Volume 93
Number 4
2006

Annals
of the
Missouri
Botanical
Garden

A SYSTEMATIC STUDY OF THE OLD WORLD GENUS *FOCKEA* (APOCYNACEAE–ASCLEPIADOIDEAE)[1,2]

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ABSTRACT

The six species of *Fockea* Endl. (Apocynaceae, Asclepiadoideae, Fockeeae) occur in Africa south of the equator from southern Kenya to South Africa. A phylogeny for all six species of *Fockea* is inferred from data obtained from two chloroplast markers (the *trn*L-F region and the *psb*A-*trn*H intergenic spacer), one nuclear marker (ITS1 region), and morphology. *Fockea* is found to be monophyletic and sister to the bitypic *Cibirhiza* Bruyns. Morphologically, *Fockea* is characterized by the deeply tubular outer corona that is filled by the erect, inflated sterile appendages of the anthers. Of the six species, the widely distributed but exclusively tropical *Fockea multiflora* K. Schum. is sister to the other five members of *Fockea*, and, among these five, the widely distributed and mainly tropical *F. angustifolia* K. Schum. is sister to the remaining four, which are endemic to southern Africa. It is shown that *Fockea* most probably originated in South Tropical Africa. A complete taxonomic account is provided for the six species of *Fockea*, and their known distribution is mapped. Lectotypes are designated for *Fockea capensis* Endl., *F. monroi* S. Moore, *F. schinzii* N. E. Br., *F. sessiliflora* Schltr., and *F. sinuata* (E. Mey.) Druce. Neotypes are designated for *Brachystelma macrorrhizum* E. Mey., *Fockea angustifolia*, and *F. comaru* (E. Mey.) N. E. Br. An isotype has been located for *F. multiflora*.

Key words: Apocynaceae, Asclepiadoideae, *Fockea*, ITS1 region, morphology, phylogeny, *psb*A-*trn*H intergenic spacer, southern Africa, taxonomy, *trn*L-F region.

The small genus *Fockea* Endl. is endemic to Africa south of the equator. It was established in 1838 by Stephan L. Endlicher for the single species, *F. capensis* Endl. He based the description of this species on a specimen cultivated at Schönbrunn Garden in Vienna (here lectotypified by *Schönbrunn Garden 488* (K, W)), which previously had been given the illegitimate name *Cynanchum crispum* Jacq. (*non C. crispum* Thunberg, 1794). This famous specimen cultivated at Schönbrunn Garden under the number 488 was collected in the Cape Colony after 1786 by Franz Boos and Georg Scholl. It was still in cultivation in Vienna in 1930 (Marloth, 1932) and, until about that time, was reputed to be the only surviving member of the species. This myth was exploded by Rudolf Marloth, who collected *F. capensis* near Prince Albert in South Africa. The plant collected by Boos and Scholl remains alive in Vienna to this day (Zecher, 1988).

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[1] This work was supported in part by a grant from the University of Cape Town Research Fund. We thank Bill and Chris Anderson, University of Michigan, for nomenclatural assistance.

[2] The editors of the *Annals* thank Sophia Balcomb for her editorial contribution to this paper.

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ANN. MISSOURI BOT. GARD. 93: 535–564. PUBLISHED ON 15 DECEMBER 2006.

The first recorded gathering of *Fockea* was made during the expedition of Simon van der Stel of 1685–1686 to the Copper Mountains of Namaqualand in South Africa. Material was found north of Clanwilliam between the Olifants River and the Doorn River and was figured in an unpublished manuscript by Jan Commelin. This figure was later identified as *F. edulis* (Thunb.) K. Schum. (Wijnands et al., 1996). However, *F. edulis* does not occur anywhere near Clanwilliam, and this plant was *F. comaru* (E. Mey.) N. E. Br. An early collection of *F. edulis* was made by C. P. Thunberg near the Gouritz River in southern South Africa in October 1772. He described this as *Pergularia edulis* Thunb. in 1794 and later placed it in the genus *Echites* P. Br. Early gatherings of the small and inconspicuous species *F. comaru* and *F. sinuata* (E. Mey.) Druce were made by Johann Franz Drège, probably between 1832 and 1833. Ernst H. F. Meyer, who worked on Drège's collections, does not seem to have been quite sure what to do with these two species and described them both as possible members of *Brachystelma* Sims (Meyer, 1838). Only after 1900 did they come to be associated with *Fockea*.

Both widely distributed and mainly tropical species, *F. angustifolia* K. Schum. and *F. multiflora* K. Schum. were described rather later by Karl Schumann (Schumann, 1893). *F. angustifolia* has by far the most extensive synonymy of any species of *Fockea*, probably because of its wide distribution and the variability in the shape of the leaves and the size of the flowers.

A further genus involving species of *Fockea*, *Chymocormus* Harv., was established by William H. Harvey (1842). He based this on *Zeyher 965* (K), which he considered to represent Thunberg's *Pergularia edulis*, with a "corona so remarkable, that I do not hesitate to propose it as the type of a new genus" (1842: 24). However, although Harvey did mention "*Pergularia ? edulis*, Thunb. (*Zeyher*, *965*)" (1842: 24) as belonging to *Chymocormus*, he made no valid new combinations (Greuter et al., 2000: ICBN Art. 33.1) and published no new names in *Chymocormus*.

Modern taxonomic investigations into *Fockea* began with an informal account by M. B. Bayer, where the various species were discussed and several previously unknown facts were brought to light (Bayer, 1976). This account was based on material at the Karoo Garden, Worcester, South Africa. A revision was prepared by Court (1982) for a Master's degree at Rhodes University, South Africa. Morphological features were investigated in this account for their taxonomic relevance and it was found that, whereas the flowers were useful for characterizing the genus, only features of the leaves could be used to distinguish the species. Five species (*F. comaru*, *F. crispa* K. Schum., *F. edulis*, *F. multiflora*, and *F. sinuata*) were recognized, but this account was never published. A summary of some of the results of Court (1982) appeared in the popular journal *Asklepios* (Court, 1987), where six species (*F. angustifolia*, *F. comaru*, *F. crispa*, *F. edulis*, *F. multiflora*, and *F. sinuata*) were discussed. This differed from the account of 1982 in that *F. angustifolia* and *F. comaru* were treated as separate species.

N. E. Brown (1902–1903: 427) mentioned that *Fockea* "appears to form a connecting link between the tribes *Secamoneae* and *Marsdenieae*," but he placed it in the Marsdenieae because the pollinia lacked a differentiated margin and are horizontal in the anther thecas (Brown, 1902–1903; 1907–1909). Kunze (1993) pointed out that many peculiar features of this genus suggested a more "basal" position in the Asclepiadoideae. Later a new tribe, Fockeeae, was published for the two genera *Fockea* and *Cibirhiza* Bruyns (Kunze et al., 1994). This tribe was said to be distinguished from the Marsdenieae and others by the shared derived characters of the complex corona, the large anther appendages, and certain characters of the translator, namely the absence of true caudicles, the attachment of the pollinia on the side of the corpuscle closest to the style head, and the lack of a floor in the corpuscle connecting its flanks.

In fact, many of these characters do not distinguish the Fockeeae from other asclepiads. A complex corona is also found in *Eustegia* R. Br., where the ontogeny has been found to follow a similar pattern to that of *Fockea* (Bruyns, 1999: 25, fig. 4). The corona of *Sarcostemma viminale* (L.) R. Br. is also of complex construction (for its ontogeny see Endress & Bruyns, 2000: 26, fig. 11). At 2–3 mm long, the appendages of the anthers are unusually large in all species of *Fockea*, but in both species of *Cibirhiza* they are less than 0.5 mm long (e.g., Kunze et al., 1994: 370, fig. 4). Certainly they are larger (at 1 mm long) in many species of *Microloma* R. Br. (e.g., Bruyns & Linder, 1991: 505, fig. 17) than they are in either species of *Cibirhiza*. Furthermore, the appendages in *Telosma africana* (N. E. Br.) N. E. Br. resemble those in *Fockea* in that they are longer than the fertile part of the anther and have somewhat inflated margins. As Kunze (1993) showed, the pollinarium of *Fockea* exhibits many features of species of *Secamone* R. Br., and one of these is the lack of true caudicles, with the pollinia attached in both cases to a dorsal process of the corpuscle. Verhoeven et al. (2003) found that the wall of the pollinia and the pollen grains differed markedly in *Fockea* and *Cibirhiza*: in *Cibirhiza* the wall is present and the grains are single (as in the Asclepiadoideae), while in *Fockea* the wall is absent and the grains are in tetrads (as in the Secamonoi-

Table 1. Vouchers for *Fockea* and other Apocynaceae used in molecular analyses with Genbank accession numbers for nuclear (ITS1) and chloroplast (*psb*A-*trn*H, *trn*L-F) gene regions.

Accession	Origin	ITS1	*psb*A-*trn*H	*trn*L-F
Cibirhiza albersiana	Tanzania, near Gulwe, *Bruyns 9652a* (BOL)	AM233381	AM231756	AM233363
Cibirhiza dhofarensis	Oman, Dhofar, *Miller 7525* (E, K)	AM233382	AM231757	AM233364
Fockea angustifolia, acc. 1	Namibia, Van Zyl's Pass, *Bruyns 8054* (BOL)	AM233385	AM231760	AM233367
Fockea angustifolia, acc. 2	South Africa, Muden, *Bruyns 9406a* (BOL)	AM233384	AM231759	AM233366
Fockea angustifolia, acc. 3	Tanzania, near Kondoa, *Bruyns 9632* (E)	AM233386	AM231761	AM233368
Fockea angustifolia, acc. 4	Zambia, Sinazongwe, *Bruyns 9587* (MO)	AM233383	AM231758	AM233365
Fockea capensis	South Africa, Plathuis, *Bruyns 7340* (NBG)	AM233387	AM231762	AM233369
Fockea comaru, acc. 1	Namibia, Numeis, *Bruyns 8821* (MO)	AM233388	AM231763	AM233370
Fockea comaru, acc. 2	South Africa, near Port Elizabeth, *Dold 2381* (GRA)	AM233389	AM231764	AM233371
Fockea edulis	South Africa, near Steytlerville, *Bruyns 7051* (BOL)	AM233390	AM231765	AM233372
Fockea multiflora, acc. 1	Namibia, Okonguati, *Bruyns 4089* (NBG)	AM233391	AM231766	AM233373
Fockea multiflora, acc. 2	Tanzania, near Gulwe, *Bruyns 9651* (E)	AM233392	AM231767	AM233374
Fockea multiflora, acc. 3	Zambia, N of Monza, *Bruyns 9593* (MO)	AM233393	AM231768	AM233375
Fockea sinuata	Namibia, near Maltahöhe, *Bruyns 5670* (MO, WIND)	AM233394	AM231769	AM233376
Raphionacme monteiroae	Tanzania, near Gulwe, *Bruyns 9652* (K)	AM233395	AM231770	AM233377
Rhyssolobium dumosum	South Africa, Alexander Bay, *Bruyns 3948* (BOL)	AM233396	AM231771	AM233378
Secamone filiformis	South Africa, Grahamstown, *Bruyns 8990* (E)	AM233397	AM231772	AM233379
Telosma africana	South Africa, Empangeni, *Bruyns 9340* (BOL)	—	AM231773	AM233380

deae). However, they still considered that the "presence of a gynostegial corona fused into an undulate annulus around the base of the gynostegium, in addition to a staminal corona of free segments" (Verhoeven et al., 2003: 70) was one distinguishing feature of the Fockeeae. This is despite a similar construction being present in *Sarcostemma viminale* and the fact that the corona in *Fockea* does not form an "undulate annulus around the base of the gynostegium" but is a tubular structure that exceeds the length of both the anthers and the style head and dominates the gynostegium.

The morphological position is therefore quite confused. Consequently the Fockeeae was abandoned in Endress and Bruyns (2000), and the two genera were again referred to the Marsdenieae.

Molecular results (Sennblad, 1997; Civeyrel & Rowe, 2001; Potgieter & Albert, 2001; Verhoeven et al., 2003) suggested that at least some members of *Fockea* and *Cibirhiza* are sisters to the remainder of the Asclepiadoideae. Sennblad (1997) found that, according to *rbc*L data, *F. tugelensis* N. E. Br. was nested within the Periplocoideae and *C. albersiana* H. Kunze, Liede & Meve was sister to the Asclepiadoideae. However the specimen (*Sennblad 237*) that had been determined by U. Meve as *F. tugelensis* was later found to be *Petopentia natalensis* (Schltr.) Bullock of the Periplocoideae (Sennblad, 1997, note added in proof) and the specimen (*Specks 248*) identified as *C. albersiana* was *Fockea multiflora* (Verhoeven et al., 2003) so that, according to *rbc*L data *F. multiflora* is sister to the Asclepiadoideae. Civeyrel & Rowe (2001) found the same position for *F. capensis* with *mat*K data. Using *trn*L-F data, Potgieter & Albert (2001) found that *F. cylindrica* R. A. Dyer, *F. edulis*, and *F. sinuata* were sister to the Asclepiadoideae. However, the credibility of these results is again called into question by the misidentification of material, since these authors found distinct positions on their cladogram for *Stapelia revoluta* Masson and *Tromotriche revoluta* (Masson) Haw., although the former is the basionym of the latter! Using data from one chloroplast gene region, Verhoeven et al. (2003) showed that *Cibirhiza dhofarensis* Bruyns, *Fockea edulis*, and *F. multiflora* formed a monophyletic group that is sister to the remainder of the Asclepiadoideae.

We build on the results of Verhoeven et al. (2003). Using both molecular and morphological data, we show that the two species of *Cibirhiza* and all six species of *Fockea* belong to a monophyletic tribe, the Fockeeae, and we elucidate the relationships among the species of *Fockea*. We give a detailed account of all species of *Fockea*, paying particular attention to the three widespread and variable species, *F. angustifolia*, *F. comaru*, and *F. multiflora*. Information on the distribution of the species has been much extended since Court (1982), and these data are included.

MATERIALS AND METHODS

Material from the herbaria BM, BOL, COI, GRA, K, KMG, LISC, M, NBG, NU, P, PRE, S, SAM, WIND, and Z was examined. Vouchers used for the molecular analyses are listed in Table 1. Table 2 provides the scoring for the morphological character states.

Table 2. Character states (0, 1) for the 13 morphological characters (1–13) (see App. 1 for definitions) used in the cladistic analyses. A dash indicates that the character is not applicable and the question mark that the state is unassignable.

	Morphological characters		
	00000	00000	111
Species	12345	67890	123
Cibirhiza albersiana	11001	10111	010
Cibirhiza dhofarensis	11001	10111	010
Fockea angustifolia, acc. 1	11001	00110	000
Fockea angustifolia, acc. 2	11001	00110	000
Fockea angustifolia, acc. 3	11001	00110	000
Fockea angustifolia, acc. 4	11001	00110	000
Fockea capensis	10100	10110	000
Fockea comaru, acc. 1	11001	00110	000
Fockea comaru, acc. 2	11001	00110	000
Fockea edulis	1010?	10110	000
Fockea multiflora, acc. 1	0--01	10110	000
Fockea multiflora, acc. 2	0--01	10110	000
Fockea multiflora, acc. 3	0--01	10110	000
Fockea sinuata	11000	00110	000
Raphionacme monteiroae	11001	110--	-1-
Rhyssolobium dumosum	0--11	000--	-11
Secamone filiformis	0--01	0110-	110
Telosma africana	0--11	1010-	101

Illustrations were made from living material in some cases and in others from material preserved in alcohol.

INGROUP AND OUTGROUP SAMPLING

Raphionacme monteiroae (Oliv.) N. E. Br., *Rhyssolobium dumosum* E. Mey., *Secamone filiformis* (L. f.) J. H. Ross, and *Telosma africana* were taken as outgroups (Civeyrel & Rowe, 2001; Verhoeven et al., 2003), with *R. dumosum* and *T. africana* chosen from the Marsdenieae, where the Fockeeae had previously been placed. *Secamone filiformis* was chosen as a representative of the Secamonoideae, while *Raphionacme monteiroae*, from the Periplocoideae, was used to root the tree (Verhoeven et al., 2003). We treated the eight species (12 accessions) of the Fockeeae as our ingroup. Representatives of all six species of *Fockea* were used, and several accessions were included for the widespread species *F. angustifolia*, *F. comaru*, and *F. multiflora*. Both species of *Cibirhiza*, *C. dhofarensis* and *C. albersiana*, were incorporated. In total, 18 accessions were included in the *trn*L-F and *psb*A-*trn*H data-sets. There were 17 accessions in the ITS1 data-set, which excluded *Telosma* because a sequence could not be obtained. For vouchers and Genbank accession numbers, see Table 1.

DNA EXTRACTION AND AMPLIFICATION OF TEMPLATE DNA

Total DNA was isolated from fresh leaf material of the 18 samples by the method of Saghai-Maroof et al. (1984) as modified by Doyle and Doyle (1987). The three DNA regions were amplified from total DNA by polymerase chain reaction (PCR). The *trn*L-F region (consisting of the adjacent *trn*L intron and *trn*L-F intergenic spacer) was amplified using primers c and f (Taberlet et al., 1991). The *psb*A-*trn*H intergenic spacer was amplified using primers *psb*AF and *trn*HR (Sang et al., 1997). The ITS region was amplified using primers ITS2 (Baldwin, 1992) and 18KRC (5′-GCACGCGCGCTACACTGA-3′). Twenty-five microliter reactions were prepared, which contained 19 μL of sterile water, 2.5 μL of 10× PCR buffer, 1 μL of 10 mmol/L dNTPs in equimolar ratio, 0.75 μL of each 10 μmol/L primer, 0.5 μL of 25 mmol/L $MgCl_2$, 0.125 μL of Taq DNA polymerase (5 U/μL), and 0.5 μL of genomic DNA. In general, a 10× dilution of the extraction product was used as template DNA. Thermal reactions were carried out as follows: first 2 min. at 97°C, initial denaturation, 1 cycle; denaturing at 95°C for 1 min.; annealing at 52°C for 45 sec.; extension at 72°C for 2 min.; the three cycles repeated 30 times, and finally followed by extension for 8 min. at 72°C. The reactions were cleaned using the QIAquick PCR purification kit from Qiagen and the purified products were eluted in 60 μL of sterile water.

SEQUENCING AND ALIGNMENTS

Both strands of the PCR products were cycle sequenced, using the ABI PRISM Dye Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems, Foster City, California, U.S.A.). The primers used for amplification were also used for the sequencing reactions. The samples were run on an Applied Biosystems 377 automated DNA sequencer.

Data files were assembled and edited using GeneDoc version 2.6.002 (Nicholas & Nicholas, 1997) and Chromas version 1.43 (McCarthy, 1996–1997). Sequences were aligned by eye. Ambiguous positions were coded using appropriate IUPAC ambiguity symbols so as to maximize retention of information. The method of simple indel coding of Simmons and Ochoterena (2000) is followed, in which all gaps were treated as single sites, coded as binary characters and added to the data matrix. Areas of ambiguity in the alignment were excluded from all analyses.

Table 3. Taxa used in the analysis of ancestral areas and their presence (1) or absence (0) in six regions: (1) Cape Region; (2) Succulent Karoo Region; (3) Nama Karoo Region; (4) Tropical and subtropical Southern Africa; (5) South Tropical Africa; and (6) Arabia.

Species	Region 1	2	3	4	5	6
Secamone filiformis	0	0	0	1	1	0
Cibirhiza albersiana	0	0	0	0	1	0
Cibirhiza dhofarensis	0	0	0	0	0	1
Fockea angustifolia	0	0	1	1	1	0
Fockea capensis	1	1	0	0	0	0
Fockea comaru	1	1	1	0	0	0
Fockea edulis	1	0	0	1	0	0
Fockea multiflora	0	0	0	1	1	0
Fockea sinuata	0	1	1	0	0	0

CLADISTIC ANALYSES

Three matrices were analyzed, one consisting of combined *trn*L-F and *psb*A-*trn*H sequences for all 18 accessions and a second of ITS1 sequences for 17 accessions (excluding *Telosma*). Due to the uniparental mode of inheritance of the plastid genome, we would not expect incongruent patterns of relationships from the different plastid regions, and so we analyzed only the combined matrices for the *trn*L-F and *psb*A-*trn*H data. A third matrix consisted of combined *trn*L-F, ITS1, and *psb*A-*trn*H spacer sequences for all 18 accessions (*Telosma* coded as "?"). No tests of congruence were performed before combining the data, because incongruent nodes were at most weakly supported (Jackknife support percentage, JK, < 63).

All cladistic analyses were performed using the parsimony algorithm of PAUP* version 4.0b4 (Swofford, 2000). Each data matrix was analyzed using 1000 replicates of random taxon-addition to find local minima in the tree-space, TBR (tree bisection-reconnection) branch swapping with MULPARS on, and all character transformations treated as equally likely (Fitch, 1971). At most two trees were saved on each replicate to minimize time spent swapping at local minima in the tree-space. All trees found in the initial 1000 replicates were then used as starting trees for a second round of TBR swapping with a tree limit of 30,000. To assess clade support, the data were analyzed using the jackknife option as implemented in PAUP*. It is known that, with a removal probability of 36.79%, JK 63 or more corresponds to a node supported by at least one uncontradicted character and may be regarded as supported by the data (Farris et al., 1996; Backlund & Bremer, 1997; Bakker et al., 1998). Therefore, the percentage of deleted characters for all jackknife analyses in this study was fixed at 36.79%. Only groups with JK greater than 50 were retained.

The ancestral area method of Bremer (1992) was used to locate the geographic origin of *Fockea*. The analysis was performed using PAUP*, with *Secamone filiformis* and the two species of *Cibirhiza* as outgroups. The area over which the species occur was divided into six regions: (1) Cape Region, (2) Succulent Karoo Region, (3) Nama Karoo Region, (4) Tropical and subtropical Southern Africa, (5) South Tropical Africa, and (6) Arabia. The occurrence of the species in these areas is given in Table 3.

RESULTS

Statistics, including numbers of variable positions and measures of consistency, are given for each analysis in Table 4.

CHLOROPLAST *trn*L-F AND *psb*A-*trn*H ANALYSIS

The strict consensus (Fig. 1) of the four trees recovered shows a monophyletic *Fockea* (JK 52), which is sister to the two species of *Cibirhiza* (JK 78). Within *Fockea*, three clades are retrieved and these form a polytomy with *F. sinuata* and the two accessions of *F. comaru*. The three clades are: (1) the four accessions of *F. angustifolia* (JK 98), (2) the three specimens of *F. multiflora* (JK 99), and (3) *F. capensis* and *F. edulis* (JK 63).

NUCLEAR (ITS1) ANALYSIS

The strict consensus (Fig. 2) of the four trees recovered shows a highly supported monophyletic *Fockea* (JK 98), which is sister (JK 100) to *Cibirhiza*. The nuclear data achieved a higher resolution among the species of *Fockea* than the chloroplast data. Within *Fockea*, the three accessions of *F. multiflora* form a monophyletic clade (JK 96), which is sister to the remainder of *Fockea* (JK 70). The remaining taxa fall into a polytomy consisting of two major clades, *F. edulis* and *F. capensis*. The two major clades are: (1) all four accessions of *F. angustifolia* (JK 71) and (2) *F. sinuata* and the two accessions of *F. comaru* (JK 75).

COMBINED MOLECULAR ANALYSIS

As in the previous analysis, the strict consensus of the two trees recovered (not shown) shows a well-supported, monophyletic *Fockea* (JK 90), which is sister to *Cibirhiza*. With both nuclear and chloroplast data, the relationships within *Fockea* are well resolved and mostly well supported. The three accessions of *F.*

Table 4. Statistics for cladistic analyses and trees for *Fockea* and related taxa. CI, Consistency index; RI, retention index; RC, rescaled consistency index.

Data partition	Total characters	Variable characters	Informative characters	No. of shortest trees	Tree length	CI	RI	RC	Indels
*trn*L-F	864	41	26	—	—	—	—	—	2
*psb*A-*trn*H	401	36	77	—	—	—	—	—	8
Chloroplast	1265	77	103	4	165	0.752	0.823	0.619	10
ITS1	637	113	69	4	134	0.761	0.799	0.608	3
All molecules	1902	190	172	2	309	0.731	0.788	0.576	13
Molecules and morphology	1915	203	185	4	327	0.722	0.781	0.563	13

multiflora are again sister (JK 82) to the remaining species of *Fockea*. The remainder forms a well-supported clade (JK 100) consisting of the four accessions of *F. angustifolia*, which is sister to a weakly supported clade (JK 53) made up of two main clades. These two clades are (1) *F. capensis* and *F. edulis* (JK 83) and (2) *F. sinuata* and the two accessions of *F. comaru* (JK 70). The two accessions of *F. comaru* are not sister taxa, since one of them is sister to *F. sinuata*. However, this relationship gained only minimal support (JK 52) and may therefore be spurious.

We show one of the two equally parsimonious trees as a phylogram (Fig. 3). The relatively long branches at the bases of the various accessions of *F. angustifolia* and *F. multiflora* show that the two tropical species are well separated from each other and from the remaining four species of *Fockea*, which have accumulated far fewer molecular changes. There are also numerous molecular changes among the four accessions of *F. angustifolia*. Similarly, in the other widespread species, *F. multiflora*, there are several molecular changes. In contrast, among the more local *F. comaru* and *F. sinuata* there is only one molecular change, which places one accession of *F. comaru* (*PVB 8821*) as sister to *F. sinuata*. These two, in turn, are sister to the second accession of *F. comaru* (*Dold 2381*).

COMBINED MORPHOLOGY AND MOLECULAR ANALYSIS

Here data for all 18 accessions were analyzed, including the 13 morphological characters listed in Appendix 1. In the strict consensus (not shown) of the four trees recovered, *Cibirhiza* and *Fockea* are monophyletic and sister to one another (JK 95 & 88, respectively). *Fockea multiflora* remains sister to the rest of *Fockea*, which forms a strongly supported clade (JK 85). Less resolution is achieved among the other species of *Fockea*, with the weakly supported southern clade (*F. comaru* and *F. sinuata*) of Figure 3 collapsing to a polytomy with *F. angustifolia*.

BIOGEOGRAPHY

Results of the ancestral area analysis (Table 5) show that the highest ratio of gain to loss occurs in the South Tropical Africa region (Area 5), followed by Tropical and subtropical Southern Africa (Area 4). The lowest ratios are in the Succulent Karoo Region (Area 2) and in Arabia (Area 6). A higher gain to loss ratio for a given area indicates a higher probability that this area is ancestral.

DISCUSSION

1. MONOPHYLY OF *FOCKEA*

In all of our analyses *Fockea* is monophyletic and sister to a monophyletic *Cibirhiza*. Although the monophyly of *Fockea* is poorly supported in our chloroplast analysis (JK 52, Fig. 1), both the nuclear (JK 98, Fig. 2) and the combined molecular analyses (JK 90, Fig. 3) show high support for the monophyly of *Fockea*. The long branch subtending the *Fockea* clade, shown in Figure 3, indicates that *Fockea* is well separated from its sister *Cibirhiza*. Morphologically the two genera are well separated too. *Fockea* is characterized by the tubular outer corona enclosing the anthers and much exceeding them, with the inner lobes partially fused to the inside of this tube, and the erect, swollen appendages of the anthers that more or less completely fill the corona tube and much exceed the style head. *Cibirhiza* is characterized by a low outer corona ring surrounding the whole gynostegium, with a tooth behind each slender and terete inner lobe. The anther appendages are short and adpressed to the style head.

2. RELATIONSHIPS AMONG THE SPECIES OF *FOCKEA*

Fockea consists of two widespread, mainly tropical species (*F. angustifolia* and *F. multiflora*) found from Kenya to Namibia and South Africa and four much more local taxa (*F. capensis*, *F. comaru*, *F. edulis*, and

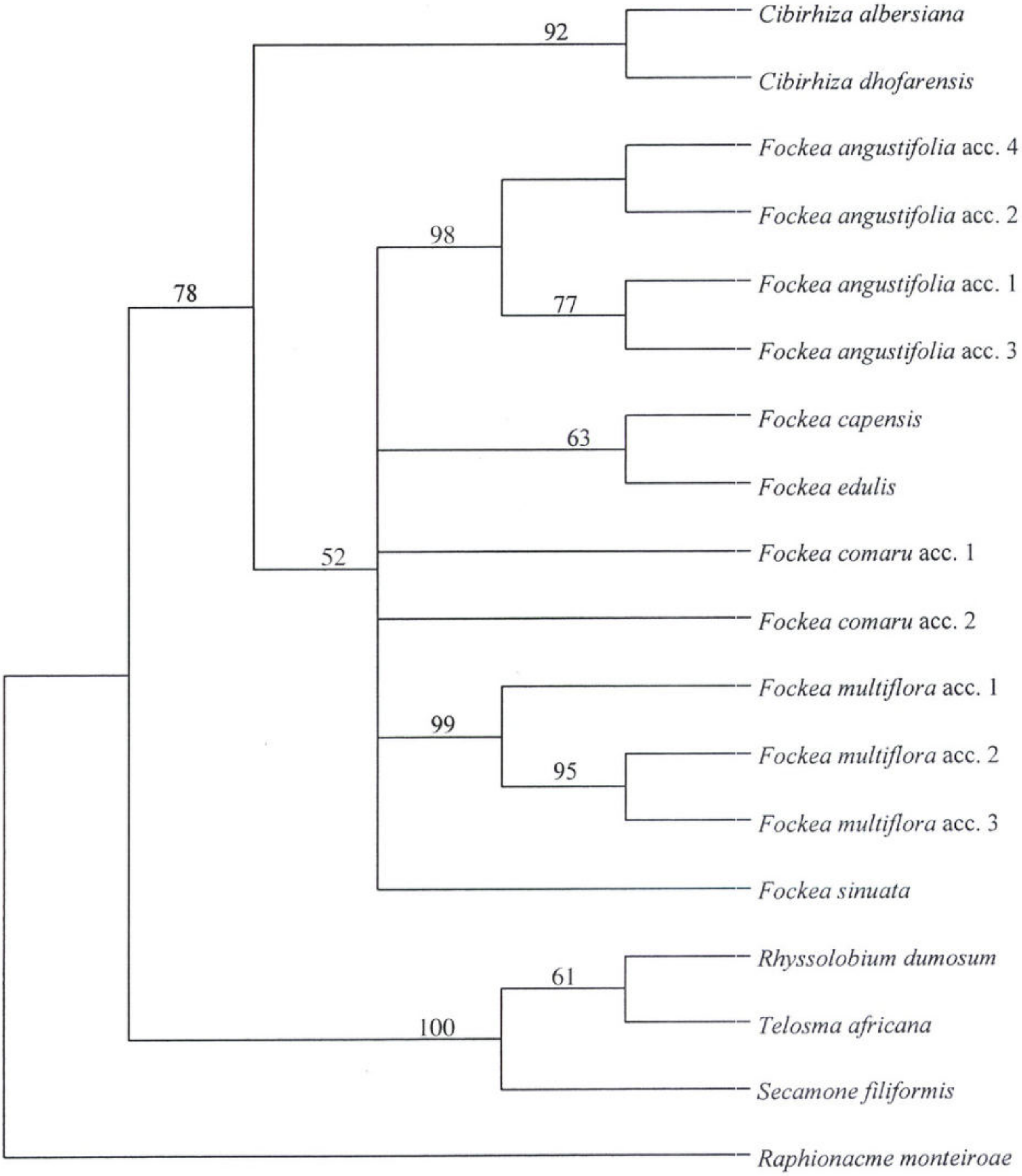

Figure 1. Strict consensus of four trees obtained from analysis of combined data from the two chloroplast genes *trn*L-F and *psb*A-*trn*H. Numbers above branches indicate jackknife support percentages.

F. sinuata) that are endemic to Namibia and South Africa. The starkest morphological contrast within the genus is beween *F. multiflora*, which is a massive, tropical liane without a tuber, and the others, which are relatively small climbers with a swollen, mostly subterranean tuber.

Relationships within *Fockea* are well resolved and mostly well supported. In addition, the relationships suggested by the molecular results are frequently congruent with those from the morphological characters. *F. multiflora* is sister to the rest of *Fockea*. Among the tuberous species, the mostly tropical *F. angustifolia*, is, in turn, sister to the remaining taxa that are endemic to southern Africa. Among the southern African taxa, *F. capensis* and *F. edulis* are well supported sisters and both have large, slightly exposed tubers, substantial stems, and elliptic to nearly circular leaves. Relationships among the small species having slender stems and mainly linear leaves are more complex, with the two southern African taxa

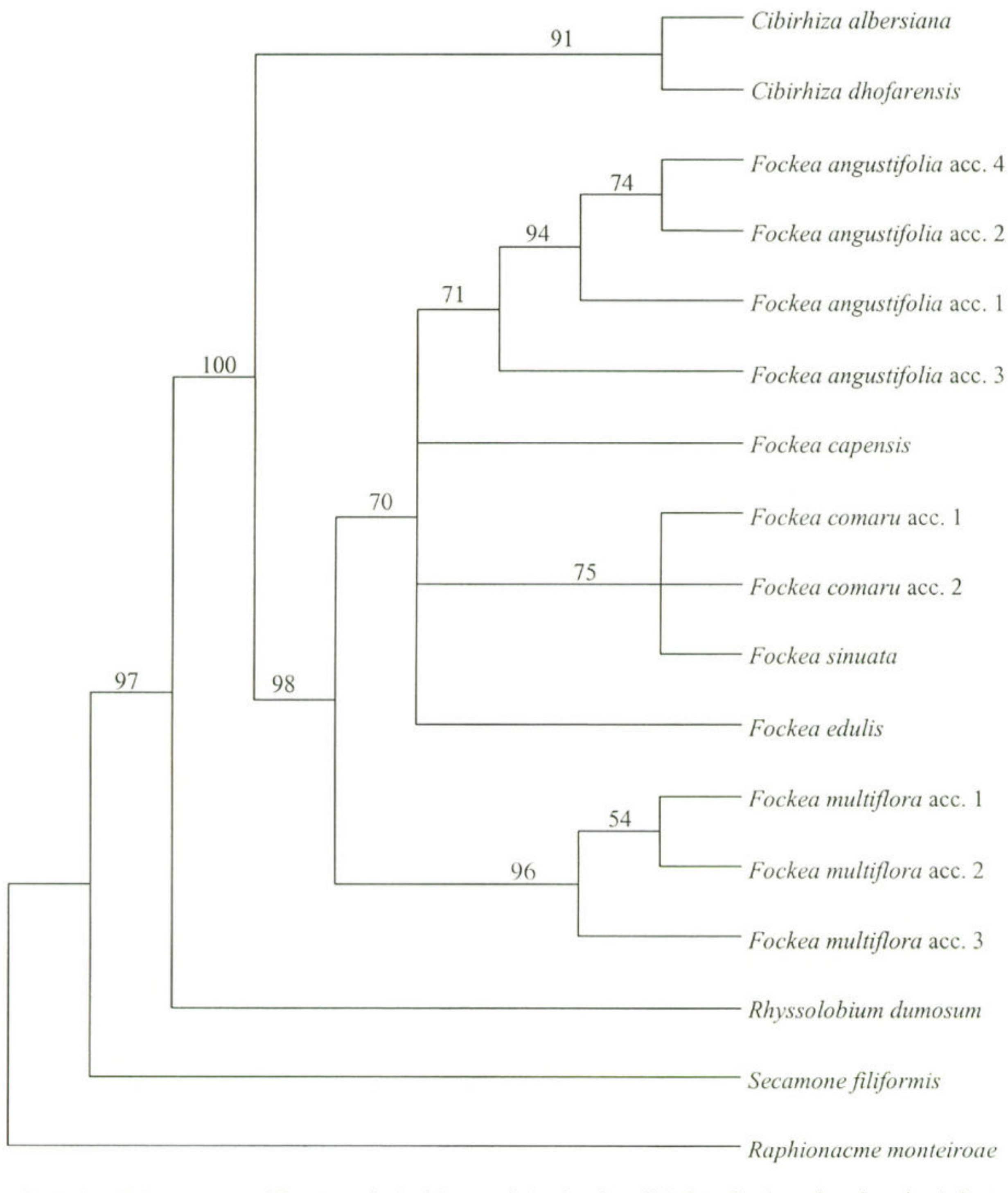

Figure 2. Strict consensus of four trees obtained from analysis of nuclear ITS1 data. Numbers above branches indicate jackknife support percentages.

(*F. comaru* and *F. sinuata*) grouping together but *F. angustifolia* remaining well outside this grouping. This is particularly interesting as *F. angustifolia* and *F. comaru* may occur together and are morphologically very similar.

The phylogram (Fig. 3) shows that both of the widespread, mainly tropical species, *F. angustifolia* and *F. multiflora*, lie on comparatively long branches, while the more local southern African endemics lie on shorter branches. This corroborates studies in other families, where extensive radiation in southern Africa has been accompanied by relatively small changes in the gene regions examined (e.g., Klak et al., 2003; 2004). As in *Fockea*, radiation in these other families is especially associated with the arid winter rainfall zone and its margins. In addition, considerable

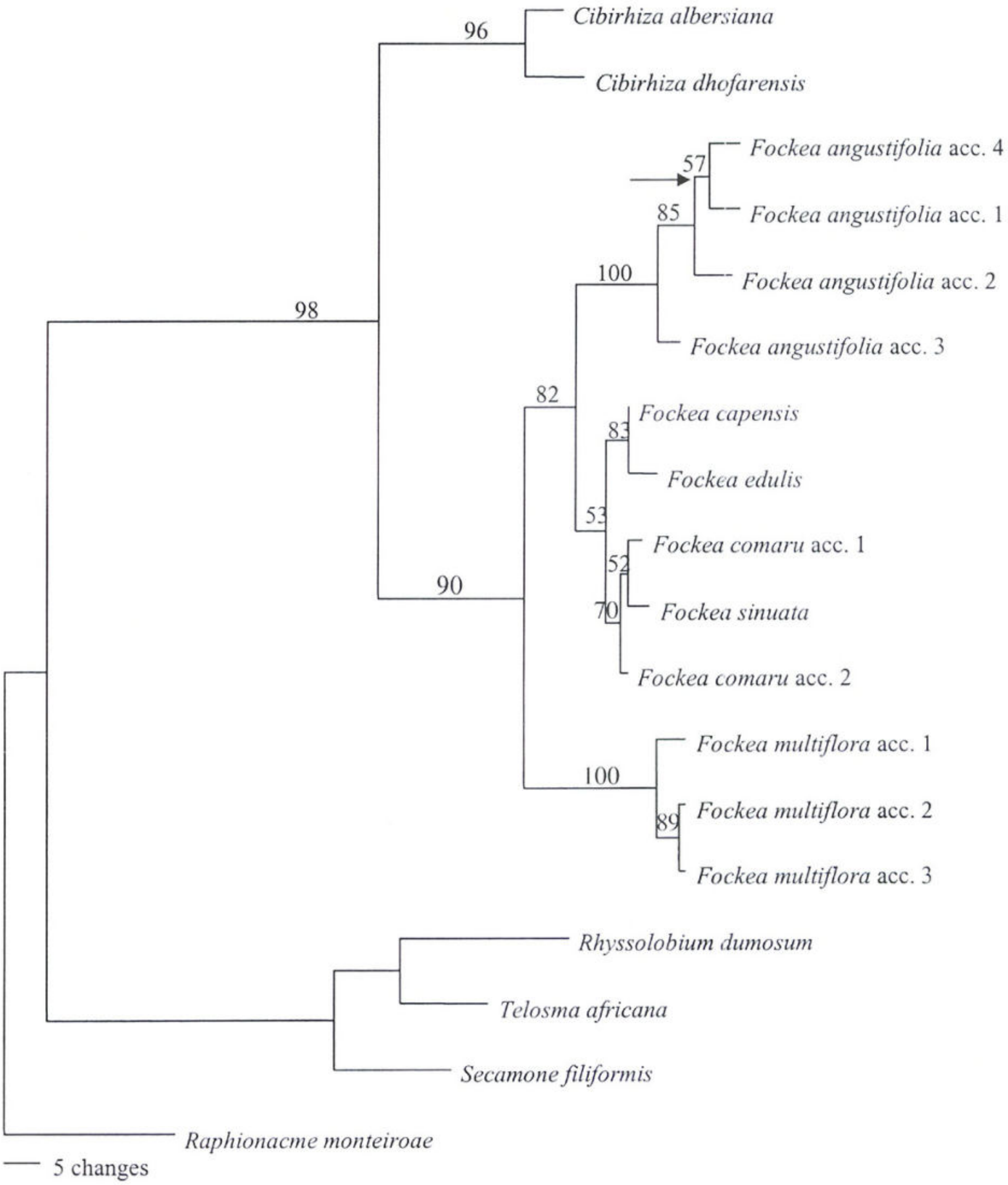

Figure 3. Phylogram of one of two trees obtained from combined analysis of chloroplast *trn*L-F, *psb*A-*trn*H, and nuclear ITS1 data. The lengths of the branches are in proportion to the number of changes in the nucleotides. The arrow indicates a node that collapses in the strict consensus tree. Numbers above branches indicate jackknife support percentages.

molecular variation is found among the different accessions of each of the widespread, mainly tropical species of *Fockea*. In fact, the phylogram shows that these accessions vary more among each other than do all the accessions in the southern clade, where relatively few molecular changes have occurred. It is possible that these tropical species of *Fockea* are much more ancient than the southern taxa.

3. RELATIONSHIPS WITHIN SPECIES IN *FOCKEA*

Our sampling contained multiple accessions of three of the most variable and widespread species.

We included three accessions of *Fockea multiflora*. In each of the molecular analyses, they formed a clade that is strongly supported. In the combined chloroplast analysis (Fig. 1) and the combined molecular

Table 5. The number of *Fockea* species gained and lost for each of six geographic areas. The proportion of gains/losses was used in the ancestral area analysis (Bremer, 1992) to determine the geographic origin of *Fockea*.

	Gains	Losses	Gains/Losses
Area 1: Cape Region	3	5	0.6
Area 2: Succulent Karoo Region	2	5	0.4
Area 3: Nama Karoo Region	2	4	0.5
Area 4: Tropical and subtropical Southern Africa	4	3	1.3
Area 5: South Tropical Africa	4	2	2.0
Area 6: Arabia	1	3	0.3

analysis (Fig. 3), the southernmost collection is sister to the others.

We included four accessions of *Fockea angustifolia* and found that they consistently formed a clade that is strongly supported in the combined chloroplast analysis (Fig. 1) and in the combined molecular analysis (Fig. 3), though less so in the ITS1 analysis (Fig. 2). In the combined molecular analysis (Fig. 3), the northernmost accession (*Bruyns 9632*) is sister to the others, which form a strongly supported clade relative to it. The wide morphological variation known in *F. angustifolia* in southern Africa and the lack of any significant morphological differences between these northern collections and those further south make the recognition of separate taxa here impossible, despite the strong support for clades within *F. angustifolia*.

We included two accessions of *Fockea comaru*. In the combined molecular analysis (Fig. 3), one accession of *F. comaru* (*Dold 2381*) comes out as sister to a clade consisting of *F. comaru* and *F. sinuata*. Figure 3 shows that this is caused by a difference in a single amino acid, which is also reflected in the weak support for the *F. comaru–F. sinuata* clade (JK 52).

4. BIOGEOGRAPHY AND ECOLOGY

Our ancestral area analysis suggests that *Fockea* originated in South Tropical Africa and radiated southward. *Fockea* is endemic to Africa south of the equator, and most species are found in southern Africa. Only two species (*F. angustifolia* and *F. multiflora*) extend north of this. Both of these reach Tanzania and are the most widely distributed members of the genus. *Fockea angustifolia* is the most widely distributed of all and is recorded from the subtropical Kimberley and Prieska area of central South Africa (in and to the east of the Nama Karoo Region of Jürgens, 1991) to southern Kenya. *Fockea multiflora*, on the other hand, is a purely tropical species occurring in northern Namibia and southern Angola, the basins of the Okavango and Zambezi Rivers, and in central Tanzania. The distributions of both *F. angustifolia* (Fig. 5) and *F. multiflora* (Fig. 9) exhibit a marked disjunction between the valley of the Zambezi River and central Tanzania. These patterns coincide largely with the more arid woodland or scrub of *Acacia* Mill., *Commiphora* Jacq., and *Balanites* Delile (where they are found) and the more mesic woodland dominated by *Brachystegia* Benth., where they tend not to occur.

The remaining four species are endemic to the semi-arid to arid, temperate to subtropical parts of South Africa and Namibia. *Fockea capensis* is the most restricted, occurring on the Little Karoo and in some of the drier surrounding mountains in southern South Africa in the Succulent Karoo Region (Jürgens, 1991). *Fockea edulis* is mainly found in semi-arid patches in the coastal parts of southern and southeastern South Africa from the Succulent Karoo Region eastward. *Fockea comaru* and *F. sinuata* are more widely distributed in South Africa and Namibia. *Fockea comaru* is strongly (but not exclusively) associated with the western part of South Africa, receiving winter rainfall, and is particularly found in the Succulent Karoo Region. Its distribution extends into the Nama Karoo Region (Jürgens, 1991) of central South Africa. *Fockea sinuata* is mainly found within the Nama Karoo and on the eastern margins of the Succulent Karoo Region. The shorter branches subtending these four species suggest that this radiation may have been more recent than the radiation within *F. angustifolia* and *F. multiflora*, where the branches are mostly longer.

Fockea angustifolia, *F. comaru*, and *F. sinuata* all occur close together in some areas on the Great Karoo of South Africa but, whereas *F. angustifolia* and *F. comaru* may actually grow in the same habitat, *F. sinuata* occupies a distinct niche in which *F. angustifolia* is rarely found and where *F. comaru* never grows. *Fockea comaru* occurs together with *F. edulis* on the Worcester-Robertson Karoo (southwestern South Africa) and very occasionally with *F. capensis* on the Little Karoo of southern South Africa.

Most species of *Fockea* occur on rocky hills, where the edible tubers are wedged tightly among stones and protected from excavation. *Fockea angustifolia* occasionally grows in flat, pan-like areas, and *F. sinuata* is almost exclusively found in calcareous, pan-like areas, which become seasonally but very intermittently moist. All species, except *F. multiflora*, have a geophytic tendency, often with the ability to die back to the tuber under very dry conditions.

5. POLLINATION

Two facts suggest that the method of pollination in *Fockea* is not the same as in most other asclepiads. Firstly, the flowers are remarkable for the extremely restricted access to the pollinaria, and, unusually, the main organs causing these restrictions are the anther appendages, which block the corona tube. Between adjacent inner corona lobes there are three narrow channels leading to the base of the corona. Two of these are on the sides of the long outer corona lobules, and a fine hair inserted down either of these is directed exactly to the base of the corpuscle. The other channel lies behind the lowest part of the outer corona, and it provides access to the nectarial orifice below the corpuscle. Secondly, the margins of the anthers are schlerenchymatous only for a very small distance near their base or are not hardened at all. The schlerenchymatous part is found below the corpuscle but does not continue below it for some distance, as is customary.

In field-collected flowers, it has been found in *Fockea* that very few pollinaria are removed from their position on the style head. The only germinating pollinia have been found in the base of the longer channels reaching the nectarial orifices, and it appears that pollination is achieved if pollinia are deposited sufficiently far down these channels. The rudimentary guide-rails appear to direct a probing proboscis toward the base of the corpuscle. This enables the pollinarium to be removed, but the guide-rails seem to play no role in the deposition of the pollinia. It seems that the weak corpuscle partly breaks up and in so doing probably causes the pollinium to be wiped off the pollinator's proboscis in the narrower parts of the channels (the guide-rails may assist in wiping them off too). Evidence suggests that the same mechanism is involved in *Cibirhiza* (Kunze et al., 1994).

Pollination in the Periplocoideae is achieved when pollen is wiped off the spoon-like receptacle of the translator onto the base of the style head (Bruyns & Klak, pers. obs.). Here guide-rails are altogether absent. In the Secamonoideae, guide-rails are present and they guide potential pollinators toward the corpuscle for removal, but it is unknown what role they play in the deposition of pollen. In the Fockeeae, rudimentary guide-rails are present and they guide potential pollinators toward the corpuscle for removal, but they appear to play no role in the deposition of pollen. These three groups are successive sisters to the rest of the Asclepiadoideae, in which the guide-rails are better developed. In the rest of the Asclepiadoideae, the guide-rails assist in the removal of the pollinarium but have the unique additional function of holding the inserted pollinium as the pollen tubes grow.

TAXONOMY

Fockea Endl., in Endl. & Fenzl, Nov. Stirp. Dec. 3: 17. 1839. TYPE: *Fockea capensis* Endl.

Chymocormus Harv., London J. Bot. 1: 23–24 (1842). TYPE: Uitenhage, *Zeyher 965* (K!).

Erect to twining herb to massive liane often with underground to slightly exposed tuber tapering into small taproot anchoring plant, with fibrous roots, sap milky. *Stems* dextrorsely twining or erect, 80 mm–15 m long, 2–300 mm thick, slightly fleshy, finely pubescent when young, later covered with a shiny gray bark. *Leaves* opposite, spreading, subcoriaceous, gray-green to green, pubescent (with fine verrucose hairs) to glabrous; *petiole* 0–25(–45) mm long, spreading; *blade* 13–60(–150) × 1.5–20(–100) mm, linear to elliptic, acute to obtuse, apiculate, margins slightly to strongly revolute, non-succulent, deciduous, midrib paler than rest. *Inflorescences* extra-axillary, 1- to 20-flowered, umbellate, pubescent; *peduncle* 0–15 mm long, stout, with several short bracts at bases of pedicels; *pedicels* 1–15 mm long. *Sepals* adpressed to corolla tube, lanceolate, acute, 1.5–3 × 1 mm, pubescent outside and glabrous inside; *corolla* rotate, 8–22(–40) mm diam.; outside pubescent, gray-green; inside puberulous to glabrous, green to brown; *tube* 1.5–5 mm long, ca. 2 mm broad at mouth, ± glabrous within; *lobes* (3–)5–12(–18) × ca. 2 mm, linear, obtuse, spreading, usually spiralling to left, often twisted to left when viewed along lobe; *corona* consisting of 2 series of lobes, white, glabrous; outer forming cylindical tube with several series of erect to spreading lobules arising at mouth of tube; inner consisting of 5 erect lobules partly fused to outer corona tube lower down and usually pressed to backs of anther appendages and exceeding them; *anthers* consisting of erect ± quadrangular fertile part pressed to style head, above this with much inflated erect, transparent-white sterile appendage 2–3 mm long, these appendages connivent and pressed to one another, filling up area inside corona tube; *style head* less than 2 mm long, not exceeding fertile part of anthers, slightly bifid at truncate apex, below this widening to base of anthers then narrowing and sessile on ovaries; *pollinarium* with 2 small translucent nearly flat and elliptical erect pollinia sessile on small brownish usually narrowly elliptical corpuscle. *Follicles* 50–220 × 8–30 mm, pendulous, broadly fusiform and narrowing into slender beak, uniformly glaucous green turning brown, glabrous, sometimes pustulate, single by abortion, containing 50 to 150 seeds; *seeds* flattened, pear-shaped in outline, 6–14 × 3–8 mm, pale beige or yellow to pale brown, with usually somewhat paler margin, slightly papillate, with coma attached at one end except in *F. sinuata* where hairs extend on margin around seed.

One of the defining features of the flower in *Fockea* is the complicated, white, tubular corona with many small lobules projecting inside and around its edges.

This corona starts off as a series of vertical ridges below the lower margins of the anthers (forming the guide-rails), with an outward swelling also occurring below these ridges (Endress & Bruyns, 2000: 18, fig. 9). Gradually three distinct parts appear to this outer corona: a horizontal lobule bridging the gap between the anthers, two diagonal ridges arising from the vertical ridges of the earliest stages, and a further lobule behind and somewhat below each anther. Thus the outer corona consists of 15 lobules. An inner corona of five lobules appears slightly after the first parts of the outer series have begun to swell, and each of these lobes lies behind the anther and a little above the outer series. In more advanced stages these structures become obscured, and the various lobules of the outer corona fuse into a tube. The longest spreading lobules around the mouth of this tube are the ones in the outer series that arose directly behind the anthers. These longest lobules are flanked on either side by a somewhat channel-forming lobule, and these are derived from the two diagonal ridges of the outer series. The remaining lobule of the outer series forms a fairly low bridge between these channel-forming lobules to complete the tubular outer corona. The lobes of the inner corona are fused to the outer corona tube nearly to its apex, and the 'dragged' vascular traces of the anthers show that at least some of the vertical expansion of this tube is achieved by growth at the base of the anther.

In the mature flower in *Fockea*, there is considerable basal fusion between the corona tube and the corolla. As can be seen in Figure 4F and G, the join between the corolla and the corona tube is much higher than that between the corolla and the calyx. However, the ontogeny of the corona shows that this fusion is a later development, and the fact that the vascular trace of the corona branches off from that of the adjacent anther also suggests that this fusion is secondary and does not imply that the corona is contributed to by the corolla, though this was suggested as a possibility by Kunze (1996: 29).

Kunze (1996: 553, figs. 3–5; 554, fig. 12) has shown that the anther in *Fockea edulis* and *F. sinuata* contains endothecial tissue that almost completely surrounds the two locules in each anther. He also found that there is some dorsal dehiscence of the anther, as if it still contained four locules rather than two.

Another defining feature of *Fockea* is the cluster of five soft, erect, inflated, translucent white sterile appendages of the anthers which fill the corona tube (Fig. 4F, G). These appendages only develop their inflated form relatively late. In the early stages there is a distinct separation of the fertile and sterile parts of the anther by slight indentations on either side at the base of the sterile part (Endress & Bruyns, 2000: 18, fig. 9), as is commonly found in the mature anther of the Asclepiadeae. Beneath each appendage the short, roughly square anther is pressed inward onto the style head. The lower margins of the anthers are slightly hardened and hyaline toward their base, forming rudimentary guide-rails just below each corpuscle.

The two ovaries in each flower are together about as broad as tall, and they contain many small ovules (Fig. 4F, G). They are only partly superior, because the ovules continue somewhat below the level of fusion of the calyx and the corolla. The comparatively short style head is sessile on the ovaries. It is broadest at the level at which the corpuscle is secreted, after which it narrows into a short, truncate, and slightly bifid apex that does not exceed the fertile parts of the anthers.

The pollinarium in *Fockea* consists of two small, usually flattened, clear to translucent white, elliptical pollinia and a corpuscle of almost equal size (Fig. 6D, I; Fig. 8G, M, S; Fig. 10H). The pollinia are often so flat that together they make up no more than the thickness of the corpuscle. Kunze (1996: 553, figs. 3, 5) has shown that in *F. sinuata* the pollinium is mostly made up of just two layers of pollen grains, while in *F. edulis* it would appear that only a single layer is present. The corpuscle is pale brown (often only brown and shiny around the top), and it is generally broader when viewed from the side than when seen from above. It is very easily broken into two halves. Near the apex of the corpuscle on the side closest to the style head there is a small process to which both the pollinia are attached, and this may be quite easily visible with the light microscope in some plants. In all species a caudicle joining each pollinium to the corpuscle is lacking. Around its base the structures by which the corpuscle is attached to the style head may be visible as slight protrusions. Kunze (1993) showed that the corpuscle has flanks and a Y-shaped floor that disappears toward the base of the corpuscle.

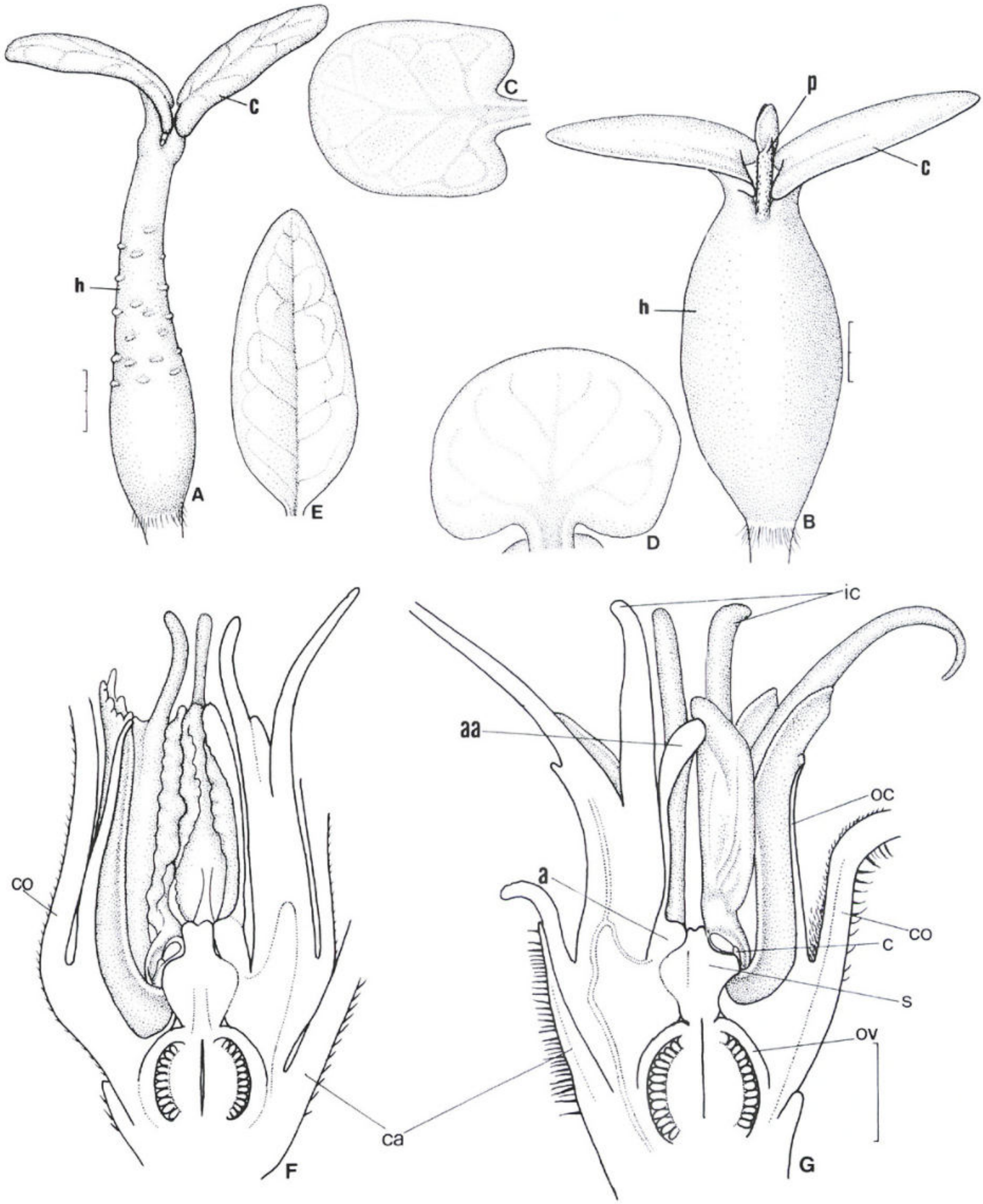

Figure 4. A–E. Seedlings in *Fockea*, about 20 days old. F, G. Half flowers in *Fockea*. —A, B. Side view of plantlet. —C, D. Face view of cotyledon. —E. Face view of one of second pair of leaves. c, cotyledon; h, swollen hypocotyl; p, primary stem; ca, calyx; co, corolla tube; a, anther; aa, sterile anther appendage; oc, outer corona tube; ic, inner corona lobes; c, corpuscle; s, style head; ov, ovary. Drawn from: A, C, E, *F. sinuata*, *Bruyns 3023* (NBG); B, D, *F. edulis*, *Bruyns 4995a* (BOL). F, *F. comaru*, *Bruyns 3329* (BOL); G, *F. edulis*, *Bayer 325* (NBG). Scales: A, C, E = 3 mm (at A); B, D = 2 mm (at B); F, G = 1 mm (at G).

Verhoeven and Venter (2001) found that in *F. angustifolia*, *F. multiflora*, and *F. sinuata* the grains are grouped into tetrads and there is no outer envelope or pollinium wall.

Seedlings (Fig. 4) have been observed in all species of *Fockea* except *F. multiflora*. Each plantlet consists of a swollen, fleshy, green hypocotyl (at least half of which projects from the soil) with two broad, green cotyledons at the apex. The primary leaves and stem emerge from between the cotyledons after one to three weeks, and the primary leaves are always much narrower than the cotyledons. Swelling of the base of the hypocotyl leads to the formation of the tuber below ground level, while the upper part of the hypocotyl above the soil does not thicken. In species such as *F. comaru* and *F. sinuata*, where the tuber can be up to 20 cm below the surface of the ground, the base of the hypocotyl elongates as well as swells so that gradually the tuber develops well below the surface.

A similarly succulent hypocotyl is common in many of the succulent Asclepiadoideae and is even known in the Periplocoideae in such species as *Ischnolepis graminifolia* (Costantin & Gallaud) Klack., *Sacleuxia salicina* Baill., and *Stomatostemma pendulina* H. Venter & D. V. Field. In the Asclepiadoideae it is found in the Fockeeae in *Fockea*, in the Asclepiadeae in *Sarcostemma* R. Br. and succulent members of *Cynanchum* L., and it is most common in the Ceropegieae (Bruyns, 2000). A succulent hypocotyl is unknown in the Marsdenieae (Forster, 1995).

KEY TO THE SPECIES OF *FOCKEA* (SOUTHERN TO EASTERN AFRICA)

- 1a. Leaves rarely more than 30 mm long and not more than 20 mm broad; stems arising via narrow neck from distinct basal (mostly subterranean) tuber, stems short and erect or climbing to 1–2 m.
  - 2a. Leaves linear, not more than 4 mm broad.
    - 3a. Margins of leaves revolute, leaves with dense adpressed pubescence, outer corona without spreading flap behind each longest terete lobule.
      - 4a. Margins of leaves strongly undulate; corpuscle relatively massive and nearly half as broad as pollinia . . . . 6. *F. sinuata*
      - 4b. Margins of leaves not undulate; corpuscle very slender and much less than half as broad as pollinia . . . . 3. *F. comaru*
    - 3b. Margins of leaves not revolute, leaves with sparse pubescence, outer corona usually with spreading flap behind each longest terete lobule . . . . 1. *F. angustifolia*
  - 2b. Leaves elliptic to nearly circular, 6–22 mm broad.
    - 5a. Outer corona without spreading flap behind each longest terete lobule; upper surface of tuber projecting from ground.
      - 6a. Leaves ± glabrous or very sparsely pubescent, margins only slightly undulate. . . . . 4. *F. edulis*
      - 6b. Leaves finely and densely pubescent, margins strongly undulate . . . . 2. *F. capensis*
    - 5b. Outer corona with spreading flap behind each longest terete lobule; tuber well below surface of ground . . . . 1. *F. angustifolia*
- 1b. Leaves usually more than 30 mm long and 25 mm broad; stems usually massive and often climbing on trees to 10 m or more, plant without distinct basal tuber . . . . 5. *F. multiflora*

1. Fockea angustifolia K. Schum., Bot. Jahrb. Syst. 17: 146. 1893. TYPE: South Africa, Cape, Griqualand West, 48 km W of Kimberley, *G. J. Lewis 67535* (neotype, designated here, PRE!; duplicate, SAM!). Figure 6A–D.

Fockea sessiliflora Schltr., Bot. Jahrb. Syst. 20, Beibl. 51: 44. 1895. TYPE: South Africa. Transvaal, Klippdam, 4500′, 14 Feb. 1894, *F. R. R. Schlechter 4493* (lectotype, designated here, drawing at W, not seen).

Fockea lugardii N. E. Br., Fl. Trop. Afr. 4 (1): 429. 1903. TYPE: Botswana. Ngamiland, Kwebe Hills, *E. J. Lugard 299* (holotype, K!).

Fockea dammarana Schltr., Bot. Jahrb. Syst. 38: 56. 1905. TYPE: Namibia. Damaraland, 1879, *T. J. G. Een* (holotype, BM!).

Fockea tugelensis N. E. Br., Fl. Cap. 4 (1): 778. 1908. TYPE: South Africa. Natal, Tugela, *W. T. Gerrard 1310* (holotype, K!; isotype, BOL!).

Fockea mildbraedii Schltr. in Mildbr., Wiss. Erg. Deut. Zentr.-Afr. Exped., Bot. 2: 545—546. 1913. TYPE: Tanzania. Lembeni, 4 Sep. 1910, *H. J. P. Winkler 3803* (holotype, K!).

Fockea monroi S. Moore, J. Bot. 52: 149. 1914. Type: Zimbabwe. Melsetter distr., Victoria, *Monro 828* (lectotype, designated here, BOL!; duplicate, SRGH).

Cynanchum omissum Bullock, Kew Bull. 10: 623. 1956. TYPE: Kenya. Kwale distr., betw. Samburu & Mackinnon road, 350 m, Aug. 1953, *R. B. Drummond & Hemsley 4045* (holotype, K!).

Small geophytic herb to climber with underground napiform tuber (sometimes somewhat irregularly shaped by pressure of surrounding rocks) up to 50 cm long and 20 cm thick with central growth point on smooth upper surface from which slender perennial and aerial stems arise, stems erect to twining to 1(–2) m, often whitish gray, softer upper parts deciduous, young growth finely tomentose. *Leaves* with petiole 1–3 mm long, grayish to brownish green (often with distinct brownish to purplish hue when young), linear to narrowly elliptic (to circular), 13–65(–105) × (0.5–)1.5–8(–22) mm, obtuse to acute, glabrous to sparsely and finely pubescent (more sparsely below), midrib translucent white, margins slightly to not at all revolute, weakly undulate to straight. *Inflorescence* 1- to 6-flowered, flowers opening in succession, covered with fine adpressed hairs; *peduncle* absent; *pedicels* 1 × 1 mm. *Sepals* 1.5–2 × 1 mm, lanceolate, outside pubescent, inside glabrous; *corolla* 10–40(–65) mm diam.; outside grayish green, pubescent; inside green to brown, sparsely and finely pubescent; *tube* 1.5–2 mm deep, ca. 2.5 mm broad at mouth, cupular; *lobes* 4–18(–28) × 1–2 mm, linear, obtuse, spreading and often spiralling to left, often twisted to left when viewed along length, with margins strongly reflexed; *corona* white, glabrous; *outer corona* forming cylindrical tube 4–6 mm long, divided at mouth of tube into 5 longer slender terete and often spreading lobules up to 5 mm long each flanked by 2 flattened spreading lobules, these groups of 3 lobes alternating with 5 linear and usually spreading lobules, longest outer lobes each usually with another flattened spreading lanceolate lobule behind it; *inner corona* of 5 terete linear lobes ca. 3 mm long adpressed to backs of anthers then erect above them. *Follicles* 70–200 × 8–12 mm, gray-green often banded with purple, smooth; *seeds* 8–10 × 4–6 mm, yellow-brown.

Phenology. Flowering October to May.

Distribution. Angola, Botswana, Kenya, Namibia, South Africa, Swaziland, Tanzania, Zambia, and Zimbabwe; 200–1700 m (Fig. 5).

Ecology. Fockea angustifolia occurs in areas receiving rainfall in summer. It is mainly found in stony places, usually on slopes but occasionally in flat areas. In parts of the Kalahari it occurs on stony calcareous flats, while in Tanzania it grows in loamy flat areas.

Discussion. The type (South Africa, Griqualand West, Groot Boetsap, 1200 m, *H. W. R. Marloth 1008*) of Schumann (1893) is missing, and a neotype has been designated here. No material seen by Schumann has been found. Consequently *Lewis 67535* was selected as a neotype, because it is from the same general area as Marloth's missing specimen and is represented in two herbaria. Moore (1914) cited two specimens of Monro in the protologue of *F. monroi*. One of these has been located and is selected as the lectotype. In the case of *F. sessiliflora*, no specimens of *Schlechter 4493* have been located, but a sketch of the flower exists at W and this is selected as lectotype.

K. Schumann (1893, 1895) and Brown (1907–1909) mentioned the name *Brachystelma circinatum* Marloth *non B. circinatum* E. Mey. This appeared in a list of Marloth's collections where, under the Asclepiadaceae, the entry "*Brachystelma circinatum* E. Meyer....bisher von den Witbergen im Kapland bekannt" appeared and the specimen *Marloth 1008* was cited (Engler, 1889: 244). No description or diagnosis was provided nor was any intent of publishing a new name expressed, so the epithet *Brachystelma circinatum* Marloth does not exist (Greuter et al., 2000: ICBN Art. 32.1, Art. 34.1 (a)).

Court (1982) treated *Fockea angustifolia* and *F. comaru* as one species, and they were treated as closely related also in Meve (2002).

Our own investigations revealed that *Fockea angustifolia* and *F. comaru* occur together over a wide area in Namibia and South Africa; the full extent of occurrence is probably still not accurately reflected by the recorded collections. In several cases both *F. angustifolia* and *F. comaru* have been noted on the same farm and have even been seen near each other on the same hillside. So far they have been recorded together in Namibia in the Tiras Mountains and the Great and Little Karas Mountains, while in South Africa they are known to grow together in the hilly southwestern part of Griqualand West. This wide sympatry leads one to suspect that they may not be closely related at all.

Analyses of the molecular data proved our suspicions to be correct. They show that *Fockea angustifolia* and *F. comaru* are two distinct species that are not particularly closely related to one another and that *F. angustifolia* is sister to all the southern species of *Fockea*.

In the areas where they occur together, *Fockea angustifolia* and *F. comaru* look superficially similar. Both are narrow-leaved with slender, often twining stems and a relatively small tuber (at least in comparison to that of *F. edulis*). A number of features can be used to separate them, and they can be distinguished mostly even without flowers. In *F. angustifolia* the main stem generally divides above the surface of the soil. In *F. comaru* the main stem divides mostly well below the surface, so that the stems of a single plant often spread extensively underground and may emerge from the soil some distance away from the central stem. The young leaves of *F. angustifolia* have a noticeably purplish to brownish hue and older leaves are grayish green, while the foliage of *F. comaru* is generally distinctly bluish green. In pressed specimens one finds that the younger stems and leaves of *F. angustifolia* are often very pale to nearly white, while they are dark brown in *F. comaru*. The whole plant in *F. comaru* is covered with fine and often adpressed hairs, while in *F. angustifolia* the hairs are extremely sparse, if present at all. A further feature of the leaves is that their margins are revolute in *F. comaru*, while in *F. angustifolia* they are mostly not revolute (this feature is often distorted by pressing, so that it is not always helpful in herbarium material). Finally, if flowers are present, the two can often be separated on the extra flap in the corona behind each large outer lobe that is usually present in *F. angustifolia* and absent in *F. comaru*.

Specimens examined. ANGOLA. Huila, Sá da Bandeira, *Santos 764* (LISC); E of Oncocua, *Bruyns 10355* (MO); 5 km W of Oncocua, *Bruyns 10363* (E); Iona, *Bruyns 10384* (WIND); near Chapeu Armado, *Bruyns 10406* (K); N of Cahama, *Bruyns 10435* (M).

BOTSWANA. Dobe, *Lee D64/61* (SRGH); 45 km W of Nokaneng, *Bruyns 6479* (BOL); 128 km WNW of Francistown, *Drummond 5283* (SRGH); 81 km W of Kuke gate,

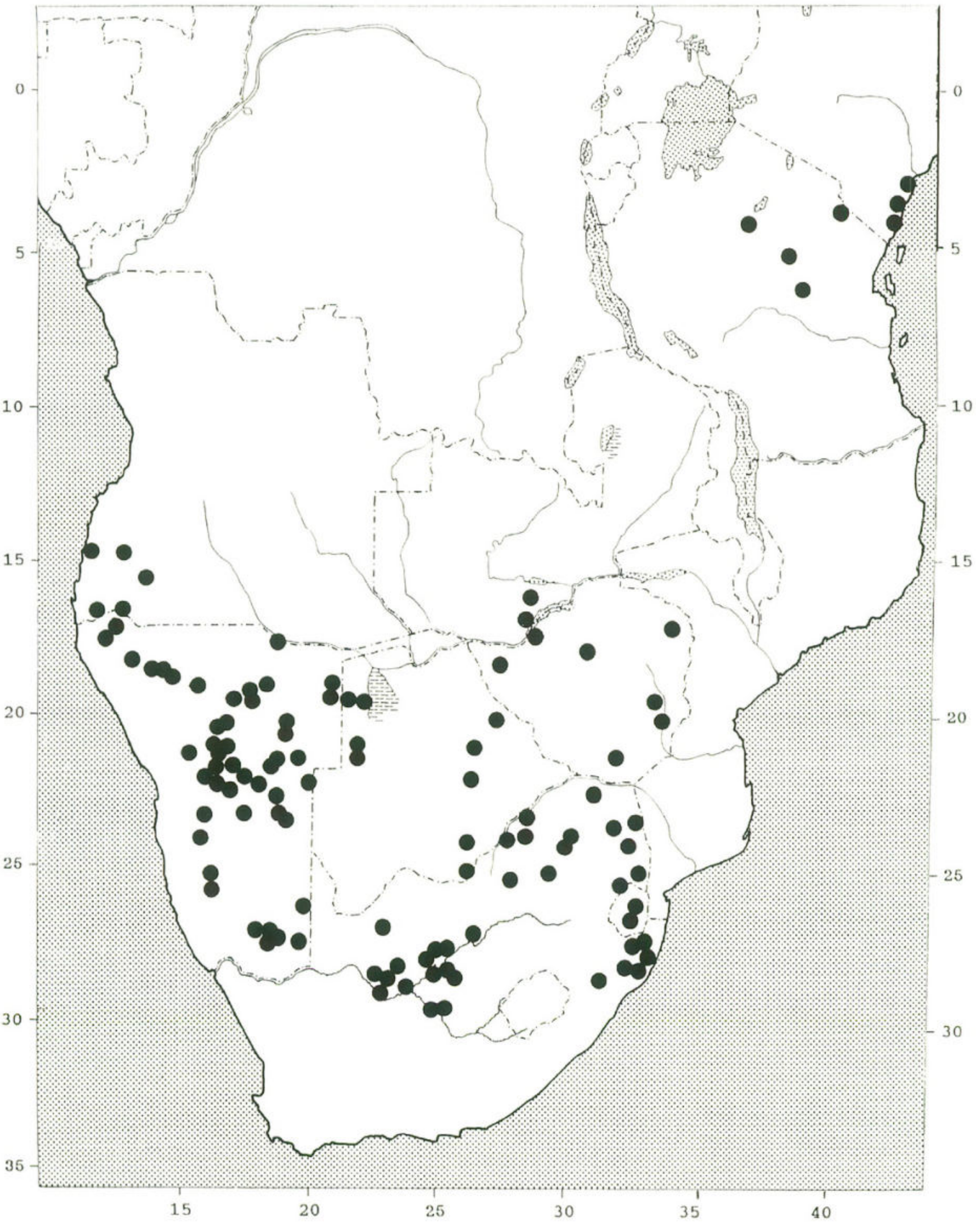

Figure 5. Map of central and southern Africa, showing distribution of *Fockea angustifolia*.

Smith 3167 (K, PRE); 9 km NE of Ghanzi, *Bruyns 6455* (BOL); D'Kar, *Bruyns 6460* (BOL); 8 km W of Lethlekane, *Wild & Drummond 7244* (M, PRE); Makunda, *Gibson 144* (WIND); N of Lephephe, *Snyman & Noailles 222* (PRE); Content farm, *Kelaole A69* (SRGH); Thorn Park, Lobatse, *Bayer 1431* (NBG).

KENYA. 2.5 km E of Dakabuko, *Luke & Robertson 2547* (K); betw. Samburu and Mackinnon Road, *Drummond & Hemsley 4045* (K); Shimba Hills, *Luke et al. 6188* (K).

NAMIBIA. Otjitande, *Rycroft 2460* (NBG); 3 km W of Etengua, *Bruyns 5577* (WIND); SW of Nzinzi, *de Winter 3985* (PRE, WIND); Okorosave, *Owen-Smith 103* (WIND); Kaoko Otavi, *Bruyns 5572* (WIND), *Barnard* (SAM); Orumana, *Grobbelaar 83* (M, WIND); 147 km N of Kamanjab, *Bruyns 4076* (BOL); Etosha Park, Okaumburu, Katspruit, *le Roux 1099* (PRE); Omuramba Onaiso, *Horn* (WIND); 4 miles SW of Okaukeujo, *Le Roux 1258* (WIND); 22 km E of Okakuejo, *Smook 7575* (PRE); Nosib, *Bruyns 2339* (WIND); Kumkauas,

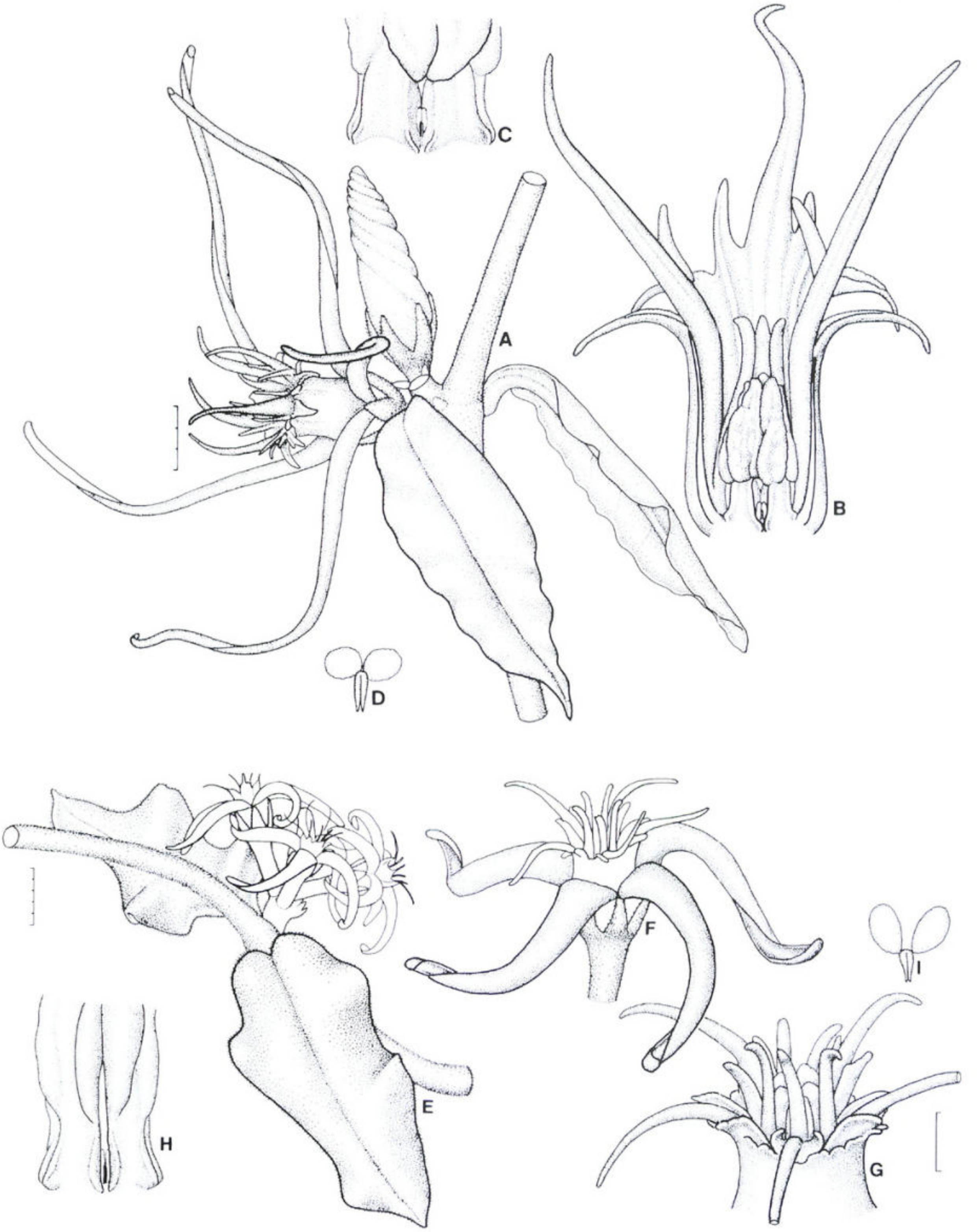

Figure 6. A–D. *Fockea angustifolia*. E–I. *Fockea capensis*. —A, E. Part of flowering branch. —F. Side view of flower. —G. Side view of gynostegium. —B. Side view of dissected gynostegium. —C, H. Side view of anthers. —D, I. Pollinarium. Drawn from: A–D, *Bayer 1431* (NBG); E–I, *Bruyns 2555* (NBG). Scales: A = 3 mm; B = 1 mm (at A); C = 0.5 mm (at A); D = 0.25 mm (at A); E = 5 mm; F = 2 mm (at E); G = 1 mm; H = 0.5 mm (at G); I = 0.25 mm (at G).

Giess & Smook 10639 (M, PRE, WIND); Auros, *Giess 12576* (M, WIND); Gobis Water, *Bruyns 5490* (WIND); 10 km toward Tsumkwe, *Bruyns 4116* (BOL); Grootfontein, *Schoenfelder S 128* (PRE); Sikereti, *Maguire 2267* (BOL, NBG, PRE); near Klein Dobe Camp, *Maggs et al. 1079* (WIND); road to Nyae-Nyae Pan, *Giess et al. 11133* (PRE, S, WIND); road to Makuri, *Hines 910* (PRE, WIND); Gautscha Pan, *Maguire 2193* (BOL, NBG, PRE), *Story 6216* (PRE, WIND);

Ozondjache, *Volk 540* (M); Otjenga, *Volk 1370* (M); Okosongomingo, *Volk 844* (M); Okakarara, *Bartsch 202* (WIND); 24 km NE of Epata, *Giess 9738* (M, WIND); 38 km NE of Epata, *Giess 9751* (WIND); Omaruru, *Bruyns 3611* (WIND); Omatako-Sicht, *Woortman 78* (WIND); Thorntrees, *Immelman 492* (PRE); Omusema, *Kers 2724* (S); Okahandja, *Bradfield 349a* (PRE); Quickborn, *Bradfield 349b* (PRE); Schoongelegen, *Seydel 2594* (M, WIND); Sturmveld, *Tölken 61* (WIND); Wilhelmsruhe, *Bruyns 2273* (WIND), *5474* (K); 64 km N of Gobabis, *Basson 238* (PRE); Epukiro, *Giess 9760* (M, PRE, WIND); Okomitundu, *Seydel 1419* (M, PRE); Ongos, *Kers 2479* (S); Neudam, *Giess 3921* (M, WIND); Ludwig, *Kers 2535* (S); Orumbo-noord, *Giess 8403* (M, PRE, WIND); Gammams, *Wanntorp 91* (PRE); Windhoek, *Dinter 275* (Z); *Hanekom 334* (WIND); *Müller 1420* (PRE, WIND), *Seydel 1704* (WIND); *Pehlemann 1243* (WIND); Voigtland, *Leippert 4355* (M, WIND); Finkenstein, *Wanntorp 185* (S); Nabitsaus, *van Vuuren 585* (M, PRE, WIND); Brack, *Volk 11198* (M); Okasewa, *Dinter 7450* (SAM); Grünental, *Merxmüller 1234* (M); 10 km W of Witvlei, *Burgoyne et al. 5221* (WIND); Witvlei, *Mason & Boshoff 2579* (PRE); Kirschberg, *Bruyns 5470* (WIND); Dawis, *Merxmüller & Giess 1200* (M, PRE, WIND); Oanob Dam Nature Res., *Sievers 168* (WIND); Klein Nauas, *Fleck 898* (Z); 64 km N of Kalkrand, *Acocks 18149* (PRE); Eersbegin, *Bruyns 5463* (WIND); Sandverhaar, *Bruyns 5462* (WIND); Naukluft, *Bruyns 4148* (BOL); Kapokvlakte, Naukluft, *Günsler 9491* (WIND); Duwisib, *Volk 12660* (M); Rooiberg Suid, *Bruyns 5672* (WIND); Barbi, *Bruyns 5709* (WIND); Lovedale, *Bruyns 5727* (WIND); Gaibis, *Bruyns 5445* (WIND); Steinfeld, *Bruyns 8143* (WIND); Dassiefontein, *Mannheimer 653* (WIND); Noachebeb, *Bruyns 5753* (WIND); Garies, *Bruyns 5801* (PRE); *Bruyns 3511* (BOL); Genadendal, *Bruyns 5781* (BOL); *Strohbach et al. 3349* (WIND); 30 km S of Narubis, *De Winter 3314* (PRE).

SOUTH AFRICA. Langkloof, *Leistner 2099* (KMG, PRE); Knockbarragh, Barkly West, *Brueckner 248* (KMG, PRE); Andaluzia, *Herre* (NBG), *Mueller-Stoll* (M); Padkloof, *Acocks 2207* (PRE); Oumeidkloof, Hay, *Cooke 6421* (BOL, KMG); Pauwfontein, *Cooke 6420* (KMG); Hay, *Acocks 2014* (PRE); Rudesheim, *Bruyns 4493* (BOL); Postmasburg, *Esterhuysen 5399* (K); Koopmansfontein, *Acocks 18792* (PRE); Newlands, *Wilman 3165* (KMG); River View, *Acocks 1503* (KMG, PRE); Best Pan, *Tapscott 119* (KMG); Riverton, *Tapscott* (BOL); 48 km W of Kimberley, *Lewis 67535* (PRE, SAM); 51 km W of Kimberley, *Hall 652* (NBG), *Hall 654* (NBG); Waverley, *Bruyns 9425* (NBG); Asbestos Mtns., *Bryant 1096* (PRE); Maselsfontein, *McDonald 77/85* (PRE); Rode Pan, near Orania, *Werger 1324* (PRE); Olifantsrug, *Power 6682* (BOL, K); Driekop, Lückhoff, *van Zyl 1046* (PRE); Magut, *Gerstner 3157* (NH, PRE); 11 km toward Jozini, *Bruyns 4459* (BOL); Nibela store, *Ward & Guy 80* (K, M, PRE); Bangonoma, *Gerstner* (NH); near Muden, *Bruyns 4437* (BOL); Bekamuzi, *Gerstner 3894* (NH, PRE); Umfolozi Game Reserve, *Mthonti 16* (PRE); Mfule Valley, *Venter 5107* (PRE); Hluhluwe Game Reserve, *Ward 2061* (PRE); Masikwaspoort, *van der Merwe 1691* (PRE); Alfred, *Codd 6606* (PRE); Gravelotte, *Bruyns 1920* (NBG); Manyeleti Game Reserve, *Bredenkamp 1784* (PRE); 3 km S of Rooibokkraal, *Leistner 3190* (K, M, PRE); Schwerin, *Leistner 3192* (K, M, Z); 9.5 km SW of Bulge R, *Louw 3545* (PUC); Sterkrivierdam Nature Reserve, *Jacobsen 2809* (PRE); Potgietersrus, *Bolus 11014* (BOL, Z); 58 km N of Marble Hall, *Vorster & Jackson 2160* (PRE); 16 km from Immerpan to Middelburg, *Meeuse 9600* (PRE, S); Kruger Park, *Gertenbach 5446* (PRE); 6.5 km WNW of Rustenburg, *Acocks 19169* (PRE); Hammanskraal, *Mogg 14864* (M, PRE); N of Gomandwane, *van der Schijf & Marais 3644* (PRE); Barberton, *Rogers 20304* (S); Maquassie, *Morris & Engelbrecht 6924/3* (PRE).

SWAZILAND. Sicusha, *Bayliss 564* (K, PRE), *2076* (NBG, Z); St. Phillips, Hlatikulu, *Dlamini* (M, PRE).

TANZANIA. Lembeni, *Winkler 3803* (K); 20 km W of Same, *Bruyns 8672* (K); Ibaya Hill, Mkomazi Game Res., *Vollesen 96/22* (K); Lake Kitangiri, *Richards 13501* (K); 31 km S of Kondoa, *Bruyns 8723* (MO); Chenene Public Land, Dodoma distr., *Rufo & Magogo 719* (K); Kiboriani Hills, *Bruyns 9635* (MO).

ZAMBIA. Gwembe, near Ntoboute village, *Scudder* (SRGH); Sinazongwe, *Bruyns 9587* (MO).

ZIMBABWE. Mwenda, *Jarman* (SRGH); Redlands, *Leach & Gosden 15014* (SRGH); 8 km W of Salt Springs, Sinamatila, *Rushworth 2550* (SRGH); 68 km W of Kadoma, *Bruyns 7454* (BOL); Devure R. bridge, *Chase 7979* (K); Umkondo Mine, *Dale 268* (SRGH); Bubye R., *Drummond 5814* (K, PRE, SRGH).

2. Fockea capensis Endl., in Endl. & Fenzl, Nov. Stirp. Dec. 3: 17. 1839. *Fockea crispa* K. Schum. in Engl. & Prantl, Pflanzenfam. 4 (1): 296. 1895. *Fockea edulis* var. *capensis* (Endl.) G. D. Rowley, Asklepios 75: 17. 1998. TYPE: South Africa. Cape, *Boos & Scholl sub Schönbrunn Garden 488* (lectotype, designated here, K!; duplicate, W, not seen). Figures 6E–I.

Perennial herb with large underground to partially exposed tuber to 80 × 60 cm with central growth point on upper warty surface from which a cluster of several more slender perennial and aerial stems arise, stems erect to twining to 1 m with some of more slender growth deciduous, young growth shortly pubescent. *Leaves* with minutely puberulous petiole 1–2 mm long, gray-green, elliptic, 15–30 × 6–12 mm, finely and densely pubescent, acute, margins strongly undulate and crisped but not revolute. *Inflorescence* 1- to 5-flowered, flowers opening in rapid succession, puberulous; *peduncle* 1–2 × 2 mm; *pedicels* 2–6 × 1–2 mm. *Sepals* 1.5–2 × 1 mm, lanceolate, outside pubescent, inside glabrous; *corolla* 15–22 mm diam.; outside grayish green, puberulous; inside green, puberulous; *tube* 2–3 mm deep, ca. 2 mm broad at mouth, cupular; *lobes* 8–12 × 1.5–2 mm, linear, obtuse, spreading and often spiralling to left, usually twisted to left when viewed along length, with margins strongly reflexed; *corona* white, glabrous; *outer corona* forming cylindrical tube 2.5–3 mm long, divided at mouth of tube into 5 longer slender terete and spreading lobules 2–3 mm long each flanked by 2 flattened spreading lobules, these groups of 3 lobes alternating with 5 truncate to emarginate, usually spreading lobules; *inner corona* of 5 terete linear lobes adpressed to backs of anthers then erect above them and slightly spreading toward tips. *Follicles* 50–80 × 10–12 mm, gray-green, often longitudinally wrinkled; *seeds* 8–10 × 4–6 mm, yellow-brown.

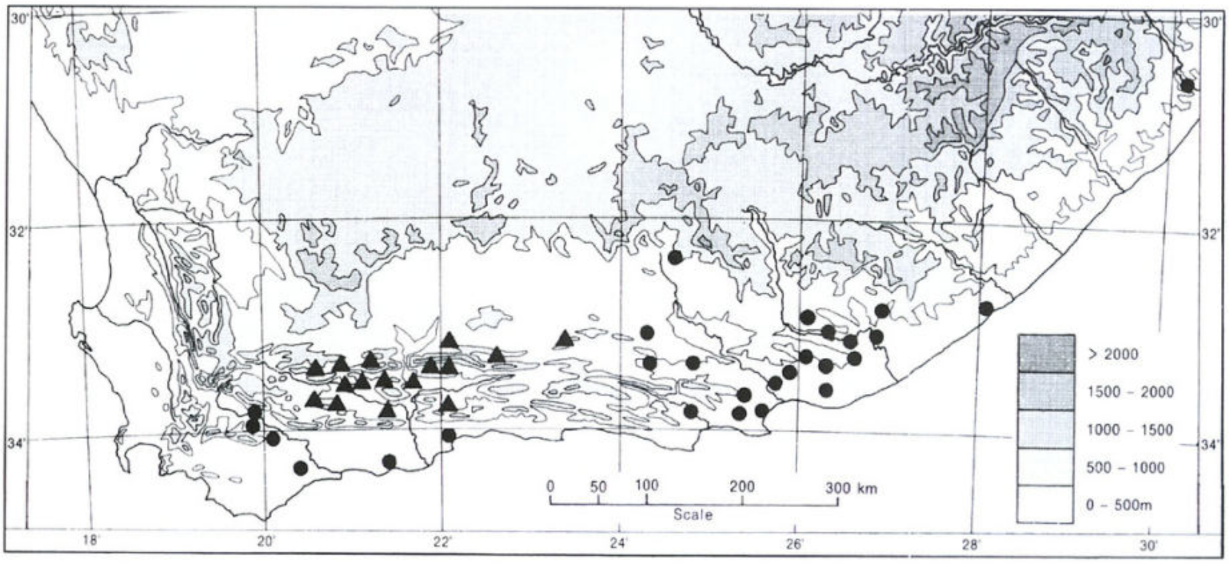

Figure 7. Map of southern Africa, showing distribution of *Fockea capensis* (triangles) and *F. edulis* (circles).

Phenology. Flowering October to May.

Distribution. South Africa; 300–1200 m (Fig. 7). *Fockea capensis* is found only in the southern portion of South Africa where it grows on the Little Karoo and in the dry mountains forming its northern border. It has been recorded from a little east of Prince Albert westward on the Little Karoo to the Warmwaterberg (Fig. 7).

Ecology. Specimens of *Fockea capensis* are always found among other succulents on rocky slopes (mostly on sandstones and quartzites but occasionally on shales as well), where the tubers are tightly wedged among the rocks and are often much misshapen by pressure from their surroundings.

Discussion. Endlicher based his description of *Fockea capensis* on the specimen in cultivation at Schönbrunn Gardens but did not cite any preserved material. As only one plant appears to have been grown there, this is assumed to be the same as the specimen *Boos & Scholl sub Schönbrunn Garden 488*, which, consequently, is selected as the lectotype of *F. capensis*.

The name *Fockea crispa* is usually cited with "(Jacq.) K. Schum." as the authors, with *Cynanchum crispum* Jacq. (1800–1809: 31, t. 34) as the basionym (e.g., Court, 1982; Meve, 2002). However, *C. crispum* Jacq. is illegitimate, being a later homonym of *C. crispum* Thunb. (of 1794, which is a synonym of *Brachystelma thunbergii* N. E. Br.). Thus, it cannot be the basionym for any later combination. The first valid publication of the epithet *crispa* for a species of *Fockea* was that of K. Schumann in 1895.

Brachystelma crispum E. Mey. (Meyer, 1838: 196: a later homonym of *B. crispum* Graham, 1830) is sometimes cited as a synonym of *Fockea capensis* (Meve, 2002). However, Meyer (1838: 196) mentioned "*tuber depressum ut in Br. tuberoso… folia 3–4 lineas longa*," so this name applies to a species of *Brachystelma* rather than a species of *Fockea*. The type of *B. crispum*, collected by J. F. Drège (Camdeboo, near Hamerkuil, Meyer, 1838), has not been located, but *F. capensis* does not occur so far to the east in South Africa.

The plants of *Fockea capensis* are not generally as large as those of *F. edulis*. As in *F. edulis*, the distinctly warty upper surface of the tuber usually projects from the ground. Noteworthy in *F. capensis* (and in *F. edulis*) is the frequent presence of a fairly large root spreading outward superficially from near the top of the tuber, which must be important for absorbing moisture close to the surface of the soil. In *F. capensis* the stems are often grazed off so as to be erect, but they may occasionally twine on surrounding bushes, if any are available. The differences from *F. edulis* are discussed under that species.

Specimens examined. SOUTH AFRICA. Skerpkrans, Vrede, *Bruyns 5314* (BOL); Keurfontein, *Bruyns 2809* (BOL); Klein Speeufontein, *Bruyns 4566* (BOL); Spreeufontein, *Bayer 4675* (NBG); 43 km NW of Ladismith, *Bruyns 2555* (NBG); Buffelsrivier Poort, *Bruyns 2554* (NBG); Patatsfontein, *Bruyns 7518* (BOL); Plathuis, *Bruyns 7340* (NBG); nr Warmwaterbron, *Bayer 4676* (NBG); 39 km SE of Laingsburg, *Bruyns 2874* (BOL); Amalienstein, *sub STE 14888* (NBG); Seweweekspoort, *Bruyns 8423* (NBG); Coetzeespoort, *Bruyns 8217* (K); N of Riversdale t'off, *Bruyns 2924* (BOL); 11 km W of Ladismith, *Hall 2592* (NBG); 5 km S of Ladismith, *Bayer & Bruyns 3648* (NBG); Naauwkloof Nat. Reserve, *Hilton-Taylor 900* (NBG); 8 km S of Vanwyksdorp, *Bayer & Bruyns 4674* (NBG); NE of Vanwyksdorp, *Bayer 317* (NBG); Tierberg, near Prince Albert, *Marloth 4465* (PRE, NBG); Boomplaas, *Hugo 21* (NBG), *Moffett 455* (NBG); Droëkloofberge, *Bruyns 8188* (MO); Brakpoort, *Hugo 148* (NBG, PRE); N of Robinson

Pass, *Bayer 458* (NBG); Leeukloof, *Bruyns 7085* (BOL); Boesmanspoortberge, *Bruyns 6315* (BOL).

3. **Fockea comaru** (E. Mey.) N. E. Br., Fl. Cap. 4 (1): 781. 1908. Basionym: *Brachystelma comaru* E. Mey., Comm. Pl. Afr. Austr.: 195. 1838. TYPE: South Africa. Cape, Nuwerus, N of Beaufort West, *M. B. Bayer 938* (neotype, designated here, NBG!; duplicate, PRE!). Figures 8A–G.

Fockea gracilis R. A. Dyer, Bull. Misc. Inform. 1933: 459. 1934. TYPE: South Africa. Grahamstown, Dikkop Flats, amongst short Karoo bushes, *R. A. Dyer 1251* (holotype, PRE!; isotypes, BOL!, GRA!, K!).

Small geophytic herb with underground napiform tuber (sometimes deformed by rocks) up to 30 × 15 cm with central growth point on smooth upper surface from which slender perennial and aerial stems arise, stems erect to twining to 50 cm (–1 m), softer upper parts deciduous, young growth finely tomentose. *Leaves* with petiole 1 mm long or less, green to bluish green, linear, 25–65 × 1.5–2(–4) mm, obtuse, upper surface darker than lower and finely adpressed pubescent, lower finely pubescent, midrib translucent white, margins strongly revolute, weakly undulate to straight. *Inflorescence* 1- to 6-flowered, flowers opening in succession, covered with fine adpressed hairs; *peduncle* absent; *pedicels* 1–2 × 1 mm. *Sepals* 1.5–2 × 1 mm, lanceolate, outside finely pubescent, inside glabrous; *corolla* 8–27 mm diam.; outside grayish green, finely pubescent; inside gray-green to brown-green, sparsely and very finely pubescent; *tube* 1.5–3 mm deep, ca. 2 mm broad at mouth, cupular; *lobes* 4–12 × 1–2 mm, linear, obtuse, spreading and often spiralling to left, often twisted to left when viewed along length, with margins strongly reflexed; *corona* white, glabrous; *outer corona* forming cylindrical tube 4–6 mm long, divided at mouth of tube into 5 longer slender terete and strongly spreading lobules 2–2.5 mm long each flanked by 2 flattened spreading lobules, these groups of 3 lobes alternating with 5 linear to truncate-emarginate usually spreading lobules; *inner corona* of 5 terete linear lobes adpressed to backs of anthers then rising erect above them. *Follicles* 50–100 × 10–12 mm, gray-green, smooth; *seeds* 8–10 × 4–6 mm, yellow-brown.

Phenology. Flowering October to May.

Distribution. Namibia, South Africa; 100–2000 m (Fig. 11).

Ecology. *Fockea comaru* is always found in stony places on hillsides and mountains, with the tubers often tightly wedged between rocks at a depth of up to 20 cm or more. It is the only species of *Fockea* that is common in the winter rainfall region of the western side of South Africa, where it always occurs with plenty of other succulents. Nevertheless, it is also found well beyond this. Many of the known localities outside the winter rainfall region are in elevated areas (such as the Tiras Mountains and the Great and Little Karas Mountains of Namibia) that receive small amounts of winter rainfall, but those in Griqualand West (for example) do not receive any significant winter rainfall.

Discussion. The specimen cited by Meyer (1838: 195, namely South Africa, Richmond distr., Uitvlugt, near Steelkloof, 4000–5000′, *J. F. Drège*) is missing, and no other suitable specimen of Drège has been located that could serve as a lectotype. Very few collections exist from the central part of South Africa where Drège's specimen came from, and other early collections are neither from this area nor are sufficiently similar to be suitable as neotypes. Consequently a recent collection, *Bayer 938*, is selected as neotype.

Although the stems in *Fockea comaru* may climb in surrounding bushes, they are often short and erect and frequently do not twine at all, forming instead small rosettes on the ground. The stems have a rhizomatous habit and often spread underground for some distance from the tuber before emerging from the soil. These subterranean stems appear to be perennial. In such situations, stems from the same plant may appear over a considerable distance, giving the appearance of several specimens growing near each other, though, on excavation, they prove to originate from the same tuber.

As shown in Fig. 8A–G, the flowers are exceptionally variable in diameter and the lobes may be quite short and not twisted at all.

Apart from the highly succulent stapeliads, asclepiads are not generally common in the winter rainfall parts of southern Africa. In this respect *Fockea comaru* (along with a few species of *Microloma*) is unusual, and it is of very wide and quite frequent occurrence in these areas. The very narrow, linear leaves and the milky sap make the plants of *F. comaru* unmistakable among the asclepiads in most areas where they occur. It is often well known where it occurs, with the tubers being dug out and consumed, and the plants are known as *kambroo* or *bergkambroo*.

The molecular data (e.g., Fig. 3) show that *Fockea comaru* and *F. sinuata* are very closely related and scarcely differ at all in the three gene regions investigated. Morphological differences between the two are discussed under *F. sinuata*.

In our molecular sampling, we included an accession of the former *Fockea gracilis* (*Dold 2381*), and this did not group strongly with the other accession of *F. comaru*. *F. gracilis* was mainly

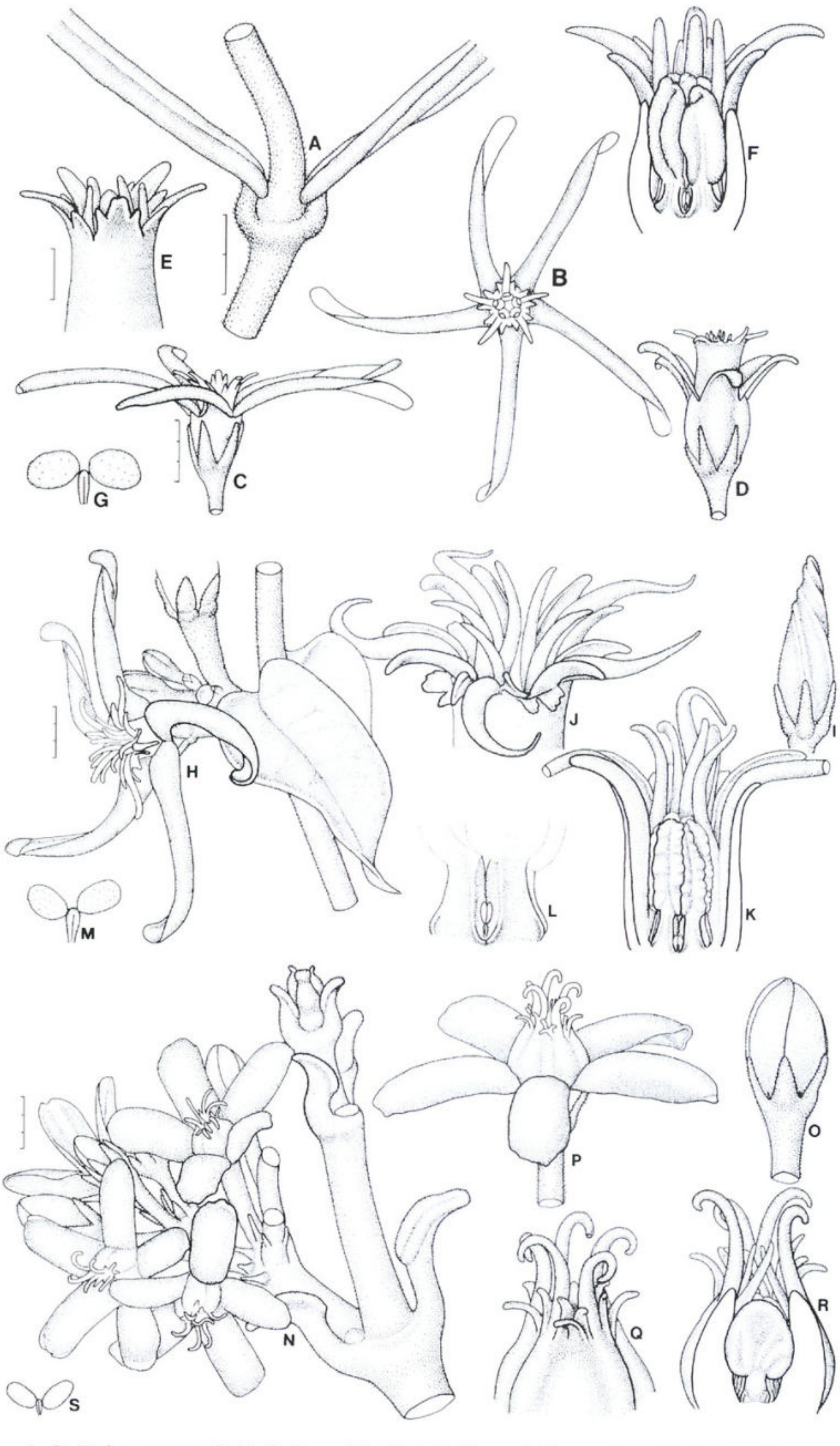

Figure 8. A–G. *Fockea comaru*. H–M. *Fockea edulis*. N–S. *Fockea multiflora*. —A, H, N. Portion of stem. —I, O. Bud. —B. Face view of flower. —C, D, P. Side view of flower. —E, J, Q. Side view of gynostegium. —F, K, R. Side view of dissected gynostegium. —L. Side view of anthers. —G, M, S. Pollinarium. Drawn from: A–C, E, F, *Bruyns 1700a* (NBG); D, E, *Bruyns 3129* (BOL); G, *Bruyns 3107* (NBG); H–M, *Bayer 325* (NBG); N–S, *D. Laing* (K). Scales: A = 2 mm; B–D = 3 mm (at C); E = 1 mm; F = 1 mm (at C); G = 0.25 mm (at C); H, I = 3 mm (at H); J, K = 1 mm (at H); L = 0.5 mm (at H); M = 0.25 mm (at H); N = 3 mm; O, P = 2 mm (at N); Q, R = 1 mm (at N); S = 0.25 mm (at N).

distinguished from *F. comaru* by its much smaller flowers. However, the wide variation in this feature within *F. comaru* makes *F. gracilis* impossible to recognize reliably, so that we are unable to distinguish it from *F. comaru*. Molecular support for its distinctness from *F. comaru* is also negligible (Fig. 3).

Specimens examined. NAMIBIA. Landsberg, *Bruyns 8112* (WIND); Naus, *Bruyns 5698* (WIND); Lovedale, *Bruyns 5724* (WIND); Tschaukaib, *Bruyns 3170* (NBG); Nooitgedacht, *Bruyns 8348a* (WIND); Nasapberg, *Bruyns 7206* (NBG); Sebrafontein, *Bruyns 3924* (BOL); Steinfeld, *Bruyns 8142* (WIND); Lord Hill, *Bruyns 8147* (WIND); Witmond, *Bruyns 5759* (WIND); *Strohbach et al. 3800* (WIND); Garies, *Bruyns 5805* (PRE); *Bruyns 3512* (WIND); Genadendal, *Bruyns 5783* (BOL).

SOUTH AFRICA. Kodaspiek, *Bruyns 8278* (K); Van Der Sterrberge, *Bruyns 7281* (NBG); summit Rosyntjie Mtn., *Bruyns 3291* (NBG); summit Cornellsberg, *Bruyns 3304* (NBG); 6 km S of Eksteenfontein, *Bruyns 8286* (MO); Kliphoogte, *Herre sub STE 12334* (NBG); Rudesheim, *Bruyns 4493* (BOL); Steinkopf, *Marloth 13300* (PRE); Hester Malan Reserve, *Rösch & le Roux 729* (PRE); Gannapoort, *Leistner 2447* (K, KMG, PRE); Waverley, *Bruyns 9424* (MO); Strydenburg, *Hall 640* (NBG); 6 km N of Ou Dam, *Bruyns 6753* (BOL); 4 km W of Paulshoek, *Bruyns 6107* (PRE); N of Kaams, *Bruyns 6348* (BOL); Stofkraal, *Bruyns 4767* (BOL); Witvlakte Oos, *Bruyns 6089* (PRE); Kubiskow, *Bruyns 6085* (PRE); Loeriesfontein, *Marloth 12848* (PRE); Nooiensberg, *Bruyns 6645* (BOL); NW of Komkans, *Bruyns 6255* (BOL); Nuwerus, *Bruyns 6786* (BOL); Kalkgat Noord, *Bruyns 6018* (BOL); 16 km S of Klawer, *Hall sub NBG 817/48* (NBG); Eselskop, *Bruyns 6824* (BOL); Blomberg, *Bruyns 7859* (NBG); Calvinia, *Marloth 7147b* (PRE); Kliprug, *Bruyns 6056* (PRE); Botterkloof, *Bruyns 6038* (PRE), *Hall 700* (NBG); Aarkolk, *Bruyns 5980* (BOL); Grootfontein, *Coetzer 59* (PRE); Boesmansberg, Juriesfontein, *Bruyns 6688* (BOL); Nuwerus, *Bayer 938* (NBG, PRE); Pakhuis, *Hall sub NBG 45/50* (NBG); Clanwilliam Dam, *Bruyns 6034* (PRE); 11 km SE of Redelinghuis, *Bruyns 4734* (BOL); 6 km N of Het Kruis, *Bruyns 6175* (BOL); E of Uitspankraal, *Bruyns 7502* (NBG); Bossiesberg, *Bruyns 7572* (BOL); 2 km N of Uitsig, *Bruyns 6708* (BOL); Aarfontein, *Bruyns 6361* (BOL); Klipfontein, *Bruyns 3107* (NBG); Amandelboom, *Bruyns 6695* (BOL); Doornhoek, *Bruyns 3991* (BOL); Prutkraal, *Bruyns 3141* (BOL), *Snyman* (NBG); Worcester Veld Reserve, *Olivier 255* (PRE); 19 km SE of Worcester, *Bayer 319* (NBG); 4 km W of Robertson, *Schwegmann* (NBG); 2 km SW of Robertson, *Bayer 136* (NBG); Doornrivier, *Stokoe* (PRE); Avondrust, *Bayer 318* (NBG); Whitehill, *Archer 18286* (BOL); Ou Tol, *Bruyns 6304* (BOL); Plathuis, *Bruyns 7341* (NBG); Coetzeespoort, *Bruyns 8216* (NBG); Calitzdorp, *Oddie 559/36* (BOL); Prince Albert, *Marloth 7147a* (PRE); Haggas, *Vlok 2440* (NBG); Vleikuil, *Bruyns 6309* (BOL); Skietkuil, *Bruyns 3129* (BOL); Zuurbergpoort, *Hall 1645* (NBG); near Steytlerville, *Compton 4998* (NBG); Korhaan Vlakte, Addo, *Dold 2381* (GRA, PRE); Dikkop Flats, *Dyer 1251* (BOL, GRA, PRE); 4 km NW of Stormsvlei Pass, *Bayer 329* (NBG).

4. **Fockea edulis** (Thunb.) K. Schum., Bot. Jahrb. Syst. 17: 146. 1893. Basionym: *Pergularia edulis* Thunb., Prodr. Pl. Cap. 1: 38. 1794. *Echites edulis* (Thunb.) Thunb., *In genus Echitis observationes*: 5. 1819. TYPE: South Africa. Cape, Gouritz River, *C. P. Thunberg 6141* (holotype, UPS, not seen). Figure 8H–M.

Brachystelma macrorrhizum E. Mey., Comm. Pl. Afr. Austr.: 197. 1838. TYPE: South Africa, Cape, Graaff-Reinet, *Marloth 7048* (neotype, designated here, PRE).

Fockea glabra Decne. in DC. Prodr. 8: 545. 1844. TYPE: South Africa. Cape, *C. L. P. Zeyher 239* (holotype, P!; isotypes, G, not seen, W, not seen).

Fockea cylindrica R. A. Dyer, Bull. Misc. Inform. 1933: 459. 1934. TYPE: South Africa. Cape, Fish River Valley, near Committees, amongst karroid scrub on dry flats, *R. A. Dyer 1635* (holotype, K!; isotypes, GRA!, PRE!).

Perennial herb with large underground to partially exposed tuber up to 50 cm long and 1 m broad with central growth point on upper usually warty surface from which 1 to several more slender perennial and aerial stems arise, stems erect to twining to 2 m with some of more slender growth deciduous, young growth puberulous. *Leaves* with minutely puberulous petiole 2–8 mm long, green often with paler midrib, elliptic, 15–45 × 6–20 mm, glabrous to sparsely pubescent, acute, margins often undulate but not revolute. *Inflorescence* 1- to 8-flowered, flowers opening in succession, puberulous; *peduncle* 1–3 × 1 mm; *pedicels* 1–3 × 1 mm. *Sepals* 1.5–2.5 × 1 mm, lanceolate, outside pubescent, inside glabrous; *corolla* 10–22 mm diam.; outside grayish green, sparsely puberulous; inside green, glabrous to puberulous; *tube* 2–5 mm deep, ca. 3 mm broad at mouth, cupular; *lobes* 6–12 × 1.5–2 mm, linear, obtuse, spreading and often spiralling to left, usually twisted to left when viewed along length, with margins strongly reflexed; *corona* white, glabrous; *outer corona* forming cylindrical tube 3–4 mm long, divided at mouth of tube into 5 longer slender terete and ascending to strongly spreading lobules 2–3 mm long each flanked by 2 flattened spreading lobules, these groups of 3 lobes alternating with 5 linear to truncate to emarginate usually spreading lobules; *inner corona* of 5 terete linear lobes adpressed to backs of anthers then erect above them and slightly spreading toward tips. *Follicles* 50–80 × 10–12 mm, gray-green, often longitudinally wrinkled; *seeds* 8–10 × 4–6 mm, yellow-brown.

Phenology. Flowering October to May.

Distribution. South Africa; 10–1200 m (Fig. 7).

Ecology. *Fockea edulis* is found in dry bush in the southern portion of South Africa, from the Worcester-Robertson Karoo and the coastal plain east of Bredasdorp to around East London and also in similar habitats in southern Natal around the Oribi Gorge. Plants occur among rocks and bushes or trees on slopes. It is rather more rarely found in flat areas, as in the low-lying areas between Steytlerville and Port Elizabeth.

Discussion. In both Schumann (1893: 146) and Schumann (1895: 296), "*Fockea edulis* (Thbg.) K. Sch." is mentioned, and no attempt is made to describe this as a new species. Consequently in Schumann (1893: 146) a valid new combination was made, because he made an indirect reference to a previously published name (Greuter et al., 2000: ICBN Art. 32.4, Art. 32.5) and the basionym for this name is *Pergularia edulis* Thunb. as given in Brown (1907–1909: 780).

For *Brachystelma macrorrhizum*, Meyer (1838: 197) cited an unnumbered collection of Drège (South Africa, Oudeberg mountain), which is missing. The neotype selected here is from the same area as Drège's collection, so that this name is unequivocally a synonym of *Fockea edulis*.

As mentioned above, Harvey (1842) made no new combinations in *Chymocormus* even though he mentioned *Pergularia edulis* as belonging to this new genus. Consequently *C. edulis* (as given in Schumann, 1895; Brown, 1907–1909; and Meve, 2002), is not valid (Greuter et al., 2000: ICBN Art. 33.1) and is not cited here.

In more bushy areas *Fockea edulis* is a vigorous climber to a height of 2 m. In more arid spots, where the vegetation is altogether shorter (such as on the Worcester-Robertson Karoo), *F. edulis* can be a small and inconspicuous climber among bushlets of *Carissa bispinosa* (L.) Desf. ex Brenan and other species. Even smaller, tufted plants that scarcely twine at all are characteristic in areas of low, mostly succulent vegetation between Steytlerville and Port Elizabeth, and one of these was described as *F. cylindrica* [= *F. edulis*].

In *Fockea edulis* the distinctly warty upper surface of the tuber usually projects slightly from the ground. The tuber may be enormous and has been recorded up to 1 m in diameter (*Bayer 326*, NBG).

Fockea edulis and *F. capensis* are similar in many respects. Both have comparatively broad leaves (6–20 mm broad in comparison to 1.5–4 mm broad in *F. comaru*) and large tubers with the upper surface projecting from or level with the surface of the ground. *Fockea capensis* is short and shrubby in habitat, but the stems will twine if provided with the opportunity. In *F. capensis* the leaves have distinctly undulate or crisped margins and are densely covered with adpressed hairs, while in *F. edulis* the leaves have at most slightly undulate margins and are more or less glabrous. This lends them a green color in *F. edulis* and a distinctly gray-green color in *F. capensis*. Florally there are no significant differences between them. This close relationship is reflected in Figure 3.

Specimens examined. SOUTH AFRICA. SW side of Graaff-Reinet, *Burchell 2916* (K); Tandjiesberg, *Bruyns 2976* (BOL); Graaff-Reinet, *Marloth 7048* (PRE); Adelaide road, *J.-Guillarmod 4929* (PRE); Keiskamma, *Bayer 323* (NBG); Gonubie Mouth, *Bayer 326* (NBG); Klaasvoogds, *Bayer 325* (NBG); Rooiberg, Goudmyn, *Bruyns 6793* (BOL); Klipplaat, *Bayer* (NBG); Witkop, *Desmet 2240* (NBG); Kleinspoort, *Bayer* (NBG); Ventershoek, *van Jaarsveld 11410* (NBG); Addo Elephant Park, *Botha 5800* (PRE); near Groendal, *Vlok 554* (PRE); 36 miles from Port Elizabeth to Steytlerville, *Long 1184* (K); Springs Reserve, Uitenhage, *Olivier 2495* (PEU); Uitenhage, *Zeyher 965* (K); near Uitenhage, *Burchell 4450, 4443, 4457* (K); betw. Port Elizabeth and Uitenhage, *Long 1469* (K); Addo, *Acocks 13661* (PRE), *Kreft 96* (BOL); Coega, *Bayer 320* (NBG), *Bursey* (NBG), *Olivier 1577* (PRE); Bluewater Bay, *Olivier 3042* (PRE); Swartkops, *Hallack 3052* (PRE); Humewood, *Dahlstrand 60* (PRE); Redhouse, *Paterson 544* (BOL, Z); Aloes stn., *Long 903* (K); Hounslow, *Galpin 13250* (BOL, PRE), *13251* (P, PRE); near Hyde's Hill, *Nicholas 912* (PRE); betw. Tootabi and Alicedale, *Archibald 5984* (PRE); 10 miles from Grahamstown toward Alexandria, *Dyer 956a* (K); Ecca Pass, *Bayer* (NBG); Pluto's Vale, *Bayer 322* (NBG); Trumpeter's Drift, *Story 2190* (PRE); Adelaide road, *Jacot Guillarmod 4929* (PRE); Nook Boosaak Forest, Alexandria, *Britten 2506* (PRE); N of Stormsvlei Pass, *Bayer* (NBG); De Hoop, *Bruyns 6656* (BOL); Kafferkuils R. mouth, *Muir 149* (PRE); Klein Brakrivier extension 4, *Taylor 8341* (NBG); Gibraltar rock, *Nicholson & Strey 1968* (PRE), *Balkwill 439* (NU).

5. Fockea multiflora K. Schum., Bot. Jahrb. Syst. 17: 145. 1893. TYPE: Tanzania. French mission in Ussambiro, *F. L. Stuhlmann 848* (holotype, B, missing; isotype, K!). Figure 8N–S.

Fockea schinzii N. E. Br., Bull. Misc. Inform. 1895: 259. 1895. TYPE: Angola. *F. Welwitsch 4194* (lectotype, designated here, K!; duplicate, P!).

Large climber to 15 m, with stout trunk (to 30 cm thick) sprawling on ground or twisting around trees for support, rarely shrub-like; stems fleshy and becoming swollen toward base but without distinct basal tuber, young stems tomentose and slightly fleshy, remaining fleshy but becoming covered with gray, shiny bark. *Leaves* with petiole 8–25(–45) mm long, gray-green, oblong to broadly elliptic, (20–)30–150 × (10–)25–100 mm, often apiculate, upper surface tomentose to glabrous, lower tomentose with raised midrib and veins, margins not revolute or undulate. *Inflorescence* (6- to)10- to 30-flowered, flowers opening ± simultaneously or in rapid succession, pubescent; *peduncle* 5–15 × 2–5 mm; *pedicels* 5–13 mm long. *Sepals* 2–3 × ca. 1 mm, lanceolate, outside pubescent, inside glabrous; *corolla* 10–15 mm diam.; outside grayish green, pubescent; inside yellowish green to brown, glabrous to sparsely pubescent; *tube* 1.5–2 mm deep, ca. 3 mm broad at mouth, shallowly cupular; *lobes* 5–10 × 2 mm, broadly linear, obtuse, spreading, with margins and apex slightly reflexed; *corona* white, glabrous; *outer corona* forming tube 2–3 mm long, becoming distinctly narrower above anthers, divided at mouth of tube into 5 longer slender terete spreading lobules 2–2.5 mm long each flanked by 2 flattened slightly spreading lobules, these groups of 3 lobes alternating with 5 linear recurved lobules; *inner corona* of 5 flattened linear lobes adpressed to backs of anthers then intertwined above them. *Follicles* 100–220 × 15–30 mm; *seeds* 10 × 7–8 mm.

Phenology. Flowering August to December.

Distribution. Angola, Botswana, Moçambique, Namibia, Tanzania, Zambia, Zimbabwe; 600–1000 m (Fig. 9).

Ecology. *Fockea multiflora* occurs in rocky areas on low hills or among rocks around the base of hills in open, often deciduous woodland consisting of an *Acacia-Commiphora-Balanites* association or *Colophospermum mopane* (Kirk ex Benth.) Kirk ex J. Léon. Plants are usually common.

Discussion. The specimen at B on which K. Schumann based *Fockea multiflora* was destroyed during World War II. However, some of the same collection is preserved at Kew and this is selected as an isotype. For *F. schinzii*, Brown (1895) cited *Welwitsch 4194* and an unnumbered collection of Schinz, which has not been located. The Welwitsch collection is selected as lectotype.

Fockea multiflora is by far the largest species, and massive specimens are probably the largest known asclepiads. The big fleshy stems sprawl on the ground or twist up the trunks of surrounding trees as massive lianes and appear to strangle them, though there is no evidence that they have any detrimental effect on these trees. Damaged specimens sometimes form a huge mass of entangled stems without any longer climbing stems, but this is exceptional. In all the other species of *Fockea*, the stems arise from a tuber that is much broader than the main stem. In *F. multiflora*, although the young plants have a thickened base, this generally disappears with age, so that in mature specimens there is no basal tuber and the rootstock consists of a network of fleshy roots radiating from the base of the stem. Only the youngest shoots and the leaves are deciduous, while the remainder of the plant is perennial. The leaves are also much larger (to 15 × 10 cm) than those of any other species of *Fockea*. The large size extends into the fruit and the seeds.

Fockea multiflora is unusual in that the inflorescences arise in large numbers around the end of the dry season between August and October (more rarely in December), on young growth produced before the true growing season begins. The sweetly scented flowers appear on the first young shoots of the new growing season among small, under-developed leaves and are sometimes used as a vegetable (*B. L. Burtt 1520* (K); Bruyns & Klak, pers. obs., Gulwe district, Tanzania). Several features of the flower are unique. They are produced in dense, more or less simultaneously opening clusters. The corolla lobes are comparatively short and relatively broad (unlike the other species where they are mostly slender and linear) and are not twisted along their length (Fig. 8N, P). The corona tube is often also noticeably constricted toward the mouth (Fig. 8P, Q). Both the corona tube and the comparatively broad anther appendages are also relatively short (Fig. 8R).

Specimens examined. ANGOLA. Bibala, *Gossweiler 13131* (LISC); Gambos, *Borges 308* (LISC, PRE, SRGH), *Pearson 2134* (BOL); Humbe, *Menezes & Sousa 3423* (LISC, PRE); Mupa, *Menezes 3152* (LISC, PRE, SRGH); Xangongo, *Santos & Barrosa 2825* (LISC, PRE); Ondjiva, *Menezes 1017* (LISC).

BOTSWANA. Ngoma on Chobe R., *Miller 1050* (PRE), *Story 4809* (P, PRE), *Munro sub PRE 6924* (PRE); Okavango, near Nokaneng, *Tinley sub PRE 51262* (PRE).

MOÇAMBIQUE. About 17 km from Mágoè toward Mágoè Velho, *Tôrre & Correia 18156* (LISC); 17 km from Zimbabwe border in Mazoe R. area, *Wild 2584* (SRGH); about 6 km from Changara, *Tôrre & Correia 18709* (LISC).

NAMIBIA. Near Ombepera, *Gibson 219* (WIND); Omupanda, *Rautanen* (Z); Ondangua, *Smuts & Pole Evans 2238* (PRE); Olukonda, *Rautanen 164* (Z); Impalela Island, *Pienaar 201a* (PRE); 6 km NE of Opuwo, *Kolberg et al. 771* (WIND); Kaoko Otavi, *Owen-Smith 128* (WIND); 7 km S of Okaruwizu, *Giess & Wiss 3310* (M, PRE, WIND); Andara Mission Stn., *de Winter & Wiss 4430* (M, PRE, WIND); Popa Falls, *Maggs 632* (WIND); Halali, *Giess 15309* (WIND); Tsumeb, *Nägelsbach 18D* (PRE); Heidelberg, *Walter 563* (WIND); 10 km N of Tsumeb, *v. Jaarsveld 3093* (NBG); 7 km SW Tsumeb, *Hardy 2122* (PRE, WIND); Ombanje, *Schinz 5* (K), *Schinz 146* (Z); Huisib Mtn., *Hilbert 31* (WIND); Strijdfontein, *Dinter 684* (SAM); Grootfontein, *Schoenfelder 5203* (PRE); *Wettstein 280* (M).

TANZANIA. E of Kakesyo, *Greenway 9056* (EA, PRE); S of Kakesyo, *Greenway 9057* (EA, PRE); N end of Lake Eyassi, *Bally 11626* (K); Lake Kitangiri, *Richards 13490* (K); Mkalama, *Burtt 293* (K); 12 miles from Singida to Itigi, *Richards 20004* (K); hills SW of Kondoa, *Burtt 1454* (K); near Dodoma, *Rigby 73* (EA); Chipogolo, *Johannson 1140* (K); Mpwapwa, *Hornby 2144* (EA); Utengule-usangu, *Leedal 2355* (EA); Noubardad, *Newbold 6307* (EA); Lake Eyasi, *Bally 10617* (EA); Badugu, Nasso, Mwanza, *Tanner 1085* (K); E of Lake Eyassi, near Mongala, *Verdcourt 4014A* (K); Magungila, Singida distr., *Burtt 1520* (K); Mtera Dam, *Bruyns 9613* (PRE); S of Mpapwa, *Bruyns 9646* (NBG); S of Gulwe, *Bruyns 9651* (E).

ZAMBIA. Luangwa Valley, *Astle 5149* (SRGH), *Trapnell 1877* (EA); Bombwe Forest Office, *Bombwe 318/32* (EA); Bombwe, *Martin 318* (K); Nkoata Isl., Mkupa, *Bullock 1186* (K); Gwembe Valley, Mazubuka distr., *Bainbridge 139/55* (K); Sinazongwe, *Bruyns 9586* (E); Monza, *Bruyns 9593* (MO).

ZIMBABWE. Chirundu, *Wild 4852* (PRE, SRGH); just S of Zambesi R. on Mazabuka–Harare rd., *Levy sub PRE 36784* (PRE); Mensa Pan, 18 km ESE of Chirundu Bridge, *Drummond 5363* (PRE, SRGH); Copper Queen purchase area, *Bingham 872* (SRGH); 35 km N of Gokwe, *Goldsmith*

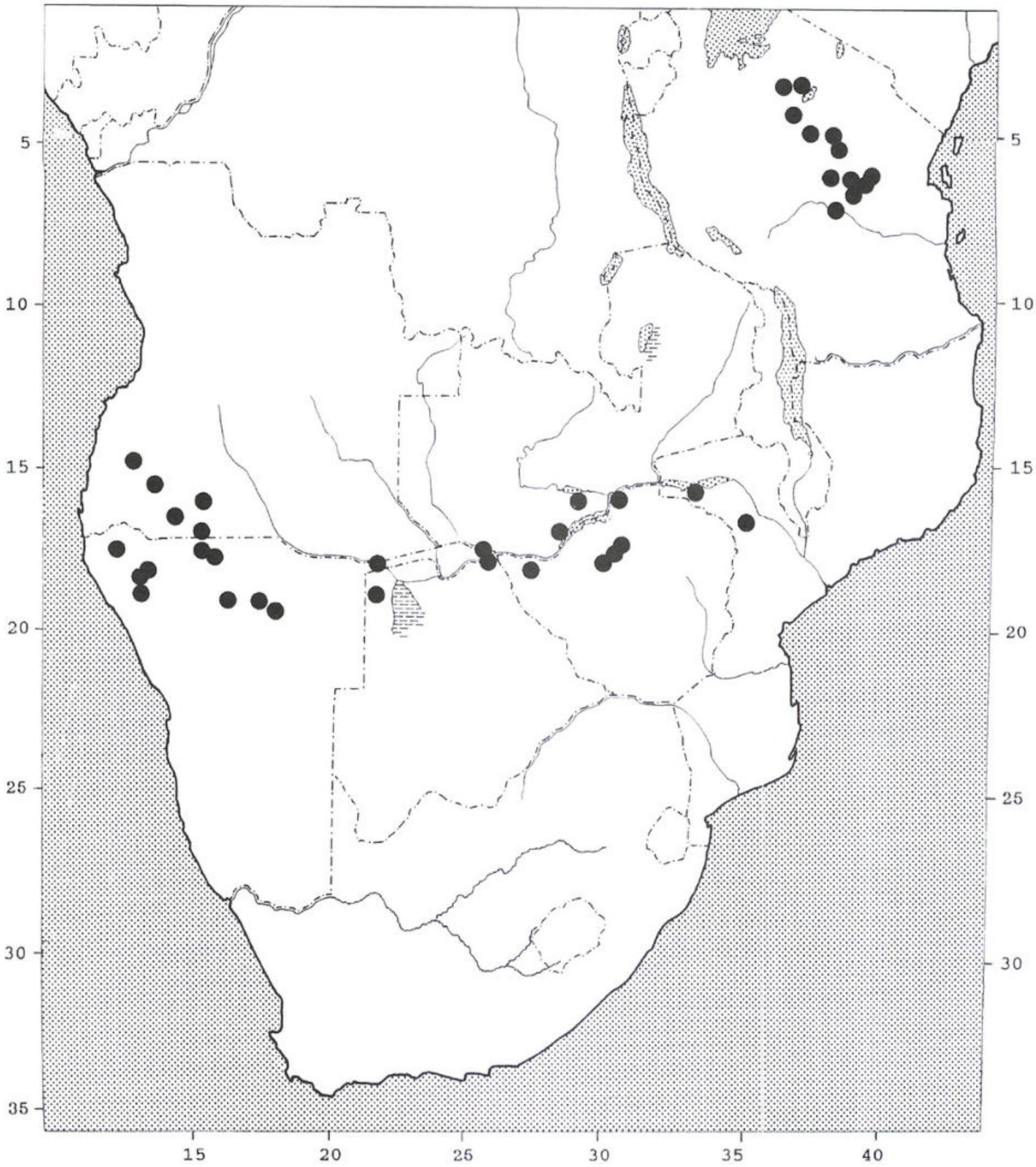

Figure 9. Map of central and southern Africa, showing distribution of *Fockea multiflora*.

21097 (SRGH); Wankie, *Levy 1123* (SRGH); betw. Sesami R. and Gokwe, *West 2998* (SRGH).

6. Fockea sinuata (E. Mey.) Druce, Bot. Soc. Exch. Club Brit. Isles: 623. 1917. Basionym: *Brachystelma sinuatum* E. Mey., Comm. Pl. Afr. Austr.: 196. 1838. TYPE: South Africa. Cape, Brakvallei, betw. Kat River & Swart River, 3500′, 15 Jan. 1827, *J. F. Drège 3439B* (lectotype, designated here, P!; duplicate, K!). Figure 10.

Fockea undulata N. E. Br., Bull. Misc. Inform. 1895: 260. 1895. TYPE: South Africa. Cape "Transvaal", Rhenosterkop, *J. Burke* (holotype, K!).

Small geophytic herb with underground napiform tuber to 30 × 10 cm with central growth point on upper surface from which slender perennial and aerial stems arise, stems erect to weakly twining to 45 cm, softer upper parts deciduous, young growth tomentose. *Leaves* sessile, brown- to gray-green, linear, 25–65 × 2–4 mm, obtuse, upper surface darker and adpressed-

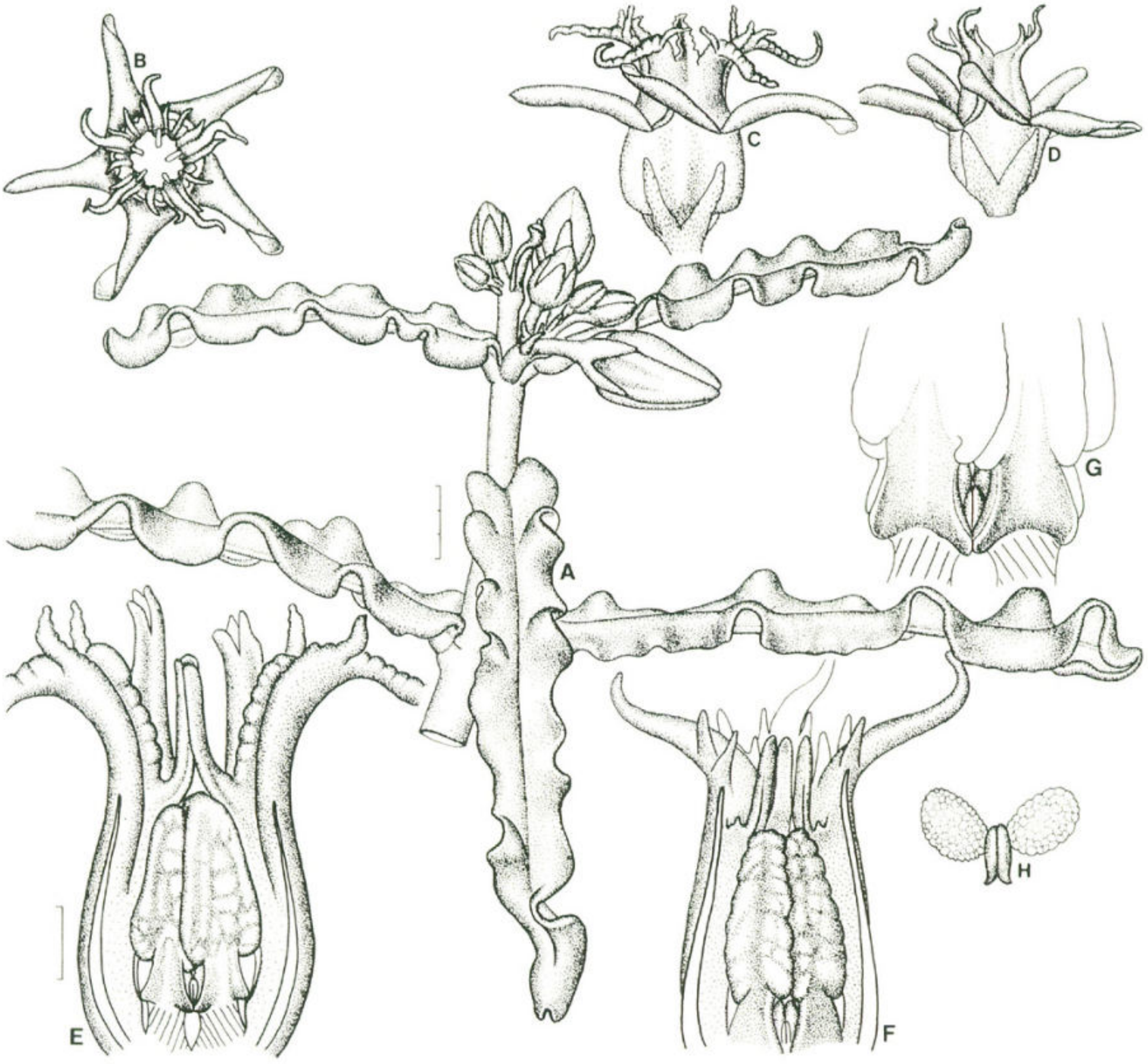

Figure 10. *Fockea sinuata*. —A. Tip of flowering branch. —B. Face view of flower. —C, D. Side view of flower. —E, F. Side view of dissected gynostegium. —G. Side view of anthers. —H. Pollinarium. Drawn from: A, B, D, H, *Bruyns 3023* (NBG); F, *Bruyns 1269* (BOL); C, E, G, *Bayer 939* (NBG). Scales: A = 3 mm; B–D = 2 mm (at A); E, F = 1 mm (at E); G = 0.5 mm (at E); H = 0.25 mm (at E).

pubescent, lower surface pubescent mainly on midrib, margins strongly undulate and revolute. *Inflorescence* 1- to 10-flowered, flowers opening in succession, covered with fine adpressed hairs; *peduncle* ca. 1 × 1 mm; *pedicels* 1–3 × 1 mm. *Sepals* 2 × 1 mm, lanceolate, outside pubescent, inside glabrous; *corolla* 8–12 mm diam.; outside grayish green, sparsely pubescent; inside green to brown, sparsely pubescent: *tube* 1.5–2.5 mm deep, ca. 3 mm broad at mouth, cupular; *lobes* 3–4.5 × 2 mm, linear, obtuse, spreading, often twisted to left when viewed along length, with margins strongly reflexed; *corona* white, glabrous; *outer corona* forming tube 4–6 mm long, becoming slightly narrower above anthers, divided at mouth of tube into 5 longer slender terete (often wrinkled) and strongly spreading lobules 2–2.5 mm long each flanked by 2 flattened erect lobules, these groups of 3 lobes alternating with 5 linear to truncate-emarginate usually erect lobules; *inner corona* of 5 terete linear lobes adpressed to backs of anthers then rising in erect column above them. *Follicles* 50–80 × 10–12 mm, gray-green, often warty; *seeds* 8–10 × 4–6 mm, yellow-brown, with hairs around margin.

Phenology. Flowering October to May.

Distribution. Namibia, South Africa; 500–1200 m (Fig. 11).

Fockea sinuata has a very scattered (and almost certainly not well-documented) distribution over the karroid parts of southern Africa from near Maltahöhe in Namibia to the Free State in South Africa and the southern portions of the Eastern Cape.

Ecology. *Fockea sinuata* is always found in open, flat, often pan-like areas and usually in loamy, slightly

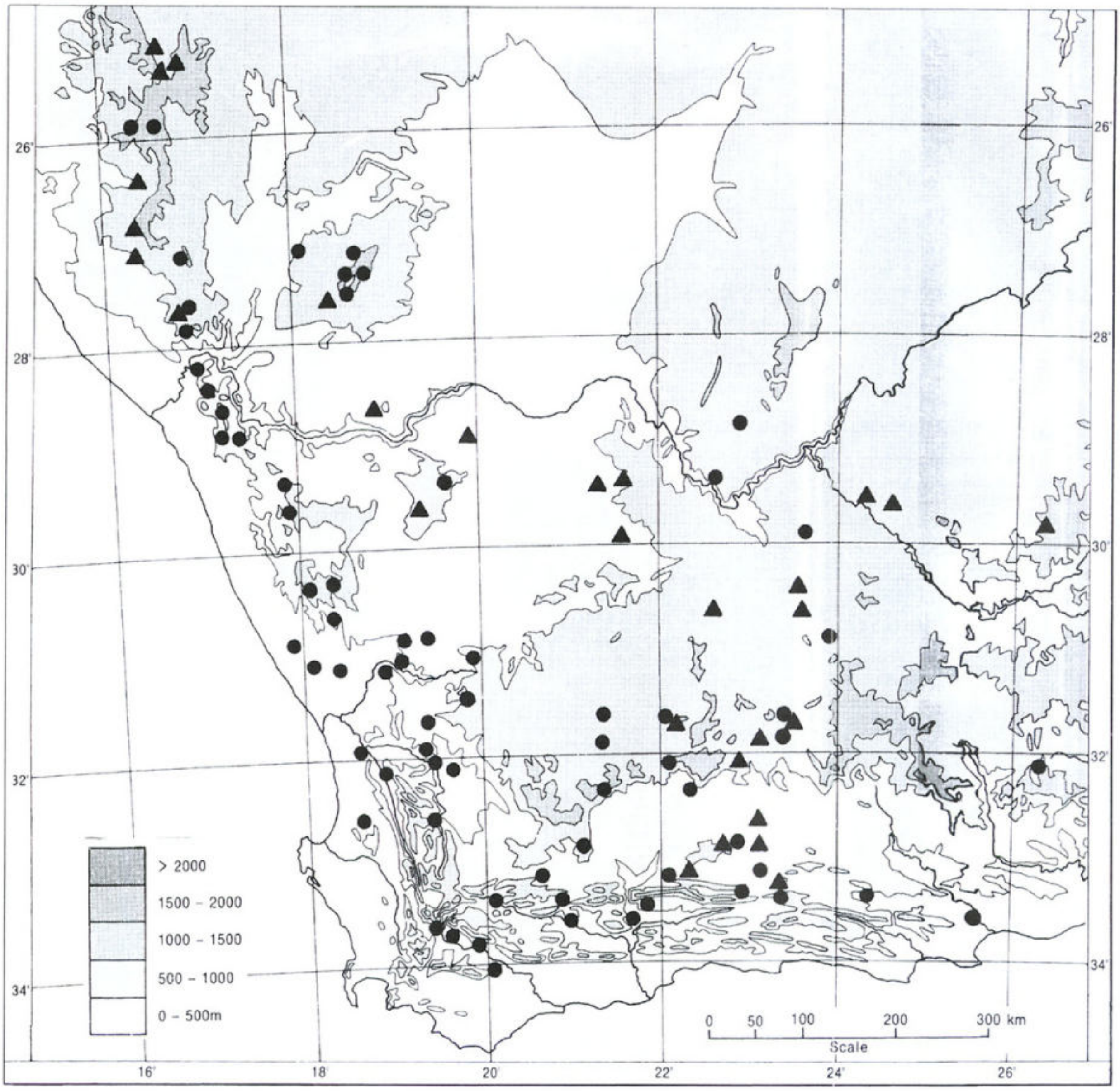

Figure 11. Map of the southwestern part of southern Africa, showing distribution of *Fockea comaru* (circles) and *Fockea sinuata* (triangles).

calcareous ground. Specimens occasionally grow among shrubs of *Rhigozum trichotomum* Burch. but more usually occur with various species of *Salsola* L. and *Zygophyllum* L. in areas of quite low diversity.

Discussion. Meyer (1838: 196) cited two specimens collected by Drège, one from "Dwyka" and the other from "Brakvalei," both without numbers. Only one, *Drège 3439B*, from Brakvallei has been located. Here we assume this to have been seen by Meyer, and it is selected as a lectotype.

In *Fockea sinuata* the plant mostly consists of only a very small erect stem 6–10 cm tall, but very occasionally the stems may twine on the lower branches of a nearby shrub. The narrow leaves have strongly undulate margins and are usually brown-green. Both of these features serve to make them exceedingly inconspicuous and lend them a strong resemblance to the stems of some of the other plants with which they grow. The leaves and some of the above-ground parts die off during the dry season. The pendulous follicles dangle down onto the ground and, in contrast to the rest of the plant, are comparatively conspicuous. In fact, the follicle may often be all that one sees of the plant, especially if the leaves are small and are not well developed.

With its mostly erect and non-twining growth and narrow leaves, *Fockea sinuata* somewhat resembles *F. comaru*. The two species never grow together, though, for *F. comaru* does not occur in low-lying places in the areas where *F. sinuata* occurs. The leaves of *F. sinuata* always have strongly undulate margins, and this is usually enough to distinguish them. Florally they are mostly easily recognizable. In *F. sinuata* the corolla is always small, with short and twisted lobes and a comparatively large and conspicuous white corona. In some flowers the corona lobes have a pustulate inner surface, but that has not proved to be constant (Fig. 10). The pollinarium is also distinctive, with fairly swollen pollinia and a larger and darker corpuscle than in the others. The pollinium is always rather flat in *F. comaru*, and the corpuscle is also particularly slender (compare Figs. 8G and 10H).

Perhaps one of the most unusual features of *Fockea sinuata* is the fact that each seed has a row of hairs all the way around the margin (Bayer, 1976). This is a rare phenomenon that is otherwise only known in *Raphionacme namibiana* Venter & Verhoeven (Bruyns, 1994). The seedling of *F. sinuata* is also unique for its comparatively long and fleshy hypocotyl, which has always been observed to have a distinctly warty surface around the middle (Fig. 4A).

Over its extremely wide distribution within South Africa, this species is generally well known where it occurs. The tubers are often excavated and eaten, and it is locally usually known as *vlak-kambroo*.

Specimens examined. NAMIBIA. 6 km NE of Nuwerus, *Bruyns 5667* (BOL); Rooiberg Suid, *Bruyns 5670* (MO, WIND); Happy Days, *Mostert* (WIND); 62 km S of Helmeringhausen, *Mueller 58* (PRU); Kubub, *Giess et al. 5300* (M, PRE, WIND); betw. Aus and Rosh Pinah, *Mannheimer 860* (WIND); Sebrafontein, *Bruyns 3914* (BOL); Grabwasser, *Bruyns 3641* (BOL, WIND); Vrede, *Bruyns 8154* (WIND).

SOUTH AFRICA. 16 km NE of Bladgrond, *Acocks 14264* (PRE); Middeldeurvlei, *Louw* (NBG); Steenkop, *Bruyns 3459* (BOL); 30 km ENE Kenhardt, *Leistner 2325* (KMG, PRE); Diemansput-Suid, *Bruyns 3444* (BOL); Ramah, *Bayer 939* (NBG); Bulberg, *Bruyns 5421* (PRE); 25 km N of Britstown, *Bruyns 6396* (BOL); Britstown commonage, *Bruyns 3023* (NBG); Boesmansberg, Juriesfontein, *Bruyns 6689* (BOL); Bulthouersfontein, *Bruyns 5404* (BOL); 16 km N of Three Sisters, *Bruyns 5106* (BOL); Schoppelmaaikraal, *Bruyns 1269* (BOL); Renosterkop, *Burke* (K); Prutkraal, *Bayer 328* (NBG), *Snyman* (NBG); Rooidam, *Bruyns 2950* (BOL); Rietbron, *Bruyns 3133* (NBG); Tierberg, *Bruyns 3695* (BOL), *Marloth 4494* (PRE); Willowmore, *Brauns sub STE 19941* (NBG); Palmietfontein, *Smith 5344* (PRE); Rosemaryn, *Henrici 3659* (PRE).

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APPENDIX 1

THE 13 MORPHOLOGICAL CHARACTERS AND THEIR CODING AS USED IN THE ANALYSES (SEE TABLE 2 FOR ASSIGNMENT OF CHARACTER STATES TO SPECIES)

Rootstock

1. Plants without tuber = 0; with tuber = 1.
2. Upper surface of tuber flush with surface of ground = 0; well below surface of ground = 1.
3. Upper surface of tuber without warts = 0; warty = 1.

The rootstock in all species of *Fockea* other than *F. multiflora* consists of a swollen, fleshy, edible, roughly turnip-shaped stem-tuber that either projects slightly from the ground (in *F. capensis* and *F. edulis*) or is well below the surface (in *F. angustifolia*, *F. comaru*, and *F. sinuata*). The upper surface of this tuber is distinctly warty in *F. capensis* and *F. edulis* and is smooth in the others.

Stems

4. Sap milky = 0; sap clear = 1.

Leaves

5. Leaves frequently narrowly linear = 0; never linear = 1.
6. Margins of leaves strongly undulating = 0; not undulating = 1.

Very narrowly linear leaves are characteristic of *Fockea comaru* and *F. sinuata* and are also prevalent in *F. angustifolia*, where, however, they are extremely variable. The margins of the leaves are very strongly undulate in *F. sinuata* and *F. capensis*, and they are strongly revolute in *F. comaru*.

Gynostegium

7. Corolline corona absent = 0; present = 1.
8. Gynostegial corona absent = 0; present = 1.
9. Gynostegial corona of one series of lobes behind anthers only = 0; with two series of lobes = 1.
10. Outer series of gynostegial corona fused into tube = 0; not forming tube = 1.
11. Lobes of inner series of gynostegial corona long, slender, and much exceeding anthers = 0; not exceeding anthers = 1.
12. Anthers with swollen appendages filling up tube of corona = 0; without swollen appendages = 1.

Pollinarium

13. Pollinarium without caudicles = 0; with caudicles = 1.

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