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REVISION OF THE DISJUNCT GENUS *CAMPYLANTHUS* (*SCROPHULARIACEAE*)

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The genus *Campylanthus* (*Scrophulariaceae*) is revised and 15 species are recognized. The genus shows a markedly disjunct pattern of distribution, with two species in Macaronesia, 12 in northeastern Africa and Arabia, and one in western Pakistan. With few exceptions all have very restricted distributions. The position of the genus within the *Scrophulariaceae* is discussed, and it is concluded that *Campylanthus* is best placed as *incertae sedis*. Morphological aspects of the genus are discussed and a cladistic analysis including all species is presented. The analysis indicates a basal split between western and eastern species in the genus. A key, descriptions and distribution maps for all species are provided, and some lectotypes and neotypes are selected.

Keywords. Biogeography, *Campylanthus*, disjunction, generic position, morphology, phylogeny, revision, *Scrophulariaceae*, taxonomy.

Introduction

Campylanthus Roth is a small genus of shrubs and subshrubs. It shows a markedly disjunct pattern of distribution, with two species in Macaronesia, 12 in northeastern Africa and Arabia, and one in western Pakistan.

The circumscription of the genus has remained stable since it was separated from *Eranthemum* L. (*Acanthaceae*) by Roth (1821). Bentham (1846) recognized two species, whereas nine were recognized in the latest complete treatment of the genus (Miller, 1980). Since 1980, four additional species and one variety have been described.

The position of *Campylanthus* within the *Scrophulariaceae* is enigmatic. In the system of Bentham & Hooker (1886) it was placed in the tribe *Digitaleae* of subfamily *Rhinanthoideae*. This treatment was also followed by Wettstein (1891), who made the latest complete treatment of the *Scrophulariaceae*. However, there are no obvious relatives of *Campylanthus* in *Digitaleae* and the proper position of the genus remains uncertain.

The present study aims at a revision of all known species of *Campylanthus* and an improved understanding of its morphology, phylogeny, biogeography, and position within *Scrophulariaceae*.

Historical outline

The first species of *Campylanthus* was discovered by Francis Masson on Tenerife in the Canary Islands in 1778, and described by Linnaeus f. (1782) as *Eranthemum salsoloides* [= *Campylanthus salsoloides* (L.f.) Roth].

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The genus *Campylanthus* was described by Roth (1821) who realized that *Eranthemum salsoloides* differed from all the other species of *Eranthemum* known to him. Roth's generic description is very exact, and he even listed six characters pointing out the differences between *Campylanthus* and *Eranthemum*.

Three additional species of *Campylanthus* were described between 1846 and 1849 (Bentham, 1846; Edgeworth, 1847; Wight, 1849). Among these, *C. junceus* Edgew. from Aden was the first in the genus to be described from the Afro-Arabian region.

A fifth species, *C. spinosus* Balf.f., was discovered by Balfour, Cockburn and Scott during their expedition to Socotra in 1880.

In 1929, the genus *Chamaecanthus* Chiov. with the single species *C. pumilus* Chiov. was described, based on material from northeastern Somalia (Chiovenda, 1929). However, this is simply a redescription of *Campylanthus spinosus* (Miller, 1982). Interestingly, Chiovenda placed his new genus in the *Acanthaceae*, where *Eranthemum* in the present sense also belongs.

The first comprehensive treatment of *Campylanthus* was published by Miller (1980). He recognized nine species, of which four were described as new, *C. incanus* A.G. Mill. from Somalia, *C. yemenensis* A.G. Mill. from Yemen, and *C. chascaniflorus* A.G. Mill. and *C. sedoides* A.G. Mill. from Oman. The plants occurring on the Canary Islands and Cape Verde Islands were treated as a single, variable species under the name *C. salsoloides* (L.f.) Roth.

Since then four additional species have been described: *C. somaliensis* A.G. Mill. and *C. mirandae* A.G. Mill. from Somalia and Oman, respectively (Miller, 1988), *C. antonii* Thulin from the Mahra region in Yemen (Thulin, 1995) and *C. parviflorus* Hjertson & A.G. Mill. from Somalia (Hjertson & Miller, 2000).

The position of *Campylanthus* within the *Scrophulariaceae*

The first attempt to place *Campylanthus* in a system was made by Reichenbach (1828), who regarded it as a member of the tribe *Selagineae* together with, for example, *Globularia* L., *Selago* L. and *Agathelpis* Choisy. The *Selagineae*, in turn, were included in the *Acanthaceae* together with the tribes *Buchnereae* and *Acantheae*. The *Buchnereae* (*sensu* Reichenbach) also included genera such as *Erinus* L. and *Manulea* L.

Lindley (1836) published a list provided by Bentham, in which *Campylanthus* was placed in the tribe *Veroniceae* of the *Scrophulariaceae*. It was also placed in *Veroniceae* by Endlicher (1839).

Webb (1845) described the monotypic subtribe *Campylanthinae* (as "*Campylantheae*") of the tribe *Salpiglossideae*, which was at that time included in the *Scrophulariaceae* (Bentham, 1835, 1846). In his first account Webb did not indicate whether this was a subtribe or a tribe, but later the same year the rank was explicitly stated to be that of subtribe (Webb & Berthelot, 1845). It was subsequently raised to tribal rank in Spicilegia Gorgonea (Webb, 1849). Bentham (1846) placed *Campylanthus* together with *Hydrotriche* Zucc. initially in the tribe *Gerardieae*, noting that both were anomalous. *Hydrotriche* is considered to belong to the tribe *Gratioleae* (Bentham & Hooker, 1886; Wettstein, 1891).

In *Genera plantarum* (Bentham & Hooker, 1886) *Campylanthus* was finally placed in the tribe *Digitaleae*, following *Erinus*, with a note that it was without any close affinities, but seemed much better placed in the *Digitaleae* than in the *Gerardieae*. Wettstein (1891) also placed *Campylanthus* in the tribe *Digitaleae*, but between *Calorhabdos* Benth. and *Oreosolen* Hook.f., instead of close to *Erinus*.

Hallier (1903) discussed the position of *Campylanthus* in more detail. He admitted that it was so different from other members of the *Digitaleae* that he had considered removing it from that tribe. He stated that judged by habit, inflorescence and flower morphology one could almost take it for a member of the tribe *Manuleae*. However, as there are differences in anther morphology between *Campylanthus* and the *Manuleae*, and as it resembles the genus *Wulfenia* Jacq. in the shape of the corolla, the two stamens, and the shape of the capsule, he concluded that it should remain in the *Digitaleae*. Concerning the seeds in *Campylanthus*, he noted that winged seeds of similar type also occur in *Alectorolophus* Zinn [= *Rhinanthus* L.], *Linaria* Mill., *Veronica* L. and *Aragoa* Kunth.

Thieret (1967) discussed Wettstein's (1891) arrangement of the *Scrophulariaceae*, and a number of tribes were discussed in more detail, with special emphasis on difficult taxa. However, Thieret did not add any new comments regarding the position of *Campylanthus*.

Kooiman (1970) investigated the occurrence of iridoid glycosides in the *Scrophulariaceae*, and found that members of the tribe *Digitaleae* are devoid of aucubin, except for *Erinus* and *Rehmannia* Libosch. ex Fisch. & C.A. Mey. *Campylanthus*, which also contains aucubin, was placed in the tribe *Veroniceae*, where most members were found to contain this substance. However, the presence of aucubin is widespread in the *Scrophulariaceae* and can be found in most tribes. Notable exceptions are the tribes *Calceolarieae* and *Antirrhineae*. A subsequent paper on iridoid glycosides (Hegnauer & Kooiman, 1978) basically confirmed the earlier results of Kooiman (1970), with the exception that *Erinus* was transferred to the tribe *Veroniceae*.

Licht (1983), in a series of papers discussing the development of the root system in the *Veroniceae*, also investigated *Campylanthus*. The root system in *Campylanthus* consists of a primary root with a variable number of lateral roots emerging from it. He also commented on the orange-red colour of the root, which is caused by a substance in the vacuole of the exodermis, according to an unpublished thesis by Albert (1976). Orange roots are also known to occur in *Craterostigma* Hochst. of the tribe *Gratioleae* (Fischer, 1992), but here the coloured substance is found in the intracellular spaces and not in the vacuole. According to Licht's investigation, the root system, including the orange-red colour, and the seedling in *Campylanthus* are completely different from other members of the *Veroniceae*, and he doubted the placement of *Campylanthus* in this tribe.

Bigazzi (1993), in a study of intranuclear inclusions in the *Scrophulariaceae*, reported lamellar inclusions in *Campylanthus* as opposed to the amorphous inclusions found in other *Veroniceae* (including *Erinus*). According to Bigazzi *Campylanthus* should be removed from the tribe *Veroniceae* to a tribe where lamellar inclusions are present, i.e. *Gratioleae*, *Verbasceae*, *Scrophularieae*, *Manuleae*, *Calceolarieae*, *Hemimerideae*, *Rhinantheae*, or *Gerardieae*, but he did not make any more precise suggestion on where to place it. The *Verbasceae* are polymorphic with regard to the presence of lamellar inclusions, as most taxa lack them or have amorphous inclusions. The presence of lamellar inclusions in the *Digitaleae* is restricted to *Rehmannia*, a genus which also has a different alkaloid content from *Digitalis* and *Isoplexis* (Kooiman, 1970; Hegnauer & Kooiman, 1978).

Miller (1980), in his revision of the genus, stated that the inclusion of *Campylanthus* in the heterogeneous tribe *Digitaleae* does not shed any light on the affinities of the genus, and that it remains an anomaly without any apparent close relatives in the family.

Molecular studies on the *Scrophulariaceae* have been performed by, for example, Olmstead & Reeves (1995), and when more taxa are added to the analyses, the patterns will hopefully get clearer. Molecular phylogenies may be very useful for the re-interpretation of characters, or simply for widening our minds that might have been too biased towards old classifications. In the case of *Scrophulariaceae*, I am convinced that future studies will lead to a complete re-evaluation of the family, at both tribal and family level, as the results of Olmstead & Reeves (1995) already imply. Results from an analysis of *ndh*F sequences of *Campylanthus* and a limited sample of other members of *Scrophulariaceae* and related families indicate a position for *Campylanthus* near *Digitalis* (Hjertson, 1997). The proper position is likely to be solved only when further DNA analyses with a much wider sampling have been made. As a consequence, I now consider *Campylanthus* as best placed in the *Scrophulariaceae* as *incertae sedis*, pending further research.

Morphology

Habit

Most species of *Campylanthus* are shrubs or dwarf shrubs, with more or less obvious xerophytic adaptations. These adaptations, as well as other characters, are discussed below.

Stems

Spine-tipped stems are a feature found, to various degrees, in *C. anisotrichus* (A.G. Mill.) Hjertson & A.G. Mill., *C. incanus*, *C. mirandae*, *C. parviflorus*, *C. pungens*, *C. ramosissimus* Wight, *C. spinosus* Balf.f. and *C. yemenensis*. The spines are most distinctly developed in *C. spinosus*, where they show no leaf traces, whereas in the other species, leaf traces can be found almost to the tips of the spines.

In some species, notably *C. antonii*, *C. junceus*, *C. pungens*, *C. ramosissimus* and

C. yemenensis, the stomata of the stems are distinctly sunken. The depressions may be shallow to deep, and the surface of the depression is covered by a granular layer that most likely consists of wax. This character is best developed in *C. pungens* (Fig. 1), where it can be seen at very low magnification. It appears that the stems play an important role in the photosynthesis of these taxa, and the leaves are usually few and very small.

Indumentum

The indumentum of the stems and leaves usually consists of eglandular, more or less erect, uniseriate hairs, which can be long and narrow to short and thick. A very different indumentum is found in *C. anisotrichus*, *C. incanus*, *C. parviflorus* and *C. spinosus*, which have appressed parallel hairs. In *C. anisotrichus*, *C. incanus* and *C. parviflorus* the hairs bifurcate, with two arms of equal length in *C. incanus*, and with one arm distinctly shorter in *C. anisotrichus* and *C. parviflorus* (Hjertson & Miller, 2000). Hairs with a distinctly swollen base are found in *C. antonii*, *C. junceus*, *C. pungens*, *C. ramosissimus* and *C. yemenensis*, a feature not found in other species of *Campylanthus*. One species, *C. somaliensis*, has an indumentum consisting of glandular hairs.

The outer surface of the corolla is usually completely glabrous, but in *C. salsoloides*, *C. sedoides* and *C. yemenensis* it is hairy. The indumentum on the inner surface of the corolla tube consists of antrorse, unicellular hairs above the insertion of the stamens and retrorse, unicellular hairs below the insertion of the stamens. Hairs below the insertion of the stamens are absent in *C. anisotrichus*, *C. incanus*, *C. parviflorus* and *C. spinosus*.

The hairs on the inside of the calyx are glandular, a condition known in other genera of the *Scrophulariaceae*, for example *Camptoloma* Benth. (Hilliard, 1994) and *Lindenbergia* Lehm. *pro parte* (Hjertson, 1997). The outer surface of the calyx may be hairy or glabrous, but there are always at least some hairs on the margins of the calyx lobes.

Flowers

The flowers are arranged in terminal racemes that can be few- or many-flowered. The flowers are very shortly to distinctly pedicellate and are subtended by a bract and two basal bracteoles.

Calyx

The calyx is always 5-lobed with free lobes. This condition is common throughout the *Scrophulariaceae* and is found, for example, in *Erinus* (Hartl, 1974), *Stemodia* L. (Minod, 1918) and *Verbascum* L. (Hartl, 1974), and in many taxa of the tribes *Antirrhineae* (Sutton, 1988) and *Manuleae* (Hilliard, 1994).

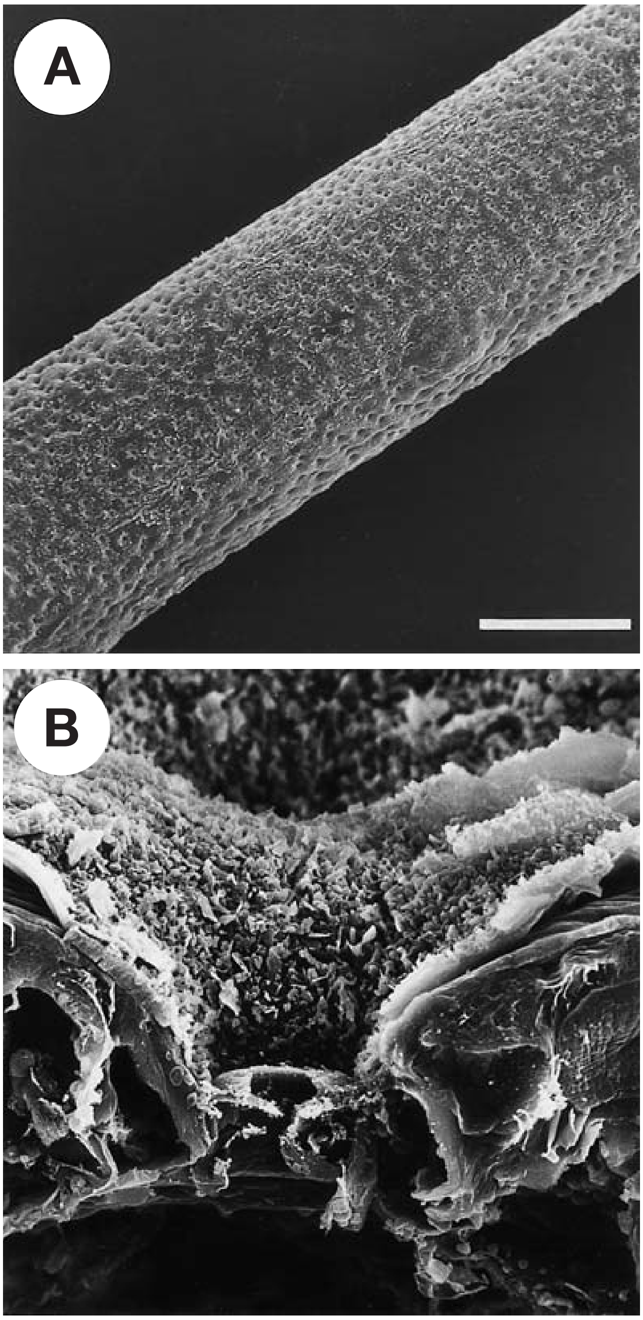

FIG. 1. SEM micrographs of sunken stomata in *Campylanthus pungens* (*Podzorski* 1188, E). Scale bar applies to A & B. A. Stem; bar = 0.5mm. B. Cross-section of stoma; bar = 12µm.

Corolla

The corolla is more or less actinomorphic with a conspicuous cylindrical tube having two geniculations where the stamens are inserted. This is one of the diagnostic characters of the genus. Geniculated corolla tubes are also known in, for example, *Jamesbrittenia* Kuntze, *Lyperia* Benth. and *Manulea* L. of the tribe *Manuleae* (Hilliard, 1994). The colour varies from white to purple and in, for example, *C. incanus* and *C. junceus*, the throat is distinctly yellow. A peculiar flower colour is found in *C. antonii*, *C. chascaniflorus* and *C. sedoides*, in which the flowers are pinkish-brown to brownish.

No obvious pollinators were observed during the field work in Yemen and no reports of pollinators have been found in the literature. However, the generally long-tubed flowers with a regular limb strongly suggest butterflies as pollinators (cf. Hilliard, 1994: 56). There is no indication that the flowers of any species are nocturnal.

Androecium

The two, very short stamens are free from each other and included in the corolla. They are borne on the corolla tube at the upper geniculation. There are no staminodes present. The anther thecae are divaricate and completely fused with a slight, central constriction.

Pollen

Two species were investigated, *C. salsoloides* (L.f.) Roth and *C. spinosus*. The pollen grains are tricolporate, prolate in shape, with a 20–23μm long polar axis and an equatorial diameter of 13–14μm, and the surface is reticulate (Fig. 2). Only minor differences were observed between the two species. This pollen type is one of the two most common types within the *Scrophulariaceae* (Minkin & Esbaugh, 1989), and it has been observed in, for example, *Lindenbergia* (Hjertson, 1996), *Antirrhinum* L. in the *Antirrhineae* (Elisens, 1986), *Zaluzianskya* F.W. Schmidt in the *Manuleae* (Argue, 1993), and *Digitalis* L. in the *Digitaleae* (Minkin & Esbaugh, 1989).

Gynoecium

The ovary is ovoid, more or less laterally compressed, and glabrous. The style is filiform and the transition from the ovary to the style may be abrupt or gradual. The stigma is capitate and oblique, and is positioned at or slightly below the anthers. In a few species, *C. chascaniflorus*, *C. sedoides* and *C. somaliensis*, the sterile, apical part of the style is distinctly bifid, whereas it is entire in all other species. The capsules are ovoid to orbicular, distinctly compressed, and dehisce septicidally.

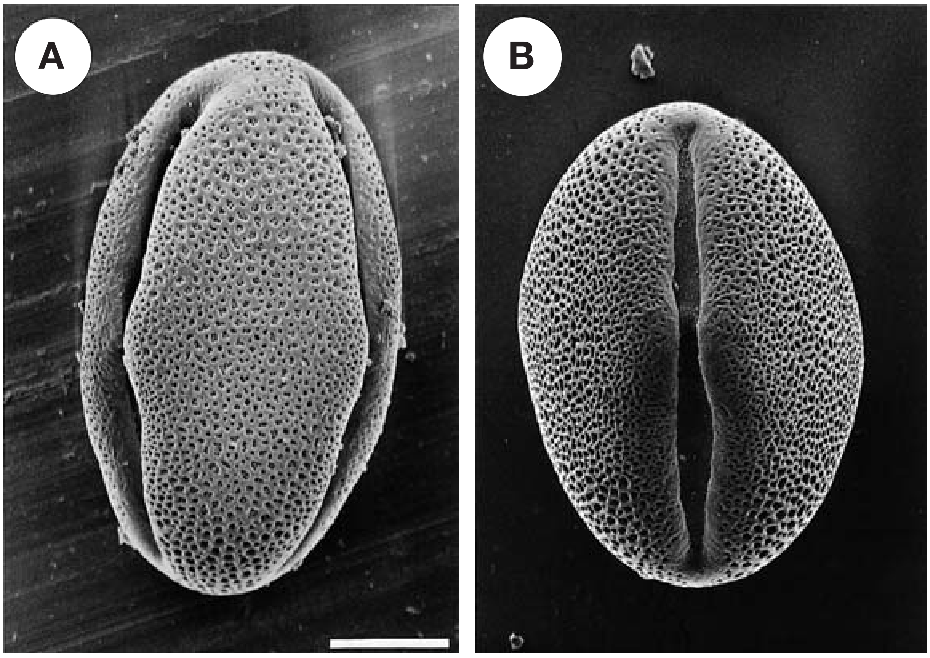

FIG. 2. SEM micrographs of *Campylanthus* pollen. Scale bar = 5µm and applies to A & B. A. *C. salsoloides* (*Davies* 67328, E). B. *C. spinosus* (*Smith* & *Lavranos* 366, K).

Seeds

The seeds are discoid in shape and around 1mm in diameter, excluding the commonly present, more or less hyaline wing around the margin. In some species the wing is restricted to the funicular region only (Fig. 3).

Chromosome numbers

Chromosome counts of *C. glaber* (Bramwell & Murray, 1972; Gomes *et al.*, 1995) and of *C. salsoloides* (Larsen, 1960; Borgen, 1970) have been published, where $2n = 14$ was found. None of the Afro-Arabian species has been investigated cytologically.

CLADISTIC ANALYSIS

Sampling and outgroup selection

The characters used are shown in Table 1, and a data matrix of the characters is given in Table 2. In this analysis *Agathelpis angustifolia* Choisy, *Anticharis glandulosa* Aschers., *Camptoloma lyperiiflorum* (Vatke) Hilliard, *Jamesbrittenia maxii* (Hiern) Hilliard, *Erinus alpinus* L. and *Freylinia tropica* S. Moore were used as outgroups. Since there are no obvious close relatives of *Campylanthus*, an approach with several,

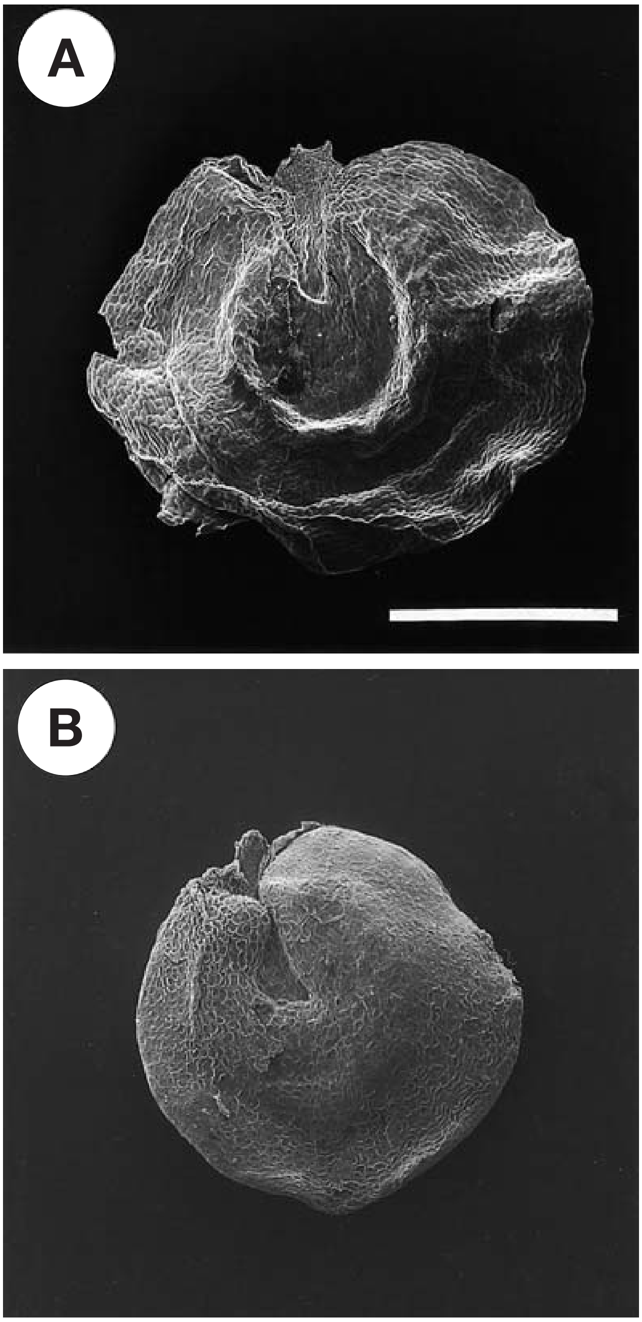

FIG. 3. SEM micrographs of *Campylanthus* seeds. Scale bar = 1mm and applies to A & B. A. *C. pungens* (*Miller* & *Nyberg* 9202, E). B. *C. somaliensis* (*Thulin* & *Warfa* 5560, UPS). Note that hyaline wing appears opaque in SEM micrographs.

TABLE 1. Characters and character states used in the cladistic analysis of *Campylanthus*

1. Plants somewhat branched or branched from below only (0); much branched (1).
2. Branches not spinescent (0); spinescent (1).
3. Sunken stomata on stems absent (0); present (1).
4. Leaves opposite (0); alternate (1).
5. Persistent leaf bases absent (0); present (1).
6. Leaves serrate to dentate (0); entire (1).
7. Glandular hairs on vegetative parts absent (0); present (1).
8. Bifurcating hairs absent (0); present, isotrichous (1); present, anisotrichous (2).
9. Hairs on vegetative parts erect (0); appressed and parallel (1).
10. Base of hairs not swollen (0); swollen (1).
11. Inflorescence frondose (0); bracteate (1).
12. Inflorescence more than 5-flowered (0); up to 3-flowered (1).
13. Bracteoles absent (0); present (1).
14. Calyx without glandular hairs inside (0); with glandular hairs inside (1).
15. Calyx lobes hairy outside and on margins (0); hairy on margins only (1); glabrous (2).
16. Corolla outside glabrous (0); pilose (1).
17. Petal venation reticulate (0); dichotomous (1).
18. Corolla tube $\leqslant$10mm long (0); $\geqslant$11mm long (1).
19. Corolla tube hairy below insertion of stamens (0); glabrous (1).
20. Geniculation at insertion of stamens absent (0); present (1).
21. Position of geniculation inside calyx (0); outside calyx (1).
22. Stamens four (0); two (1).
23. Anther thecae confluent with a ± distinct central constriction (0); monothecous (1).
24. Anther thecae parallel (0); divaricate (1).
25. Ovary/style transition gradual (0); abrupt (1).
26. Apical, sterile part of style entire (0); bifid (1).
27. Stigma non-oblique (0); oblique (1).
28. Capsule with septicidal dehiscence (0); loculicidal and septicidal dehiscence (1); indehiscent (2).
29. Capsule not laterally compressed (0); laterally compressed (1).
30. Seeds oblong-elliptic, not winged (0); discoid with entire wing (1); discoid with wing restricted to the funicular region (2).

not necessarily closely related, outgroup taxa has been preferred. The rationale for using single species as representatives of the genera is to avoid variable states as far as possible.

Methods

A maximum parsimony analysis, using all species of *Campylanthus*, was performed using PAUP 3.1.1 (Swofford, 1993). Heuristic search options included: 1000 random addition replicates and tree-bisection-reconnection (TBR) branch swapping, saving all equally parsimonious trees, with all characters equally weighted and unordered (Fitch parsimony; Fitch, 1971). Characters were optimized using ACCTRAN. Clade stability was estimated using Bremer (Bremer, 1988, 1994) and bootstrap support

TABLE 2. Data matrix assembled using the characters in Table 1 for the outgroup and *Campylanthus*. Polymorphic or variable taxa in characters with more than two states are coded with letters in the matrix: a = 0/1, and inapplicable states are coded as ‘i’

	Character number					
		1	11111	11112	22222	22223
Taxon	12345	67890	12345	67890	12345	67890
Agathelpis angustifolia	00011	10000	00002	00010	i1010	00200
Anticharis glandulosa	00010	11000	00100	00010	i1000	00100
Camptoloma lyperiiflorum	00010	01000	00010	00110	i01i0	00000
Erinus alpinus	00010	00000	10000	10010	i0001	00100
Freylinia tropica	00001	00000	10001	00010	i0000	00101
Jamesbrittenia maxii	00000	01000	00000	00111	i01i0	00000
Campylanthus anisotrichus	11010	10210	01110	01011	01011	01012
Campylanthus antonii	00110	10001	00111	01101	11010	01012
Campylanthus chascaniflorus	00010	10000	00110	01101	11011	11011
Campylanthus glaber	00011	10000	1011a	01001	11011	01011
Campylanthus incanus	11010	10110	01110	01011	01011	01012
Campylanthus junceus	00110	10001	00111	01001	11011	01011
Campylanthus mirandae	11110	10001	00110	01001	01011	01011
Campylanthus parviflorus	11010	10210	01110	01011	01011	01012
Campylanthus pungens	11110	10001	00111	01001	11011	01011
Campylanthus ramosissimus	11110	10001	00111	01001	01011	01011
Campylanthus salsoloides	00011	10000	10110	11001	11011	01011
Campylanthus sedoides	00011	10000	01110	11001	01011	11011
Campylanthus somaliensis	00110	11000	00110	01101	11010	11012
Campylanthus spinosus	11010	10010	01110	01011	01011	01012
Campylanthus yemenensis	11110	10001	01110	11001	01010	01012

values (Felsenstein, 1985). Bremer support values were calculated using topological constraints in PAUP. Bootstrap was calculated using 30,000 replicates, each with a single, random additional sequence of the taxa and nearest-neighbour-interchanges (NNI) branch swapping saving a single tree. The mapping of characters onto one of the equally parsimonious trees was done using the ‘show reconstructions’ option in PAUP.

Results

The analysis yielded three equally parsimonious trees, with a length of 64 steps, a retention index of 0.76 and a consistency index of 0.53. The strict consensus tree is presented in Fig. 4, and one of the equally parsimonious trees is presented in Fig. 5.

The results show that the monophyly of *Campylanthus* with its current circumscription is well supported (96% bootstrap value). An unresolved but well-supported clade (90% bootstrap value) consisting of *C. spinosus*, *C. incanus*, *C. anisotrichus*

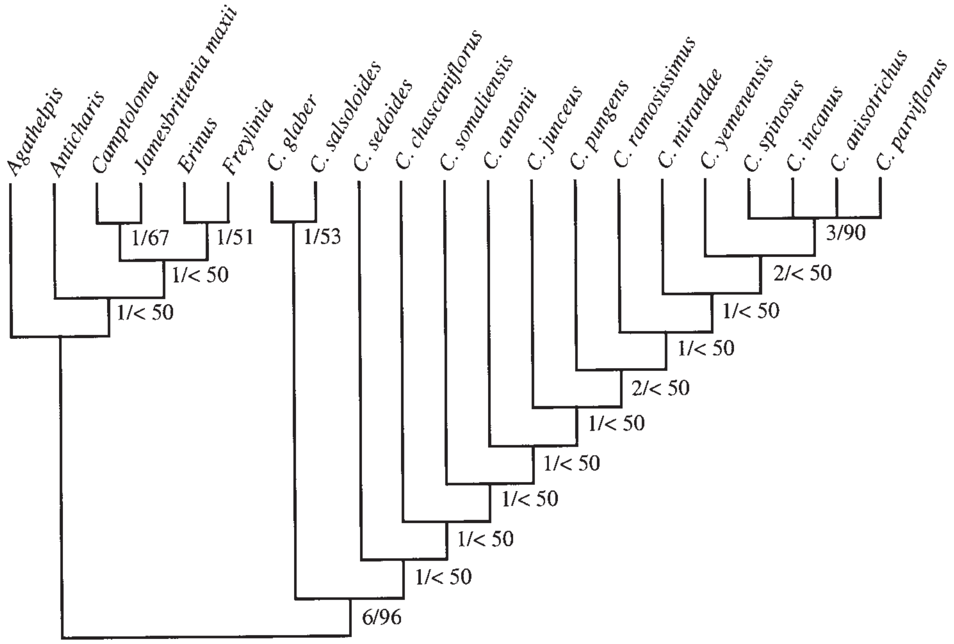

FIG. 4. Strict consensus tree of three most parsimonious trees resulting from the analysis of the morphological data in Table 1. Decay indices followed by bootstrap values are given to the right of each node.

and *C. parviflorus* is found at the top of the tree. The support values for all other nodes in the tree are low, including the basal branch (53% bootstrap value) with *C. glaber* and *C. salsoloides*.

The *Campylanthus* clade is supported by nine characters, three of which are not homoplastic: the dichotomous corolla lobe venation (character 17), the oblique stigmas (character 27) and the laterally compressed capsules (character 29). The clade consisting of *C. glaber* and *C. salsoloides* is supported by character 11 (distinctly bracteate racemes), which also occurs as a parallelism in *Erinus* and *Freylinia*. The clade containing *C. spinosus*, *C. incanus*, *C. anisotrichus* and *C. parviflorus* is supported by three reversals: sunken stomata absent (character 3), base of hairs not swollen (character 10), and corolla tube glabrous below insertion of stamens (character 19); and a unique synapomorphy: indumentum of vegetative parts consisting of parallel, appressed hairs (character 9). For additional notes on characters, see discussion under 'Morphology' above.

Discussion

Since all taxa inhabit dry regions, water economy is obviously a problem. Two different means of reducing evaporation have developed in *Campylanthus*. Sunken

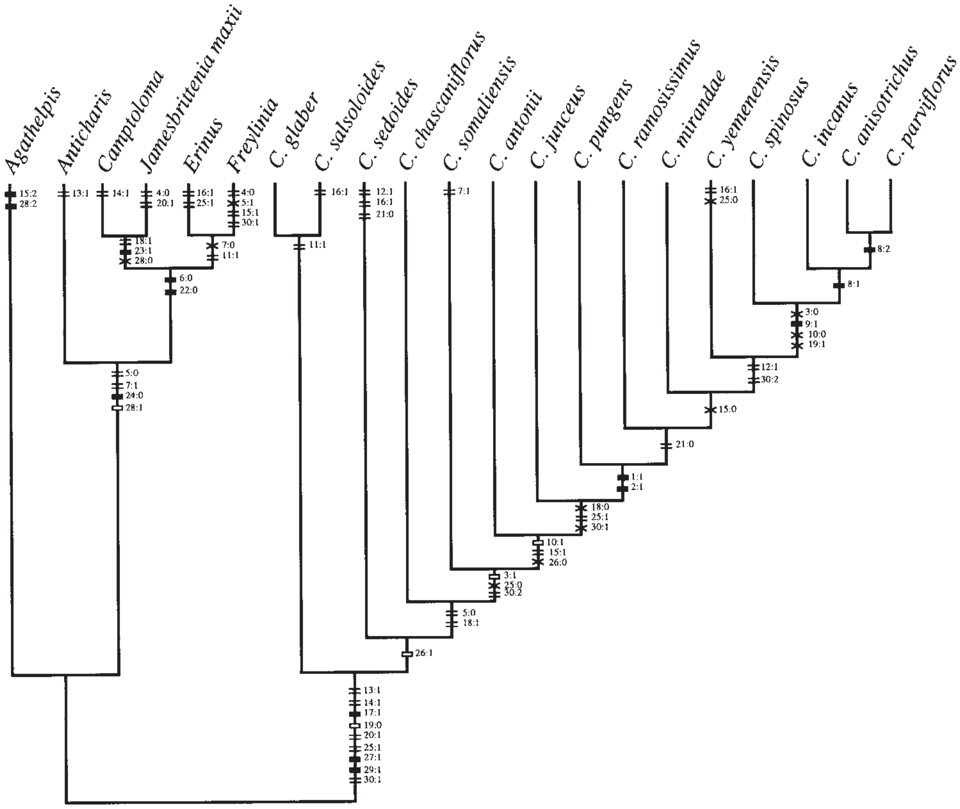

FIG. 5. One of three equally parsimonious trees from the cladistic analysis of *Campylanthus* with the characters optimized on the branches using ACCTRAN optimization. Black boxes indicate unique changes. Homoplasies are given as open boxes with parallel bars representing parallelisms, and crossed bars reversals.

stomata on stems (character 3:1) developed once with a later reversal. Interestingly, the reversal appears in a clade where the vegetative parts are covered in appressed parallel hairs (character 9:1), indicating that hairs have taken over the function of protection against excessive evaporation. The taxa with appressed parallel hairs, *C. spinosus*, *C. incanus*, *C. anisotrichus* and *C. parviflorus*, are all restricted to Somalia, with the exception of *C. spinosus*, which is also found on Socotra and the adjacent island of Abd el Kuri. A much-branched habit (character 1:1) has developed once in *Campylanthus*; this appears to be coupled to the development of spinescent branches (character 2:1).

Corolla evolution in *Campylanthus* is a bit ambiguous. Corolla tubes longer than 11mm (character 18:1) are found only in *C. chascaniflorus* (Oman), *C. somaliensis* (Somalia) and *C. antonii* (Yemen), which are placed in ascending order in the topology. From a biogeographical point of view it seems fairly unlikely that this character has developed only once, with a later reversal; a more likely scenario would be that it has developed independently three times in these taxa.

A complete analysis of *Campylanthus* using molecular data would certainly help to improve the understanding of character evolution in the genus. However, until such a study is performed, and given the fact that the analysis presented above is based solely on morphological characters, one must be very cautious when speculating on character evolution. Also, the fact that the support for most branches is low further weakens such discussion.

BIOGEOGRAPHY

The genus *Campylanthus* is distributed in the Canary Islands, Cape Verde Islands, northeast tropical Africa, southern Arabia and Pakistan, with a centre of diversity in northeast tropical Africa and southern Arabia, where 12 of the 15 species occur.

The known distributions of all species of *Campylanthus* are given in Figs 6–8. Note that one dot may represent more than one collection.

Campylanthus is confined to arid regions, and the species are generally found in rocky, gravelly or sandy places. They can be found at altitudes from sea level up to about 2500m.

The 15 species of *Campylanthus* have been grouped according to their distribution within floristic regions. For the species occurring on the Cape Verde Islands and the Canary Islands I have used the same circumscription of Macaronesia as that used by, for example, Engler (1882), Bramwell (1972), Sunding (1979) and Takhtajan (1986). The African and Arabian species have been arranged according to the regions proposed by White (1983) and the revised circumscription of the Somalia-Masai

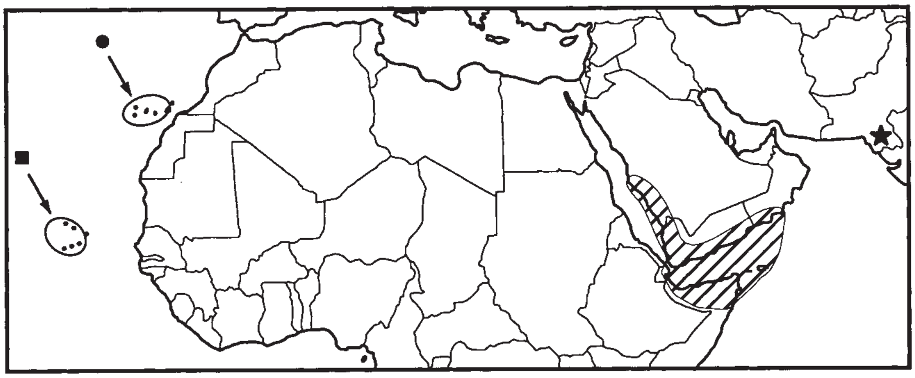

FIG. 6. Map of northern Africa and the Middle East showing total distribution of the genus *Campylanthus*. Hatched area: 12 species presented in more detail in Figs 7–10. *C. glaber* (■), *C. salsoloides* (●), and *C. ramosissimus* (★).

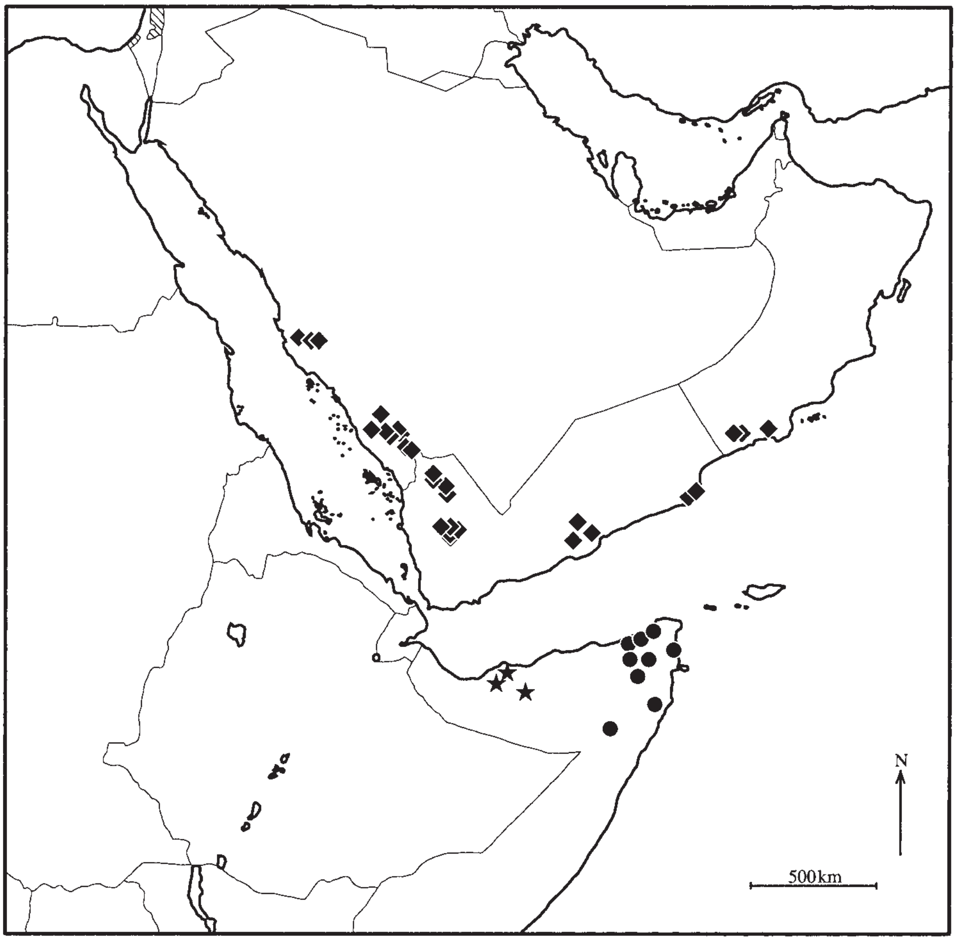

FIG. 7. Map of the Arabian peninsula and NE Africa showing distribution of *C. anisotrichus* (★), *C. incanus* (●), and *C. pungens* (◆).

region of White & Léonard (1991). For the Pakistani species I have used the Saharo-Sindian region as defined by White & Léonard (1991). The species have been divided into the following groups: the Macaronesian group, the Somalia-Masai group, and finally the Saharo-Sindian group.

Macaronesian group

Two species are known from this region, *C. glaber* from the Cape Verde Islands and *C. salsoloides* from the Canary Islands (Fig. 6). These two species are the western outliers of the genus and they show a remarkable disjunction with the rest of the species, which occur in the Horn of Africa region and Pakistan. Similar patterns of

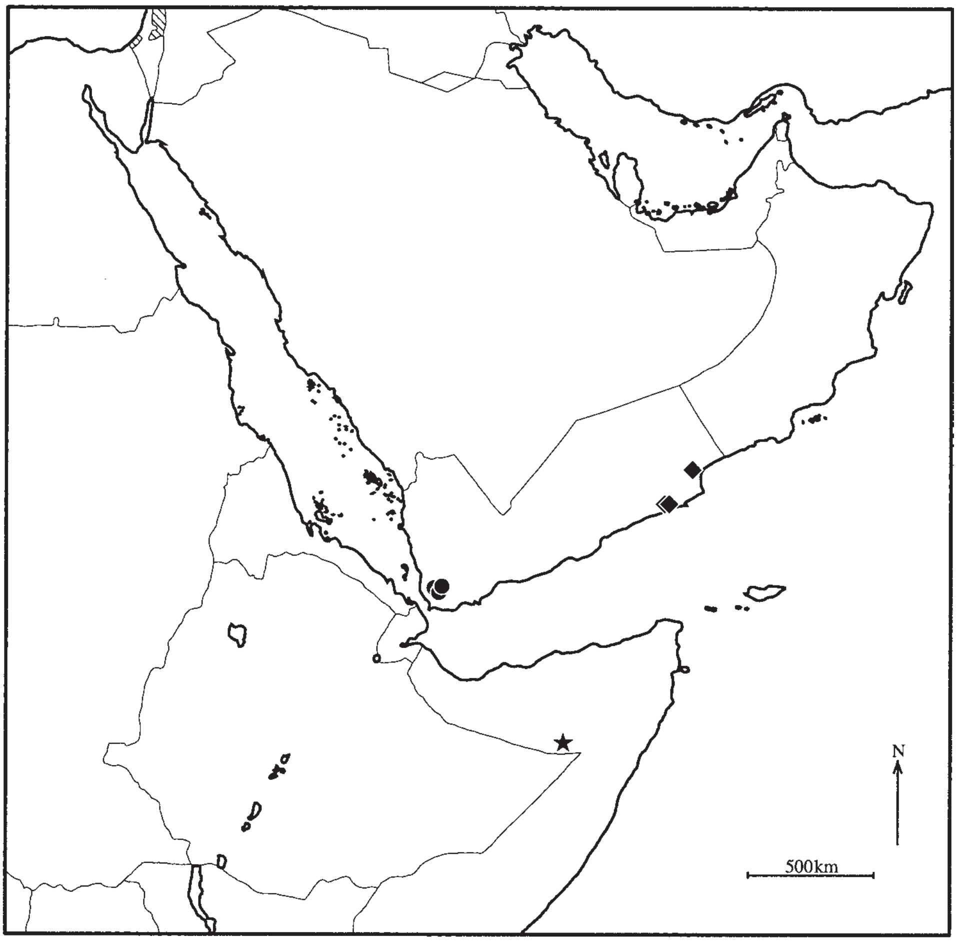

FIG. 8. Map of the Arabian peninsula and NE Africa showing distribution of *C. parviflorus* (★), *C. yemenensis* (●), and *C. antonii* (◆).

distribution are also known in other taxa, for example *Aeonium* Webb & Berthel. (Lems, 1960; Liu, 1989), *Dracaena* Vand. ex L. (Sunding, 1979), *Drusa* DC. (Hedge & Miller, 1977), and *Euphorbia balsamifera* Aiton (Bally, 1965).

The endemic Macaronesian flora is at least partly considered to be a relic of the Tethyan-Tertiary Region (e.g. Meusel, 1953; Bramwell, 1976). It is thus quite logical to argue that some of the disjunct elements in the Horn of Africa region are also relics of the same time, as stated by Thulin (1994). The reason for the disjunctions between the two opposite sides of Africa may be found in the spreading of a drier climate in Africa during the late Miocene (Axelrod, 1975), eliminating populations between these two outposts.

Somalia-Masai group

The vast majority of the species, namely *C. anisotrichus*, *C. antonii*, *C. chascaniflorus*, *C. incanus*, *C. junceus*, *C. mirandae*, *C. parviflorus*, *C. pungens*, *C. sedoides*, *C. somaliensis*, *C. spinosus* and *C. yemenensis*, belong to this region (Figs 7–10), as it was shown by White & Léonard (1991) that southern Arabia and Socotra with adjacent islands are also part of the Somalia-Masai region. However, the delimitation of floristic regions in Arabia has been disputed, and in the work of Zohary (1973), using another terminology, the Arabian species would be placed in the large Sudanian region, which includes the Somalia-Masai region of White & Léonard (1991). The Sudanian region of Zohary was later enlarged by Mandaville (1984) to include most of the Arabian peninsula.

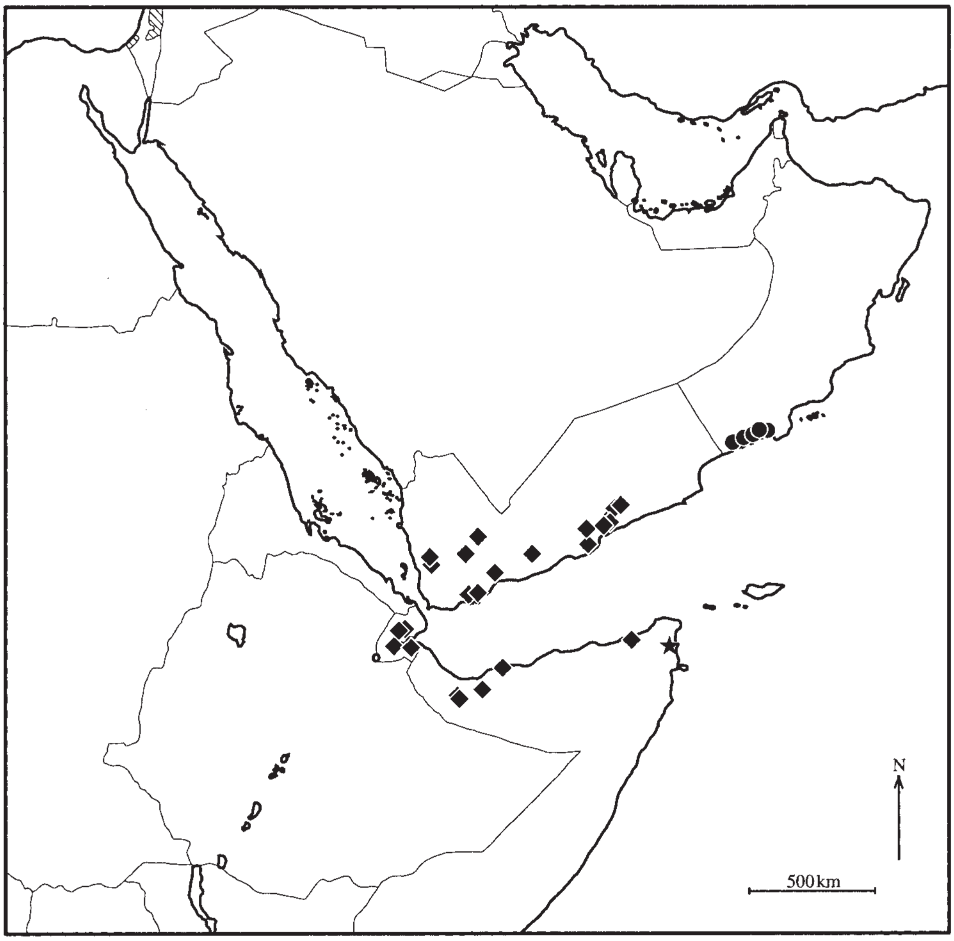

FIG. 9. Map of the Arabian peninsula and NE Africa showing distribution of *C. somaliensis* (★), *C. chascaniflorus* (●), and *C. junceus* (◆).

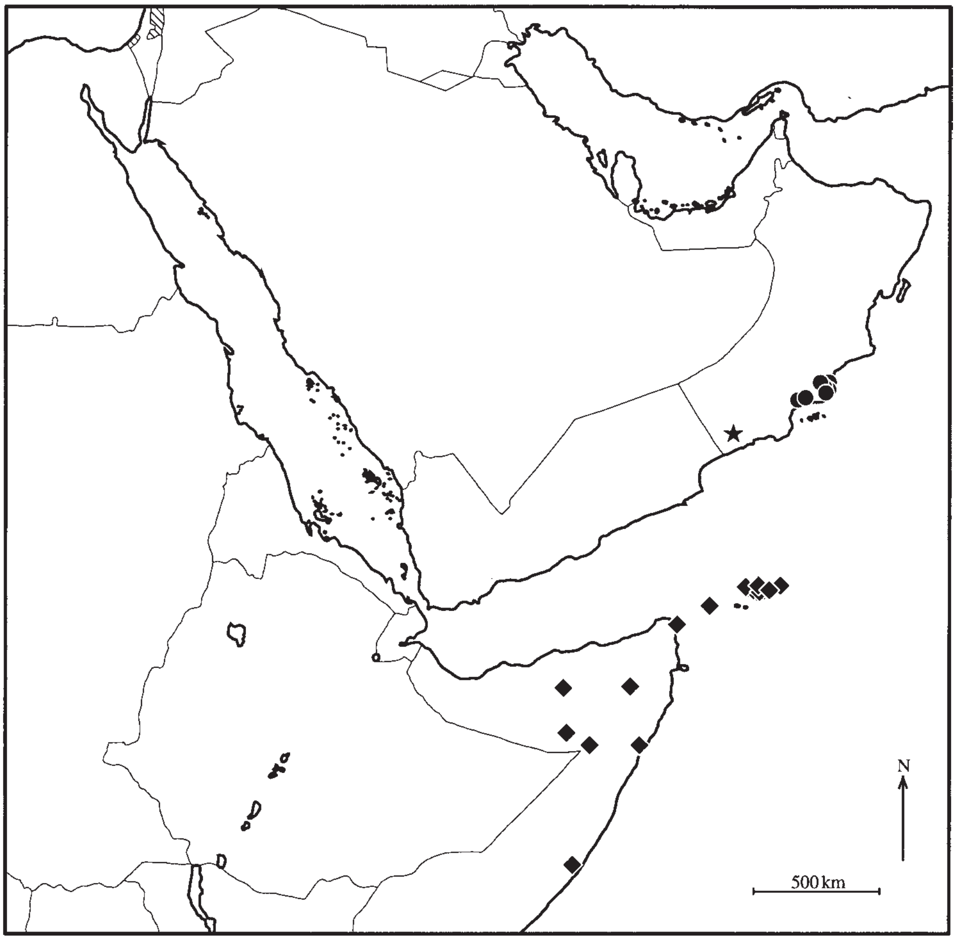

Fig. 10. Map of the Arabian peninsula and NE Africa showing distribution of *C. mirandae* (★), *C. sedoides* (●), and *C. spinosus* (◆).

Most species in Africa and Arabia have strongly restricted distributions, the only exceptions being *C. pungens* in Saudi Arabia, Yemen and Oman, *C. spinosus* on Socotra and the adjacent Abd el Kuri and in eastern Somalia, and *C. junceus*, which is the only species that occurs on both sides of the Gulf of Aden.

Miller & Nyberg (1991) recognized eight local centres of endemism on the Arabian peninsula, apart from Socotra and neighbouring islands. *Campylanthus yemenensis* has a distribution just outside their local area of endemism around Ibb in northern Yemen, an area that is very rich in endemics. *Campylanthus antonii* is found in the Jol area that corresponds to the Hadramaut and Mahra Governorates in south-eastern Yemen which contains about 40 endemics. In Oman *C. chascaniflorus* and *C. mirandae* both occur within the local area of endemism in Dhofar (c.35 endemics), while *C. sedoides* is found in the floristically poor region of Central Oman which has about 15 endemics.

Socotra and neighbouring islands constitute an area well known for its many endemics, which account for 30% of the total flora, or 240 species (Miller & Nyberg, 1991). *Campylanthus spinosus* was long considered endemic on Socotra and Abd el Kuri, but Verdcourt (1958) reported a collection made in Somalia in 1956 (*Simmons* B50). However, the first collection in Somalia had already been made in 1924 by Stefanini & Paoli, and this collection later became the type of *Chamaeacanthus pumilus* Chiov. (Chiovenda, 1929), a name now placed in the synonymy of *C. spinosus* (Miller, 1982).

Apart from the relatively widespread *C. junceus* and *C. spinosus*, all species occurring in Africa have strongly restricted distributions. Of these, *C. somaliensis* is found in the northeastern corner of Somalia, which is one of the two areas in this country pointed out by Thulin (1994) to be particularly rich in endemics. Most collections of *C. incanus* are also from this area, but its distribution also extends further south. *Campylanthus anisotrichus* is restricted to an area around Berbera in the northwest, which is fairly high in endemics, whereas *C. parviflorus* occurs near Laascaanood [= Las Anod], an area with rather few endemic species.

It is interesting to note that the southernmost collection of *C. spinosus* is from near Hobyo, an area which besides its many endemics also has disjunct distributions of otherwise north-Somalian taxa, for example *Buxus hildebrandtii* Baill. and *Maytenus undulata* (Thunb.) Blakelock (Thulin, 1994).

Saharo-Sindian group

According to the definition of White & Léonard (1991) only one species belongs to this region, namely *C. ramosissimus* from Sind in southeast Pakistan. Among species endemic to this area (Pakistan and northern India) *Moringa concanensis* Nimmo can be mentioned and perhaps also *M. oleifera* Lam., although the distribution of the latter has been much extended by cultivation (Verdcourt, 1985). *Moringa*, like *Campylanthus*, is disjunct between Sind and northeast tropical Africa/Arabia, where nine of the 14 species occur (Thulin, 1994). The phytogeographical link between the Somalia-Masai region and Sind was also discussed by Thulin (1985).

Vicariance biogeography

Originally, *Campylanthus* might have been more or less evenly distributed throughout northern Africa, and the present disjunction between Macaronesia and the Horn of Africa region was most likely caused by extinctions in the area between these regions when the climate became drier as discussed above. This hypothesis is congruent with the phylogeny of the genus, which indicates a basal split between western and eastern species.

Of the five archipelagos in Macaronesia, the Cape Verde Islands is the one that differs most from the other four with respect to the total vascular flora and phytogeographical spectrum (Sunding, 1979). However, apart from *Campylanthus*, the Cape Verde Islands also host a considerable number of taxa, for example *Dracaena draco* L., *Sideroxylon marmulano* Banks ex Lowe, and species of *Aeonium* Webb & Berth., *Echium* L. and *Sonchus* L., that are identical to or related to those of the Canary Islands or Madeira, supporting the inclusion of the Cape Verde Islands in the biogeographic region of Macaronesia (Sunding, 1979).

The species occurring in northeast Africa, Arabia and Pakistan, with the exception of *C. junceus*, *C. pungens* and *C. spinosus*, largely show a vicariant pattern of distribution. It has been shown that during the Paleocene Africa was connected to Asia via Arabia (Raven & Axelrod, 1974). It is quite possible that *Campylanthus* had a more or less even distribution from what is now Macaronesia in the west to Sind in the east. The subsequent continental break up forming the Red Sea, the Gulf of Aden and the Persian Gulf, along with further vicarious events followed by speciation, then formed the basis of the picture we see today. The only species occurring on both sides of the Gulf of Aden, *C. junceus*, is also partially sympatric with the closely related *C. pungens* in Arabia as well as with *C. anisotrichus* in Somalia. This distribution is probably due to secondary dispersal. *Campylanthus pungens*, in turn, is also partially sympatric with *C. chascaniflorus* and *C. mirandae* in Oman.

In the strongly supported clade comprising *C. anisotrichus*, *C. incanus*, *C. parviflorus* and *C. spinosus* all species are allopatric except for *C. spinosus* which may have dispersed to Somalia from the Socotra archipelago.

TAXONOMY

Materials and methods

This work is based mainly on herbarium material obtained on loan from or studied in the following herbaria: B, BM, BONN, BR, EA, FT, HBG, K, O, P, UPS, W, WAG and WU (abbreviations according to Holmgren *et al.*, 1990). Field work was performed in southern Yemen in 1992, where *Campylanthus junceus* Edgew., *C. pungens* O. Schwartz and *C. antonii* Thulin were studied.

Morphology. Plant parts were measured with a hand-ruler or under a dissecting microscope. Flowers were softened in hot water before dissection. Seeds and various hair types were studied by light microscopy (LM) or scanning electron microscopy (SEM). For the SEM studies seeds and small pieces of stems were put on double-sided adhesive tape on stubs and coated with gold-palladium.

Maps. The distribution maps were computer-drawn using CANVAS 5.0.2 for Macintosh.

Species concept. Since this study is based mainly on herbarium material, a morphological species concept has been applied. Species concepts, especially the morphological, are discussed by several authors (DuRietz, 1930; Cronquist, 1978; Stuessy, 1990).

Collection lists. Type specimens are not repeated in the collection lists. Names of localities have been used in accordance with various gazetteers as far as possible. Altitudes, where originally given in feet, have been transformed into metres. All collections cited have been seen by the author, unless otherwise stated.

Campylanthus Roth, Nov. Pl. Sp. 4 (1821).
Type: *Campylanthus salsoloides* (L.f.) Roth.
Syn.: *Chamaeacanthus* Chiov., Flora Somala: 266 (1929). Type: *Chamaecanthus pumilus* Chiov.

Shrubs, subshrubs or woody-based perennial herbs; stems terete, erect to decumbent, often much branched, sometimes with spine-tipped branches, almost glabrous to pilose or hirsute. *Leaves* simple, alternate, sessile to subsessile, subulate to distinctly flattened, often succulent, entire. *Flowers* white to purplish or pinkish-brown, pedicellate or subsessile, arranged in terminal, few- to many-flowered racemes; bracts usually leaf-like and similar to the ordinary leaves. *Bracteoles* 2, inserted at the base of the pedicel. *Calyx* with 5 more or less equal lobes. *Corolla* hypocrateriform to infundibuliform; lobes 5, subequal; tube cylindric with two geniculations, glabrous or pilose to hirsute outside, pilose with antrorse hairs above the insertion of the stamens and glabrous or more commonly with erect to retrorse hairs below the insertion of the stamens inside. *Stamens* 2, anterior; filaments filiform, inserted in the corolla tube at the upper geniculation, glabrous; anther thecae fully confluent with a slight constriction in the middle, longitudinally dehiscent. *Ovary* ovoid; style filiform, glabrous; stigma capitate, oblique. *Capsule* laterally compressed, orbicular to ovate in outline, septicidally dehiscent. *Seeds* numerous, discoid, with a scarious wing around the margin, sometimes in the funicular region only; embryo curved, peripheral.

Key to the species

1a. Plants with parallel, bifurcating hairs 2
1b. Plants glabrous, at least above, or with unbranched hairs only 4

2a. Bifurcating hairs with arms of equal length **13. C. incanus**
2b. Bifurcating hairs with one arm distinctly shorter than the other 3

3a. Flowers to 4mm long, white; stems divaricately branched in three or more orders **15. C. parviflorus**
3b. Flowers at least 6mm long, purple; stems divaricately branched in two orders **14. C. anisotrichus**

4a. Plants with glandular hairs **5. C. somaliensis**
4b. Plants glabrous, at least above, or with eglandular hairs 5

5a. Corolla tube at least 14mm long 6
5b. Corolla tube to 10mm long 7

6a. Virgate, almost leafless shrub; glabrous, at least above **6. C. antonii**

6b. Ascending, woody-based herb, distinctly leafy; shortly hirsute to villous **4. C. chascaniflorus**

7a. Corolla shortly hirsute to hirsute or shortly sericeous outside 8
7b. Corolla glabrous outside 11

8a. Corolla shortly sericeous; plants shortly sericeous, silvery grey **12. C. spinosus**
8b. Corolla shortly hirsute to hirsute; plants glabrous or shortly hirsute, never silvery grey 9

9a. Shrubs to 2m tall, distinctly leafy, leaves 10–50mm long **2. C. salsoloides**
9b. Dwarf shrubs to 20cm tall, leaves to 8mm long 10

10a. Plants subaphyllous, branches ± spinescent; corolla mauve **11. C. yemenensis**
10b. Plants with succulent, broadly elliptic to obovate or spathulate leaves; branches not spinescent; corolla pink to reddish-brown **3. C. sedoides**

11a. Plants densely sericeous, silvery grey; distinctly spinescent **12. C. spinosus**
11b. Plants glabrous or with a different indumentum, never silvery grey 12

12a. Virgate shrub to 2m tall; geniculations of the corolla tube very prominent and well exserted from the calyx **7. C. junceus**
12b. Shrubs or dwarf shrubs to 1m tall; geniculations of the corolla tube not very prominent, positioned at mouth of calyx 13

13a. Leaves at least 10mm long (usually much longer) **1. C. glaber**
13b. Leaves to 7mm long 14

14a. Stems and leaves shortly hirsute to shortly pilose **10. C. mirandae**
14b. Stems and leaves papillose or glabrous 15

15a. Leaves acute; corolla tube at least 8mm long **8. C. pungens**
15b. Leaves obtuse; corolla to 7mm long **9. C. ramosissimus**

1. Campylanthus glaber Benth. in DC., Prodromus 10: 508 (1846). Type: Cape Verde Islands, *Forbes* s.n. (lecto., selected here: K).

Syn.: *Campylanthus benthamii* Webb in Hooker, Icones Plantarum tab. 776 (1848).

Campylanthus benthamii Webb var. *glaber* (Benth.) Webb in Hooker, Icones Plantarum tab. 776 (1848).

Campylanthus benthamii Webb var. *hirsutus* Webb in Hooker, Icones Plantarum tab. 776 (1848). Type: Cape Verde Islands, "In montibus ins. S. Vincentii" at 240m, *Vogel* 72 (lecto., selected by Brochmann *et al.* (1997): FI-WEBB, not seen; isolecto. K).

Campylanthus glaber Benth. var. *puberulus* Cout., Arq. Univ. Lisboa 1: 310 (1914). Type: Cape Verde Islands, Santo Antão, iv–v 1894, *Cardoso* s.n. (holo. LISU, not seen).

Campylanthus spathulatus A. Cheval., Rev. Bot. Appliq. 15: 897 (1935). Type: Cape Verde Islands, Santo Antão, between Pombas and Janela, 11 ix 1934, *Chevalier* 45278 (holo. P, not seen).

Campylanthus glaber Benth. ssp. *spathulatus* (A. Cheval.) Brochmann, N. Kilian, Lobin & Rustan, Sommerfeltia 24: 277 (1997).

Campylanthus glaber Benth. var. *pumilus* Pett., Comm. Biol. Soc. Scient. Fenn. 22: 43 (1960). Type: Cape Verde Islands, São Nicolau, 9 xii 1953, *H. Lindberg* s.n. (holo. H, not seen).

Nomenclatural notes. Two syntypes were mentioned in the protologue of *C. glaber*, *Forbes* s.n. and *Hooker* s.n., both of which are at Kew. The single sheet of *Hooker* s.n. is in rather poor condition compared with the two collections of *Forbes* s.n. Of the Forbes collections, the one with two plants mounted along with a drawing is in best condition, and is therefore selected as lectotype.

Webb included the older name *Campylanthus glaber* Benth. in his *C. benthamii*, and *C. benthamii* is thus superfluous and illegitimate. Furthermore, there has been confusion regarding the correct date of the publication of *C. benthamii*. Most authors have cited Spicilegia Gorgonea (Webb, 1849), included in the *Niger Flora* (Hooker, 1849), as the place of publication. However, that work was published in November or December 1849 according to Stafleu & Cowan (1979: 298), whereas the first publication of the name was in May 1848 (Stafleu & Cowan, 1979: 294–295), in *Icones Plantarum* (Webb, 1848). Webb, who wrote both accounts, obviously intended to publish Spicilegia Gorgonea before the account in *Icones Plantarum*, but for some reason Spicilegia Gorgonea was delayed. That this was Webb's intention is shown by the fact that he cited Spicilegia Gorgonea in the account in *Icones Plantarum*.

There are some uncertainties regarding the syntypes of *Campylanthus benthamii* var. *hirsutus.* In Spicilegia Gorgonea, where Webb intended to publish the name (see notes above), only *Vogel* 72 is explicitly stated to belong to var. β (=*hirsutus*), whereas *Vogel* 35 could possibly be referred to the var. β citation given as "(*Th. Vogel*, n. 35. b. sp. procera et fruct.)". The statement by Brochmann *et al.* (1997) that *Forbes* 17 is also a syntype of var. *hirsutus* is erroneous since no reference to this is made in Spicilegia Gorgonea. Furthermore, Brochmann *et al.* (1997) wrongly stated that the lectotype of *Campylanthus benthamii* var. *hirsutus* was selected by Lobin (1986). In fact Lobin erroneously proposed a lectotype of *C. benthamii*, which in fact is homotypic with the older *C. glaber* (see notes above). To add to the confusion, Lobin also stated that *C. benthamii* var. *hirsutus* is homotypic with *C. benthamii*. These errors were pointed out by Brochmann *et al.* (1997), but they made no attempts to correct them. Therefore I consider that the name was first properly lectotypified by Brochmann *et al.* (1997).

I have not seen the type of *C. spathulatus*. However, a photograph of the type was included in the protologue (Chevalier, 1935: pl. 14).

I have not seen the types of *Campylanthus glaber* var. *puberulus* and *C. glaber* var. *pumilus*. However, photographs of the types were reproduced by Lobin (1986: 101, 103).

Description. Shrub to 100cm high. *Stems* erect, branched; young branches leafy, old ones with persistent leaf bases, glabrous to shortly hirsute, particularly at axils. *Leaves* succulent, linear to narrowly elliptic or narrowly obovate, acute, glabrous or sometimes shortly hirsute, 10–55 × 0.7–7mm. *Flowers* c.10–30 in simple or somewhat branched racemes to 15cm long; *pedicels* 3–8mm long, glabrous to shortly hirsute; *bracts* 2.5–10mm long, glabrous to shortly hirsute; *bracteoles* 1–5mm long, glabrous to shortly hirsute. *Calyx lobes* narrowly ovate to triangular, acute, 3.5–6 × 1–1.8mm, glabrous or sometimes shortly hirsute outside, ciliate. *Corolla* hypocrateriform to infundibuliform, pink to mauve or sometimes white, glabrous outside; *tube* 7–10 × 2mm, geniculate at level of calyx mouth, with retrorse hairs below insertion of stamens inside; *lobes* elliptic to broadly obovate, obtuse to acute at apex, 3–7 × 2.5–7mm, glabrous. *Anthers* 1.7–2.3mm long; *filaments* 0.5–1mm long. *Ovary* slightly compressed, tapering abruptly into style. *Style* 1–2mm long. *Capsule* broadly elliptic to ovate, 3.5–5.5 × 2.7–3.5mm, brown to black. *Seeds* 0.5–0.9 × 0.6–0.9mm, reddish brown, winged around margin.

Distribution and habitat. *Campylanthus glaber* is endemic to the Cape Verde Islands, where it is known from Santo Antão, São Vicente, São Nicolau, Brava, Fogo and Santiago (Fig. 6). It can be found on cliffs, rocky or sandy slopes and gravel from 10 to 1750m. The greatest altitudinal ranges are found on Santo Antão (10–1620m) and Fogo (50–1750m), whereas the smallest ranges are found on São Vicente (200–900m) and Brava (60–740m). On São Nicolau (500–1300m) and Santiago (60–1150m) the ranges are intermediate.

Variation and taxonomic remarks. *Campylanthus glaber* is variable in leaf shape, which ranges from linear and c.0.7mm wide to distinctly flattened and up to 7mm wide. The wide-leaved form is mainly found at lower altitudes on Santo Antão, and it has been described as *C. spathulatus*. However, since intermediate forms occur on Santo Antão (e.g. *Rustan & Brochmann* 1499 and *Rustan & Brochmann* 1826) and São Vicente (e.g. *Brochmann & Rustan* 762/82), and given the fact that wide-leaved forms also occur in the normally narrow-leaved *C. junceus* and *C. spinosus*, I see no reason to retain *C. spathulatus* at any rank.

Recently, Brochmann *et al.* (1997) proposed recognition of *C. spathulatus* as a subspecies of *C. glaber*. However, since there is considerable infraspecific variation in other genera in the Cape Verde Islands, for example *Campanula* L. (Figueiredo, 1995) and *Kickxia* Dumort. (Sutton, 1988; Ghebrehiwet, 2001), and given the facts discussed above, I cannot agree with their conclusion. If *C. spathulatus* is to be retained as an infraspecific taxon of *C. glaber*, one must recognize infraspecific taxa in several other species of *Campylanthus* as well and this would serve no useful purpose.

The plants described as *C. glaber* var. *puberulus* and *C. glaber* var. *pumilus* fall well within the range of *C. glaber* and do not merit recognition.

In the latest revision of the genus (Miller, 1980), *C. glaber* was treated as a synonym of *C. salsoloides*, the two species being very similar. *Campylanthus glaber* differs however in the glabrous outer surface of the corolla (distinctly pilose in *C. salsoloides*) and to some extent the more low growing habit.

Selected specimens (from 125 examined). CAPE VERDE ISLANDS. **Santo Antão**: NE facing, steep coastal cliffs between Ribeira Paul and Ribeira das Pombas, 10–50m, 21 xii 1993, *Kilian & Leyens* 2803 (BONN); Ribeira do Paul, along levada on NW-side of Tope Cavaleiro, 17°07′N, 25°02′W, 350m, 11 i 1982, *Rustan & Brochmann* 1499 (O); Morossos, between the old crater Espadana and Monte Morossos, steep NE facing escarpments into Ribeira da Garca, 1300–1620m, 23 xii 1993, *Kilian & Leyens* 2887 (BONN). **São Vicente**: NNE of Mindelo, at the top of Monte Vigia, 16°54′N, 24°59′W, 300m, 5 ii 1982, *Rustan & Brochmann* 2108 (O); Monte Verde, 400–500m, 4 xii 1985, *Kilian* 774 (B); Near the top of Monte Verde, 750m, 1976, *Sunding* 3357 (O); Tope da Caixa, 16°49′N, 25°00′W, 300m, 6 ii 1982, *Brochmann & Rustan* 762/82 (O). **São Nicolau**: Monte Gordo, at the top, 16°37′N, 24°21′W, 1300m, 29 i 1982, *Rustan & Brochmann* 1865 (O); E part, small peak just 1km W of Tope Julanga, 16°35′N, 24°06′W, 500–550m, 14 vi 1994, *Kilian & Leyens* 3186 (BONN); On the coastal road immediately before Vila da Ribeira Brava, 12 x 1979, *Lobin* 1016 (BONN, O). **Brava**: NW-slope of Monte Gambia between Ponta do Sorno and Ponta do Gambia, 14°53′N, 24°43′W, 80m, 26 ii 1982, *Rustan & Brochmann* 2584 (O); Ribeira da Fajã de Agua, along levada close to Ribeira Pau do Corro, 14°51′N, 24°44′W, 230m, 22 ii 1982, *Brochmann & Rustan* 1104/82 (O); S of Cachaçao, Monte Miranda, 14°49′N, 24°42′W, 740m, 25 ii 1982, *Brochmann & Rustan* 1181/82 (O). **Fogo**: Chã das Caldeira, between the village and the "exit" to Monte Velha, 1600–1750m, 24 i 1994, *Kilian & Leyens* 3337 (BONN); N of São Filipe, W of Monte Almada on the plains near Ribeira do Pico, 14°55′N, 24°30′W, 80m, 14 ii 1982, *Rustan & Brochmann* 2243 (O); Ribeira São Jorge, between Galinheiros and São Jorge, somewhat above road, 150–200m, 21 i 1994, *Kilian & Leyens* 3260 (BONN). **Santiago**: Serra da Malagueta, 1km E of Quebrada, 15°10′N, 23°41′W, 60m, 20 xii 1981, *Brochmann & Rustan* 454/81 (O); SW slope of Serra do Pico da Antonia, SW of Ribeira Longueira, 1100m, 18 xi 1976, *Sunding* 3710 (O); The more western of the two volcano cones between Ribeira São João and Ribeira Fundura, in the upper slopes on the Ribeira Fundura NW below the volcano cone, 14°59′N, 23°41′W, 400–460m, 13 xii 1993, *Kilian & Leyens* 2699 (BONN).

2. Campylanthus salsoloides (L.f.) Roth, Nov. Pl. Sp. 4 (1821). Type: Canary Islands, Tenerife, "Habit in Barrancas circa oppidum St. Crux", 1778, *Masson* s.n. (lecto., selected by Miller (1980): BM; isolecto. UPS-THUNB.).

Syn.: *Eranthemum salsoloides* L.f., Suppl. Pl. 82 (1782).

Teucrium filiforme Poir., Encycl. (Lamarck) Suppl. 2: 769 (1812). Type: Canary Islands, *Broussonet* s.n. (P?, not seen).

Campylanthus salsoloides (L.f.) Roth var. *penduliflorus* Pitard in Pitard & Proust, Flore de l'Archipel les Iles Canaries 293 (1909). Type: Gran Canaria, Guia, Barranco de San Felipe, 200m, *Pitard* 1577 (lecto., selected here: P).

Campylanthus salsoloides (L.f.) Roth var. *leucanthus* Svent., Indices Seminum Horti Acclimat. Plantarum Arautapensi 4: 47 (1967). *Nom. inval.* (Art. 37.1).

Nomenclatural notes. There is one sheet of *Campylanthus salsoloides* in the Thunberg herbarium at UPS under the name *Selago salsoloides*. The fact that the specimen was collected by Fr. Masson (see reverse of sheet) and that it is very similar to the lectotype in BM makes it clear that this represents an isolectotype of *Eranthemum salsoloides*. The locality data in the protologue says: "…circa oppidum…", whereas the label on the sheet in question says: "…prope oppidum…".

I have seen only the protologue of *Teucrium filiforme* Poir., but according to Webb

& Berthelot (1845), who had seen the appropriate material, it belongs to *Campylanthus salsoloides*.

Pitard (1909) did not cite any specimens in the protologue of *C. salsoloides* var. *penduliflorus*, but a detailed locality description was given. There are two sheets present in P: *Pitard* 1577 and *Pitard* 1578, both collected in Barranco de San Felipe, Gran Canaria. The data given on the label of *Pitard* 1577 conform most closely with the protologue and this sheet is therefore selected as lectotype.

Sventenius (1967) did not cite a type for *C. salsoloides* var. *leucanthus*, and thus the name is not validly published.

Description. Shrub to 200cm high. *Stems* erect, branched; young branches leafy, old ones with persistent leaf bases, glabrous to shortly hirsute above, particularly at axils. *Leaves* succulent, linear, more or less terete, acute, glabrous, 10–50 × 0.8–2mm. *Flowers* c.10–30 in simple or somewhat branched, hirsute racemes to 20cm long; *pedicels* 3.5–6.5mm long, hirsute; *bracts* 2.5–6mm long, hirsute; *bracteoles* 1.3–2.5mm long, hirsute. *Calyx lobes* narrowly ovate to triangular, acute, 4–6 × 1.5–2mm, hirsute outside, ciliate. *Corolla* hypocrateriform to infundibuliform, pink to mauve, or sometimes white, shortly hirsute outside; *tube* 7–9 × 1.5–2mm, geniculate at level of calyx mouth, with retrorse hairs below insertion of stamens inside; *lobes* elliptic to broadly obovate, obtuse to acute at apex, 3.5–7.5 × 3–4mm, shortly hirsute outside. *Anthers* 2.2–2.5mm long; *filaments* 0.5–0.7mm long. *Ovary* ovoid, slightly compressed, tapering abruptly into style. *Style* 1–1.5mm long. *Capsule* broadly elliptic to ovate, 4–6.5 × 3.5–4mm, brown to black. *Seeds* 0.8 × 0.9–1mm, reddish brown, winged around margin.

Distribution and habitat. *Campylanthus salsoloides* is endemic to the Canary Islands, where it is found on Gran Canaria, Gomera, Fuerteventura and Tenerife (Fig. 6). It grows on cliffs, on rocky slopes and hillsides, and on dry banks from 10 to 660m. Associated plants include *Asparagus umbellatus* Link, *Euphorbia canariensis* L. and *Periploca laevigata* Aiton.

Variation and taxonomic remarks. *Campylanthus salsoloides* is a uniform species, showing some variation only in leaf length and colour of the corolla. The plant described as *C. salsoloides* var. *penduliflorus* is merely a form with hanging inflorescences, and it is not worth retaining at any rank.

Campylanthus salsoloides is closely related to the very similar *C. glaber* from the Cape Verde Islands. For differences between the two, see under *C. glaber*.

Selected specimens (from 117 examined). CANARY ISLANDS. **Fuerteventura**: Risco Blanco, about 1.5km S of Vega de Rio Palmas, 470m, 28 iii 1979, *Halvorsen* 103 (O). **Gomera**: Agula, 150m, 19 ix 1924, *Czeczott* 216 (K); Just before Tamargada on road from Vallehermoso to Hermigua, 450m, 9 iii 1973, *Aldridge* 1138 (BM); Puerto de Hermigua, 150m, 3 iv 1957, *Lid* s.n. (O). **Gran Canaria**: Cuesta de Silva, 23 v 1933, *Asplund* 1368 (K, O, UPS); Caldera de Bandama, 400–500m, 17 v 1900, *Bornmüller* 1037 (HBG, W, WU); Barranca de Tirajana on cliffs SW of Temisas, 600m, 20 iii 1971, *Bramwell & Humphries* 3028 (BM). **Tenerife**: NW part, 2km WNW of Buenavista near the seashore, 17 iv 1974, *Moberg* 2231 (UPS); Montañas de Teno, Punta de Teno, 28°21′N, 13°12′W, 50m, 8 iv 1977, *Jarvis & Murphy* 197 (BM); Guimar, Mirador de Don Martin, 28°17′N, 16°24′W, 20 iii 1997, *Swenson, Schmidt & Almeida* 478 (UPS).

3. Campylanthus sedoides A.G. Mill., Notes Roy. Bot. Gard. Edinburgh 38: 382, fig. 2a & 5Aa–e (1980). Type: Oman, Dhofar, Shuwamiyah, in shallow sand over rocky ledges, 50m from high tide mark, 0m, 14 x 1979, *Miller* 2727 (holo. E).

Description. Subshrub to 20cm high. *Stems* procumbent; young branches greyish-green often tinged red, hirsute; old branches light yellowish brown with ± peeling bark, glabrescent. *Leaves* succulent, broadly elliptic to broadly obovate or spathulate, obtuse, shortly hirsute to hirsute, 1.5–8 × 1.5–4mm. *Flowers* 2–4 at ends of branches; *pedicels* 0.5–1(–2)mm long, hirsute; *bracts* 1.5–3 × 0.8–3mm, hirsute; *bracteoles* 1–2.5 × 0.8–2.5mm, hirsute. *Calyx lobes* narrowly elliptic to narrowly triangular, acute, 2.5–5.5 × 0.8–1.5mm, hirsute. *Corolla* hypocrateriform, pink to reddish-brown, hirsute outside above the upper geniculation; *tube* 6.5–9 × 1–1.5mm, geniculate at level of calyx mouth, with retrorse hairs below insertion of stamens inside; *lobes* furrowed in middle at apex, broadly obovate, acute at apex, 2.5–3.5 × 2.2–3.2mm, hirsute outside. *Anthers* 1.6–2.2mm long; *filaments* c.0.5mm long. *Ovary* ovoid, slightly compressed, tapering abruptly into style. *Style* c.2–4.5mm long. *Capsule* broadly obovoid, 3–5 × 3.7–5mm, brown. *Seeds* c.0.7–1 × 1–1.2mm, bluish black, winged around margin.

Distribution and habitat. *Campylanthus sedoides* is known from coastal areas in Oman from around Shuwamiyah and eastwards to Sawqirah (Fig. 10). It is found on sparsely vegetated sandy beaches or gravel plains between sea level and 600m.

Vernacular name. Gunerain (Oman, *JAS* 75).

Variation and taxonomic remarks. *Campylanthus sedoides* shows no notable variation. It is easily distinguished from all other members of the genus by its dwarfish habit and by its succulent, broadly obovate to spathulate leaves.

Specimens examined. OMAN. **Dhofar**: 19°N, 56°E, 13 ii 1968, *Popov* 68/17 (BM); *Popov* 68/24 (BM); Wadi Ghadun, Sahil al Jazir, 18°45′N, 56°43′E, 50m, 13 v 1983, *Gallagher* 6763/10 (E); R'as Sawqirah c.5km W of Sawqirah, 19 ix 1989, *Miller & Nyberg* 9451A (E, K); Sawqirah, 0m, 29 ix 1984, *Miller* 6477 (K); Plateau above Sharbithat, 200m, 19 ix 1989, *Miller & Nyberg* 9444 (E, K); Limestone cliffs above Sharbithat, 18°00′N, 56°27′E, 100m, 29 ix 1984, *Miller* 6453 (E); Sharbithat, 240km NE of Salalah, 20m, 14 x 1979, *Miller* 2754 (E); Without precise locality, iv 1989, *JAS* s.n. (E).

4. Campylanthus chascaniflorus A.G. Mill., Notes Roy. Bot. Gard. Edinburgh 38: 380, fig. 2c & 5Ba–d (1980). Type: Oman, Dhofar, Ra's Hamar, 6km W of Raysut, on sea cliffs, 50m, 28 ix 1979, *Miller* 2312 (holo. E).

Description. Perennial woody-based herb to 25cm high. *Stems* prostrate or ascending, branched from below or somewhat branched above; branches greyish-green, shortly hirsute to villous. *Leaves* obovate to elliptic, obtuse to acute, shortly hirsute to villous, 2–18 × 0.5–7mm. *Flowers* c.4–10 in ± secund racemes to 10cm long; *pedicels* 2.5–6(–8.5)mm long, shortly hirsute to villous; *bracts* 1–4mm, shortly hirsute to villous; *bracteoles* 1–2mm long, shortly hirsute to villous. *Calyx lobes* narrowly ovate to narrowly triangular, acute, 0.7–1.2 × 1.8–4mm, with narrow scarious margin at least at base, shortly hirsute to villous outside and with villous margins. *Corolla* hypocrateriform, pinkish yellowish-brown, glabrous outside; *tube* 14–18 × 1mm, geniculate in the middle, with retrorse hairs below insertion of the stamens inside; *lobes* recurved, narrowly oblong to narrowly ovate, acute at apex, 4.2–6.7 × 1–2.5mm, glabrous. *Anthers* 2.2–2.5mm long; *filaments* 0.3–0.5mm long. *Ovary* slightly compressed, tapering abruptly into style. *Style* c.9mm long. *Capsule* broadly elliptic to round, c.4–5.5 × 3–4mm, brown. *Seeds* c.1 × 1.2mm, reddish brown, winged around margin.

Distribution and habitat. *Campylanthus chascaniflorus* is a common species (Miller & Morris, 1988) restricted to southwestern Oman (Fig. 9); it can be found on rocky slopes and cliffs, in wadi beds and in coastal sand. The vegetation at the type locality is dominated by *Commiphora* sp. Other plants associated with *C. chascaniflorus* include *Boswellia sacra* Flueck., *Ziziphus leucodermis* (Baker) O. Schwartz and *Aloe dhufarensis* Lavranos. The altitudinal range is from sea level to 100m.

Variation and taxonomic remarks. *Campylanthus chascaniflorus* is a uniform species, showing some variation in leaf size and indumentum only. It is readily distinguished by its more or less herbaceous habit. In floral characters it is similar only to *C. antonii*, which also has a very long-tubed corolla; however, *C. antonii* is an almost glabrous, virgate shrub with minute leaves. Apart from the illustrations in the protologue, a colour drawing was published in Miller & Morris (1988: 261, fig. 2A–F).

Specimens examined. OMAN. **Dhofar**: Salalah plain, 5km E of Wadi Hinnah, 10m, 20 ix 1985, *Miller* 7731 (E); Arzat, near Salalah, 17°00′N, 54°18′E, 10m, 8 x 1984, *McLeish* 68 (E); Wadi Adawnib, near turnoff to Wadi Nar, 30m, 26 v 1985, *Miller* 7003 (K); Mughsayl, 80km W of Salalah, 10m, 19 x 1979, *Miller* 2772 (E, K); Kharfat, lower Wadi Sayq, Jabal al Qamar, 9km E of Thalfut, 2km W of Rakhyut, 16°44′N, 53°19′E, 0m, 26 ix 1977, *Radcliffe-Smith* 5263 (E, K); Salalah plain, i 1966, *Lavranos* 4350 (K).

5. Campylanthus somaliensis A.G. Mill., Notes Roy. Bot. Gard. Edinburgh 45: 73, fig. 1Ba–g (1988). Type: Somalia, Bari, 60km S of Bargaal, Tug Giael, 26 xi 1985, *Thulin & Warfa* 5560 (holo. UPS; iso. E, K, MOG (destroyed)).

Description. Low shrub to 50cm; most parts with glandular hairs. *Stems* subaphyllous, ascending, somewhat branched, weakly ribbed, pale green. *Leaves* linear-oblong, 1.5–10 × 0.6–1.3mm, subacute. *Flowers* 3–8 in racemes to 7cm long; *pedicels* 2–3mm long; *bracts* ovate, c.2–2.3 × 0.5–0.9mm; *bracteoles* ovate, 1.5–2 × 0.5–0.6mm. *Calyx lobes* narrowly elliptic to narrowly ovate, acute, 3.5–4.5 × 0.7–1.5mm. *Corolla* hypocrateriform, pale violet with a purple tube, glabrous outside; *tube* 11–14 × 1mm, geniculate in the middle, with retrorse hairs below insertion of stamens inside; *lobes* obovate, acute at apex, 4.5–6 × 1.8–3mm. *Anthers* c.2mm long; *filaments* c.0.5mm long. *Ovary* ovoid, slightly compressed, tapering gradually into style. *Style* c.5–6mm long. *Capsule* round, c.4–5.5 × 4.2–5mm, brown. *Seeds* 1.2–1.3 × 1.8–1.9mm, purplish brown, wing minute, restricted to funicular region.

Distribution and habitat. *Campylanthus somaliensis* is known only from the type collection, which was made in northeastern Somalia (Fig. 9). It was found on a limestone slope growing together with *Acacia ankokib* Chiov., *Commiphora* sp. and *Boswellia frereana* Birdw. between 100 and 200m.

Taxonomic remarks. *Campylanthus somaliensis* is distinguished from all other members of the genus by its dense indumentum of glandular hairs. It differs from the superficially similar *C. mirandae* in the longer corolla tube (11–14mm vs. 7.5–9mm) and by the longer style (5–6mm vs. 2–2.5mm).

6. Campylanthus antonii Thulin, Nord. J. Bot. 15: 191, fig. 1 (1995). Type: Yemen, Al Mahrah, 13km from Sayhut along road to Qishn, 15°15′N, 51°20′E, c.50m, 16 x 1992, *Thulin, Eriksson, Gifri & Långström* 8407 (holo. UPS, iso. K).

Description. Slender shrub to 50cm high. *Stems* subaphyllous, erect, sparsely branched, weakly ribbed, greenish, glabrous above, with short spreading hairs or sometimes shortly pilose with a few longer hairs below. *Leaves* linear to narrowly elliptic, acute, minutely pubescent or ciliate, lower leaves sometimes shortly pilose with a few longer hairs, 1.5–5 × 0.5–2mm. *Flowers* c.5–13 in racemes to 10cm long; *pedicels* 2–5mm long, glabrous; *bracts* c.1mm, ciliate; *bracteoles* c.0.8mm, ciliate. *Calyx lobes* narrowly ovate, acute, c.2–3 × 0.8–1.2mm, ciliate. *Corolla* hypocrateriform, brownish yellow, glabrous outside; *tube* 14–15 × 1mm, geniculate in upper third, with retrorse hairs below insertion of stamens inside; *lobes* linear, recurved, acute at apex, c.4 × 1mm. *Anthers* c.1.6mm long; *filaments* c.0.4mm long. *Ovary* slightly compressed, tapering gradually into style. *Style* c.10mm long. *Capsule* broadly elliptic to round, 4–5 × 4–5mm, brown. *Seeds* 1 × 1.2mm, purplish brown, wing minute, restricted to funicular region.

Distribution and habitat. *Campylanthus antonii* is known from a few localities in the Mahrah region in southeastern Yemen (Fig. 8), where it grows on open rocky slopes and along gravelly wadis at altitudes between 5 and 70m, together with, for example, *Ochradenus gifrii* Thulin and *Isoleucas arabica* O. Schwartz.

Variation and taxonomic remarks. The few collections seen show only a little variation in the amount and length of the indumentum. *Campylanthus antonii* is a distinct species related to *C. junceus*, which is very similar in vegetative characters. However, in floral characters it differs significantly. The corolla tube is much longer in *C. antonii* than in *C. junceus*, the colour is different (brownish yellow in *C. antonii* vs. white to pink to blue in *C. junceus*), as also is the shape of the corolla lobes, which are linear in *C. antonii* and broadly obovate in *C. junceus*. Similar flowers are found in *C. chascaniflorus* from Oman. However, this taxon is a prostrate or ascending perennial herb, with villous vegetative parts and densely set leaves up to 18mm long and 7mm wide. *Campylanthus somaliensis* from northeastern Somalia is similar in habit but differs in the glandular indumentum and in the violet corolla with the geniculations in the middle of the tube whereas they are in the upper third in *C. antonii*.

Specimens examined. YEMEN. **Mahrah**: Along road between Al Ghaydah and Al Fatk, 16°30′N, 52°40′E, 5–20m, 10 xi 1998, *Thulin, Beier & Mohammed A. Hussein* 9679 (UPS); 21km NE of Sayhut, 15°16′N, 51°23′E, 10m, 5 xi 1998, *Thulin, Beier & Mohammed A. Hussein* 9534 (UPS); 31km NE of Sayhut, 15°18′N, 51°24′E, 70m, 5 xi 1998, *Thulin, Beier & Mohammed A. Hussein* 9539 (UPS).

7. Campylanthus junceus Edgew., J. Asiat. Soc. Bengal 16: 1217 (1847). Type: Yemen, Aden, 19 xii 1847, *Hooker* 98 (neotype, selected here: K).

Nomenclatural notes. The original material, *Edgeworth* s.n. (Yemen, Aden, x 1846), was not found in K where the main set of Edgeworth's material is deposited (Wickens, 1982). Further requests to G and OXF, two herbaria known to hold Edgeworth material (Wickens, 1982), also gave negative results. Finally, a request to CAL confirmed that no material was present there either. It is thus concluded that the original material has been lost, and as a consequence a neotype has been selected. *Campylanthus junceus* has been collected in Aden many times over the years, and I have selected *Hooker* 98 (see above) at K as a neotype, since it matches the original description accurately, dates back to the time of the description of *C. junceus* and is placed in the herbarium where Edgeworth's original material should have been.

Description. Slender shrub to 200cm high. *Stems* subaphyllous, sprawling, somewhat branched, young branches green, old ones brownish-green, glabrous to sparsely pilose, particularly below and at axils. *Leaves* semi-succulent, linear to elliptic, acute, glabrous to sparsely pilose, 2–22 × 0.5–2.8mm. *Flowers* c.10–35 (occasionally fewer) in ± secund racemes to 30cm long; *pedicels* 2–4.2mm long, glabrous; *bracts* 1–2.6(–5)mm long, glabrous to ciliate, rarely hairy on upper surface as well; *bracteoles* 0.5–1.7mm long, ciliate. *Calyx lobes* narrowly ovate to ovate, acute, 1.8–4 × 0.7–1.2mm, almost glabrous to sparsely pilose inside, usually ciliate. *Corolla* hypocrateriform, pale to bright blue, pale lilac, mauve, pink or white, glabrous outside; *tube* 7–10 × 1mm, pronouncedly geniculate in the middle, with retrorse hairs below insertion of stamens inside; *lobes* broadly obovate, obtuse to acute at apex, 2.8–5.5 × 2.1–4.5mm, glabrous. *Anthers* 1.5–1.7mm long; *filaments* 0.3–0.5mm long. *Ovary* slightly compressed, tapering gradually into style. *Style* 2–5(–7)mm long. *Capsule* broadly elliptic to round, 4–5.2 × 3.8–5mm, brown. *Seeds* 1–1.3 × 1.2–1.5mm, reddish brown, winged around margin.

Distribution and habitat. *Campylanthus junceus* is distributed in Djibouti and northern Somalia in Africa and in Yemen on the Arabian peninsula (Fig. 9). It is thus the only species of *Campylanthus* found on both sides of the Gulf of Aden. As well as the three collections cited below, further collections from Djibouti are cited in Moggi (1963: 589) and Lebrun *et al.* (1989: 208).

Throughout its distribution, *Campylanthus junceus* is generally found in rocky places on volcanic ground, but it also grows on sandstone hills, gravel plains and sandy coastal plains. It often grows inside shrubs of, for example, *Acacia* spp., *Indigofera* spp. and *Leptadenia pyrotechnica* Decne. The altitudinal range is from sea level to 2100m.

Vernacular names. Merko Dabera (Somalia, *Gillett* 4775); Mirroh (Somalia, *Glover & Gilliland* 1185); Marekh (Yemen, *Maxwell Darling* 170); 'Alat al Jabal (Yemen, *Wakefield Expedition* 4A).

Variation and taxonomic remarks. *Campylanthus junceus* is rather uniform throughout its area of distribution, showing some variation in indumentum, leaf length and colour of the corolla. However, this variation is not geographically correlated. One collection, *Gillett & Watson* 23672, from Somalia is notable for its exceptionally large leaves and indumentum of very long hairs. However, comparable leaf lengths are found in, for example, *Miller & Long* 3488 from northern Yemen and in *Thulin, Eriksson, Gifri & Långström* 8047 from Hadramaut in Yemen.

Campylanthus junceus is obviously closely related to *C. antonii*, which is very similar in vegetative characters. However, the corolla differs both in size (tube to 10mm long in *C. junceus*, at least 15mm in *C. antonii*), colour (white to pink to blue in *C. junceus*, brownish yellow in *C. antonii*) and in the shape of the lobes (broadly obovate in *C. junceus*, linear in *C. antonii*). It is also related to *C. pungens*, from which it differs in habit (*C. junceus* is a virgate, little-branched shrub, whereas *C. pungens* is a low, much-branched shrub), number of flowers per raceme (usually 10 to more than 15 in *C. junceus*, usually around 5 in *C. pungens*), the longer pedicels (2–4.2mm in *C. junceus*, 0.8–1.5mm in *C. pungens*), the position of the geniculations of the corolla (in middle of tube in *C. junceus*, in lower third of tube in *C. pungens*), and in the wider corolla lobes. Furthermore, the geniculations of the corolla tube are much more pronounced in *C. junceus* than in any other species of *Campylanthus*.

Selected specimens (from 66 examined). Djibouti. Near turning to Arta, 11°31′N, 42°52′E, 400m, 10 ii 1994, *Thulin* 8909 (UPS); Yager, 800m, iv 1957, *Chedeville* 1164 (FT); Djibouti to Al Sabieh, 14 viii 1960, *Giraud* s.n. (FT). Somalia. **Woqooyi Galbeed**: Halkulan tug above Anlah pool, Karin near Berbera, 100m, 3 v 1945, *Glover & Gilliland* 1185 (BM, K); E of Duwi, 10°01′N, 44°14′E, 1100m, 30 vi 1981, *Gillett & Watson* 23672 (E, K); Foot of Dubriyaad, 10°22′N, 45°10′E, 150m, 3 i 1933, *Gillett* 4775 (K). **Sanaag**: Abdo, Ceelaayo, 3 iv 1945, *Glover & Gilliland* 897 (K). **Bari**: Qandala, 11°28′N, 49°52′E, 2 ix 1957, *Newbould* 1033 (K). Yemen. **Hodeida**: Northern side of Jabal ar R'as, M'kahl, Wadi Zabid, 600m, 15 x 1976, *Wood* 1418 (BM); Jabal ar R'as, 14°04′N, 43°36′E, 1300m, 14 xi 1995, *Thulin, Ghebrehiwet & Gifri* 9366 (K, UPS); Jabal ar R'as, 15km NE of Hays, 1450m, 8 iv 1981, *Miller & Long* 3488 (E). **Dhamar**: Sandstone hills just E of Rida, 2100m, 28 iv 1979, *Wood* 2267 (BM, K). **Marib**: Between Naqil Hagla and Harib, 5 iii 1980, *Wood* 3158 (K). **Lahij**: Coastal plain N of Lahij, in the vicinity of the foothills, 9 x 1962, *Popov* P32/1 (BM). **Aden**: Aden, Gold Mohur valley, 12°46′N, 44°59′E, 10–40m, 28 ix 1992, *Thulin, Eriksson, Gifri & Långström* 7847 (K, UPS); Aden, above the tanks and on the terrace to the foot of Jabal Shamsan, 50–200m, 18 iv 1931, *Wissmann* 1292 (HBG); Aden, slopes towards NE, above Steamer Point, 100m, 16 iv 1931, *Wissmann* 1305 (HBG). **Abyan**: Hinterland of Aden, Hadjer Djûel – Aqabet Marma, 31 iii

1939, *Wissmann* 2836 (BM); 10km W of Shaqra', 0m, 8 iv 1954, *Grierson* 137 (E). **Hadramaut**: Wadi Hajr, Mintaq, 100km W of Al Mukalla, 420m, 13 ii 1989, *Miller et al.* 8165 (E); Al Mukalla, near College of Education, 14°32′N, 49°08′E, 50–75m, 5 x 1992, *Thulin, Eriksson, Gifri & Långström* 8065 (UPS); 23km on the pipeline route starting 15km NE of Riyan, 14°50′N, 49°31′E, 200m, 4 x 1992, *Thulin, Eriksson, Gifri & Långström* 8047 (K, UPS).

8. Campylanthus pungens O. Schwartz, Mitt. Inst. Bot. Hamburg 10: 245 (1939). Type: Yemen, Hadramaut [without precise locality], 1931, *Wissmann* 661 (holo. HBG).

Description. Dwarf shrub to 100cm high, usually much lower. *Stems* subaphyllous, much branched, young branches tinged purple, old ones grey-green, more or less spinescent, glabrous or sometimes scabridulous at base. *Leaves* linear-subulate, acute, glabrous, 1–5(–7) × 0.2–0.5(–0.8)mm. *Flowers* usually up to 5 at ends of branches, occasionally up to c.15 in a 1–4cm long raceme; *pedicels* 0.8–1.5mm long, glabrous; *bracts* 0.9–1.6mm long, glabrous to ciliate; *bracteoles* 0.5–1.2mm long, ciliate. *Calyx lobes* linear to narrowly triangular, acute, 2–5 × 0.7–1.3mm, usually ciliate, at least at tips. *Corolla* hypocrateriform, purple, maroon, mauve, pink or white, glabrous outside; *tube* 8–10 × 1–1.5mm, geniculate in lower third, with retrorse hairs below insertion of stamens inside; *lobes* ovate, acute at apex, 2.2–3.6 × 1.2–2.2mm, glabrous. *Anthers* 1.8–2.5mm; *filaments* 0.3–0.5mm long. *Ovary* slightly compressed, tapering abruptly into style. *Style* 2–3mm long. *Capsule* round, 4–5.5 × 3.8–5.2mm, reddish-brown to dark-reddish brown. *Seeds* 1.3–1.5 × 1.3–1.8mm, light reddish-brown, winged around margin.

Distribution and habitat. *Campylanthus pungens* is known from Saudi Arabia, Yemen and Oman (Fig. 7) and is thus one of the most widespread species in the genus. However, the distribution is not even throughout its range. There are gaps between the populations around At T'aif and Abha in Saudi Arabia and also between the populations in northern Yemen and those in southeastern Yemen (Hadramaut and Mahrah) and southwestern Oman (Dhofar).

Campylanthus pungens can be found on limestone rocks or slopes, on sandstone hills, in rocky places on granite, on volcanic ground and in sandy loam in wadi flood plains. It usually grows on open ground, but can also be found in open scrub consisting of, for example, *Acacia* spp., *Commiphora* spp. and *Euphorbia* spp. The altitudinal range is from 200 to 2500m.

Vernacular name. Ghaban (Saudi Arabia, *Tothill* 75).

Variation and taxonomic remarks. *Campylanthus pungens* is a uniform species and apart from slight variation in stem indumentum and corolla colour, the only variation worth noting is that some of the collections from Dhofar in Oman are rather tall and have leaves up to 7mm long (e.g. *McLeish* 323) compared with a maximum of 5mm in other collections. It appears that this species is heavily grazed in many areas, creating plants with very stunted growth.

The closest relatives of *Campylanthus pungens* seem to be *C. yemenensis* and *C.*

ramosissimus. It is easily distinguished from *C. yemenensis* by its glabrous to papillose vegetative parts (shortly hirsute in *C. yemenensis*) and by the glabrous corolla (shortly hirsute in *C. yemenensis*), and from *C. ramosissimus* by its linear-subulate leaves with acute apices (linear to obovate with obtuse apices in *C. ramosissimus*), by the longer corolla tube (8–10mm vs. 6–7mm) and by the position of the geniculations of the corolla tube (lower third in *C. pungens* vs. below the calyx in *C. ramosissimus*). It is also related to *C. junceus*; for distinguishing characters, see under the latter.

Selected specimens (from 39 examined). SAUDI ARABIA. **Makkah**: At T'aif road near Hadda', 1680m, sine coll. (K); Alongside At T'aif – Hadda' road, 1650m, 24 ii 1979, *Collenette* 822 (K); At T'aif, 30 v 1971, *Popov* 71/155 (BM). **Asir**: Wadi al Arin, 18 iii 1952, *Tothill* 75 (BM, HBG); North of Abha, 1km from Bani Rizam, 2200m, 6 v 1982, *Podzorski* 1188 (E); 70km S of Abha on road to Najran, 2200m, 11 iii 1980, *Lavranos & Collenette* 18269 (E). **Najran**: Base of Qarn Shithath, 17°41′N, 43°30′E, 2100m, 21 x 1969, *Mandaville* 2544 (BM). YEMEN. **Sadah**: 27km W of Sadah, 2200m, 15 xi 1985, *FJM* 47 (K); Track from Marashi to Al Batan, 16°42′N, 44°16′E, 2160m, 27 v 1979, *Wood & Heckel* Y1246 (E); Sadah to Sanaa road, 20km S of Sadah, 1700m, 23 iii 1981, *Miller* 3178 (E, K). **Sanaa**: Naqil Ghaylan, Beni al Harith-Nehm, 2500m, 31 vii 1980, *Wood* 3338 (E, K); Sanaa to Ma'rib road, 10km from Sanaa, 2200m, 3 iv 1981, *Miller & Long* 3396 (E, K); Huth to Sadah road, 10km N of Al Harf, 1600m, 21 iii 1981, *Miller* 3157 (E). **Dhamar**: Hill 79 on W of Dhamar road, 79km S of Sanaa, 2500m, 25 vii 1977, *Radcliffe-Smith & Henchie* 4761 (K). **Hadramaut**: Mola Matar area, near Bayn Al-Jibal, 14°47′N, 48°45′E, 1950m, 6 x 1992, *Thulin, Eriksson, Gifri & Långström* 8110 (K, UPS); 50km NW of the coastal road, along the road to Sayun, shortly after Aqabat Abd Allah Gharib, 930m, 20 vi 1987, *Boulos et al.* 16997 (E, K); Jol, Ras Kureth, 13 iv 1939, *Wissmann* 3099 (BM). **Mahrah**: 16km NE of Itab, 15°25′N, 51°32′E, 400m, 5 xi 1998, *Thulin, Beier & Mohammed A. Hussein* 9554 (UPS). OMAN. **Dhofar**: 4.4km on Uyun turnoff, 17°19′N, 53°55′E, 23 iii 1985, *McLeish* 505 (E); Mirbat Plain, c.15km E of Mirbat, 200m, 8 ix 1989, *Miller & Nyberg* 9202 (E, K); 40km W of Salalah, 2km from Mughsayl, 16°45′N, 53°40′E, 9 ix 1984, *McLeish* 323 (E).

9. Campylanthus ramosissimus Wight, Ic. Pl. Ind. Or. 4, t.1416 (1849). Type: Pakistan, Limestone range, Hyderabad, 21 iv 1847, *Stocks* s.n. (holo. K).

Description. Dwarf shrub to 20cm high. *Stems* subaphyllous, much branched, more or less spinescent, papillose. *Leaves* linear to obovate, obtuse, papillose, 3–7 × 0.7–2mm. *Flowers* up to 5 at ends of branches; *pedicels* 1.5–3mm long, papillose; *bracts* c.1mm long, papillose; *bracteoles* 0.5–0.7mm, papillose. *Calyx lobes* narrowly triangular, acute, 2–3 × 1–1.2mm, papillose, ciliate at least at the tips. *Corolla* hypocrateriform, colour not known, glabrous outside; *tube* 6–7 × 1mm, geniculate below level of calyx mouth, with retrorse hairs below insertion of stamens inside; *lobes* narrowly ovate, acute at apex, c.2.5 × 1.5mm. *Anthers* c.1.8mm long; *filaments* c.0.3mm long. *Ovary* ovoid, slightly compressed, tapering abruptly into style. *Style* 0.8–1.2mm long. *Capsule* somewhat transversely elliptic, 3.5–4 × 4.2–5mm, dark brown to blackish. *Seeds* c.1 × 1mm, light reddish brown, winged around margin.

Distribution and habitat. *Campylanthus ramosissimus* is apparently restricted to Pakistan, and it is the easternmost representative of the genus (Fig. 6). I have seen only the two collections cited, but three additional collections were cited by Stewart (1972: 646). There are no records of habitat or altitudinal range.

Variation and taxonomic remarks. The two collections seen show no notable variation.

In general appearance, *Campylanthus ramosissimus* is similar to *C. pungens*; for distinguishing characters see discussion under the latter.

Specimen examined. Pakistan. Hills of Sind, 1849, *Stocks* 522 (K).

10. Campylanthus mirandae A.G. Mill., Notes Roy. Bot. Gard. Edinburgh 45: 75, fig. 1Aa–h (1988). Type: Oman, Dhofar, Jabal al Qamar, plateau area of western mountains, on southward facing stony steps above seacliffs, x 1984, *Morris* 258 (holo. E).

Description. Subshrub to 20cm high. *Stems* subaphyllous, much branched, grey-green, more or less spinescent, older stems shortly hirsute, younger branches shortly pilose. *Leaves* linear-oblong, ± subulate, acute, shortly hirsute, 3–7 × 0.5–1mm. *Flowers* c.6 at ends of branches; *pedicels* c.2mm long, shortly hirsute; *bracts* linear-subulate, 2–3.5mm long, shortly hirsute; *bracteoles* linear-subulate, 1.5–2mm long, shortly hirsute. *Calyx lobes* linear to narrowly triangular, acute, 3.7–4 × 0.5–0.6mm, shortly hirsute on both sides. *Corolla* hypocrateriform, purple, glabrous outside; *tube* 7.5–9 × c.1mm, lower geniculation below level of calyx, upper geniculation level with mouth of calyx, with retrorse hairs below insertion of stamens inside; *lobes* broadly obovate, acute at apex, c.4 × 2mm. *Anthers* c.2mm long; *filaments* c.0.4mm long. *Ovary* slightly compressed, tapering abruptly into style. *Style* 2–2.5mm long. *Capsule* rounded, 3.5–4.5 × 3.5–4.5mm, brown. *Seeds* c.1 × 1.1–1.3mm, light reddish brown, winged around margin.

Distribution and habitat. *Campylanthus mirandae* is known only from a restricted area of stony terraces in western Dhofar (Fig. 10) at an altitude of c.500m (Miller, pers. comm.). According to Miller (1988), this area is affected by the monsoon and is shrouded in mist between June and September.

Variation and taxonomic remarks. The two specimens seen show no notable variation.

Campylanthus mirandae is likely to be confused only with *C. pungens* among the species occurring in Oman. However, it is easily distinguished by its shortly hirsute vegetative parts (glabrous to papillose in *C. pungens*). It also resembles *C. yemenensis* from northern Yemen, from which it differs in its longer leaves (3–7mm vs. 0.8–2mm) and the glabrous outside to the corolla (shortly hirsute in *C. yemenensis*), and *C. somaliensis*, from which it differs in the shorter corolla tube (7.5–9mm vs. 11–14mm), the shorter style (2–2.5 vs. 5–6mm) and the eglandular indumentum (glandular in *C. somaliensis*).

Specimen examined. Oman. **Dhofar**: Jabal al Qamar, x 1984, *Morris* 561 (E).

11. Campylanthus yemenensis A.G. Mill., Notes Roy. Bot. Gard. Edinburgh 38: 378, fig. 2d (1980). Type: Yemen, Taizz, slopes of Jabal an Nar [Taizz to Al Mukha road, 25km E of Al Mukha], 100m, 21 iv 1977, *Lavranos & Newton* 15914 (holo. E).

Description. Dwarf subshrub to 20cm high. *Stems* subaphyllous, much branched, grey-green, more or less spinescent, scabridulous to very shortly hirsute. *Leaves* linear-subulate, acute, very shortly hirsute, 0.8–2 × 0.2–0.3mm. *Flowers* c.2–3 at ends of branches; *pedicels* 1.5–2.5mm long, shortly hirsute; *bracts* 0.5–1mm long, shortly hirsute; *bracteoles* 0.5–1mm, shortly hirsute. *Calyx lobes* linear to narrowly triangular, acute, 2.5–4 × 0.5–1mm, shortly hirsute on both sides. *Corolla* hypocrateriform, mauve, shortly hirsute outside; *tube* 6–8 × 1–1.2mm, lower geniculation below level of calyx, upper geniculation level with calyx mouth, with retrorse hairs below insertion of stamens inside; *lobes* narrowly ovate, acute at apex, 3.5–4 × 1.5–1.7mm. *Anthers* c.2mm long; *filaments* c.0.4mm long. *Ovary* ovoid, slightly compressed, tapering gradually into style. *Style* 2–2.5mm long. *Capsule* broadly ovoid to round, 3.5–4.5 × 3–4mm, brown. *Seeds* c.1.5 × 1.7mm, light reddish brown, wing restricted to funicular region.

Distribution and habitat. *Campylanthus yemenensis* is known only from three collections from a rather restricted area east of Al Mukha in Yemen (Fig. 8). The plant represented by *Wood* 75/225 was found on a rocky bank, otherwise there are no habitat data or records of associated plants. It is found at altitudes between 100 and 300m.

Variation and taxonomic remarks. The few collections available show no notable variation.

The closest relative of *Campylanthus yemenensis* is obviously *C. pungens*, which grows at much higher altitudes in northern Yemen (1600–2500m vs. 100–300m). However, *C. yemenensis* is easily distinguished by its shortly hirsute vegetative parts (glabrous to papillose in *C. pungens*) and by the shortly hirsute outside of the corolla (glabrous in *C. pungens*).

Specimens examined. YEMEN. **Taizz**: On a rocky bank near Al Mafraq between Al Mukha and Taizz, 300m, 26 v 1975, *Wood* 75/225 (BM, E); Al Bara, on Taizz to Al Mukha road, shortly after Al Mukha turn-off, 300m, 15 iii 1981, *Miller* 3076 (K).

12. Campylanthus spinosus Balf.f., Proc. Roy. Soc. Edinburgh 12: 84 (1884). Type: Yemen, Socotra, without precise locality, “in campis prope mare abundans”, ii–iii 1880, *Balfour* 101 (lecto., selected here: K).
Syn.: *Chamaeacanthus pumilus* Chiov., Fl. Somala: 267 (1929). Type: Somalia, Bari, Xaafuun, 23 v 1924, *Stefanini & Paoli* 616 (holo. FT, not seen).

Campylanthus spinosus Balf.f. var. *kuriensis* A.R. Smith, Kew Bull. 25: 189 (1971). Type: Yemen, Abd al Kuri, c.5.7km NE of Jabal Hassala (Qarat Salih), 12°14′N, 52°15′E, 3m, on a stony slope above a coastal salting, 8 v 1967, *Smith & Lavranos* 706 (holo. K; iso. EA, not seen, FT, not seen, PRE, not seen, W, not seen, WAG).

Nomenclatural notes. Two syntypes were cited in the protologue of *Campylanthus spinosus*, *Balfour* 101 and *Schweinfurth* 261, both mounted on the same sheet at Kew. Since the name has never been typified, a lectotype needs to be designated. Of the two syntypes *Balfour* 101 is more complete and in better condition than *Schweinfurth* 261 and is therefore selected as a lectotype.

Description. Densely branched dwarf shrub to 60cm high, but usually much lower; most parts sericeous. *Branches* distinctly spiny; spines glabrescent, straw-coloured. *Leaves* linear to elliptic-oblanceolate, fleshy, apex obtuse, 1.5–8 × 0.5–2mm. *Flowers* 2–3 at ends of branches, below the spine; *bracts* 1.5–4.5 × 0.5–1.6mm; *bracteoles* 1–3 × 0.3–1mm; *pedicels* 0.5–1mm long. *Calyx lobes* linear to narrowly ovate, 2.5–5 × 0.5–1.1mm. *Corolla* pink to mauve, sometimes almost glabrous outside; *tube* 6.5–9 × 1–1.3mm, geniculate below level of calyx mouth, glabrous below insertion of stamens inside; *lobes* obovate to broadly obovate, 3–5 × 2–3mm, apex acute to obtuse with an irregular margin. *Anthers* 1–1.5mm long; *filaments* c.0.3–0.5mm long. *Ovary* slightly compressed, tapering abruptly into style. *Style* 1–1.5mm long. *Capsule* ovoid to oblong, 3–5 × 2–3mm, blackish brown. *Seeds* 0.6–0.7 × 0.7–0.9mm, kidney-shaped; wing restricted to funicular region.

Distribution and habitat. *Campylanthus spinosus* is found on Socotra (Yemen), the adjacent island of Abd el Kuri and in eastern Somalia (Fig. 10).

Throughout its range *Campylanthus spinosus* can be found in rocky places on limestone where it grows in low scrub consisting of *Acacia* spp., *Commiphora* spp. and *Croton* spp. It can also be found on sandy or gravelly coastal plains or in gypsum-rich areas. The altitudinal range is between sea level and 1650m.

Vernacular name. Hamhama (Yemen, Socotra, *Miller et al.* 8566).

Variation and taxonomic remarks. The protologue of *Campylanthus spinosus* was rather brief, but a more comprehensive description, accompanied by an excellent illustration, appeared five years later (Balfour, 1888: 203, tab. 61, fig. 1–6).

Campylanthus spinosus is liable to some variation in leaf size, flower size and leaf shape. The variation in leaf shape resulted in the description of *C. spinosus* var. *kuriensis* by Smith (1971) from a single collection. This collection (*Smith & Lavranos* 706) does indeed have unusually wide leaves, but as intermediate specimens are known from Abd el Kuri (*Simony* s.n.), Socotra (*Thulin & Gifri* 8566) and Somalia (*Thulin & Warfa* 5891) I see no reason for retaining *C. spinosus* var. *kuriensis* at any rank.

Chiovenda (1929) described *Chamaeacanthus pumilus* (*Acanthaceae*) from Somalia, but subsequent research has shown this to be a synonym of *Campylanthus spinosus* (Miller, 1982).

Campylanthus spinosus is a distinctive species characterized by its dense, shortly sericeous indumentum and spinescent branch tips. It is probably related to *C. incanus*, which has a similar habit and very similar flowers.

Specimens examined. Somalia. **Sanaag**: Ceerigaabo, 10°38′N, 47°22′E, 1500m, 7 ix 1956, *Simmons* B50 (EA, K); 1650m, 3 x 1941, *Peck* 205 (EA, K). **Bari**: Gees Gwardafuy, 11°50′N, 51°17′E, 100–150m, 19 xi 1986, *Thulin & Warfa* 5891 (K, UPS); 1km E of Qardho town, 9°30′N, 49°05′E, 720m, 26 iii 1981, *Beckett* 947 (EA, K); "Bur Hossa Wein", SE of Dhuudo, 4 iv 1954, *Merla, Azzaroli & Fois* s.n. (FT); Sagaleh, near Bandarbeyla, 8 i 1954, *Merla, Azzaroli & Fois* s.n. (FT); Nafagallo, near Bandarbeyla, 7 i 1954, *Merla, Azzaroli & Fois* s.n. (FT). **Nugaal**: Laascaanood, 12 x [year unknown; 20th C.], *Richards* s.n. (K); 95km E of Sinujiif, 40km NW of Eyl airstrip, 1 i 1973, *Bally & Melville* 15467 (K); 28km SW of Garoowe on Gaalkacyo road, 8°12′N, 48°16′E, 600m, 5 v 2001, *Thulin, Abdi Dahir, Abdulkadir Khalid & Ahmed Osman* 10439 (UPS). **Mudug**: 43km S of Hobyo, 60m, 28 xi 1985, *Lavranos & Carter* 23477 (EA, K); Without precise locality, *Puccioni & Stefanini* s.n. (FT). Yemen. **Socotra**: R'as Qatanan, 12°21′N, 53°33′E, 20m, 16 i 1994, *Thulin & Gifri* 8566 (K, UPS); 15m, 18 ii 1953, *Popov* GP/So/135 (EA, BM); Base of R'as Mami on south side, 400m, 2 iii 1989, *Miller et al.* 8566 (UPS); Below Majah escarpment, Hammaderoh, 12°35′N, 54°17′E, 360m, 6 iv 1967, *Smith & Lavranos* 285 (K); Above path to Qadub, which follows round the base of the N slopes of Jabal Rughid, 12°37′N, 53°58′E, 450m, 13 iv 1967, *Smith & Lavranos* 366 (EA, K, W, WAG); Jabal Rughid, 450m, 4 iv 1953, *Popov* GP/So/353 (BM); Qallansiya, NE Diorit Peak, 10 iv 1881, *Schweinfurth* 261 (K); Coast between Qallansiya and Qaysuh, 12°40′N, 53°29′E, 0m, 26 iii 1967, *Smith & Lavranos* 128 (K); Without precise locality, 1897, *Bent* s.n. (K); Abd al Kuri, northern slopes of Jabal Eimali, 21 i 1899, *Simony* s.n. (WU).

13. Campylanthus incanus A.G. Mill., Notes Roy. Bot. Gard. Edinburgh 38: 376, fig. 2i (1980). Type: Somalia, Bari, above Galgalo, 1150m, 28 xi 1972, *Lavranos & Horwood* 9038 (holo. E). **Fig. 11.**

Description. Densely branched dwarf shrub, forming cushions to 30cm high, most parts with dense, bifurcate, isotrichous hairs. *Young branches* somewhat spinescent; *older stems* glabrescent. *Leaves* linear, slightly fleshy, with somewhat revolute margins, 3–17 × 0.5–1mm. *Flowers* 2–3 at ends of branches; *bracts* and *bracteoles* shorter than the pedicels; *pedicels* 1–2mm long, almost glabrous to densely hairy. *Calyx lobes* narrowly elliptic, 2.5–4.5 × 0.7–1.5mm, with acute apices, sparsely hairy, denser at the apices, also with a few very short glandular hairs. *Corolla* pink to pale lilac to pinkish blue with a yellow centre, 9–14mm long, almost glabrous but with a few hairs outside; *tube* 6–9 × 0.8–1.1mm, geniculate below level of calyx mouth, glabrous below insertion of stamens inside; *lobes* broadly obovate, c.3.2–6 × 2.2–5.5mm. *Anthers* c.1.5 × 0.5mm; *filaments* 0.4–0.5mm long. *Ovary* somewhat compressed laterally, abruptly tapering into style. *Style* 1–2mm long; *stigma* with papillose surface. *Capsule* 3.5–4 × 2.2–2.8mm, elliptical, dark brown. *Seeds* c.0.7mm in diam., rounded, wing restricted to funicular region.

Distribution and habitat. *Campylanthus incanus* occurs in northeastern Somalia (Fig. 7), where it usually grows on rocky limestone slopes or escarpments with sparse, low shrub vegetation (e.g. *Commiphora* spp.), but it has also been found on gypsum hills. Apart from the cited material it was also observed and photographed by Mats Thulin at Al Miskaat in the Bari region in January 1997 (Thulin, pers. comm.). The altitudinal range is from 20 to 1550m.

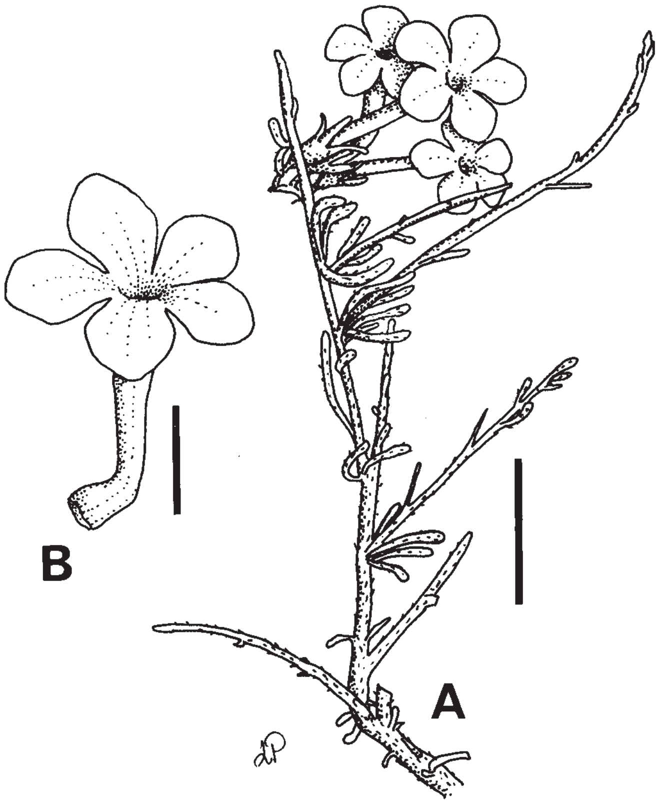

FIG. 11. *Campylanthus incanus*. A. Habit; bar = 1cm. B. Corolla; bar = 5mm.

Variation and taxonomic remarks. *Campylanthus incanus* is a uniform species, showing some variation in leaf size and flower size only.

Campylanthus incanus is related to *C. anisotrichus* and *C. parviflorus*, but is easily distinguished from both these species by the indumentum of bifurcating isotrichous hairs, in contrast to the bifurcating anisotrichous hairs in *C. anisotrichus* and *C. parviflorus*.

Specimens examined. SOMALIA. **Bari**: 8km S of Dhurbo on road towards Ceel Gal, 11°35′N, 50°21′E, 800m, 22 xi 1986, *Thulin & Warfa* 5961 (K, UPS); Ceel Gal, 10 iv 1954, *Merla, Azzaroli & Fois* s.n. (FT); Mijertein, 11°35′N, 50°20′E, 450m, 22 v 1957, *Everard* 7 (BM); Bugo Caleed, 11°12′N, 49°55′E, 1200m, 7 ix 1957, *Newbould* 1078 (K); Cal Miskaat, 5km S of Dadar, 11°06′N, 49°53′E, 1400m s. m., 8 i 2000, *Thulin, Abdi Dahir & Ahmed Osman* 10207A (UPS); 30km S of Bargaal, 11°04′N, 51°03′E, 20m, 24 xi 1985, *Thulin & Warfa* 5511 (K, UPS); 8km from Dalweyn along road to Qardho, 10°11′N, 49°01′E, 850m, 22 v 2001, *Thuli, Abdi Dahir, Abdulkadir Khalid & Ahmed Osman* 10720 (UPS); Above Galgalo, 1150m, 28 xi 1972, *Lavranos & Horwood* 9038 (E); 9°21′N, 50°12′E, 370m, 30 x 1980, *Beckett* 493 (EA, K); 114km N of Garooe on road to Qardho, 5km S of Dan Gorayo, 8°41′N, 49°18′E, 12 xi 1986, *Lavranos & Carter* 24629 (EA, K).

14. Campylanthus anisotrichus (A.G. Mill.) Hjertson & A.G. Mill., Edinburgh J. Bot. 57: 224 (2000). Type: Somalia, Woqooyi Galbeed, Maledere, Gowambohale, 24 i 1945, *Glover & Gilliland* 616 (holo. EA, not seen; iso. K).
Syn.: *Campylanthus incanus* var. *anisotrichus* A.G. Mill. [as "*anisotricha*"], Notes Roy. Bot. Gard. Edinburgh 40: 331 (1982).

Description. Densely branched dwarf shrub to 30cm high. *Older branches* greyish brown, densely covered with appressed, bifurcate, anisotrichous hairs, with longest arm retrorse, glabrescent below; *young branches* spinescent, with purplish, glabrescent tips. *Leaves* linear to very narrowly obovate, fleshy, with somewhat revolute margin, 2–14 × 0.5–1.5mm, covered with simple and bifurcate hairs. *Flowers* c.2–3 at ends of branches; *bracts* and *bracteoles* shorter than pedicels; *pedicels* 2–2.5mm long, glabrous above, with bifurcate hairs below. *Calyx lobes* narrowly ovate to narrowly triangular, 3.5–4 × 0.7–1mm, almost glabrous with a few very short glandular and simple hairs, particularly along the margins of the lobes, sometimes some bifurcate hairs also present. *Corolla* purple, 8–11mm long, almost glabrous, with a few anisotrichous hairs externally; *tube* 6–8 × 1mm, geniculate below level of calyx mouth, glabrous below insertion of stamens inside; *lobes* broadly obovate, c.3 × 2.5mm. *Stamens* inserted c.3mm above the corolla base; *filaments* c.0.5mm long; *anthers* c.1.6 × 0.6mm. *Ovary* tapering abruptly into style. *Style* c.0.6mm long; *stigma* with markedly papillose surface. *Capsule* c.2.7 × 2mm, ovoid, glabrous, dark brownish red. *Seeds* c.0.8mm in diam., rounded, wing restricted to funicular region.

Distribution and habitat. *Campylanthus anisotrichus* is known only from three collections from northern Somalia (Fig. 7), where it grows on open, stony ground on limestone at altitudes from 100 to 1500m. Associated taxa from the 1500m locality included *Dracaena ombet* Kotschy & Peyr., *Tarchonanthus camphoratus* L., *Monotheca buxifolia* (Falc.) A. DC., *Buxus hildebrandtii* Baill., *Dodonaea angustifolia* L.f., *Euphorbia* sp., *Aloe* sp. and *Kalanchoe* sp.

Variation and taxonomic remarks. The few collections studied show no notable variation. *Campylanthus anisotrichus* is closely related to *C. parviflorus*; for the differences between the two, see under the latter.

Specimens examined. SOMALIA. **Woqooyi Galbeed**: Anberoh, near Karin near Berbera, 100m, 2 v 1945, *Glover & Gilliland* 1180 (EA, K). **Sanaag**: 140km WSW of Ceerigaabo, 10°24′N, 46°06′E, 1500m, 27 xi 1980, *Hemming & Watson* 3316 (EA, K).

15. Campylanthus parviflorus Hjertson & A.G. Mill., Edinburgh J. Bot. 57: 221 (2000). Type: Somalia, Sanaag, 9km S of Laascaanood, 8°23′N, 47°21′E, 28 xi 1986, *Lavranos & Carter et al.* 24973 (holo. K, iso. EA).

Description. Densely branched, ± aphyllous shrublet, forming cushions c.15cm high and 30cm in diam.; most parts with appressed, bifurcate, anisotrichous hairs with longest arm retrorse. *Older branches* somewhat gnarled, whitish brown, densely hairy; *ultimate branches* ± divaricate, dark brown, 3–10mm long, glabrescent, tips spinescent, light brown. *Leaves* linear, fleshy, 1–8 × 0.3–0.7mm, sparsely covered with simple and bifurcate hairs, glabrescent. *Flowers* apparently 2–3 at ends of branches; *bracts* and *bracteoles* shorter than the pedicels; *pedicels* 1–2mm long, sparsely covered with simple and bifurcate hairs. *Calyx lobes* narrowly ovate to narrowly triangular, 1.5–2 × 0.3–0.6mm, pilose with simple and ± antrorse bifurcate hairs. *Corolla* white, c.4mm long, with sparse hairs externally; *tube* c.3 × 1mm, glabrous below insertion of stamens inside, upper geniculation above calyx mouth; *lobes* broadly obovate, c.1.75 × 1.75mm. *Anthers* c.1.6 × 0.3mm; *filaments* c.0.3mm long. *Ovary* abruptly tapering into style. *Style* c.0.5mm long. *Capsule* c.2.2 × 2mm, ovoid, brownish red. *Seeds* (immature) c.0.8mm in diam., ± comma-shaped, wing restricted to funicular region.

Distribution and habitat. *Campylanthus parviflorus* is known only from the type locality (Fig. 8), where it grows on rocky slopes and gypsum hills with denuded sparse *Lannea* scrub at an altitude of c.730m.

Taxonomic remarks. *Campylanthus parviflorus* with its small white flowers and divaricate, glabrescent and spinescent branches is a distinctive species. Its closest relative seems to be *C. anisotrichus*, which grows some 300km further to the northwest in Somalia. The latter also has an indumentum of bifurcating, anisotrichous hairs, and branches that are usually somewhat spinescent, albeit not so pronounced as in *C. parviflorus*. However, it differs in the branching pattern, which is not divaricate as in *C. parviflorus*, and in purple flowers that are 8–11mm long, as opposed to white and up to about 4mm long in *C. parviflorus*.

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