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Revision of the genus *Faucaria* (Ruschioideae: Aizoaceae) in South Africa

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Keywords: Aizoaceae, distribution, Eastern Cape, ecology, *Faucaria*, morphology, phylogeny, South Africa, stat. nov., taxonomy

ABSTRACT

Faucaria Schwantes is a small genus of succulents, concentrated in south-central Eastern Cape. Distinguishing features of *Faucaria* are the characteristically dotted and toothed leaves and the structure of the seed capsule. A taxonomic review of the genus is presented, including relationship, diagnostic features, variation, distribution and ecology. The revision reduces the number of species from 33 to six: *F. bosscheana*, *F. felina*, *F. gratiae*, *F. nemorosa*, *F. subintegra*, and *F. tigrina*. Two new subspecific combinations, *F. felina* subsp. **britteniae** and *F. felina* subsp. **tuberculosa** have been made. A cladogram is included. A key to the taxa is provided and each species is described and illustrated.

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INTRODUCTION

The earliest record of a *Faucaria* dates from before 1707, and consists of a watercolour of *F. felina* subsp. *felina* in the *Moninckx Atlas* (Wijnands 1983). The *Moninckx Atlas* is a collection of nine volumes of watercolours, painted from plants in the *Hortus Medicus Amstelodamensis*. Material of this specimen was probably collected at a location near Algoa Bay, [the present-day Port Elizabeth region], during a search for fresh water by a Dutch vessel. Herbarium material from this period could not be traced. The earliest known herbarium sheet of *F. felina s.l.* was made by Thunberg, who visited the Eastern Cape on his second journey, from September 1773 to January 1774 (Juel 1918; Dyer 1937). After Thunberg, only a few herbarium specimens of this succulent genus were deposited in herbaria until ± 1925. Even Ecklon and Zeyher, who collected extensively in the Eastern Cape between 1831 and 1832, left only a few herbarium specimens. More herbarium collections were made between 1930 and 1938 by Mmes W. van Ryneveld, G.V. Britten, L.L. Britten, I.E. King, Messrs H.W. James, G.G. Smith, and other (often amateur) collectors. Plants from these collectors were often introduced into living collections, especially those of the then acknowledged expert on the Mesembryanthema, Louisa Bolus in Kirstenbosch and Rondebosch.

Haworth (1803) subdivided *Mesembryanthemum* and placed the two species known at that time, *M. tigrinum* and *M. felinum*, later considered to be species of *Faucaria*, in the section *Denticulata*. Both species recur in the new section *Ringentia* (Haworth 1812) together with some species now placed in the genus *Stomatium*. Schwantes (1926) erected *Faucaria*, accommodating *M. bosscheanum*, *M. felinum*, *M. lupinum*, *M. tigrinum* and *M. tuberculosum*. Field collections during the nineteen-thirties enabled Louisa Bolus to describe 25 species between 1933 and 1938 from living material. Her species concept was very narrow, and often based on minor differences. With the exception of *F. subintegra* these species turned out to be synonyms of already known *Faucaria* species. Hartmann placed *Faucaria* in the *Stomatium* group, one of the 11 groups in the Ruschioideae (Hartmann 1991). This group is charac-

terised by homocellular xeromorphic leaves with crystals in irregular zones, flowers with five separate nectaries, capsule with or without covering membranes, without closing bodies, and with valve wings broad to reduced.

MATERIAL AND METHODS

Live material of more than 60 field collections were studied over the period 1985–1992. An extensive field study in 1991 completed the taxonomic research. SEM studies of epidermis, pollen and seed of fresh material were carried out with a JEOL JSM–5200. This material was dried using a Balzers Union CPD 020 critical point dryer with carbon dioxide and subsequently sputter-coated with platinum using a Polaron Sputter Coating Unit E5100. The morphological studies were made with a Zeiss Axiophot photomicroscope. Germination experiments with seeds of 11 accessions harvested in the wild were carried out in Petri dishes, placed in a germination incubator for 12 hours at 25°C, and 12 hours at 20°C. The material for microtome sectioning was embedded in Kulzer's Technovit 7100 and stained with 1 % Toluidine blue in 1 NHCl. A 4% solution of formalin was used to examine the idioblasts (Hartmann 1977). The presence of tannins was established by blue colouring of tannin with a 1% FeCl3 solution (Hartmann 1977). Cytotaxonomic studies were done on root tips of germinating seeds, stained with Feulgen reagent. Besides the living accessions, 300 herbarium sheets were studied from B, BOL, G, GRA, HBG, K, MO, NBG, PRE, SAM and WAG. A cladistic analysis was carried out with all eight taxa of *Faucaria* using *Orthopterum* L. Bolus as the outgroup. Thirteen characters were investigated (Table 1). The most parsimonious cladogram was determined using Hennig86 (Farris 1988).

TAXONOMY

Faucaria *Schwantes* in Zeitschrift für Sukkulentenkunde 2: 176 (1926); Schwantes: 105 (1927); N.E.Br. et al.: 212 (1931); L.Bolus: 22 (1933a); H.Jacobsen: 129 (1933); Poelln.: 41 (1933); L.Bolus: 109 (1937); L.Bolus: 114 (1938); E.Phillips: 320 (1951); Schwantes: 20 (1952); H.Jacobsen: 1362 (1955); Schwantes: 129 (1957); H.Jacobsen: 422 (1970); Herre: 156 (1971); H.Jacobsen: 1141 (1978); H.Jacobsen: 454 (1981); F.McIntosh: 167 (1989). Type: *Faucaria tigrina* (Haw.) Schwantes 3: 105 (1927).

Mesembryanthemum L.: 487 (1753) p.p.; Haw.: 161 (1794/1795); DC.: t. 152 (1805); Haw.: 216 (1812); Haw.: 89 (1821); Haw.: 109 (1824); DC.: 419 (1828); Salm-Dyck: t. 5, 6 (1836); Salm-Dyck: t. 2 (1854); Sond.: 388 (1862); A.Berger: 265 (1908).

Prelinnean: *Mesembryanthemum rictum felinum repraesentans*, Dill.: 240, t. 187, fig. 230 (1732); L.: 218, No. 12 (1738)[1737].

Plants perennial, forming clumps or tufts, 20–100 (–150) mm high and up to 200 mm across; stems sometimes developing with age; thick, turnip-shaped taproots sometimes present; isophyllous. *Leaves* succulent, 2–4 crowded pairs at top of stem, fused at base, covering short internodes, upper side flat, smooth or rough, ovate-rhomboid to linear-spatulate, underside rounded in lower part, keeled and 3-angled in cross section towards tip, leaf margins in upper half with 0–12 cartilaginous, often bristle-tipped teeth on each leaf margin; epidermis homocellular xeromorphic, often with whitish dots. *Flowers* solitary, terminal; pedicel flattened, (0–)1–4(–6) × 2.5–4.0 mm, 0.4–1.5 mm thick, not scented; receptacle 2-keeled, sometimes slightly constricted at apex, base broadly bell-shaped, often flattened, top with 5 or 10 grooves, in middle usually raised; bracts absent. *Sepals* (4)5(6), unequal, 2 outer sepals keeled with small dorsal subapical appendage, 3 inner sepals not keeled, all free to base. *Petals* many, free, in 3 or 4 series, linear, narrowed to base, on inside shining yellow, outer petals dull yellow, rarely white or reddish. *Nectaries* free, crest-like,

TABLE 1.—The characters (1–13), character states and coding in the cladistic analysis of *Faucaria*. The first state of a character is coded 0, the second 1, the third state 2

	Characters												
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13
Orthopterum waltoniae	0	0	0	0	0	0	0	0	0	0	0	0	0
F. bosscheana	0	0	2	0	0	0	0	0	0	1	1	0	0
F. felina subsp. *felina*	1	1	1	0	1	1	1	0	1	2	1	0	0
F. felina subsp. *britteniae*	1	1	1	1	1	2	1	0	1	2	2	0	0
F. felina subsp. *tuberculosa*	0	1	1	0	0	1	1	1	2	2	1	1	0
F. gratiae	0	1	1	0	0	0	1	0	1	1	0	0	0
F. nemorosa	1	0	0	0	0	0	0	0	0	2	0	0	1
F. subintegra	1	0	0	0	0	0	1	0	0	1	0	1	1
F. tigrina	0	1	1	1	2	2	1	1	2	2	2	1	0

1 = Some plants stem-forming with age/stem-forming absent
2 = Keel of leaves sharp/rounded at top
3 = Whitish leaf margins not present/not continuously/continuously
4 = Teeth less than 4/usually more than 5
5 = Bristles shorter than 2 mm/sometimes/always longer than 2 mm
6 = Bristles not papillate/sometimes/always papillate
7 = Whitish dots on upper surface absent except on margins/dots always present
8 = Whitish dots on upper surface small/large dots
9 = Epidermis smooth/somewhat uneven/rough
10 = Cuticular folds absent/not very developed/well-developed cuticular folds
11 = Petals fewer than 100/sometimes/always more than 100
12 = Nectaries greenish or ochreous/brownish
13 = Tumble fruits sometimes present/absent

(4)5(6), yellow, greenish to dark brown. *Staminodes* absent. *Stamens* numerous, 7–11 mm long; filaments sparsely papillate at base, yellowish, at base whitish; pollen yellow. *Gynoecium* inferior, (4)5(6) fused carpels with parietal placentation. *Style* absent; stigmas (4)5(6), filiform, erect, in medium-aged flowers about as long as stamens, top usually curved, yellowish, with elongated blunt papillae ± 10–16 µm wide on inside. *Capsule* hygrochastic, woody, long-persistent, sometimes breaking off and forming tumble fruits, brownish, obovate, usually laterally slightly compressed; forming a flattened to nearly semiglobose top, flattened to globose in lower part, often flattened on one side; valves when closed, with small slits between them, each concave, ascending to form a central peak, expanding keels surrounded by broad, expanding sheets, ending in a short awn and extending into locules; covering membranes absent; closing bodies absent; stiff, small valve wings present; fruit stalk flattened, 0–4(–6) × 2.5–4.0 mm, 0.4–1.5 mm thick. *Seeds* 60–100(–200) per capsule, broadly ovate to tetrahedral, dark-brown, 1.4–1.7 × 0.9–1.4 mm, covered with warts. Chromosome number: 2n = 18 (Moore 1973).

The generic name is derived from *faux* (= jaw, throat); *Faucaria* = a collection of jaws, likening the toothed leaves to the open jaws of an animal.

Diagnostic features

Leaves usually toothed, rarely toothless, dispersed calcium oxalate crystal concentrations usually visible as small dots. Flowers opening during late afternoon, closing at sunset; petals 1.0–1.25 mm wide. Fruit locules hidden by split septa (resembling covering membranes). Covering membranes and closing bodies absent. Valve wings stiff, straight and standing erect over locules in open fruits.

Key to species

1a Upper leaf surface shiny green, usually without white dots, with conspicuous, often continuous, white cartilaginous margins and keel, with 0–3 white cartilaginous teeth without papillae ..... 1. *F. bosscheana*
1b Upper leaf surface rarely shiny green, with white dots, without continuous, white cartilaginous margins, teeth absent to many, usually partly greenish:
2a Leaves with a blunt keel, only present at tip, dots minute, rare or absent, teeth and bristles very reduced to absent; fruits often firmly attached:
3a Leaves ovate-rhomboid in upper part, epidermis hard, somewhat glossy, green to yellowish, teeth absent or conical, 1–2 mm long, usually not bristle-tipped; sepals thicker than wide ..... 5. *F. subintegra*
3b Leaves oblong-lanceolate in upper part, epidermis soft, dull greyish green, with (0–) 2–4 teeth, reduced to small whitish tubercles, shorter than 1 mm; sepals longer than wide ..... 4. *F. nemorosa*
2b Leaves often with sharp keel, present from halfway up, distinct dots usually present, teeth and bristles often well developed; fruits often easily detached (tumble-fruits):
4a Stem at base obscured by leaves which have numerous white distinct dots, confluent into patches, teeth well developed, ending in long bristles ..... 6. *F. tigrina*
4b Stem often leafless at base, dots on leaves present, not confluent into patches, teeth poorly to well developed, with or without long bristles:
5a Leaves olive-green to reddish, margins irregularly undulate, large-lobed or obscurely toothed with up to 5 small teeth, usually ending in short bristles, 1–3 mm long ..... 3. *F. gratiae*
5b Leaves mostly greyish green, margins regularly few- to many-toothed, very rarely absent, teeth well developed, usually ending in short or long bristles:
6a Leaves with some to many whitish tubercles on upper surface ..... 2c. *F. felina* subsp. *tuberculosa*
6b Leaves without tubercles on upper surface, some tubercle-like teeth on margins may be present:
7a Leaves fresh green to greyish green but not glaucous, dots clearly visible, minute dots with (0–)3–8(–10) teeth ..... 2a. *F. felina* subsp. *felina*
7b Leaves partially or completely whitish or glaucous, caused by very numerous, barely visible dots, with 6–10(–13) teeth ..... 2b. *F. felina* subsp. *britteniae*

1. **Faucaria bosscheana** *(A.Berger) Schwantes* in Zeitschrift für Sukkulentenkunde 2: 177 (1926); L.Bolus: 153 (1930); L.Bolus: 22 (1933a); H.Jacobsen: 129 (1933); L.Bolus: 110 (1937); H.Jacobsen: 1363 (1955); Schwantes: 131 (1957); H.Jacobsen: 423 (1970); H.Jacobsen: 1141 (1978); H.Jacobsen: 454 (1981); F.McIntosh: 167 (1989); S.A.Hammer: 1, 3 (1991). Type: De Wildeman: 108, fig. 230 (1908) (neo.!, here designated).

Mesembryanthemum bosscheanum A.Berger: 269 (1908).

F. albidens N.E.Br.: 349 (1927); L.Bolus: 153 (1930); H.Jacobsen: 1362 (1955); H.Jacobsen: 423 (1970); H.Jacobsen: 1141 (1978); H.Jacobsen: 454 (1981); F.McIntosh: 166 (1989). Type: *J.Frith s.n.* (K, lecto.!, here designated).

F. haagei Tischer: 20 (1929); G.D.Duursma: 128 (1930). *F. bosscheana* var. *haagei* (Tischer) H.Jacobsen in H.Jacobsen & G.D.Rowley: 80 (1955); H.Jacobsen: 1363 (1955); H.Jacobsen: 423 (1970); H.Jacobsen: 1142 (1978); H.Jacobsen: 455 (1981). Type: Tischer: 21 (1929), unnumbered plate (lecto.!, here designated).

F. paucidens N.E.Br. et al.: 210 (1931). Type: N.E.Br. et al.: 210, fig. 100 (1931) (holo.!).

F. kendrewensis L.Bolus: 469 (1934). Type: Kendrew, *Van der Berg NBG1619/34*, fl. 28 April 1934 (BOL, holo.!).

F. peersii L.Bolus: 108 (1937). Type: near Klipplaat, *Peers BOL21979*, fl. 15 March 1937 (BOL, holo.!).

Plants small, clumped or tufted (Figure 1A). *Leaves* 4–8 per rosette, crowded, thick ovate-lanceolate or linear-spatulate, 15–40(–50) × 5–15(–25) mm, margins undulate or with 0–3(–5) short whitish stout teeth on each leaf margin, without or with short stout smooth bristles; margins and keel with almost semiglobose epidermal cells; leaf surface smooth, often without obvious white dots, numerous small, dark green subepidermal idioblasts visible, wax rugose; leaf margins and keel at least partially whitish cartilaginous, glossy or shiny fresh green, turning reddish in very sunny conditions. *Flower* with 70–90 petals; stamens 120–180. *Nectaries* largely

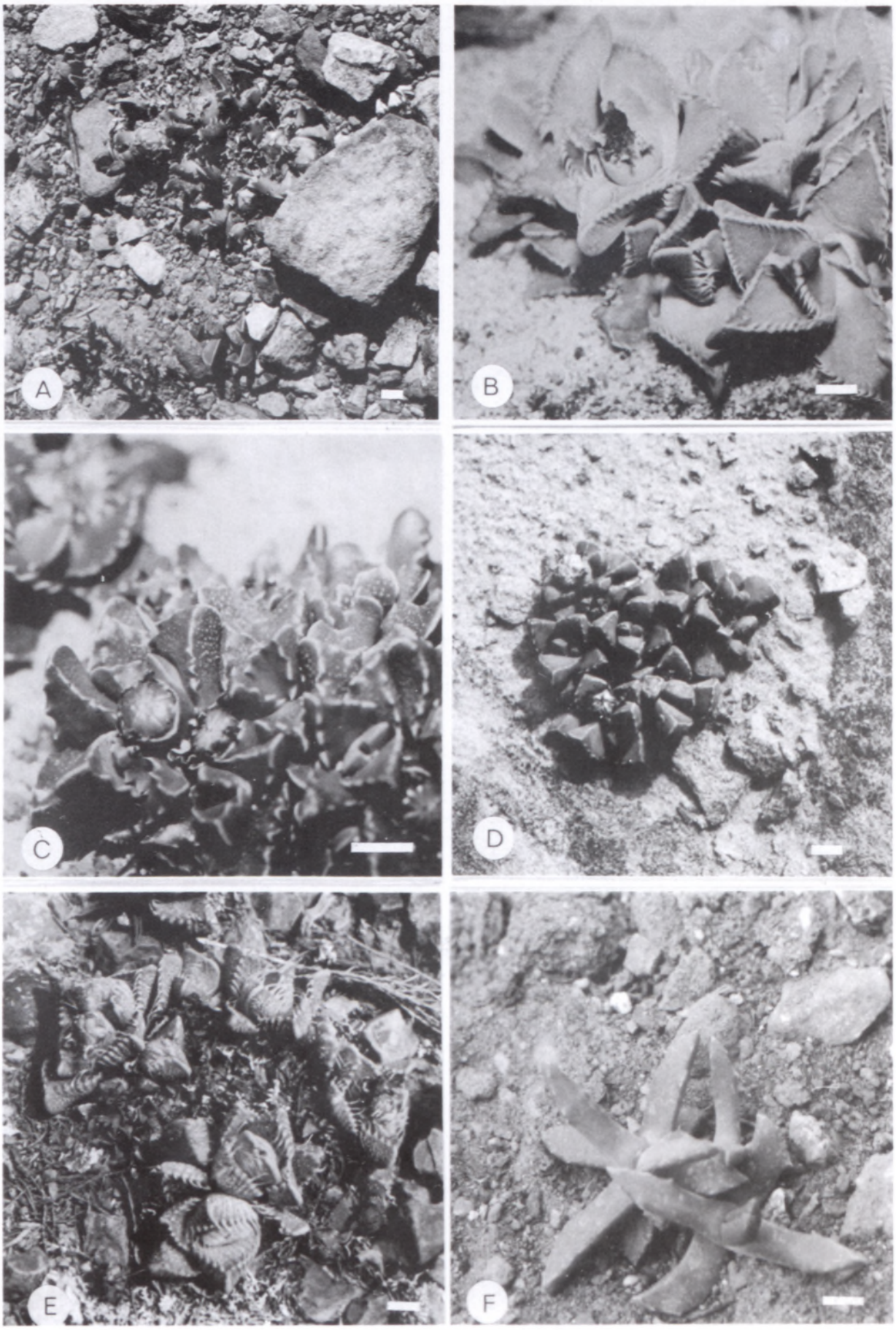

FIGURE 1.—*Faucaria* species. A, *F. bosscheana*, *Van Jaarsveld 11120*; B, *F. felina* subsp. *britteniae*, *Van Jaarsveld 11106*, pl. culta; C, *F. gratiae*, *Van Jaarsveld 11110*, pl. culta; D, *F. subintegra*, *Groen 1082*; E, *F. tigrina*, *Groen & Marx 1052b*; F, *F. nemorosa*, *Van Jaarsveld NBG878/85*. Scale bars: A–F, 10 mm.

greenish. *Fruit stalk* mostly absent or (0.5–)2.8–5.8 × 2.0–2.6 mm, 0.7–1.4 mm thick. *Fruits* often easily falling off (tumble fruits), 7.0–11.3 × 6.5–12.0 mm, 7.0–10.5 mm thick; lower half of fruit mostly flattened at one side, or more rarely convex on 2 sides, valves on top of fruit bent downwards in the middle forming a depression there. *Seeds* 1.35–1.6 × 0.9–1.45 mm. *Flowering period*: Feb.–July, main period March.

Distribution: western part of the Eastern Cape, widespread in scattered populations (Figure 2A).

Ecology: restricted to Karoo Biome, altitude 750 m and up, open vegetation, flat terrain, north-facing foothills, in flat cavities of rock plates, between stones on slopes. Rainfall: 200 mm (arid Karoo) to about 350 mm (False Karroid Broken Veld), mainly in March and November. Geological formation: often sandstone of Beaufort Group, Adelaide Subgroup; Dwyka tillite, pH(H_2O) 7.5.

F. bosscheana was named after Van den Bossche of Tirlemont (Belgium), in whose garden the first plants were grown from seed received from H. Bolus, Cape Town in December 1904.

The descriptions of Berger and De Wildeman have been based on two different plants: De Wildeman sent seedlings to Berger in la Mortola (Italy), whose description (Berger 1908) predates the description of De Wildeman (1908) by a month. Berger did not conserve herbarium specimens of *F. bosscheana*. Both descriptions indicate a form with narrow leaves, *F. albidens*, which occurs around Graaff-Reinet and Kendrew. The type specimen of *F. albidens* is very similar to the picture of the De Wildeman specimen. The confusion of what should be regarded as *F. albidens* is already noted by Bolus (1930). She noted that the chief difference between *F. albidens* and *F. bosscheana* seemed to be the length of the stamens. The broad-leaved form is common in cultivation and has therefore been regarded by growers as the real *F. bosscheana*. All listed synonyms of *F. bosscheana* are based on characters such as leaf form and number of teeth. These characters are quite variable and may vary from koppie to koppie according to Hammer (1991). They have in common the smooth epidermis, often without conspicuous white dots, the few-toothed, uniform green to brownish coloured leaves and (not) continuous white margins. *F. haagei* was a cultivated variant of *F. bosscheana*, characterised by dark green broad leaves, undulating or often entire leaf margins. *F. paucidens*, like *F. albidens*, is a narrow-leaved form of *F. bosscheana*, described from a plant in cultivation. According to Hammer this form varies considerably around Graaff-Reinet. *F. peersii* is a normal variant of *F. bosscheana*, not distinct at specific level.

Specimens examined

WESTERN CAPE.—3222 (Beaufort West): Beaufort West, (–BC), *Perold NBG2657/35* (BOL); ibid., *Grant 13748* (PRE); *Otzen NBG1153/36* (BOL). 3322 (Oudtshoorn): Prince Albert, (–AA), *J.A.C. Koorts BOL46534* (BOL).

EASTERN CAPE.—3123 (Victoria West): Murraysburg, (–DD), *Hort. Stell. Univ. Garden s.n.* (BOL). 3224 (Graaff-Reinet): Graaff-Reinet, (–BC) *Van Jaarsveld 11170* (NBG); 30 km from Pearston and Jansenville, *Smith 7251* (BOL); Graaff-Reinet Dist., (–BC), *Barkhuizen BOL46594* (BOL); Graaff-Reinet, (–BC), *Luckhoff BOL46596* (BOL); near Oatland Railway station, 24 km north of Klipplaat, (–CD) *Marx 202* (WAG); Kendrew, (–DA), *Peers BOL46595* (BOL); ibid., *Cook & Long s.n.* (BOL); dry plains, near Graaff-Reinet, *H.Bolus 574* (BOL); Karoo Nat. Park, Graaff-Reinet, *Groen 1025, 1027, 1035* (GRA, WAG). 3323 (Willowmore): Willowmore, (–AD), *Hort. Stell. Univ. Garden 9337, 9861* (BOL); 29 km from Willowmore, on road between Willowmore and Uniondale, (–CA), *Mrs N.R. Urton s.n.* (BOL). 3324 (Steytlerville): Klipplaat, between Miller and Mount Steward, (–AB), *Long s.n.* (BOL); Klipplaat Dist., *Peers BOL46537* (BOL); Baroe station, near Klipplaat, (–AB), *Stayner BOL22191* (BOL); Steytlerville, (–AD), *Hort. Stell. Univ. Garden 8659* (BOL).

2. **Faucaria felina** *(L.) Schwantes* in Zeitschrift für Sukkulentenkunde 2: 177 (1926); L.Bolus: 22 (1933a); H.Jacobsen: 129 (1933); L.Bolus: 110 (1937); H.Jacobsen: 1364 (1955); Schwantes: 131 (1957); H.Jacobsen: 423 (1970); H.Jacobsen: 1143 (1978); H.Jacobsen: 455 (1981); Wijnands: 148 (1983); Van Jaarsv.: 53 (1984). Type: Dill.: 240, t. 187, fig. 230 (1732) (lecto.!, here designated).

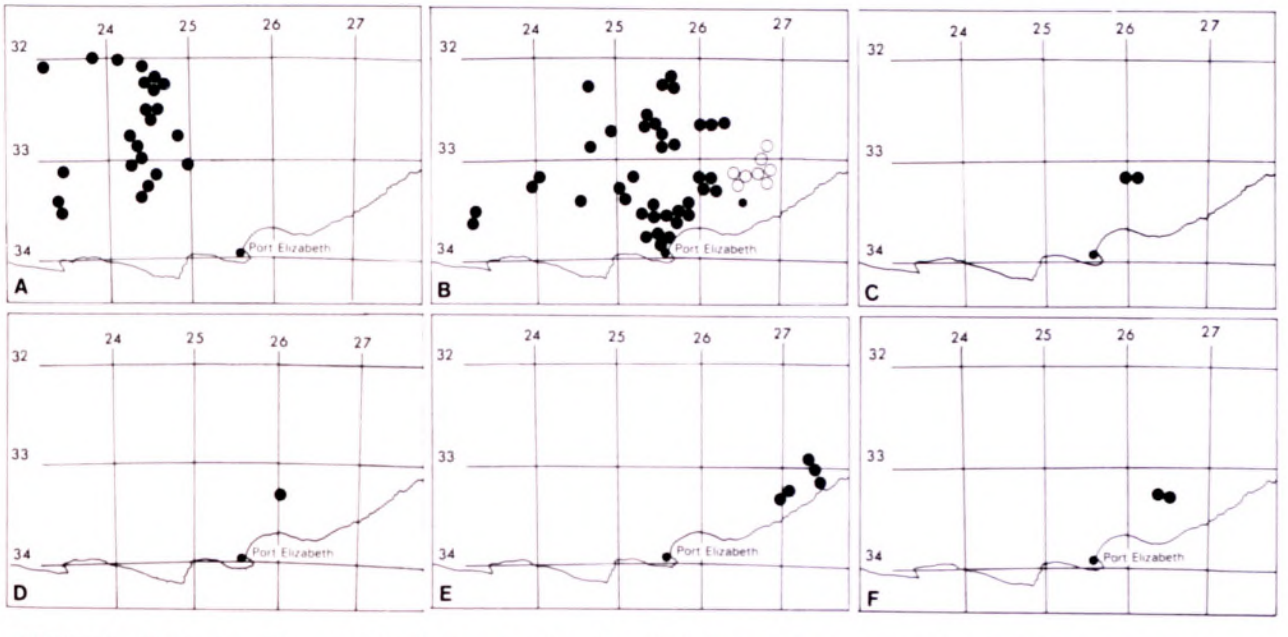

FIGURE 2.—Distribution of *Faucaria* in South Africa: A, *F. bosscheana*; B, *F. felina s.l.*: *F. felina* subsp. *felina*, ●, *F. felina* subsp. *brittenae*, ○. C, *F. gratiae*; D, *F. nemorosa*; E, *F. subintegra*; F, *F. tigrina*.

2a. subsp. **felina**

Mesembryanthemum ringens L. ß *felinum* L.: 487 (1753). *M. felinum* (L.) Weston: 172 (1770); Lam.: 486 (1788); Haw.: 161 (1794/1795); Haw.: 31 (1803); DC.: t. 152 (1805); W.T.Aiton: 218 (1811); Haw.: 216 (1812); Haw.: 89 (1821); DC.: 419 (1828); G.Don: 128 (1834); Eckl. & Zeyh.: 308 (1834–1837); Salm-Dyck: t. 6 (1836); Sond.: 397 (1862); A.Berger: 267 (1908); N.E.Br.: 76 (1920).

M. lupinum Haw.: 111 (1824). *F. lupina* (Haw.) Schwantes: 176 (1926). Type: watercolour, *Bowie s.n.*, in 1823 (K, lecto.!, here designated).

F. militaris Tischer: 280 (1932). Type: Tischer: 280 (1932), unnumbered plate (lecto!, here designated).

F. duncanii L.Bolus: 22 (1933a). Type: Port Elizabeth Dist., Coega Kop, *W. Duncan BOL19645* (BOL, holo.!).

F. felina (L.) Schwantes var. *jamesii* L.Bolus: 395 (1933b). Type: Somerset East Dist., near Halesowen, alt.1 200–1 525 m, *James 8*, fl. 3-02-1933, (BOL, lecto.!, here designated).

F. acutipetala L.Bolus: 443 (1934). Type: Somerset East Dist., Bruintjeshoogte, *W. van Ryneveld NBG686/34*, fl. 21 Feb. 1934 (BOL, holo.!).

F. cradockensis L.Bolus: 448 (1934). Type: Somerset East Dist., Cradock, *B. Rogers NBG687/34* (BOL, holo.!).

F. crassisepala L.Bolus: 442 (1934). Type: Somerset East Dist., Bruintjeshoogte, *W. van Ryneveld NBG2352/33*, fl. 22 April 1934 (BOL, holo.!).

F. jamesii L.Bolus ex Tischer: 99 (1934) nom. nud.

F. latipetala L.Bolus: 443 (1934). Type: Fort Beaufort Dist., *W. van Ryneveld NBG686/34*, fl. 14 April 1934 (BOL, holo.!).

F. laxipetala L.Bolus: 444 (1934). Type: Grahamstown Dist., near Grahamstown, comm. *Long & Cook NBG286/33*, (BOL, holo.!).

F. longidens L.Bolus: 470 (1934). Type: Somerset East Dist., Yester Farm, *W. van Ryneveld NBG2355/33*, fl. 7 July 1934 (BOL, holo.!).

F. longifolia L.Bolus: 471 (1934). Type: Fort Beaufort Dist., *W. van Ryneveld NBG690/34*, fl. 3 May 1934 (BOL, holo.!).

F. montana L.Bolus: 448 (1934). Type: Somerset East Dist., hill near Cradock, *H.W. James NBG685/34*, fl. 2 April 1934 (BOL, holo.!).

F. multidens L.Bolus: 450 (1934). Type: Fort Beaufort Dist., *W. van Ryneveld NBG1412/33*, fl. 5 April 1934 (BOL, holo.!).

F. ryneveldiae L.Bolus: 446 (1934). Type: Fort Beaufort Dist., *W. van Ryneveld NBG688/34*, fl. 31 March 1934 (BOL, holo.!).

F. candida L.Bolus: 105 (1937). Type: Somerset East Dist., Scanlan, near Cradock, *Mrs C.H. Mclane NBG651/37* (BOL, holo.!).

F. kingiae L.Bolus: 106 (1937). Type: Grahamstown Dist., near Alicedale, *I.E. King 15* (BOL, holo.!).

F. multidens L.Bolus var. *paardepoortensis* L.Bolus: 107 (1937). Type: Port Elizabeth Dist., Klein Winterhoek Mountains at Paardepoort, *I.E. King 4*, fl. 4 May 1937 (BOL, holo.!).

F. plana L.Bolus: 107 (1937). Type: collector and locality unknown, *BOL21978*, fl. 1 May 1937 (BOL, holo.!).

F. uniondalensis L.Bolus: 106 (1937). Type: Willowmore Dist., near Uniondale, *E. Markoetter SUG10662*, fl. 24 March 1936 (BOL, holo.!).

Plants clump-forming or shrubby, short-stemmed with age. *Leaves* spreading, crowded, 4–8, variable, ovate-rhomboid to linear-lanceolate, 15–70 × 5–15(–20) mm, keeled; keel at an oblique angle with tip of leaf, with (0–)3–8(–10) teeth on each margin; teeth 0.5–3.0 × 1–4 mm, usually bearing more or less papillate bristles of 1–5(–6) mm long, sometimes one or more small teeth present on keel, rarely teeth with very broad base up to 4 mm broad, between teeth furrows often visible; leaf surface nearly smooth to rough from a variable number of small epidermal whitish dots (Figure 3), emerging from subepidermal crystals, sometimes confluent into larger flecks present on leaf margins and keel; epidermis with cuticular folds, wax cover thin; light green-olive, dark green, grey-green, or glaucous. *Flowers* yellow, white-flowering plants occasionally found; petals 100–130, (1.0–)1.25 mm wide, acute; stamens 200–250. *Nectaries* variable in colour, greenish, yellowish, yellow-brown, brownish. *Fruit stalk* absent or 1–4 × 2.5–4.0 mm, 0.4–1.5 mm thick. *Fruits* easily falling off, top of capsule variable in shape, lower part of capsule often flattened on one side, (5.0–)9.0–13.5 × (5.0–)7.5–12.0 mm and 5.0–8.5 mm thick. *Seeds* 1.4–1.6 × 1.0–1.3 mm. *Flowering period*: March–August, main flowering period March to June. Differences in flowering date between locations in the large area of distribution are small. In several cases it has been noticed that the plants start to flower after rain.

Distribution: Eastern Cape; the area between Graaff-Reinet, Cradock, Bedford, Uitenhage, Oudtshoorn, Uniondale and the coast. Large populations occur near Cradock, in the valleys of the Sundays, Swartkops and Fish Rivers, around Port Elizabeth and Addo (Figure 2B).

Ecology: (open) Grassland, Karoo, Valley Bushveld. Rainfall: from about 200 mm or less (Karoo) to 700 mm (Valley Bushveld, Grahamstown). Geological formation: quartzite sandstone of Witteberg Series, Kommadagga Subgroup (Cape system); shale Karoo Succession, Beaufort Group; tillite Dwyka formation; sandstone of Uitenhage Group, pH (H_2O) 6.3–7.5.

Faucaria felina s.l. is variable and is distributed over a vast region in the centre of the area of the genus. The majority of the diagnostics between *Faucaria* segregates were based on local, variable forms of this species, as already mentioned. Judging from the available field data it is impossible to maintain them as separate taxa. Plants

FIGURE 3.—*Faucaria felina* subsp. *felina*, *Van Jaarsveld 11120*, pl. culta, papillae and calcium oxalate dots above subepidermal idioblasts clearly visible. Scale bar: 5 mm.

with long leaves and many thin teeth grow in more humid conditions, usually within the boundaries of the Tongaland-Pondoland phytochorological regions. Plants with shorter, stout leaves and teeth, described as *F. felina s.str.*, grow in the harsher conditions of the dry Karoo-Namib phytochorological region.

After the publication of a watercolour of *F. felina* in the *Moninckx Atlas* before 1707 (Wijnands 1983), Boerhaave (1719) published a short description that Martyn (1728) used in his more detailed paper together with an excellent watercolour of *F. felina* subsp. *felina*. Linnaeus (1738, 1753) published the species referring to Dillenius (1732). Very variable in their vegetative characters, most described *Faucaria* 'species' are to be considered as mere populations and fall into synonymy with *F. felina s.l.* Details are discussed with the synonyms.

Faucaria felina subsp. *tuberculosa* has been regarded as a distinct species up till now. However, this taxon differs from *F. felina* only in the tubercles on the leaves. As such *F. tuberculosa* can not be classified as a species on the tubercles only and should be regarded as a subspecies of *F. felina*. Some succulent lovers will have problems with the rejection of *F. ryneveldiae* and *F. longifolia* as separate species. The long, narrow, few-toothed leaves seem distinct. However, this rare leaf form occurs on widely diverging localities, e.g. in Addo (*Liebenberg 7697*). As genetically isolated populations develop the same leaf type, it is still hard to describe them as a single taxon, as *F. longifolia* and *F. ryneveldiae* differ in other characters. The ovary top of the type specimen of *F. longifolia* is hollow, whereas that of *F. ryneveldiae* is acute. Intermediates with rather long leaves and more teeth also occur. Further research must indicate whether *F. ryneveldiae* should remain a synonym of *F. felina s.l.* or regain species status. With some hesitation *F. lupina* is regarded here as conspecific with *F. felina*. The differences are small, the leaves are greener, slender, more glossy, and the teeth normally have rather long bristles. The number of teeth is variable, from 0–10. In the notes of Haworth (1824), *F. lupina* was described as having longer and narrower glaucous leaves, and with longer and twice as many teeth as *F. felina*. Salm-Dyck (1836) gives a more detailed description and says that this plant differs from *F. felina* by having greener, shiny leaves, without points and more teeth with bristles. The teeth on the keels described for *F. militaris* occur occasionally in *F. felina*.

F. felina subsp. *felina* grows together with *F. bosscheana* in a large area. However, they do not grow sympatrically, *F. bosscheana* prefers a more karroid area than *F. felina*. Intermediate populations are short-leaved, and the leaves are partly white margined and have a smooth epidermis. The leaves bear 3–6, long-needled teeth.

Specimens examined

WITHOUT LOCALITY: Cape of Good Hope, *Thunberg sheet 12009* (UPS-Thunb., microfiche).

EASTERN CAPE.—3224 (Graaff-Reinet): between Graaff-Reinet and Beaufort, *Ecklon & Zeyher 1983* (SAM); Halesowen, *James BOL22728, BOL24959* (BOL); near Jansenville, (–CC), *King 56* (BOL). 3225 (Somerset East): Somerset East, (–BA), *Ferguson s.n.* (BOL); Somerset East, near Cradock, (–BA), *James BOL21977, BOL22725* (BOL); between Cradock & Bedford, (–BC), *James BOL22193, BOL22194, BOL46646, BOL46647* (BOL); Mortimer, (–BC), *Groen 1106* (WAG). 3226 (Fort Beaufort): Bedford, (–CA), *Van Ryneveld s.n.* (BOL); Farm Richfontein, near Yester, (–DC), *Van Ryneveld BOL46708* (BOL). 3322 (Oudtshoorn): (–CA), *s.c., BOL46579* (BOL). 3323 (Willowmore): 8 km NE Uniondale, (–CA), *Markoetter s.n.* (BOL). 3324 (Steytlerville): Brakfontein, (–BB), *Van Ryneveld BOL46711* (BOL); Sandpoort, Springbokvlakte, (–BD), *Marx 207* (WAG). 3325 (Port Elizabeth): 4 km south of Lake Mentz, (–AA), *Marx 210* (WAG); road to Jansenville, about 8 km beyond Glenconnor, (–AC), *King 3* (BOL); ± 32 km from Uitenhage on mountain road to Steytlerville, (–AD), *King 12* (BOL); near Bluecliff Station, (–AD), *King 62* (BOL); Addo Bush, (–BC), *King 6* (BOL); Addo Drift, (–BC), *King 8* (BOL); 48 km from Port Elizabeth on Uitenhage-Steytlerville road, (–BC), *Stayner BOL22189* (BOL); hills ± 8 km south of Selborne, in Sundays River Valley, (–CA), *King 9a, b* (BOL); 'am Zwartskoprivier Uitenhage', (–CB), *Ecklon & Zeyher 1981* (SAM); Swartskoprivier, (–CB), *Zeyher 2580* (B, G); hills north of Uitenhage, (–CB), *Muir 3999* (K); 19 km out of Port Elizabeth on Uitenhage road, (–CD), *King 2* (BOL); Soutpoort, near Addo, (–DA), *Groen 1092* (WAG); near Addo, (–DA), *Long & Cook NBG282/33* (BOL); Coegakop, (–DA), *King 1* (BOL); Coega, *G.V. Britten s.n.* (BOL); Perseverance, (–DC), *Groen 1119* (WAG); New Brighton, (–DC), *L.Bolus BOL46580, BOL46581* (BOL, HBG); Port Elizabeth, (–DC), *Dahlstrand 1884* (STE, MO); near Port Elizabeth, (–DC), *King 52* (BOL). 3326 (Grahamstown): near Swartwaterpoort, (–AA), *King 41, 42* (BOL); ibid., *Van Jaarsveld 11142* (NBG); near Middleton, (–AB), *Van Ryneveld BOL22205* (BOL); Tootabie, (–AC), *Groen 1080* (WAG); near Alicedale, (–AC), *King 16, 17, 39, 43* (BOL); Eagles Craig, near Alicedale, (–AC), *King 35* (BOL); near Grahamstown, (–BC), *G.V. Britten BOL21986* (BOL).

2b. subsp. **britteniae** *(L.Bolus) L.E.Groen*, stat. nov.

Faucaria britteniae L.Bolus in South African Gardening & Country Life 23: 22 (1933a); H.Jacobsen: 1363 (1955); H.Jacobsen: 423 (1970); H.Jacobsen: 1142 (1978); H.Jacobsen: 455 (1981); F.McIntosh: 167 (1989). Type: Grahamstown Dist., on the road to Committees, 20 miles from Grahamstown, *L.L. Britten 5395*, coll. 12 July 1926 (BOL, holo.!).

F. coronata L.Bolus: 446 (1934). Type: Grahamstown Dist., between Carlisle Bridge and Riebeeck East, *G.V. Britten 34*, fl. 15 April 1934 (BOL, holo.!).

F. speciosa L.Bolus: 445 (1934). Type: Grahamstown Dist., near Grahamstown, *L.L. Britten & A.H. Harcourt-Wood NBG691/34*, fl. 10 April 1934 (BOL, holo.!).

F. smithii L.Bolus: 32 (1936). Type: Albany Dist., Fish River valley, near the foot of Pluto's Vale, about 20 miles E of Grahamstown, *G.G. Smith 90*, fl. 15 March 1936, (BOL, holo.!).

F. grandis L.Bolus: 125 (1938). Type: Albany Dist., exact locality unknown, probably coll. by *G.V. Britten BOL21986*, fl. 28 March 1936, (BOL, holo.!).

Plants clump-forming or shrubby, stem-forming with age; stems up to 120 mm long (Figure 1B). *Leaves* spreading, ovate-rhomboid, 30–55(–70) × 12–33 mm, keeled; keel sharp, forming a pronounced chin in almost rectangular arrangement as seen from side, toothed; 6–10(–13) teeth on each margin, 3–5 mm broad at base, 2.5–5.0 mm long normally with long, papillate bristles; epidermis with well-developed wax cover, thicker than in subsp. *felina*; uniform or partially whitish green with numerous small greyish white dots, or dull green with white clearly visible dots. *Flowers* large for genus, 60–80 mm diam.; petals 125–160; stamens 260–350. *Nectaries* mostly yellowish. *Fruit stalk* absent or (0.5–)2.2–3.8(–6.5) × 2.3–6.5 mm, 0.50–1.4 mm thick. *Fruits* easily falling off (tumble fruits), 7–13 × 10.5–13.0(–15.0) mm, 7–10 mm thick. *Seeds* 1.4–1.6 × 1.0–1.3 mm. *Flowering period*: March–August, occasionally throughout the year.

Distribution: northeast of Grahamstown, Fish River Ridge, northern hills on foot of mountain range at Riebeeck East (Figure 2B). It occurs near the areas where *F. felina* subsp. *felina* and *F. tigrina* are found. Intermediate populations with *F. felina* subsp. *felina* are found at Fish River Ridge, north of Grahamstown. These plants are robust, have few but large teeth with bristles, and the whitish sheen of *F. felina* subsp. *britteniae*.

Ecology: (dense) Valley Bushveld, Noorsveld, Arid Savanna, open karroid Valley Bushveld, on slopes between stones. *F. felina* subsp. *britteniae* is found in open rocky spots in dense thicket, in open grassy spots or under small bushes with a preference for north-facing slopes. Rainfall: 350–500(–700) mm. Geological formation: Karoo System, Ecca Series, tillite; Dwyka Series; Bokkeveld Series, pH (H_2O) 6.7–7.7.

Faucaria felina subsp. *britteniae* is unique in the genus because of the (partially) whitish grey epidermis. This taxon deserves the rank of subspecies by the presence of numerous very small dots on the leaves, papillate bristles and restricted area of distribution. Additional features are the large number of teeth and the size. The most characteristic specimens with many, but rather small teeth are found at Ecca Pass, north of Grahamstown.

Specimens examined

EASTERN CAPE.—3226 (Fort Beaufort): Kat River hills, 15.5 km south of Fort Beaufort, (–DC), *Marx 196* (WAG). 3326 (Grahamstown): Signalkop, near Carliste Bridge, (–AA), *Van Jaarsveld 11090* (NBG); Buffelsdrif, (–AA), *Van Jaarsveld 11095* (NBG); Fish River Ridge, (–AB), *G.V. Britten BOL22120, BOL46640, BOL46641* (BOL); Hellskloof, (–AB), *G.V. Britten s.n.* (BOL); Hell's Poort, (–AB), *R.A. Dyer s.n.* (K); Pigots Bridge, (–AB), *Smith 1992* (BOL); Clifton Farm, (–BA), *Groen 1061* (WAG); Botha's Hill, *Ecklon & Zeyher 1982* (SAM); near Grahamstown, *L.L. Britten s.n.* (BOL); Ecca's Pass Nature Reserve, (–BA), *Groen 1057* (GRA, WAG); near foot of Pluto's Vale, (–BA), *Smith 598* (BOL, K); Committees Flats, *G.V. Britten s.n.* (BOL); Uplands, Kransdrift, (–BA), *Groen 1071* (WAG); Fort Brown, (–BA), *A. Walton BOL22195, BOL46557* (BOL); 32 km from Grahamstown on road to Committees, (–BB), *G.V. Britten s.n.* (BOL); near Committees Hotel, (–BB), *Smith 5456, 5457* (BOL). 3327 (Peddie): between Chalumna and Committees, (–AB), *Herre s.n.* (BOL).

2c. subsp. **tuberculosa** *(Rolfe) L.E.Groen*, stat. nov.

F. tuberculosa (Rolfe) Schwantes in Zeitschrift für Sukkulentenkunde 2: 177 (1926); L.Bolus: 382 (1930); N.E.Br. et al.: 212 (1931); H.Jacobsen: 130 (1933); L.Bolus: 110 (1937); H.Jacobsen: 1369 (1955); Schwantes: 131 (1957); H.Jacobsen: 424 (1970); H.Jacobsen: 1146 (1978); H.Jacobsen: 456 (1981); F.McIntosh: 167 (1989). Type: *Rolfe s.n.*, aquaprint Curtis's Botanical Magazine t. 8674b (1916), (holo.!).

Mesembryanthemum tuberculosum Rolfe: t. 8674b cum fig. (1916).

Plants clumped or single. *Leaves* spreading, 4–8 per rosette, crowded, thick, ovate-rhomboid, 15–20 × 15–20 mm, keeled, with 3–6 short, whitish stout teeth on each margin, almost without bristles, some teeth may be rudimentarily developed; surface with many epidermal whitish dots, sometimes confluent on leaf margins and keel; upper surface with blunt, whitish tooth-like tubercles (this may vary from a single tubercle, to, very rarely, a complete tuberculate surface). *Flowers* yellow, as *F. felina*. *Stigmas* 5, filiform, free to the base. *Nectaries* yellow-brown, large. *Fruits* and *seed* as in *F. felina* subsp. *felina*.

Distribution: Bedford surroundings; field data very scarce (Figure 4).

Ecology: grassland, often camouflaged by grasses in association with many herbs. Rainfall: 493 mm. Geological formation: Beaufort group, Adelaide subgroup (Karoo Succession).

As Bolus (1930) already noticed, the aquaprint of the united stigmas in *Curtis' Botanical Magazine* is not correct, in *Faucaria* these are free to the base.

At a glance *F. felina* subsp. *tuberculosa* can be identified by the tubercles on the leaves which are unique in the genus. A typical plant is compact, with whitish dots and patches and resembles *F. tigrina*. Cultivated hybridised plants often show tubercles more prominent than in wild material.

Specimens examined

WITHOUT LOCALITY: photo original plant, Oct 1921 (BM); *N.S. Pillans 281* sin. loc. (SAM); Hort. *Pillans s.n.*, May 1915 (BOL); *N.E. Brown s.n.*, Oct. 6 1913 (K).

EASTERN CAPE.—3226 (Fort Beaufort): Bedford, (–CA), *Van Ryneveld BOL46630* (BOL); Normandale, south of Bedford, *Van Jaarsveld 11115* (NBG); ibid., *Groen 1118* (WAG); Adelaide, (–CB), *Van Ryneveld s.n.* (BOL); (–CB), *W.E. Armstrong BOL46691, BOL22190* (BOL); Kat River Hills, (–CD), ± 64 km from Grahamstown and 5 km from the Kat River, *G.G. Smith 10* (BOL). 3326 (Grahamstown): 32 km west of Grahamstown (–AA), on road to Bedford, *G.G. Smith* 710 (BOL); between Fort Beaufort and Grahamstown, *A.P.J. Kluth BOL46628* (BOL).

3. **Faucaria gratiae** *L.Bolus* in Notes on Mesembryanthemum and allied genera 2: 394 (1933b); H.Jacobsen: 1365 (1955); H.Jacobsen: 423 (1970); H.Jacobsen: 1143 (1978); H.Jacobsen: 455 (1981). Type: Albany Dist., Mitford Park, near Riebeeck East, *G.V. Britten 35*, fl. 23-3-1933, (BOL, holo.!).

F. hooleae L.Bolus: 447 (1934). Type: Albany Dist., Mitford Park, near Riebeeck East, *Hoole & G.V. Britten NBG684/34*, fl. 10 April 1934 (BOL, holo.!).

Plants clump-forming, very short-stemmed (Figure 1C). *Leaves* erect, ovate-lanceolate, 21.5–35.0 × 10.0–16.5(–20.0) mm; leaf margins irregular, sometimes undulating or with (0–)2–5(–7) obscure, normal to

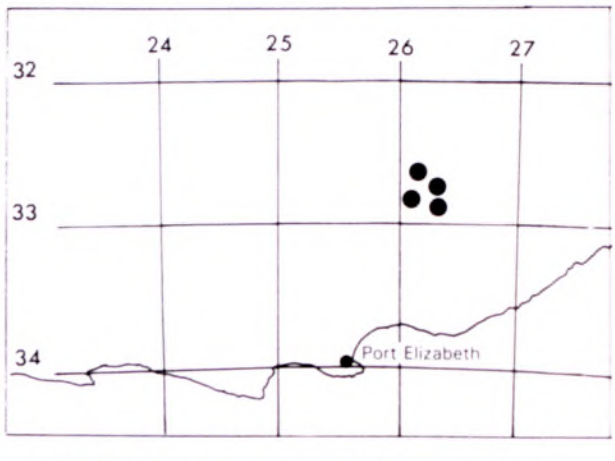

FIGURE 4.—Distribution of *Faucaria felina* subsp. *tuberculosa*.

coarse teeth, without or with few bristles of 0.1–4.0 mm long; shiny green, often with a reddish lustre, base reddish, with many small white crowded dots, margins and keel whitish. *Flowers* yellow; sepals 5, 8–10 mm long, base 2.5–5.0 mm broad, unequal; petals 70–84, emarginate to acuminate, 15.0–21.0 × 1.0–1.75 mm; stamens 8–9 mm long; filaments white. *Nectaries* brown-orange. *Stigmas* 8–11 mm long, shorter than longest stamens. *Fruit stalk* absent or up to 1 × 3 mm wide, 1 mm thick. *Fruits* sessile, when closed with rounded top, 0.65–9.0 × 0.5–0.8 mm, 0.6–0.9 mm thick. *Seeds* 0.85–1.0 × 1.15–1.30 mm. *Flowering period*: March–May.

Distribution: restricted to a radius of 3 km around Riebeeck East (Figure 2C).

Ecology: Grassy Fynbos with forest groups. The ecology of the plant is peculiar: without shelter in compact clumps in sandy soil in cracks and hollows of flat sandstone plates. Rainfall: about 380 mm per annum. Geological formation: sandstone, Karoo System, Witteberg Series, Kommadagga Subgroup.

F. gratiae and *F. hooleae* are known only from three herbarium sheets. The descriptions do not differ significantly, the type specimens originate from the same population. The plants are very small with short leaves and irregular margins, rather different from those of *F. felina*. Van Jaarsveld (1990) visited the locality and rediscovered these plants. I examined this rare species at the same location in 1992, and collected it, 3 km further away.

Specimens examined

EASTERN CAPE.—3326 (Grahamstown): Mitford Park, near Riebeeck East, (–AA), *G.V. Britten s.n.* (BOL); ibid., *Van Jaarsveld 11110* (NBG); Palmietfontein, near Riebeeck East, *Groen, Brink & Marx 1068* (WAG).

4. **Faucaria nemorosa** *L.Bolus ex L.E.Groen* in Succulenta 73: 39 (1994). Type: Fort Beaufort Dist., near Alicedale, Swartwaterpoort, *Archibald 960*, 29-7-1937 (BOL, holo.!).

Plants stem-forming, branching from base, forming small clumps, (Figure 1F). *Stems* up to 150 × 7–13 mm, internodes 5–10 mm long. *Leaves* spreading, 3–5 leaf pairs together per branch, crowded, connate at base, oblong-lanceolate, 25–45 × 9–14 mm, slightly triangular in upper part, with leaf sides often unequal, keeled towards apex; keel often asymmetric, flat on face, margin each with (0–)2–4 reduced teeth, smaller than 1 mm, bristles 0.1–1.0 mm long or absent; epidermis dull grey-green, soft, without any white dots or flecks, numerous small subepidermal idioblasts visible as dark green dots. *Flowers* yellow; sepals 5, 8–12 mm long, at base 0.3–0.65 mm wide; petals 70–90, conspicuously narrowed downwards, some of innermost row very small, linear, (15–)20–25 × (1.0–)2.0–2.3 mm in upper part, at base (0.1–)0.2–0.5 mm wide, yellow, top emarginate or obtuse, some very small ones acute. *Receptacle* 8–9 × 7–9 mm. *Stamens* 150–200, 5–8 mm long; anthers yellow, 1 mm long. *Nectaries* olive-green, smooth. *Ovary* top 5-lobed, almost flat but very slightly raised in middle, stigmas 5, filiform, 10 mm long, in young flowers shorter or as long as stamens, in old flowers longer. *Fruit stalk* 1–2 × up to 4 mm, 1 mm thick. *Fruits* tightly attached, dark brown, 9.5 × 7–8 mm, 5–7 mm thick, valves bend to a central depression. *Seeds* 1.3–1.5 × 0.9–1.0 mm. *Flowering period*: June–September.

Distribution: from a single locality near Alicedale (Figure 2D) in the Eastern Cape.

Ecology: hills, (300–)600–900 m altitude, Fish River Scrub in which *Portucalaria afra* and small succulents are dominant. *F. nemorosa* is solitary or grows in small groups among a *F. felina* subsp. *felina* population on a hill (E. van Jaarsveld pers. comm.). Rainfall: 350–400 mm, mainly in summer months. Geological formation: quartzite sandstone, Dwyka Series, Karoo System.

When verifying the *Faucaria* sheets from BOL, three sheets could not be determined satisfactorily. The specimens looked similar to *F. subintegra* but their leaves were different. They originate from a single locality near Alicedale, and have been collected between 1937 and 1939 by Mrs E.E.A. Archibald and Grace Britten, both from Grahamstown. Louisa Bolus grew field accessions in her garden, and recognised these specimens as somewhat different. She made an additional note on the sheet: 'may be only a variety of *F. subintegra*'. She referred to the habitat by her note on the sheet *Faucaria nemorosa*, i.e. *Faucaria* from the forest. She did not publish this name. The live collection of the Kirstenbosch Botanic Garden includes a plant, collected by Ernst van Jaarsveld in 1985, very much like the Archibald specimen in the Bolus Herbarium. This peculiar plant bears soft dull greyish green leaves without any sign of whitish dots, and the teeth are small and indistinct. Like the herbarium specimens of *F. nemorosa* the leaves are similar to those of *F. subintegra*, but longer and narrower. Moreover this plant has been collected in the same area as the original *F. nemorosa*. The scarce, conserved fruiting material was of the normal *Faucaria* type, but not like those of *Orthopterum*. Unfortunately the plant could not be traced again in 1991, even after repeated efforts.

Study of the living material confirmed some relationship between *F. nemorosa* and *F. subintegra*. The reduction of the teeth in *F. nemorosa* is almost complete, being reduced to small tubercles. The fruits are similar, rather small, tightly attached on the plants and often broader than long. The scarce ecological data on *F. subintegra* indicate differences in habitat between the two taxa. *F. subintegra* is restricted to shallow hollows or crevices in bare sandstone rocks in full sun under very dry circumstances. *F. nemorosa* grows in soil in the understorey of shrubs in partial shade. SEM micrographs of *F. nemorosa* show cuticular folds which are also found in *F. subintegra* (Figure 5D), a common feature for *Faucaria*, that is missing in *Orthopterum* (Figure 5H).

Specimens examined

EASTERN CAPE.—3326 (Grahamstown): near Alicedale, Swartwaterpoort, (–AA), *G. Britten s.n.* (BOL); ibid., *Van Jaarsveld NBG878/85* (WAG!).

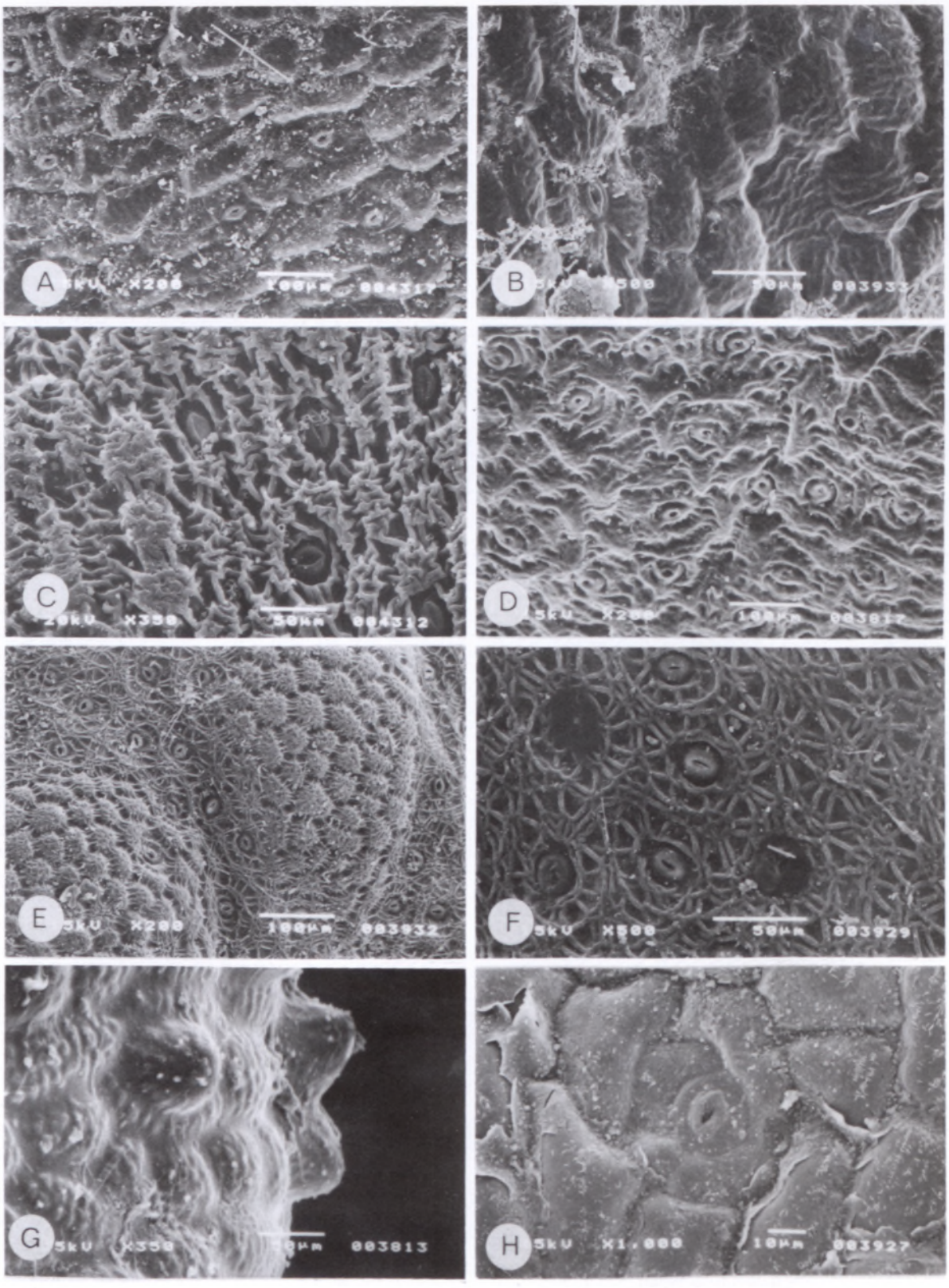

FIGURE 5.—Scanning electron micrographs of leaf epidermis. A, B, *F. bosscheana, Bayer 4965*: A, epidermis above showing rather even surface with small dispersed wax particles; B, under surface with a ribbed structure of the cuticle and few wax particles. C, *F. felina, Van Jaarsveld 6897*, under surface with cuticular folds. D, *F. subintegra, Van Jaarsveld 6950*, under surface with coarse ribbed structure. E, F, *F. tigrina, Mullins s.n.*: E, under surface with raised dots and stomata between them; F, upper surface with well-developed cuticular folds. G, *F. bosscheana, Bayer 2011b*, margin with semi-globose epidermis cells. H, *Orthopterum waltoniae, Hammer s.n.*, under surface without cuticular folds and with large flakes of wax. Scale bars: A, D, E, 100 µm; B, C, F, G, 50 µm; H, 10 µm.

5. **Faucaria subintegra** *L.Bolus*, Notes on Mesembryanthemum and allied genera 2: 449 (1934); H.Jacobsen: 1368 (1955); H.Jacobsen: 424 (1970); H.Jacobsen: 1146 (1978); H.Jacobsen: 456 (1981); F.McIntosh: 167 (1989). Type: Peddie Dist., Chalumna River Bank, *J.I. Browlee s.n.*, fl. 12 April 1934 (BOL, lecto.!, here designated).

F. subindurata L.Bolus: 444 (1934). Type: Peddie Dist., near Peddie, *G.G. Smith 102*, fl. 12-4-1934 (BOL, holo.!).

Plants clump-forming, in older stages stem-forming; stems 4–7 mm diam. (Figure 1D). *Leaves* 4–8, crowded, very thick, spreading, ovate-rhomboid, 20–35 × 10–15 mm, bluntly keeled at top, margins with 0–8 very short conical teeth having short bristles on each side that disappear in older leaves; often shiny, glaucous, sometimes with a violet lustre, with minute white dots, margins and keels indistinctly whitish. *Flowers* with 80–92 linear petals; stamens 150–180. *Nectaries* yellowish green. *Fruit stalk* absent or 2–4 × 2–4 mm, 1.0–1.4 mm thick. *Fruits* tightly attached on plant, 7–10 × 9–12 mm, 6–9 mm thick; top of capsule flat, or in most fruits a raised centre. *Seeds* dark brown, 1.1–1.4 × 1.0–1.1 mm. *Flowering period*: March–May.

Distribution: the most south-central part of the Eastern Cape (Figure 2E).

Ecology: Subtropical Coast, Open Valley Bushveld with grassveld in between, overgrazed, in full sun on open places on top of north-facing river bank, cavities in rock plates in flat sandstone rock under very dry circumstances. Rainfall: 500–900 mm (Valley Bushveld) or more (Subtropical Coast). Geological formation: Sandstone of the Beaufort Group, Adelaide Subgroup (Karoo Succession).

F. subintegra possesses leaves with indistinct teeth and often rounded leaf margins and keel. The epidermis is smooth with indistinct small whitish dots. *F. subindurata* was described from the same area in the same publication, and is very clearly conspecific. The two names therefore have the same priority but the name *F. subintegra* is chosen here because it better describes the almost entire leaf margins in older leaves.

Intermediate plants have been found between *F. felina* subsp. *britteniae* and *F. subintegra*. The leaf shape was that of *F. subintegra*, the number and shape of the teeth those of *F. felina* subsp. *britteniae*. It is unknown if these intermediate populations are the result of natural hybridisation.

Specimens examined

EASTERN CAPE. —3327 (Peddie): Wooldridge, (–AB), *King 76* (BOL); a couple of km west of Wooldridge, (–AB) *Smith 3146* (BOL); Chalumna River, (–BA), *G.V. Britten s.n.* (BOL); East London, (–BB), collector unknown, *SUG10855* (BOL); Farm Kamaskraal, *King 53* (BOL); Chalumna River bank, (–BA), *Groen 1082* (WAG); Chalumna River bank, near King Williams Town, (–CD), *Henderson 2041* (NBG).

6. **Faucaria tigrina** *(Haw.) Schwantes* in Zeitschrift für Sukkulentenkunde 2: 177 (1926); L.Bolus: t. 267 (1927); G.D.Duursma: 128 (1930); N.E.Br. et al.: 211 (1931); L.Bolus: 22 (1933a); H.Jacobsen: 130 (1933); L.Bolus: 110 (1937); H.Jacobsen: 1369 (1955); Schwantes: 129 (1957); H.Jacobsen: 424 (1970); Herre: 156 (1971); H.Jacobsen: 1146 (1978); B.P.Barkhuizen: 126 (1978); H.Jacobsen: 456 (1981); J.A.Retief: 23 (1989); F.McIntosh: 167 (1989); S.A.Hammer: 4 (1991). Type: Edwards, 1817, t. 260, unnumbered plate, (1817) (neo.!, here designated).

Mesembryanthemum tigrinum Haw.: 164 (1794/1795); Haw.: 31 (1803); W.T.Aiton: 218 (1811); Haw.: 216 (1812); Edwards: t. 260 cum fig. (1817); Haw.: 89 (1821); DC.: 419 (1828); G.Don: 128 (1834); Salm-Dyck: t. 5 (1836); Sond.: 397 (1862); Eckl. & Zeyh.: 308 (1834–1837); A.Berger: 266, fig. 57 (1908).

F. tigrina (Haw.) Schwantes forma *splendens* H.Jacobsen & G.D. Rowley: 81 (1955); H.Jacobsen: 1369 (1955); H.Jacobsen: 424 (1970); H.Jacobsen: 1146 (1978); H.Jacobsen: 456 (1981). Type: not designated.

F. tigrina 'Superba' nom. nud., Weber: 12 (1968).

Plants forming compact clumps, stem-forming absent (Figure 1E). *Leaves* very crowded, pressed against each other, more or less erect, ovate-rhomboid in upper half, lowest half of leaves square, sharply keeled at top, 30–40(–50) × 15–20(–25) mm, toothed; teeth on leaf margins (5–)9–10(–12) with long bristles, pointed backwards; grey-green, turning to bluish purple, margins and keel whitish; epidermis with numerous clearly visible white dots, confluent into larger flecks, often arranged in curved lines towards keel, minute white dots absent. *Flowers* with 100–120 petals, linear, acute, 1.0–1.25 mm wide; stamens 250–300. *Nectaries* brownish, surface often 3-ribbed. *Fruit stalk* absent or (0.5–)2.5–3.8 × 3.0–4.0 mm, 0.9–1.6 mm thick. *Fruits* coming loose rather easily, top of fruit flattened to slightly spherical, 7.0–9.5 × 8.0–10.0(–12.0) and (6–)8–9 mm thick. *Seeds* 1.15–1.50 × 1.0–1.25 mm. *Flowering period*: March–May.

The species was discovered as early as 1790 (Bolus 1927), probably because of its accessibility. *Faucaria tigrina* is a compact, crowded, distinctly flecked plant having 9–10 distinct teeth with long bristles on the short leaves. The many white-coloured flecks on the often reddish leaves resemble the lichens and reddish rocks in its natural surroundings. Some populations of *F. felina* subsp. *britteniae* at Hell's Poort, 35 km west of Grahamstown and near Fort Beaufort, look like *F. tigrina* because of the numerous large flecks on the leaves and the long bristles. However, the leaves of *F. felina* subsp. *britteniae* are larger, not pressed against each other and the number of teeth is reduced to 5 or 6. Forma *splendens*, published by Jacobsen & Rowley in 1955, was recognised on the basis of its reddish leaves, typical for some populations. *F. tigrina* 'Superba' is a superfluous synonym, used in seed catalogues to differentiate good plants and seed, reintroduced by Mrs Dudley Ryder, from the usually inferior hybrids named *F. tigrina* (Weber 1968).

Distribution: narrow endemic at the edge of Grahamstown (Figure 2F). These populations are endangered because of cultivation and urbanisation (Retief 1989; Van Jaarsveld 1990; Groen 1991; Chan 1992).

Ecology: Fynbos, Renosterbosveld on open rocky patches. Rainfall: 681 mm per annum (Grahamstown). Geological formation: sandstone, Dwyka Series, Karoo System, pH(H_2O) 4.7–5.7.

Specimens examined

EASTERN CAPE.—3326 (Grahamstown): Gowieskloof, near Grahamstown, (–BC), *Gowie s.n.* (K); ibid. *G.V. Britten* 36 (BOL); ibid., *Van Jaarsveld 11104* (NBG); ibid., *A.J. Mullins comm. E. Brink* (GRA); Burnt Kraal, near Grahamstown, (–BC), *Groen & Marx 1052b, 1054* (GRA, WAG).

CYTOTAXONOMY

The chromosome number of *Faucaria* is usually listed as 2n = 18 (Moore 1973). The chromosome number of the studied material of all species was also 2n = 18. The chromosomes are however difficult to study, and this number is therefore based on a few plates only.

CHARACTER ASSESSMENT

The classification of *Faucaria* is based on a combination of variable characters (Table 1). There could be even more variation within taxa than between taxa. These difficulties are reflected in the key; it proved quite difficult to construct a usable one. In this treatment, considerable importance is awarded to epidermis characters, being one of the few fairly usable characters. Other characters such as number of teeth or leaf shape proved to be too variable for making reliable taxonomic decisions. Cladistic analysis is also hampered by this lack of usable information and must be regarded as uninformative. Despite these shortcomings, the authors find this monograph important as the first taxonomic treatment of this horticulturally important genus.

Morphology

Stems

Stems of *Faucaria* taxa are short, erect or creeping, or may be virtually absent. The stems increase in length, to a maximum of about 150 mm long and up to 10 mm thick. The woody stems show a limited secondary anomalous growth and cork development. The internal structure consists of successive rings of meristem in the phloem or pericycle. Cork develops in the inner part of the cortex or inside the endodermis. The stems are branched, so that small clumps develop. The leaves at the top of the branches cover the stem completely, whereas older parts of the stems are mostly leafless.

Leaves

The leaves of *Faucaria* show a distinct interspecific variation, whereas the variation in separate populations of one species is usually smaller. In the pre-juvenile stage, all species lack flecks and teeth, are fresh green, often with white margins. In the juvenile stage the subsequent leaves gradually develop the characteristics of the adult leaves (Figure 6A). In the adult stage the successive leaves are similar. In conditions of poor light the plants stay longer in the pre-juvenile and juvenile stage than in full sunlight. The ontogeny of *F. bosscheana* is very short, compared to the other species; it reaches the flowering stage while still in possession of juvenile leaves; the neoteny of this species could be initiated by the very dry circumstances of its habitat, which tend to induce a shortening of its development. It has been noticed that extreme conditions promote the development of taxa with neotenic character states (Ihlenfeldt 1971a).

The shape of adult leaves may vary from ovate-rhomboid to ovate-lanceolate, depending on species, population and environment. Individual populations could be recognised in some cases on the basis of leaf characters.

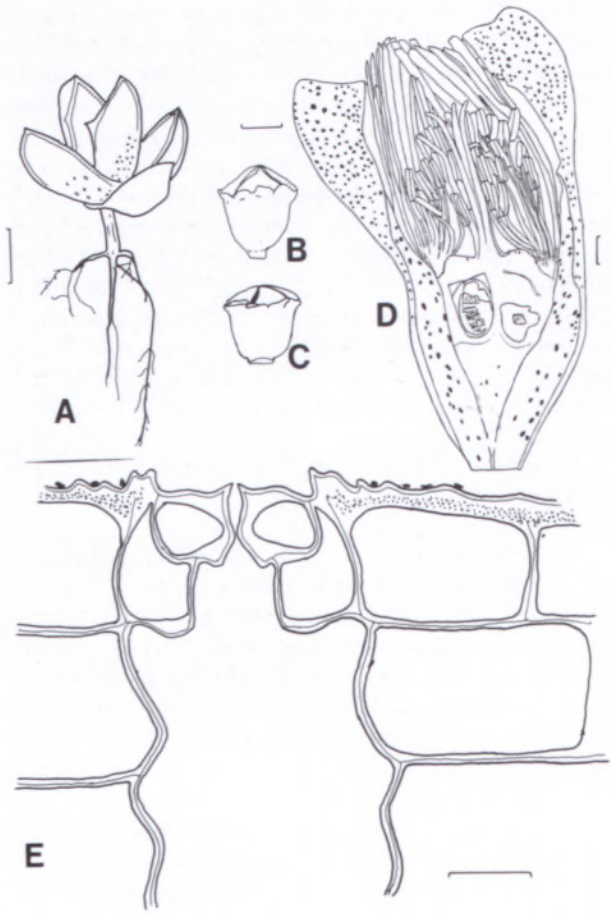

FIGURE 6.—A, Seedling of *F. bosscheana*, *Marx 202*, cotyledons still visible and 2 pairs of leaves developed, 252 days after sowing; B, *F. felina* subsp. *britteniae*, *Groen 1058*, fruit, central part raised; C, *F. tigrina*, *Groen 1054*, central part of fruit not raised; D, *F. felina* subsp. *felina*, *84BG41408*, flowerbud just before anthesis; E, *F. felina* subsp. *britteniae*, *Groen 1057*, epidermis of under surface of leaf, superficial stoma surrounded by cuticular folds, wax particles dispersed. Scale bars: A, D, 1 mm; B, C, 5 mm; E, 10 µm.

Leaves exposed to full sun are shorter, wider, more intensely coloured and flecked than leaves sheltered from the sun. Old withered leaves turn brownish, reddish, greyish to blackish. Plants of *Faucaria* are isophyllous. All leaves are narrow at the base, flat on the upper side, with the lower side keeled and triangular in cross section towards the top. The keel becomes rounded lower down so that towards the base the leaf is hemispherical. Towards the base the leaves are fused for a short distance and consequently the internodes are hidden by a leaf sheath. The leaf margins are often sharp at the apex, a mucro is absent on the ± rounded leaf tip. The differences in leaf form can be remarkable (Huber 1943; Bolus 1937), this taxonomically variable character proves, however, to be useful in the key.

The leaves of *Faucaria* very often bear teeth on the leaf margins in the upper part. Their development is simultaneous with that of the leaf, but very young leaves bear relatively large teeth. These teeth develop successively, the differences in size could be large in young stages; e.g. in a leaf primordium of 1.5 mm length with the largest tooth at 1.3 mm, the ratio with two other teeth

is 16:3:1. In later stages the differences between the teeth become gradually smaller. The teeth are emergences of the leaf because deeper tissue layers contribute to the formation of the projections. The teeth consist of epidermal and hypodermal cell layers that are characterised by strongly thickened collenchymatic or sclerenchymatic cell walls. Some populations have leaves with small, poorly developed teeth on the upper side, the so-called tubercles. These usually functionless tubercles may be present on the margins or elsewhere on the upper side. Plants with tubercles on the upper surface have often been cultivated under the name *F. tuberculosa*. In the ontogeny, teeth appear in the 3rd or 4th leaf pair. In adult leaves the teeth are most prominent in the young stage, normally decreasing in size with age. The number and size of teeth vary with each taxon, growing circumstances, and even the population.

The teeth often bear bristles, depending on the taxon. Certain taxa like *F. tigrina* always possess bristles, whereas others, like *F. bosscheana*, usually lack them. A strong development of bristles seems to be correlated with well-developed oxalate dots in the epidermis. The presence of papillae on the teeth is also variable, they are only numerous on the teeth of *F. tigrina*. In *F. felina s.l.* the teeth are smooth to moderately papillate, some accessions are very papillate, whereas other populations are hardly or not papillate. *F. bosscheana*, *F. gratiae*, *F. nemorosa* and *F. subintegra* show no or only a few papillae.

Idioblasts

Idioblasts occur on the stem, leaves and receptacle of *Faucaria* (Figure 7A, B). They are roundish, spherical or elongated. The elongated idioblasts in the lower part of the leaves and the central tissue are orientated in the growth direction of the leaves. The subhypodermal idioblasts are visible as longitudinal or roundish dots in the epidermis. They are very often obscured by calcium-oxalate dots that develop above the idioblasts. They may or may not contain bundles of needle-like calcium oxalate raphides. The idioblasts vary considerably in size: small roundish raphide idioblasts are about 80–185 µm whereas only liquid-containing idioblasts may vary between 100 and 650 µm. The most and largest idioblasts may be found at the strongly cutinized edges. Subepidermal idioblasts contain mostly tannin-like substances, idioblasts in the central tissue are often tannin-free. Dark brown-coloured tannin idioblasts occur especially in old leaves. From the outside they can be localised as small dark brown or blackish dots. It could not be established whether the percentage of tannin-like substances in decayed leaves is higher than in younger leaves.

Flowers

Flower shape and colour within *Faucaria* is not very variable, and only some differences in petal and stamen number can be observed between species. Variation in colour in the nectaries has some taxonomic value as was suggested by Schwantes (1957). But even within populations the colour can vary between green and brown. The single flower (Figure 6D) is a termination of the shoot, produced by the more developed of the two buds of the distal leaf pair. Sometimes both buds become fertile or stay sterile. The flower is produced on the topmost internodium (homologous to the flower pedicel), resulting in (almost) sessile flowers. The study of Troll & Weberling (1981) of *F. felina* proves that the reduction of the stem region is important, resulting in the absence of bracts.

The free sepals often show membraneous margins. The calyx consists of five sepals of which the two outer sepals are leaf-like (Ihlenfeldt 1960, 1971a; Haas 1976). The three-keeled inner sepals are produced by the edge of the receptacle. Difference in thickness of the sepals is of some taxonomic importance. The two keeled outer sepals are slightly longer than the inner three and bear small dorsal subapical appendages, homologous with the protruding keel of the leaf (Kaussmann & Schiewer 1989).

The yellow linear-lanceolate petals are whitish at the base, dull yellow below, sometimes reddish at the tip, outer surface reddish, especially in fading flowers. Very occasionally a white-flowering mutant can be found among many yellow-flowering ones. One of these mutants has been described as *F. candida*. The yellow colour originates from 90–95% dopaxanthin and free lemon-yellow betalamic acid (Hofmann 1973; Reznik *et al.* 1988). The petal number depends on the species and size of the flower and varies between 70 and 160 (Figure 8). Staminodes are absent. The 100–350 erect stamens fill the centre of the flower, providing abundant pollen. The presentation of large amounts of pollen and the hidden nectaries characterise the pollination type of

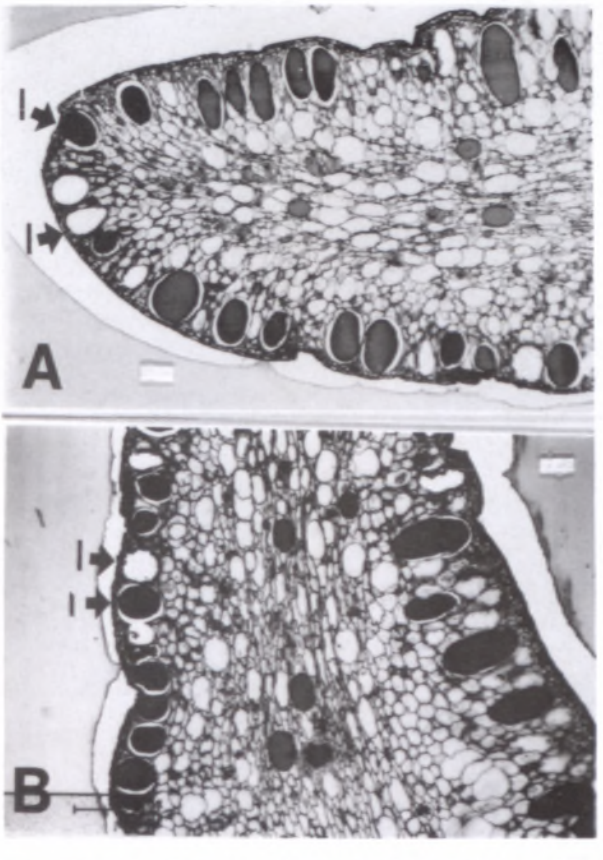

FIGURE 7.—Subepidermal idioblasts in leaf section. A, B *F. subintegra*, *Van Jaarsveld 6950*. The dark coloured tannin contents have disappeared in some cases during preparation. Scale bar: 160 µm.

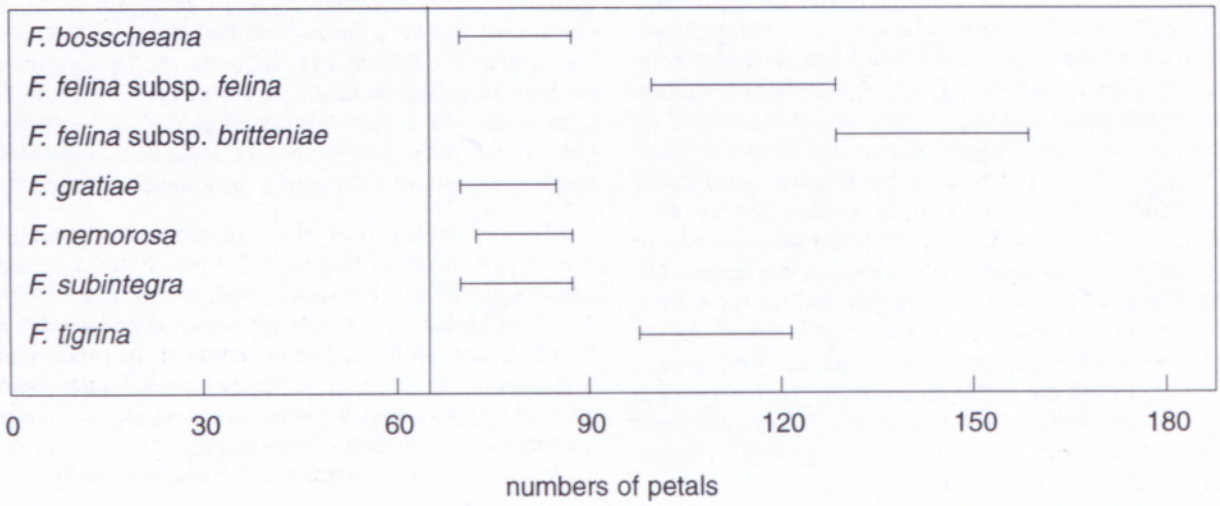

FIGURE 8.—Variation in numbers of petals of *Faucaria* species.

Faucaria as melittophilous (Vogel (1954). Because of the flat, open flower and the stamen-filled centre, the flower subtype could be classified as stamen carpet flower (Vogel 1954; Hartmann 1991).

The anthers consist of thin-walled cells, usually weakly papillate at the base. The papillae are hair-like projections from the basal cells, which may occur higher up. Variation in papillae occurs and in some flowers almost epapillate stamens have been found. The stamens vary in length from 7 to 11 mm, depending on their position, the longest are placed at the outside of the cone, the innermost are the shortest. The stamens are colourless except for a somewhat yellowish apex. Pollen grains are spherical-subprolate, 28–32 µm diam., 3-colpate (Figure 9A, B); with microreticulate, microspinulose tectum. Our

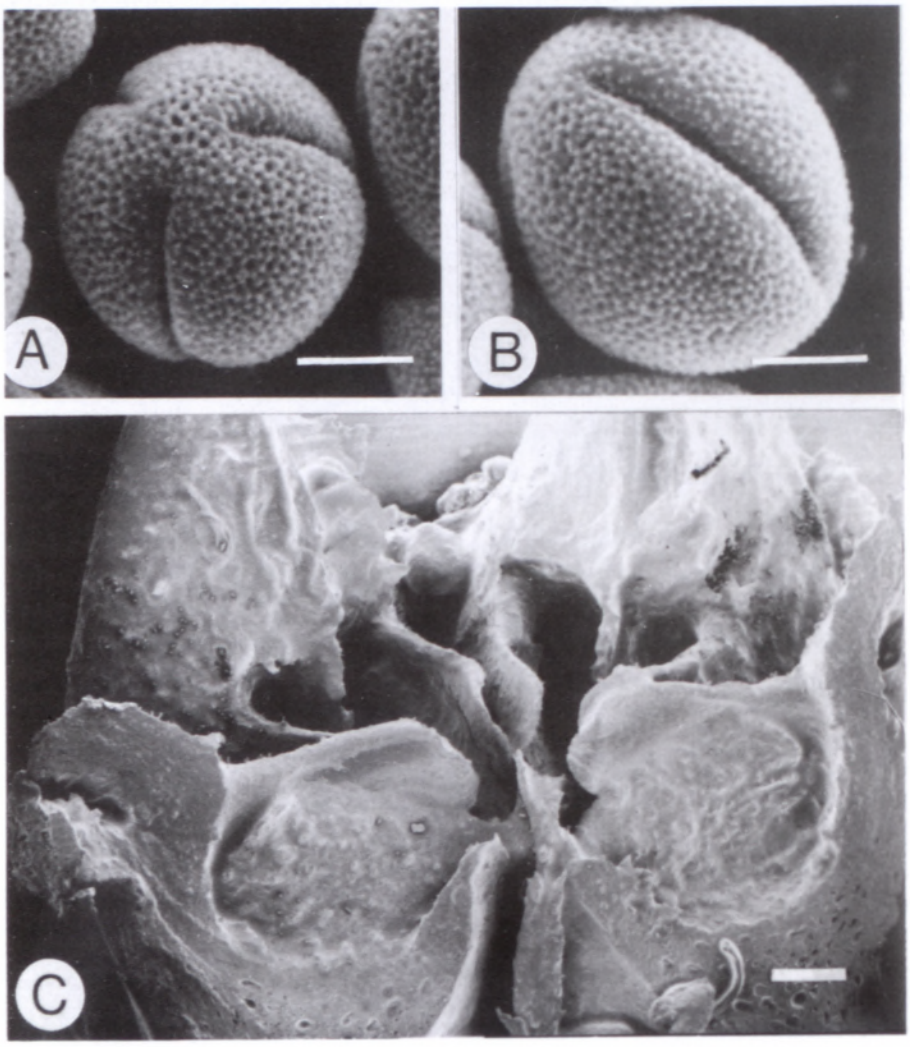

FIGURE 9.—Scanning electron micrographs of *F. felina* subsp. *felina*, *Van Jaarsveld 6897*. A, B, pollen grain: A, polar view; B, equatoral view. C, valve wings have been dissected from valves in background for a view of open fruit; split septa with their hollows clearly visible. Scale bars: A, B, 10 µm; C, 1 mm.

observations do not indicate any differences between taxa. The style is absent, usually five stigmas are present, free to the base. On the inner side they bear elongated blunt papillae of about 10–16 µm wide, which may form small bunches. The stigmas continue to grow during flowering, at anthesis they are shorter than or as long as the stamens, in old flowers they overtop them. The stigmas can be curled or recurved, especially in old stages.

The green to brown nectaries of *Faucaria* vary in size, and form, even within species. They may be button-like, elongated, crest-like, smooth or ribbed. Mostly they are slightly less then 1 mm long. Nectaries in *F. bosscheana* and *F. subintegra* are button-like, 1 mm or less long and 0.5 mm wide, with a smooth or slightly uneven surface. Those of *F. hooleae* are smooth, and button-like to elongated. The nectaries of *F. felina s.l.* vary from smooth button-like to elongated or crest-like. The surface may be smooth to ribbed. The variation is clearly depicted in the watercolour drawings of *F. ryneveldiae*. One drawing shows smooth, crest-like nectaries, the other drawing, button-like, smooth ones. The nectaries of *F. tigrina* are ribbed and elongated.

The receptacle is 2-keeled and sometimes slightly constricted at the apex, and may form a short tube up to 1 mm long. The top of the inferior ovary is flattened to conical, with 5 grooves, sometimes with another 5 alternating less prominent grooves. Bolus (1934, 1937) emphasised especially the number of these grooves in *Faucaria* and the slope of the tissue between them to the centre. The middle of the ovary itself is usually elevated for 1–2 mm. A considerable variation exists in the construction of the top of the ovary, and may even vary between flowers of the same plant.

Fruits

The top of the ovary, and immature and mature *Faucaria* fruits vary in shape between the taxa (Bolus 1937). The variation in shape of the top of the ovary and the immature fruits is so large that this character is not used in this study. The mature fruits show less variation among the taxa and is included only in the species description.

In the developing fruit, parenchyma tissue develops from the valves downwards, and splits the lamellae of the five septa. The top of the ripening fruit is often conically swollen by this developing parenchyma tissue, the grooves are well developed at this stage. In ripe capsules the parenchyma has disappeared and only five empty hollows remain of the pulp masses, so that, together with the real locules, the fruit seems to be 10-celled (Figure 9C). At first sight the capsule seems empty, because only the hollows are visible, but in fact the locules are hidden by the bent lamellae. The ripe capsule is 5-(6)-locular, woody, persistent, light brown to dark brown, with a flattened or subglobose base, and a flat to globose or raised top (Figure 6B, C). The closed valves may be bent upwards or show inwardly folded margins, leaving small fissures between them. The deep locules are covered by the split and bent cell lamellae (Figure 10B). Ordinary covering membranes and closing bodies are absent. The combined closing mechanism of deep locules and cell lamellae is very effective, since very old fruits normally still contain some seed for late distribution. The expanding keels end in an awn. The two expanding keels of one valve are lateral on each side of the valve, parallel with those of the neighbouring valve. The valve wings are stiff and straight, and when the fruits are fully opened, they stand over the locules. The capsules of *Faucaria* are variable in opening, some fruits open rapidly within minutes, whereas others need half an hour or more.

Seeds

A capsule contains 60–100(–200), broadly ovate, dark brown, warty seeds of 1.0–1.5 mm diam. Taxonomically important differences between the seeds could not be observed. The exotesta is more or less uniform, however, a longitudinal row of elongated cells on the rear is absent. The warts on the seeds exist on the papillae of the exotesta and are common in the Ruschioideae. Ehler & Barthlott (1978) found with the aid of the scanning electron microscope that the warts of *Faucaria* are covered with an epicuticular dimorphic layer of erect rodlets. One

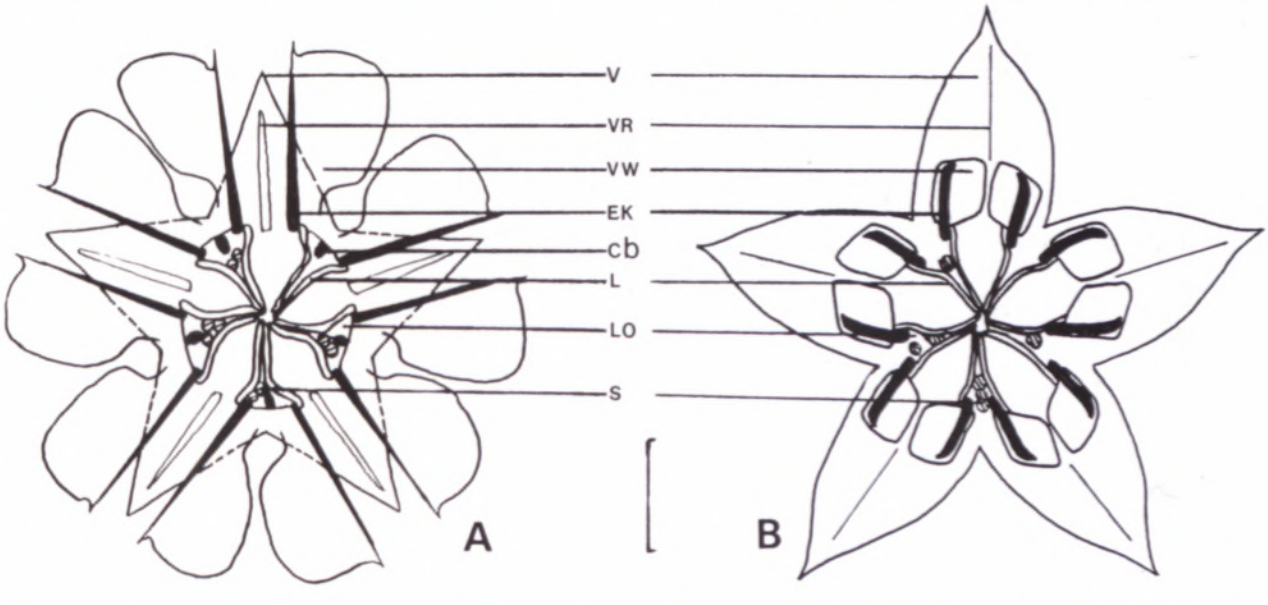

FIGURE 10.—Fruit of A, *Orthopterum waltoniae*, *Groen* 1090; B, *Faucaria tigrina*, *Groen 1054*. cb, closing body; EK, expanding keel; L, lamella; LO; locule; S, seeds (lined); V, valve; VR, valve membrane; VW, valve wing. Scale bars: A–C, 1 mm.

layer consists of rodlets of about 6 × 1 µm. On and between these rodlets other small, often bent rodlets are present that measure 1–4 × 0.4 µm. They also found small differences in the shape of these rodlets between *F. tigrina* and *F. felina* subsp. *tuberculosa*. From SEM preparations it could only be concluded that slight differences between the species exist, but these do not seem to be of any taxonomic use (Figure 11A–F).

Anatomy of epidermis

The wax cover on the epidermis may occur as small particles of different size (Figure 5A, B), but is obscured by the cuticular folds of the epidermis. Form, structure and occurrence of the cuticular folds of 21–36 µm wide depends on the position on the leaf and on the taxon. The folds may form cobweb-like structures in combination with small epidermal elevations of the whitish dots (Figure 5E). A more ribbed structure can be found in species without pronounced elevated dots such as *F. subintegra* or *F. bosscheana*. The most developed cuticular fold structures can be found in species with strongly oxalate-encrusted epidermis, like *F. tigrina*. The cuticular folds are generally less developed on the upper surface than the lower surface of the leaves. A flake-like wax cover is strongly developed in the related *Orthopterum waltoniae*, where the cuticular folds are absent (Figure 5H).

The epidermis of *Faucaria* is of the xeromorphic type (Ihlenfeldt & Hartmann 1982; Ihlenfeldt 1983) and is encrusted with calcium-oxalate crystals in the outer walls. Strongly encrusted parts of the epidermis are visible as whitish dots and flecks of 0.15–5.0 mm or more diam., very often developed above subhypodermal tannin idioblasts. The outer walls of the epidermal cells in these dots are dome-like and 16–26 µm thick with a thick layer of oxalate crystals, compared to the 8–13 µm thick outer epidermis of the surrounding epidermal cells. These dome-like epidermal structures may be further developed in papillae of 20–150 × 20–50 µm that are located on margins, keels and teeth of the leaves (Figure 5G). Their presence is however variable (see description of leaf). Besides these large papillae, small club-shaped papillae occur on the epidermis, which are about 7.1–9.1 × 2.8–3.9 µm in size. The outer wall of the strongly encrusted epidermis cells reaches to about half-way down the tangential walls, the thickness may vary from 2–4 µm. The inner walls of the epidermis of these cells are 3–6 µm thick, in less encrusted cells 2 µm.

The development of the epidermal calcium-oxalate crystal dots, flecks or zones differs from species to species and may be restricted to the leaf margins, as in *F. bosscheana*, or even absent in some populations of *F. felina* subsp. *felina*. The crystal concentrations are slightly elevated, giving the leaves a pattern of depressions and elevations. These elevations are also partially due to the presence of subepidermal idioblasts in the mesophyll (Figure 3).

The stomata on upper and lower leaf surfaces generally occur in relatively less oxalate-encrusted parts between the strongly oxalate-encrusted elevated dots.

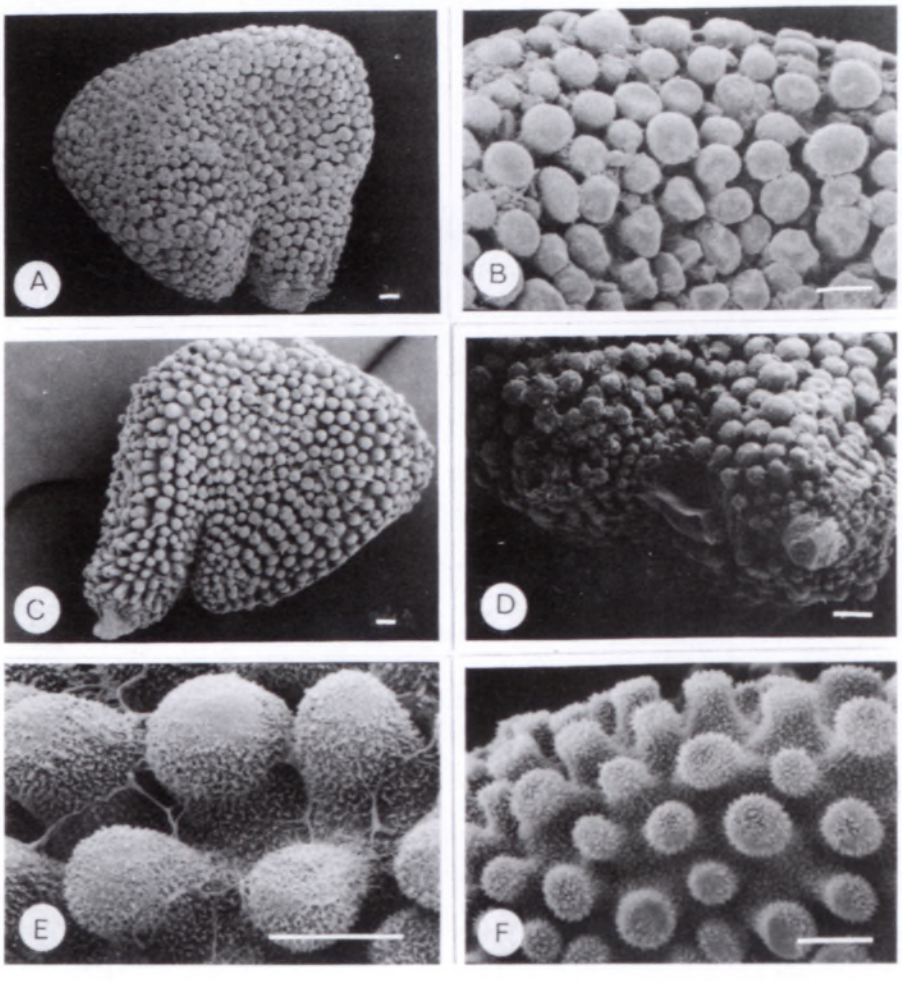

FIGURE 11.—Scanning electron micrographs of seeds. A, B, *F. tigrina*, *G.V. Britten s.n.* (BOL); C, *F. felina* subsp. *felina*, *James 8* (BOL); D, *F. felina* subsp. *felina*, *N.S. Pillans NBG446/16* (BOL); E, *F. bosscheana*, *Bayer 2395* (BOL); F, *F. subintegra*, *NBG1046/33* (BOL). Scale bars: 100 µm.

The stomata occur regularly in these areas, whereas their density is very variable, ranging from 6–128 per mm^2. The anisocytic and paracytic stomata are level with the surrounding epidermal cells. These superficial stomata (Figure 6E) occur also in other genera with a xeromorphic epidermis e.g. *Nananthus* and *Rhombophyllum* (Ihlenfeldt & Hartmann 1982). The guard cells measure 22–37 × 6–12 µm. The stomata may be surrounded partially or completely by cuticular folds of the neighbouring cells. These projections partially form a secondary outer surface. The epidermal protection of the stomata of *Faucaria* may be absent or almost sunken in the cuticular folds and/or protected by the elevated leaf surface (Figure 5A–F). This type of differentiation was described earlier from the genera *Odontophorus*, *Octopoma* and some species of *Cheiridopsis* (Ihlenfeldt & Hartmann 1982). Instead of surface sculpturing in the form of papillate epidermis cells like these taxa, *Faucaria* has cuticular folds.

Anatomy of leaves

The leaves possess a large central vascular bundle, occasionally accompanied by some parallel lateral vascular bundles. A ring of lateral vascular bundles is also present. The distinction between assimilation parenchyma and chloroplast-free, central, water-storing, spongy parenchyma is not very sharp. Assimilation parenchyma is absent in the dorsally lower part. A faint ring of lateral vessels could be observed in the transition zone between the two tissues.

Germination and development

Fresh seed of *Faucaria* will germinate within a few days after sowing. The germination curve is bimodal like that of *Trichodiadema* spp. (Ihlenfeldt 1971b). The first seedlings appeared three days after sowing and the first germination peak appeared after six days, the second one after 12 days. New seedlings appeared up to 33 days after sowing. The percentage germination varied from 34 to 94%, with an average of 67%. In the first stage the germination is by means of a true operculum, which breaks off before the embryo emerges. Bregman & Bouman (1983), who studied seeds of numerous Cactaceae and a few Portulacaceae, found that all operculate species studied were succulents, whereas the inoperculate species were not. The cracks may be dorsal or lateral near the micropyle. The germination does not depend on disintegration of the tough testa. The empty testa may still be attached to the cotyledons. It was noticed in the present study that with germination, the primary root stayed enclosed in the inner integument in some seeds. The primary root in these seeds may break finally through the inner integument after days or even several weeks. This delay in germination is advantageous if only a single short rain shower has fallen.

The succulent green cotyledons of the seedlings are slightly broader than long (5:4), with a clear slit between them. With their fused base they form a flat semicircular or elliptic top of the seedling. After germination they grow to about 5 mm in length and width. Dupont (1968) has observed seedlings of 79 genera in the Aizoaceae *s.l.* and found that the cotyledons of *Faucaria* are about average in their degree of succulence. Differences between species of this genus in size, form and colour are hardly noticeable in the seedling stages. Within some months after sowing, the seedlings develop their first leaf pair. These leaves are uniformly shiny green and possess a white, cartilaginous margin without teeth. At this stage differences between species are not yet noticeable. After a vegetative development of ± seven months to three years the first flowers develop. The flowers appear in autumn, mostly around April/May in the southern hemisphere and in September/November in the northern hemisphere.

Pollination biology

Faucaria sets seed easily after cross-pollination. The main flowering period is in autumn, from March till June, but occasionally flowering occurs outside this period. Differences in the flowering time between species are usually small; *F. bosscheana* flowers one month earlier than *F. felina s.l.* in culture in the southern hemisphere. Rain may be important to induce flower development, in several cases the plants start flowering after the onset of the rains. Nectar does not seem to play an important role in pollination. The nectaries are not so easy to reach, insects have to pass the stamen brush. This unspecialised floral type is a representative of the cantharophilous syndrome, where pollination takes place by small malachiid beetles. Gess & Gess (1989) found small wasps (Hymenoptera, Masaridae) as one of the main pollinators of the Aizoaceae. Liede *et al.* (1991) found in a similarly structured flower of *Conophytum subfenestratum* Schwantes *(= C. pillansii)* that both insects play a role in the pollination, but that the beetles outnumbered the wasps. Wind pollination is unlikely, as the stigmas are not exposed and dry pollen is not present (Chan 1992). The flowers of *Faucaria* open around 15:00–17:00, and close at sunset. It has been observed in the field that mixed populations of *Faucaria*, *Bergeranthus* and *Orthopterum* flower simultaneously. This could indicate a combined pollinator attraction by flower synchrony.

Fruit and seed dispersal

Faucaria has variable fruit dispersal. Some capsules become detached easily, others are persistent. The fruits can either be detached actively from the plant by the next developing leaf pair or passively when the very short pedicel withers. The seed is not specially adapted for dispersal and combined with the effective closing mechanism seed dispersal of *Faucaria* depends on capsule dispersal. There is a close correlation between hygroscopic opening, ombrochory and germination (Hartmann 1988). In *Faucaria*, ejection of seeds is prevented by a combination of deep locules and overgrown cell lamellae. In old capsules most seeds are usually still present and only after complete deterioration, which could be after years, these seeds come free from the fruits. This is an ingenious method for these plants to overcome drought conditions and re-establish populations after long periods of low rainfall. Observations and small experiments with seed dispersal also indicated that seeds of *Faucaria* are difficult to wash out from the capsules. This means that

ombrochory in *Faucaria* is not very important. Fruit and seeds of *Faucaria* are not wind-dispersed (anemochorous) like nearly half of the species of the central lower Karoo community (Cowling & Roux 1987). The relatively large and heavy capsules usually stay within a few centimetres of the plants. The re-establishment on locations after unpredictable long periods of drought in the south-central Eastern Cape is probably more important than dispersal. The establishment of new populations is difficult, because of the absence of vegetative dispersal and the poor seed dispersal.

Cultivation

Like many other species of the Eastern Cape, *Faucaria* is rather easy to grow in cultivation. In nature, leaf succulents in the Eastern Cape grow throughout the year, but a summer peak is apparent (Hoffman 1989). In cultivation it is attempted to restrict growth to spring and summer. The best results in the Netherlands were obtained by growing plants in a sunny place in a heated winter frame, protected from rain in the growing season by glass, watered generously in summer and early autumn. Species of *Faucaria* overwinter without watering at a minimum of 5°C. Under these conditions plants grow well and remain compact. If grown in a warm greenhouse, plants at low light intensity produce long etiolated leaves. Soil is not very critical; in nature *Faucaria* grows in several soils. An appropriate potting mixture is 1 part compost to 2 parts sharp sand and a small amount of clay. Pots of 70–120 mm diam. are suitable. The pH can probably be below 7 according to field data (see species descriptions). Propagation is easy by seed or cuttings. *Faucaria* species hybridise easily in cultivation, causing frequent confusion (Hammer 1991). To obtain unhybridised seed it is necessary to isolate species when in flower. Plants sometimes suffer from (root) mealy bugs or they may be attacked by the vine weevil, *Otiorhynchus sulcatus* (F.). Watering during cold or moist periods may result in rotting of the leaves, ultimately killing off the plant.

Ecology

Faucaria is found very often under the shelter of open bushes. This 'nurse plant' phenomenon whereby seedlings readily establish themselves beneath the canopy of certain plants is common in most arid and semi-arid areas, including the Karoo (Cowling & Roux 1987). *Faucaria* usually grows on rocky hill slopes, on top of koppies, on open spots in the bush or more rarely in cracks of rocks. The plant has a preference for sun-facing north slopes, but is not restricted to that position. Field data recorded plants growing in gravel, sand, tillite, sandstone, shale, loam, and clay. The plants are probably not sensitive to low pH.

In this genus a very compact growth is not an adaption against aridity; *F. subintegra* grows in very dry circumstances and develops a rather long stem. Correlation between location factors and species seems small. The genus occurs in different rainfall regimes, the southernmost populations of *F. felina* subsp. *felina* thrive exclusively in a maximum winter rainfall area. *F. bosscheana* occurs in regions with mainly autumn and summer rainfall. The remaining taxa grow in areas with mainly spring and autumn rainfall. *Faucaria* does not grow at very high altitudes, and is mostly recorded between 600–850 m, rarely up to 1 500 m. A comparison of the distribution area with the vegetation maps of Lubke *et al.* (1986) indicates that *Faucaria* is for the greater part an element of the Tongaland-Pondoland and Karoo-Namib phytochorological regions, which contain many succulent species from karroid origin, distributed in the thicket (Lubke *et al.* 1986). The distribution area of *F. tigrina* is within the boundaries of the southern phytogeographical centre of the Cape Floral Kingdom as defined by Olivier *et al.* (1983); Bond & Goldblatt (1984); Ellis (1988). The dry thickets of these river valleys were defined by Cowling (1983) as Kaffrarian Succulent Thicket, and as Valley Bushveld Thicket by Lubke *et al.* Like Noorsveld (Acocks No. 24) and Spekboomveld (Acocks No. 25) these thickets are classified by Lubke *et al.* (1986) as Subtropical Thicket. *Faucaria* has been reported in all three.

Distribution and habitat

The genus is found south of 31° S and between 22° and 28° E. The main distribution area is within the south-central region of the Eastern Cape, but it extends slightly into the Western Cape. The genus occurs from the southeastern coast at about sea level to 1 500 m in the interior of the Namib-Karoo region. Few locations are reported from the dry northwestern districts of the area, but these have been botanically poorly explored (Gibbs Russell *et al.* 1984). *Faucaria* shows a patchy distribution; the plants are scattered in populations of different size. Temperature and rainfall change markedly from the coast towards the interior. The more extreme temperatures occur in the north and west of the area, with maximum air temperatures of more than 43°C in summer, and winter minimum falling below –3°C at Graaff-Reinet (Palmer 1989). The unpredictable rainfall diminishes gradually from south to north, the river valleys receive 500–900 mm per annum and the area at Graaff-Reinet has recorded extreme annual precipitation between 144 and 664 mm (Acocks 1988; Palmer 1989). Part of the distribution area of *Faucaria* is situated in the 'stem succulent zone' as defined by Jürgens (1986). This vegetation type, characterised by tall long-lived succulents, only exists in regions with a moderate variability in rainfall. The diagram of Ellenberg (1981) indicates that *Faucaria* can grow in regions with a rainfall of 400–700 mm and a rainfall variability index of 2.5–3.5.

The present distribution of *Faucaria* partially fits the hypothesis of Cowling (1983). He postulated that the semi-arid river valleys of the south-central Eastern Cape, where *Faucaria* is concentrated, comprise an endemic centre and a relatively ancient centre of karroid taxa. He suggested that karroid species in the south-central Eastern Cape river valleys were more widespread during the last glacial era. Thicket taxa of tropical origin e.g. *Euphorbia* were established in the Holocene (White *et al.* 1941). The present-day succulent thicket communities consist of these immigrants and newly evolved species. The semi-arid climate promotes the division of large or medium-sized populations into smaller ones.

These small populations become isolated from each other, resulting in small, but often distinct differences between the populations of *Faucaria*.

Conservation status

Only Hall *et al.* (1980) listed a conservation status for two *Faucaria* taxa, *F. candida* and *F. longidens* synonyms of *F. felina* subsp. *felina*. The conservation classification was listed as indeterminate resp. uncertain, which means that insufficient data are available. As for other plant taxa it seems to be more important to protect the habitat than that of *Faucaria* itself. *Faucaria felina s.l.* prefers Eastern Cape transitional thicket, comprised of Valley Bushveld, Noorsveld and Spekboomveld. This subtropical thicket is extremely poorly conserved (Noorsveld = 0%, Spekboomveld = 1.8%, Valley Bushveld = 1.2%) (Hoffman & Everard 1987). More than 30% has been converted to wheat cultivation or degenerated to wasteland by overgrazing. The southern form of *F. felina* subsp. *felina* (published as *F. lupina*), is threatened by human activities in its habitat around Algoa Bay.

It is preferable to assign the IUCN code 'Vulnerable' to *F. tigrina*, as this species is restricted to the surroundings of Grahamstown, where it is threatened by human activity such as housing development. There are about 1 700 plants in seven colonies in the wild, according to a field study of Chan (1992). According to Hilton-Taylor (1996), *F. tigrina* is also listed as Vulnerable. Two other species with a very limited distribution, *F. nemorosa* and *F. gratiae*, are not threatened at the moment, but must be regarded as Vulnerable. About 800 plants of *F. gratiae* exist in two populations according to Chan and the size of the population of *F. nemorosa* is small but unknown.

DISCUSSION

Classification of species of *Faucaria* and the genus itself is problematic. On species level, taxa with striking but taxonomically difficult characters such as *F. ryneveldiae*, remain a subject for discussion. Hartmann (1988) described eight fruit types in the Ruschioideae. *Faucaria* had been regarded in this scheme as being of uncertain position. In Hartmann (1993) *Faucaria* fruits had been classified as similar to the *Leipoldtia* type but lacking tubercles. However, *Orthopterum*, the close relative of *Faucaria*, with its small tubercles, does not fit properly in the *Leipoldtia* type, as will be discussed later.

Relationship with other genera

Faucaria is included in the subfamily Ruschioideae of the Mesembryanthema, a monophyletic branch without taxonomic rank within the Aizoaceae (Caryophyllales). The Ruschioideae comprise 107 genera (Bittrich & Hartmann 1988) and are distributed mainly in southern Africa.

The Ruschioideae are characterised by: ovary almost always with parietal to basal placentation; nectaries crest-shaped, either as separate nectaries or in a ring, rarely flat and inconspicuous, very rarely absent; fruits with expanding keels of mainly valvular origin, never reaching to the centre of the fruit, if not hygrochastic, xerochastic, or breaking into mericarps.

The Ruschioideae are divided into 11 groups, mainly on epidermal, flower and fruit characters by Hartmann (1991). The epidermal characters employed are: epidermis mesomorphic or xeromorphic and homocellular or heterocellular. Flower features used are form and structure of the nectaries and the presence/absence of filamentous staminodes. Fruit characters are very important for this classification. Hartmann (1991) placed *Faucaria* in the *Stomatium* Group, mainly on the basis of epidermis features. The problems in classifying *Faucaria* fruits will be discussed later (see phylogeny).

The *Stomatium* Group comprises nine genera with the following diagnostic characteristics:

Plants are perennial. *Leaves* two to three pairs to a branch, homocellular xeromorphic, the crystals in irregular zones; surface rough or warty, from elevations above subhypodermal tannin idioblasts, often denticulate. *Flowers* with five separate nectaries. *Capsule* with or without covering membranes; closing bodies absent; valve wings broad to reduced. Genera: *Chasmatophyllum*, *Faucaria*, *Frithia*, *Mossia*, *Neohenricia*, *Orthopterum*, *Rabiea*, *Rhinephyllum*, *Stomatium*.

Frithia, *Mossia* and *Neohenricia* have morphologically little in common with *Faucaria* (Table 2). *Rabiea* with its different floral structure and 7–10-locular *Titanopsis*-type capsule is also not close to *Faucaria*. *Faucaria* and *Stomatium* differ mainly in flower, fruit and seed features; morphologically the latter often looks like a small *Faucaria* with compact growth and toothed leaves. Flower types are, however, different, the recess flower of *Stomatium* with a shallow hypanthium contrasts with the large carpet flower of *Faucaria* (Table 2). The scented flowers of *Stomatium* with small petals 0.25–0.5(–1.0) mm wide can readily be distinguished from the scentless flowers of *Faucaria* where the petals are 1.0–1.25 mm wide. The often club-shaped stigmas of *Stomatium*, 1–3 mm long, differ markedly from the 8–11 mm long filiform stigmas of *Faucaria*. The light brown, non-woody *Delosperma*-type fruit of *Stomatium* is not clearly distinct from the dark-coloured woody *Faucaria* capsule (Figure 10A, B). The parallel expanding keels and seed pockets are in contrast to the diverging keels and the seed-retaining syndrome of *Faucaria* by means of bent, split septa. The seeds of the two genera are also different, the light brown *Stomatium* seeds have a smooth or papillate brown testa, those of *Faucaria* are dark brown and tuberculate.

The similarities between *Chasmatophyllum* and *Rhinephyllum* and *Faucaria* are restricted to compact growth and similar flower shape. Teeth on the often rounded leaves of the former two are, however, generally indistinct or even missing, whereas in *Faucaria* the teeth are usually well developed and often the leaves have white margins. In *Rhinephyllum*, furthermore, the nectaries are often hardly separated, but in *Chasmatophyllum* and *Faucaria* they are clearly distant.

TABLE 2.—Morphological similarities in the Stomatium Group

Character states	Fa	Or	Rh	Ch	St	Ra	Fr	Mo	Ne
Taproot absent	+	+	+	+	+	-	+	+	+
Clump-forming	+	+	-	-+	+	+	+	-	-
Leaves more or less toothed	+	+	+	+	+	-	-	-	-
Leaves conspicuously dotted	+	-	+	+	+	+	-	-	+
Large carpet flower	+	+	+	+	-	-	-	-	-
Petals yellow	+	+	+	+	+	+	-	-	+
Hypanthium absent	+	+	+	+	-	-	-	-	+
Meronectary present	+	+	+	+	+	+	+	+	-
Not *Delosperma* fruit type	+	+	-	+	-	+	-	-	-
Keel present	+	+	-	-	-	-	-	-	-
Split septa	+	+	-	+	+	-	-	+	-
Septa not upright, extended	+	-	+	+	+	+	-	+	+
Septa bent	+	+	-	-	-	-	-	-	-
Valve wings present	+	+	-	+	-	+	-	+	-
Valve wings small or absent	+	-	+-	-	+	-	+	-	+
Covering membranes absent or endocarpal tissue only	+	+	+	-	+	-	+	+	+
Closing body absent	+	-	+	-+	+	+	+	+	+
Fruit dark-coloured, woody	+	+	+	+	-	+	-	-	-
Testa tuberculated, dark-coloured	+	+	+	-	+-	+	-	-	-
Characters shared with *Faucaria*	19	15	13	13	12	10	8	7	8

+ character states present; - character states absent. Fa, *Faucaria*; Or, *Orthopterum*; Rh, *Rhinephyllum*; Ch, *Chasmatophyllum*; St, *Stomatium*; Ra, *Rabiea*; Fr, *Frithia*; Mo, *Mossia*; Ne, *Neohenricia*.

The fruit of *Chasmatophyllum* and *Rhinephyllum* can not be misidentified as *Faucaria* fruits, mainly because of the absence of the unique stiff, upright valve wings of the latter.

Vegetatively *Orthopterum* is closer to *Faucaria* than to any other genus. Non-fruiting plants of *Orthopterum* with their smooth, more or less shiny appearance resemble forms of *Faucaria felina*, described as *F. lupina*, even though the leaves of *Orthopterum* usually have fewer teeth and white dots.

The flowers are almost identical and those of *Orthopterum* also open in the late afternoon. The real difference between the two genera lies in the fruits. Nevertheless the fruits of *Orthopterum* are the only ones within the Ruschioideae that have close similarities to those of *Faucaria* fruits (see Phylogeny).

Hybridisation between *Faucaria* and other members of the *Stomatium* group is unknown. Up to now only one natural intergeneric hybrid has been reported by Hammer & Liede (1990) between *Faucaria* and *Rhombophyllum*.

Phylogeny

The *Stomatium* Group is polyphyletic, a cladogram could not be constructed. The artificial character of the *Stomatium* Group is reflected by the absence of any diagnostic feature common to all taxa. The diversity of the group is also shown by the presence of three of the eight described Ruschioideae fruit types (Hartmann 1991). *Orthopterum*, *Stomatium*, *Rhinephyllum* and *Chasmatophyllum* resemble *Faucaria* as mentioned earlier (Table 2). Only the fruits are considered suitable for a meaningful examination of relationships within the *Stomatium* Group. Five out of the nine genera in the group possess *Delosperma*-type fruits (Hartmann 1988). The fruits of this type have parallel expanding keels, probably an apomorphic character (Hartmann 1988), quite different from the diverging expanding keels of *Faucaria* and *Orthopterum*. The fruits of *Stomatium* and *Rhinephyllum* belong to the *Delosperma* type, those of *Chasmatophyllum* to the *Drosanthemum* type. This last-mentioned type has translucent covering membranes which are absent in *Faucaria*. Out of the genera involved, only the fruits of *Orthopterum* show similarities with those of *Faucaria* (Figure 10B, C).

Close examination reveals that the fruits of *Faucaria* might be derived from those of *Orthopterum* by reduction and lignification. They share split septa, which bend over the locules to resemble covering membranes. The fruits of both genera lack real covering membranes. The upper part of the split septa of *Orthopterum* is translucent, flexible and raised, the lower part is partially lignified. This expanded part has disappeared in *Faucaria* and the lamellae are completely lignified. Both fruits have divergent, non-broadened expanding keels. The expanding keel of *Orthopterum* is long, that of *Faucaria* short. The long awn of the expanding keel of *Orthopterum* is reduced to a short subulate point in *Faucaria*. The large, broad, reflexed, flexible valve wings of *Orthopterum* have been reduced to small upright wings in *Faucaria*, standing rigidly over the locules. The valve wings of *Orthopterum* are reflexed, away from the opening fissure of the locules. In spite of differences in lamellae, expanding keels and valve wings, the basic fruit structure of the genera is the same. The common features indicate a common ancestor, confirming the hypothesis of Schwantes (1957) that they are related. The presence of closing bodies in *Orthopterum* has no influence on this relationship, as the taxonomic importance of these structures cannot be determined (Hartmann 1988). The ontogeny of the fruits also suggests that *Orthopterum* and *Faucaria* are close relatives. Mature fruits of *Orthopterum* are conical and acute, providing space for the raised septa. The ripening fruits of *Faucaria* also develop this conical top (Figure 6C), but this plesiomorphic feature disappears in later developmental stages, as the septa are lower, and the ripe fruits are flat- or low-topped.

Hartmann (1993) assumed that *Faucaria* fruits are similar to the *Leipoldtia* type, the striking feature of the genus being firm, stout valve wings fused to the valves in their basal part only and standing rigidly above the locules after the capsule has opened. *Faucaria* shares with the *Leipoldtia* type the distinct, non-broadened radial awn and expanding keels. Other fruit types (*Drosanthemum*, *Titanopsis*) show broadened expanding keels. However, the two apomorphic characters of the *Leipoldtia* type (Hartmann 1983): large closing bodies and the elaborate covering membranes, are missing. The large valve wings of *Orthopterum* and the small valve wings of *Faucaria* both occur in the *Leipoldtia* type. The large valve wings are common, the reduced valve wings of *Faucaria* are only shared with *Antimima*. *Orthopterum* fits even better into this fruit type, as it has small closing bodies similar to those in *Jordaaniella* and *Fenestraria*. The presence of these small closing bodies does not prevent classification of *Orthopterum* in the *Leipoldtia* fruit type. The pentamerous fruits of *Orthopterum* and *Faucaria* are also represented in this fruit type, e.g. in *Antimima* fruits. The absence of covering membranes in *Faucaria* and *Orthopterum* is the single, but essential feature, preventing them from being readily classified in the *Leipoldtia* type. If the presence of this character prevents classification in this type, then *Faucaria* and *Orthopterum* fit into none of the fruit types described by Hartmann (1988). It must be concluded that in the present classification *Faucaria* cannot be satisfactorily placed. Only *Orthopterum* is closely related to *Faucaria* and together they appear to form an isolated group within the Ruschioideae. Therefore it is proposed to re-introduce the *Faucaria* fruit type of Schwantes (1952). This will fit into the fruit scheme of Hartmann (1988) with the following characters:

Faucaria type of fruit (Schwantes 1952)

Expanding keels stout, divergent with distinct radial awn, not broadened, connate in their basal part only, extending rigidly above the locules, expanding sheet present. Covering membranes absent. Closing body absent or small. Genera: *Faucaria* Schwantes, *Orthopterum* Schwantes.

For a cladistic analysis of the genus *Faucaria* itself only a few characters are usable, such as crystal dots and teeth. Four *Faucaria* species show good visible crystal dots dispersed over the leaves in the outer epidermal layer. The three remaining species, *F. bosscheana*, *F. nemorosa* and *F. subintegra*, share with the outgroup *Orthopterum* the presence of, mostly only a few, concentrations of crystals around the teeth and margins on the leaves. The size and number of crystal dots and teeth are dictated by the taxa and are influenced in a minor way by the habitat. In culture all species turn more greenish than in nature.

The development of hypodermal crystal concentrations, teeth or bristles reflects the phylogeny in the ontogeny, and indicates the polarity of these characters. The ontogenetic transformations are an invaluable tool in the recognition of characters (sets of homologous states). The absence of oxalic crystal dot concentration in the leaves in the juvenile stage of *Faucaria* indicates that this feature is an advanced character. Because of the neotenic character of *F. bosscheana*, this species is considered basal in the genus by the phylogenetic analysis (Figure 12). The differences with the other species are, however, not so large as the diagram suggests. The diagram reflects a close relation between *F. nemorosa* and *F. subintegra*. Both show a reduction in tooth development. The fruits are similar in form and attachment on the plant, and the two species have the same, somewhat shrubby growth. The ecology of the two species, however, differs markedly: *F. subintegra* grows in the open, on very dry river banks. *F. nemorosa* is found under shrubs. A close relationship exists between *F. felina s.l.* and *F. gratiae*. *F. tigrina* is also related to the *F. felina* Group, but is distinct in morphological and epidermal features.

CONCLUSIONS

Faucaria together with *Orthopterum* forms an isolated group within the Ruschioideae. The genus consists of six species. Two species, *F. bosscheana* and *F. felina s.l.* occur over a large area, four are much more localised. The most common and widely distributed species, *F. felina s.l.*, covers most of the diversity in *Faucaria*, more than three quarters of the names in the genus were based on forms of this species. The variation is continuous, only three forms could be recognised as separate taxa, giving rise to subsp. *britteniae*, subsp. *felina* and subsp. *tuberculosa*. Macro-morphological information was sufficient for a proper taxonomic analysis in the genus.

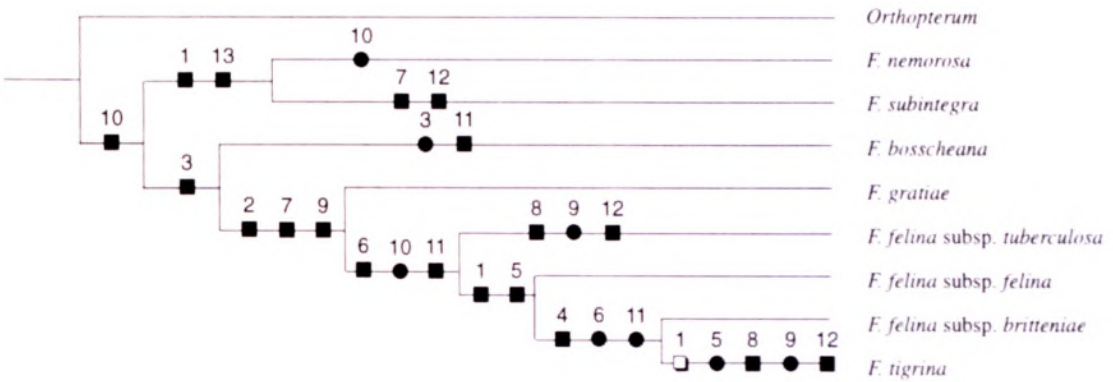

FIGURE 12.—Cladogram for the species in *Faucaria*. Characters, represented by numbers in the cladogram are given in Table 1. Symbols: 0–1 character state changement, ■, 1–0 homoplasy, ❑, 1–2 character state changement, ● Consistency index 67, retention index 72.

Epidermal characters proved important in this genus. Neither seed surface, nor pollen morphology provide taxonomically important data; similarly the structure of flowers and fruits is of limited taxonomic value.

The cladistic analysis is based on only 13 characters (Table 1) and must be regarded as preliminary. The cladogram reflects the impression that *Faucaria* has arisen from a toothless or few-toothed ancestor. *F. bosscheana*, with its neotenic tendencies, is probably the less advanced species with a relatively simple epidermis and leaf structure, with little ecological specialisation in karroid circumstances. *F. tigrina*, on the other hand, shows a complicated epidermis structure, is ecologically specialised, even showing mimicry with reddish lichens.

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REFERENCES

ACOCKS, J.P.H. 1988. Veld types of South Africa, 3rd edn. *Memoirs of the Botanical Survey of South Africa* No. 57. Botanical Research Institute, Pretoria.

AITON, W.T. 1811. *Hortus kewensis* edn 2, Vol. 3. London.

BARKHUIZEN, B.P. 1978. *Vetplante van Suidelike Afrika met spesifieke verwysing na die vetplantfamilies van die Republiek van Suid-Afrika en Suidwes-Afrika*: 124–127. Perskor-Uitgewery, Johannesburg.

BERGER, A. 1908. *Mesembrianthemen und Portulacaceen*: 265–269. Eugen Ulmer, Stuttgart.

BITTRICH, V. & HARTMANN, H.E.K. 1988. Aizoaceae—a new approach. *Botanical Journal of the Linnean Society* 97: 239–254.

BITTRICH, V. & STRUCK, M. 1989. What is primitive in Mesembryanthemaceae? An analysis of evolutionary polarity of character states. *South African Journal of Botany* 55: 321–331.

BOERHAAVE, H. 1719 [1720]. *Index alter plantarum, quae in horto academico Lugduno-Batavo aluntur*: 290, Nr. 12. Leiden.

BOLUS, H.M.L. 1927. *Faucaria tigrina*. *The Flowering Plants of South Africa* 7: t. 267.

BOLUS, H.M.L. 1930. *Mesembrianthemum* and allied genera. *South African Gardening & Country Life* 20: 153, 381, 382.

BOLUS, H.M.L. 1933a. New or noteworthy plants. *South African Gardening & Country Life* 23: 22, 23.

BOLUS, H.M.L. 1933b. *Notes on* Mesembryanthemum *and allied genera*, part 2: 394–396. Bolus Herbarium, University of Cape Town, Cape Town.

BOLUS, H.M.L. 1934. *Notes on* Mesembryanthemum *and allied genera*, part 2: 442–450, 469–471. Bolus Herbarium, University of Cape Town, Cape Town.

BOLUS, H.M.L. 1936. *Notes on* Mesembryanthemum *and allied genera*, part 3: 32, 33. Bolus Herbarium, University of Cape Town, Cape Town.

BOLUS, H.M.L. 1937. *Notes on* Mesembryanthemum *and allied genera*, part 3: 105–115. Bolus Herbarium, University of Cape Town, Cape Town.

BOLUS, H.M.L. 1938. *Notes on* Mesembryanthemum *and allied genera*, part 3: 114, 115. Bolus Herbarium, University of Cape Town, Cape Town.

BOND, P. & GOLDBLATT, P. 1984. Plants of the Cape Flora. *Journal of South African Botany*. Suppl. Vol. 13: 330.

BREGMAN, R. & BOUMAN, F. 1983. Seed germination in Cactaceae. *Botanical Journal of the Linnean Society* 86: 357–374.

BROWN, N.E. 1920. New and old species of *Mesembryanthemum*. *Journal of the Linnean Society Botany* 45: 76.

BROWN, N.E. 1927. *Faucaria albidens* N.E.Br. *Journal of Botany British and Foreign* 65: 349.

BROWN, N.E., KARSTEN, M.C. & TISCHER, A. 1931. *Mesembryanthema*: 210–212. Reeve, Kent, England.

CHAN, J. 1992. *Field study on* Faucaria. B.Sc. Hons., Rhodes University, Grahamstown.

COWLING, R.M. 1983. Phytochorology and vegetation history in the south-eastern Cape. *South African Journal of Biogeography* 10: 393–419.

COWLING, R.M. & ROUX, P.W. (eds). 1987. *The karoo biome: a preliminary synthesis. Part 2—vegetation and history*. South African National Scientific Programmes Report No. 142. Pretoria.

DE CANDOLLE, A.P. 1805. *Plantarum historia succulentarum* (Histoire des plantes grasses): t. 152. Paris.

DE CANDOLLE, A.P. 1828. Ficoideae Juss. *Prodromus systematis naturalis regni vegetabilis* 3: 415–455. Paris, Strasbourg, London.

DE WILDEMAN, E.A.J. 1908. *Mesembrianthemum bosscheanum* Berger. *Icones selectae horti Thenenensis*: 108–111 cum fig. 230. Brussels.

DILLENIUS, J.J. 1732. *Hortus Elthamensis seu plantarum rariorum, quas in horto suo Elthami in Cantio coluit J. Sherard*. London.

DON, G. 1834. *A general system of gardening and botany* 3: 128. London.

DUPONT, S. 1968. Epidermes et plantules des Mésembryanthémacées. Systematique. Evolution. *Bulletin de la Societé d'Histoire Naturelle de Toulouse* 104: 1–64.

DUURSMA, G.D. 1930. *Succulenten in beeld en woord*. Amsterdam, Haarlem.

DYER, R.A. 1937. The vegetation of the divisions of Albany and Bathurst. *Memoirs of the Botanical Survey of South Africa* No. 17.

ECKLON, C.F. & ZEYHER, C.L.P. 1834–1837. *Enumeratio plantarum africae australis extratropicae*. Hamburg.

EDWARDS, S.T. 1817. *Mesembryanthemum tigrinum*. *Botanical Register* 3: 260 cum fig.

EHLER, N. & BARTHLOTT, W. 1978. Die epicuticulare Skulptur der Testa-Zellwände einiger Mesembryanthemaceae. *Botanische Jahrbücher für Systematik* 99: 329–340.

ELLENBERG, H. 1981. Ursachen des Vorkommens und Fehlens von Sukkulenten in den Trockengebieten der Erde. *Flora* 171: 114–169.

ELLIS, W.N. 1988. Biogeografie. *Wetenschappelijke Mededelingen Koninklijke Natuurhistorische Vereniging* Nr. 190. Utrecht.

FARRIS, J.S. 1988. *Hennig86 reference, version 1.5*. University of Stoney Brook, New York.

GESS, S.K. & GESS, F.W. 1989. Flower visiting masarid wasps in southern Africa (Hymenoptera: Vespoidea: Masaridae). *Annals of the Cape Provincial Museums, Natural History* 18: 95–134. Cape Provincial Museums & Albany Museum, Grahamstown.

GIBBS RUSSELL, G.E., RETIEF, E. & SMOOK, L. 1984. Intensity of plant collecting in southern Africa. *Bothalia* 15: 131–138.

GROEN, L.E. 1991. *Studiereis. Veldonderzoek naar* Faucaria *en verwante genera in de oostelijke Kaapprovincie*. Internal report. Department of Plant Taxonomy, Wageningen.

GROEN, L.E. 1994. *Faucaria nemorosa* L.Bolus ex L.E.Groen. *Succulenta* 73: 39–41.

HAAS, R. 1976. Morphologische, anatomische und entwicklungsgeschichtliche Untersuchungen an Blüten und Früchten hochsukkulenter Mesembryanthemaceen-Gattungen. *Dissertationes Botanicae* 33: 44. Cramer, Vaduz.

HALL, A.V., DE WINTER, M., DE WINTER, B. & VAN OOSTERHOUT, S.A.M. 1980. *Threatened plants of southern Africa*. South African National Scientific Programmes Report No. 45. Cooperative Sciences Programmes, Council for Scientific and Industrial Research, Pretoria.

HAMMER, S.A. 1991. *Faucaria bosscheana* and its relatives. *Aloe* 28: 3–5.
HAMMER, S.A. & LIEDE, S. 1990. Natural and artificial hybrids in Mesembryanthemaceae. *South African Journal of Botany* 56: 356–362.
HARTMANN, H.E.K. 1977. Monographie der Gattung *Argyroderma* N.E.Br. (Mesembryanthemaceae Fenzl). *Mitteilungen aus dem Institut für Allgemeine Botanik Hamburg* 15: 121–235.
HARTMANN, H.E.K. 1983. Untersuchungen zum Merkmalsbestand und zur Taxonomie der Subtribus Leipoldtiinae (Mesembryanthemaceae). *Bibliotheca Botanica* 136: 1–67.
HARTMANN, H.E.K. 1988. Fruit types in Mesembryanthema. *Beiträge zur Biologie der Pflanzen* 63: 313–349.
HARTMANN, H.E.K. 1991. Mesembryanthema. In systematics, biology and evolution of some South African taxa. *Contributions from the Bolus Herbarium* 13: 75–157.
HARTMANN, H.E.K. 1993. Aizoaceae. In K. Kubitzki, J.G. Rohwer & V. Bittrich, *The families and genera of vascular plants* II. *Flowering plants—Dicotyledons*. Springer Verlag, Berlin, Heidelberg.
HAWORTH, A.H. 1794/1795. *Observations on the genus* Mesembryanthemum: 161–164. Barker, London.
HAWORTH, A.H. 1803. *Miscellanea naturalia*. Taylor, London.
HAWORTH, A.H. 1812. *Synopsis plantarum succulentarum*. Taylor & Socii, London.
HAWORTH, A.H. 1821. *Revisiones plantarum succulentarum*. R. & A. Taylor, London.
HAWORTH, A.H. 1824. An account of the Mesembryanthema Ringentia. *Philosophical Magazine and Journal*: 109–111. London.
HERRE, H. 1971. *The genera of the Mesembryanthemaceae*: 156, 157. Tafelberg-Uitgewers Beperk, Cape Town.
HILTON-TAYLOR, C. 1996. Red Data List of southern African plants. *Strelitzia* 4.
HOFFMAN, M.T. 1989. A preliminary investigation of the phenology of subtropical thicket and karroid shrubland in the lower Sundays River Valley, SE Cape. *South African Journal of Botany* 55: 586–597.
HOFFMAN, M.T. & EVERARD, D.A. 1987. Neglected and abused—the eastern Cape subtropical thickets. *Veld & Flora* 73: 43–45.
HOFMANN, U. 1973. Morphologische Untersuchungen zur Umgrenzung und Gliederung der Aizoaceen. *Botanische Jahrbücher für Systematik* 93,3: 247–324.
HUBER, J.A. 1943. Morphologische Studien an Mesembryanthemen. *Beiträge zur Sukkulentenkunde und -pflege*: 1–60.
IHLENFELDT, H.-D. 1960. Entwicklungsgeschichtliche, morphologische und systematische Untersuchungen an Mesembryanthemen. *Feddes Repertorium* 63: 1–104.
IHLENFELDT, H.-D. 1971a. Über ontogenetische Abbreviationen und Zeitkorrelationsänderungen und ihre Bedeutung für Morphologie und Systematik. *Berichte der Deutschen Botanischen Gesellschaft* 84: 91–107.
IHLENFELDT, H.-D. 1971b. Some aspects of the biology of dissemination of the Mesembryanthemaceae. In H. Herre, *The genera of the Mesembryanthemaceae*: 28–34. Tafelberg-Uitgewers Beperk, Cape Town.
IHLENFELDT, H.-D. 1983. Epidermis structure in Mesembryanthemaceae. *Bothalia* 14: 931–937.
IHLENFELDT, H.-D. & HARTMANN, H.E.K. 1982. Leaf surfaces in Mesembryanthemaceae. In D.F Cutler, K.L. Alvin & C.E. Price, *The plant cuticle*: 397–424. Academic Press, London.
JACOBSEN, H.J.H. 1933. *Die Sukkulenten*: 129, 130, 153–160. Verlagsbuchhandlung Paul Parey, Berlin.
JACOBSEN, H.J.H. 1955. *Handbuch der Sukkulenten Pflanzen* 3: Mesembryanthemum: 1362–1369. Fischer Verlag, Jena.
JACOBSEN, H.J.H. 1970. *Das Sukkulentenlexikon*: 422–424. Fischer Verlag, Jena.
JACOBSEN, H.J.H. 1978. *A handbook of succulent plants*, 3rd edn, 3: *mesembryanthemums (Ficoidaceae)*: 1141–1146. Blandford Press, London.
JACOBSEN, H.J.H. 1981. *Das Sukkulentenlexikon* 2. Auflage: 454–456. Fischer Verlag, Stuttgart, New York.
JACOBSEN, H.J.H. & ROWLEY, G.D. 1955. Some name changes in succulent plants. Part II. *National Cactus & Succulent Journal* 10: 80, 81.
JUEL, H.O. 1918. *Plantae Thunbergianae*. Almqvist & Wiksells Boktryckeri, Uppsala.
JÜRGENS, N. 1986. Untersuchungen zur Ökologie sukkulenter Pflanzen des südlichen Afrika. *Mitteilungen aus dem Institut für Allgemeine Botanik Hamburg* 21: 139–365.
KAUSSMANN, B. & SCHIEWER, U. 1989. *Funktionelle Morphologie und Anatomie der Pflanzen*. Fischer Verlag, Stuttgart, New York.
LAMARCK, J.B.A.P.M. DE 1788. Ficoïde. *Encyclopédie Méthodique*, Vol. 2,2: 486, 487. Liége, Paris.
LIEDE, S., HAMMER, S. & WHITEHEAD, V. 1991. Observations on pollination and hybridization in the genus *Conophytum* (Mesembryanthemaceae). *Bradleya* 9: 93–99.
LINNAEUS, L. 1738 [‘1737’]. *Hortus cliffortianus*: 218. Amsterdam.
LINNAEUS, L. 1753. *Species plantarum*, edn 1. Salvius, Stockholm.
LOVEGROVE, B. 1993. *The living deserts of southern Africa*. Fernwood Press, South Africa.
LUBKE, R.A., EVERARD, D.A. & JACKSON, S. 1986. The biomes of the eastern Cape with emphasis on their conservation. *Bothalia* 16: 251–261.
MARTYN, J. 1728. *Historia plantarum rariorum*: t. 30 (cum fig.).
MCINTOSH, F. 1989. *Faucaria* Schwantes. In S.M. Walters *et al.*, *The European Garden Flora* 3: 166, 167.
MOORE, R.J. 1973. *Index to plant chromosome numbers 1967–1971*. International Bureau for Plant Taxonomy and Nomenclature. Oosthoek's Uitgeversmaatschappij B.V., Utrecht.
OLIVER, E.G.H., LINDER, H.P. & ROURKE, J.P. 1983. Geographical distribution of present-day Cape taxa and their geographical significance. *Bothalia* 14: 427–440.
PALMER, A.R. 1989. The vegetation of the Karoo Nature Reserve, Cape Province. I. *South African Journal of Botany* 55: 215–230.
PHILLIPS, E.P. 1951. The genera of South African flowering plants, edn 2. *Memoirs of the Botanical Survey of South Africa* No. 25.
POELLNITZ, K. VON 1933. Die Aufteilung der Gattung *Mesembryanthemum* L. Feddes Repertorium Spec. Nov. *Regni Vegetabile* 32. Berlin-Dahlem.
RETIEF, J.A. 1989. *Faucaria tigrina*. *Aloe* 26: 23.
REZNIK, H., ENGEL, U. & WAMBACH, C. 1988. Untersuchungen über die Betalainfarbstoffe der Aizoaceae. I. Die Betaxanthine der Ruschieae. *Beiträge zur Biologie der Pflanzen* 63: 209–219.
ROLFE, R.A. 1916. *Mesembryanthemum tuberculosum*. Curtis's Botanical Magazine: t. 8674b.
SALM-REIFFERSCHEID-DYCK, PRINCE J.M.F.A.H.I. VON J. FÜRST ZU, 1836. *Monographia generum Aloes et Mesembryanthemi* 1: t. 5, 6. Henry & Cohen, Düsseldorf & Bonn.
SALM-REIFFERSCHEID-DYCK, PRINCE J.M.F.A.H.I. VON J. FÜRST ZU, 1854. *Monographia generum Aloes et Mesembryanthemi* 6: t. 2. Henry & Cohen, Düsseldorf & Bonn.
SCHWANTES, G. 1926. Zur Systematik der Mesembrianthemen. *Zeitschrift für Sukkulentenkunde* 2, 11: 176, 177.
SCHWANTES, G. 1927. Zur Systematik der Mesembrianthemen. *Nachtrag Zeitschrift für Sukkulentenkunde* 23: 105.
SCHWANTES, G. 1952. Die Früchte der Mesembryanthemaceen. *Vierteljahrsschrift der Naturforschenden Gesellschafft Zürich* 97, Beiheft 2: 1–38.
SCHWANTES, G. 1957. *Flowering stones and midday flowers*: 129–131, 340. Benn, London.
SONDER, O.W. 1862. Mesembryaceae Lindl. In W.H. Harvey & O.W. Sonder, *Flora capensis* 2: 388, 389, 396, 397. Dublin.
TISCHER, A. 1929. *Faucaria haagei* Tisch. spec. nov. *Monatsschrift der Deutschen Kakteen-Gesellschaft* 1: 20, 21.
TISCHER, A. 1932. Einige neue Mesembryanthema. *Monatsschrift der Deutschen Kakteen-Gesellschaft* 3: 280.
TISCHER, A. 1934. *Faucaria jamesii* L.Bolus ex Tischer. *Kakteenkunde*: 99.
TROLL, W. & WEBERLING, F. 1981. Infloreszenzstudien an Aizoaceen, Mesembryanthemaceen und Tetragoniaceen. *Tropische und Subtropische Pflanzenwelt* 35: 195–289.
VAN JAARSVELD, E. 1984. The family Mesembryanthemaceae with special reference to *Faucaria felina* and *Glottiphyllum muirii*. *Cactus and Succulent Journal* (USA) 56: 53.
VAN JAARSVELD, E. 1990. *Kougadam en Oos Kaap versameltog*. Internal report, Kirstenbosch Botanic Gardens.
VOGEL, S. 1954. Blütenbiologische Typen als Elemente der Sippengliederung. In W. Troll & H. von Guttenberg, *Botanische Studien* 1. Fischer Verlag, Jena.
WEBER, C. 1968. Notes on the nomenclature of some Aizoaceae. *Baileya* 16: 12.
WESTON, R. 1770. *Botanicus Universalis et Hortulanus* (Weston's Nurseryman) I: 172. London.
WHITE, A., DYER, R.A. & SLOANE, B.L. 1941. *The succulent Euphorbieae (southern Africa)*. Abbey, Pasadena.
WIJNANDS, D.O. 1983. *The botany of the Commelins*. Balkema, Rotterdam.

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