The genus Leysera (Compositae)

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Bremer, K. 1978 09 30: The genus Leysera (Compositae). *Bot. Notiser 131:* 369–383. Stockholm. ISSN 0006-8195.

Leysera L. (Compositae-Inuleae-Athrixiinae), a genus of four species, is revised. *L. longipes* Bremer from the SW Cape (S Africa) is described. *L. gnaphalodes* (L.) L. and *L. tenella* DC. are two widespread species in southern Africa. *L. leyseroides* (Desf.) Maire is a closely related species, the sister species of *L. tenella,* distributed in N Africa, S Spain, and SW Asia. The plant known as *L. montana* Bolus is excluded from the genus *Leysera.* Chromosome numbers 2n = 8 are reported for *L. gnaphalodes* and *L. tenella.*

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Leysera L. is a genus of the Compositae-Inuleae-Athrixiinae. In its present circumscription it comprises three southern African species and one species from N Africa, S Spain, and SW Asia. I have studied the genus in the field in southern Africa and two species (*L. gnaphalodes* and *L. tenella*) have been grown in greenhouses in Stockholm. I have examined collections from the following herbaria: B, BM, BOL, G, G-DC (only microfiches), K, L, LINN, M, MO, NBG, P, PRE, S, SAM, U, UPS, UPS-THUNB (Herbarium Thunberg at UPS), W, and Z (abbreviations according to Holmgren & Keuken 1974). A list of examined specimens is kept at the Museum of Natural History, Section for Botany, Stockholm.

History and nomenclature

One of the four *Leysera* species, to us known as *L. gnaphalodes,* is not uncommon on the hills and slopes surrounding Cape Town. There it was gathered and brought to Europe by the early collectors at the Cape. Paul Hermann (1687 p. 68) was probably the first to name it, as *"Aster Aethiopicus, Stoechadis foliis flore aureo"*. Vaillant (1722) established the genus *Asteropterus* with three species and the first of these is our *L. gnaphalodes,* then named *"Asteropterus luteus, Laricis foliis lanuginosis"*.

Linnaeus probably got to know the plant from a specimen in Oldenland's herbarium, which was brought to Uppsala by Burman (fil.) for examination by Linnaeus. Most of the plants described in 'Plantae rariores africanae' (Linnaeus 1760) were based on Oldenland's specimens (Nordenstam 1961 p. 278). This should also apply to *Callisia gnaphalodes,* which is the name that Linnaeus (1760) originally gave to the plant. This Oldenland herbarium has not been traced but it is possible that it is preserved at the Institut de France in Paris (Nordenstam 1968 p. 92). There is no doubt about the identity of Linnaeus' species, however, since there are specimens of *L. gnaphalodes* in the Linnaean herbarium in London (LINN specimen no. 1008: 1, 2, 4, and 5). Linnaeus had himself changed the genus from *Callisia* to *Leysera.* In 'Plantae rariores africanae' (Linnaeus 1760) he had certainly used the former name by mistake, since *Callisia* was already occupied for an American genus of the Commelinaceae (Loefling 1758) Possibly Linnaeus had discussed the plant with Burman, and by mistake named it *Callisia gnaphalodes* instead of *Callicornia gnaphaloides,* which is the name that Burman (1768) later gave to this species.

In October 1760 the young German botanist Friedrich Wilhelm von Leysser sent his new 'Flora halensis' (Leysser 1760) to Linnaeus and Leysser was rewarded with the new generic name *Leysera*. It was published in 1763 in the second edition of 'Species plantarum' and in the sixth volume of 'Amoenitates academicae', where the dissertation 'Plantae rariores africanae' was reprinted, now with the generic name of *Callisia gnaphalodes* changed to *Leysera*. Leysser was overwhelmed by the honour bestowed upon him and in a letter dated October 1764 he wrote to Linnaeus that he was "touched to the depth of his heart".(Leysser's correspondence with Linnaeus has been published by Schmid 1928.) Leysser originally spelled his name with one s only and this is the spelling Linnaeus used in the generic name *Leysera*. Later authors have changed it to *Leyssera* but we should adopt the original spelling *Leysera*. This also applies to the specific epithets *gnaphalodes* (not *gnaphaloides* or *gnaphalioides)* and *leyseroides* (not *leysseroides)*.

The same year as Linnaeus published *Leysera,* Adanson (1763) adopted the old generic name *Asteropterus* of Vaillant (see above). Adanson did not mention any species but he cited Hermann's (1687 p. 71) figure of *Leysera gnaphalodes* so that there is no doubt which plant he had in mind. It is not definitely settled which book was first published, volume two of the second edition of 'Species plantarum' or volume two of Adanson's 'Famille des plantes'. Rothmaler (1944) ascribed the priority to *Asteropterus* Adans., and made a number of new combinations. He has been followed by Täckholm (1974), whereas most other recent authors, e.g. Tutin (1976) and Levyns (1950) have adopted *Leysera* L. According to F. A. Stafleu (pers. comm.) it is likely that Linnaeus' book came out in July 1763 and that Adanson's book came out in August 1763. A statement to this effect is also planned in the third volume of the second edition of 'Taxonomic literature', where Linnaeus will be treated. Consequently, and in concordance with general practice, I have adopted *Leysera* L. rather than *Asteropterus* Adans.

Thunberg (1800) described a number of new *Leysera* species. Only *L. incana* Thunb. belongs to *Leysera,* however, and it is here regarded as conspecific with *L. gnaphalodes*.

In the beginning of the nineteenth century rich collections were made by Burchell, Drège, Ecklon, and Zeyher in South Africa. De Candolle had access to these collections and he described (De Candolle 1838 a) the second species, *Leysera tenella,* which occurs in the drier, inner parts of S Africa.

In the Mediterranean–SW Asian region there is a third species, known as *Leysera leyseroides*. It was first described by Desfontaines (1799). Its isolated systematic position, not in the otherwise S African genus *Leysera* but among other Mediterranean Compositae, is probably the reason for the establishment of three monotypic genera based on this species (*Longchampia* Willdenow 1811, *Leptophytus* Cassini 1817, and *Pseudocrupina* Velenovský 1923 according to Merxmüller et al. 1977 p. 581). The combination *Leysera leyseroides* should be ascribed to Marie (1929) and not to Dandy (in Andrews 1956) as indicated by some authors.

The fourth species, *Leysera longipes,* is from the Cape. It is described here from recently collected material.

Delimitation and systematic position

In their systematic review of the Inuleae Merxmüller et al. (1977) reduced the number of subtribes to three, Inulinae s. ampl., Gnaphaliinae s. ampl. and Athrixiinae s. ampl. Within Inuleae-Athrixiinae they recognized 24 genera with c. 220 species, arranged into 7 informal groups. The *Athrixia* group comprises *Antithrixia, Arrowsmithia, Athrixia, Leysera, Macowania, Relhania,* and *Rosenia*. Of these genera *Antithrixia, Leysera, Relhania,* and *Rosenia* constitute a monophyletic group, defined by their ventrally furrowed and pubescent (if not secondarily glabrous) leaves, otherwise a most uncommon feature (Bremer 1976 a p. 9).

Within this group the four genera are defined by pappus characters. In the Inuleae-Athrixiinae the pappus generally consists of several barbellate bristles. This is also the case in *Antithrixia,* whereas the other three genera show derived pappus features, reductions in number of bristles and development of pappus scales. In *Leysera* the disc-floret pappus consists of scales and 5 (or sometimes fewer) bristles, in *Rosenia* it consists of scales and generally 1–2 bristles (Bremer 1976 b), and in *Relhania* there is a disc-floret pappus of scales only (Bremer 1976 a). In all three genera there are only scales and no bristles in the ray-floret pappus. These differences are rather slight and the derived conditions might conceivably have been reached more than once but there is no information indicating that the genera should be polyphyletic or paraphyletic. *Leysera* is also distinguished by its solitary capitula on long peduncles.

The plant known as *Leysera montana* Bolus (1905) is here excluded from the genus *Leysera*. This species has a pappus of many barbellate bristles, as in *Antithrixia* and many other Inuleae-Athrixiinae. It has solitary capitula on long peduncles, a derived feature shared by the remaining *Leysera* species, but keeping *L. montana* within *Leysera* for that reason would severely weaken the definition of the genus as outlined above. *L. montana* cannot be transferred to *Antithrixia* on account of the similar pappus, since this is a primitive feature, which cannot indicate a monophyletic group. Such a grouping would make *Antithrixia* a symplesiomorphous, paraphyletic genus. The remaining solution is to describe a new genus for *L. montana* and this will be done in a forthcoming issue of this journal.

Morphological aspects

Habit. Most of the species of Inuleae-Athrixiinae are perennial shrubs or shrublets. *L. gnaphalodes* is also a perennial shrublet and there is no doubt that this is the primitive condition in *Leysera*. *L. tenella* and *L. leyseroides* are annuals and *L. longipes* is a suffrutex with subterranean, woody rhizomes, adaptations for survival during dry periods and veld fires, respectively.

Leaves. The genera *Antithrixia, Leysera, Relhania,* and *Rosenia* are characterized by their ventrally furrowed and pubescent leaves. The leaves of *L. gnaphalodes, L. tenella,* and *L. leyseroides* are of this type, whereas *L. longipes* and several other species within this group of genera have glabrous leaves, a derived condition in the group. However, all species of *Leysera* have ± glandular leaves and in *L. longipes* the glands are particularly conspicuous with rather long, stiff stalks.

Peduncles. All species of *Leysera* have solitary capitula on long peduncles. In related genera sessile capitula is a prevailing and primitive condition, even if some species in *Relhania* have developed peduncles independently.

Receptacle. The receptacle is epaleate in all species of *Leysera* but in *L. gnaphalodes, L. tenella,* and *L. leyseroides* there are projections, i.e. outgrowths from the receptacle between the florets. At the ventral side of each ray-floret these outgrowths are developed into scales, sometimes several mm long. After anthesis the ray-floret achenes remain clasped between these scales and the innermost involucral bracts long after the dispersal of the disc-floret achenes. The condition is easily observed on fruiting specimens with spreading involucral bracts, where the scales and their corresponding ray-floret achenes are arranged like the rays of a star around the empty receptacle. A similar condition with the marginal achenes held by the involucral bracts only is known in *Hedypnois, Rhagadiolus,* and other genera (Zohary 1950), obviously a case of convergent evolution.

Florets. The *Leysera* species have bisexual, perfect or in *L. longipes* possibly ♀-sterile disc-florets and female, fertile ray-florets. In *L. leyseroides* the ray-floret lamina is much reduced and not exceeding the involucre.

In *L. longipes* the floret tubes are glandular. The multicellular glands are rather long-stalked with a small head. In *L. gnaphalodes, L. tenella,* and *L. leyseroides* the floret tubes are furnished with multicellular, subulate–conical hairs (Fig. 2 A). These hairs consist of the stalks of reduced glands. A parallel development is known in *Relhania,* where conditions intermediate between glands and hairs occur (Bremer 1976 a p. 20).

The anthers have a sterile, acute–obtuse or truncate apical appendage and sterile, subulate, minute tails (Fig. 1 C, F). The disc-floret styles have narrowly oblong, apically penicillate and rounded–truncate style-branches and the stigmatic areas are arranged in two discrete lines (Fig. 1 A, D).

Achenes. The hairs on the achenes of *L. gnaphalodes, L. tenella,* and *L. leyseroides* are the common Compositae twin hairs (Hess 1938), tricellular with two parallel, elongated cells and a lateral, basal cell. In these *Leysera* species pubescent achenes is thus the primitive condi-

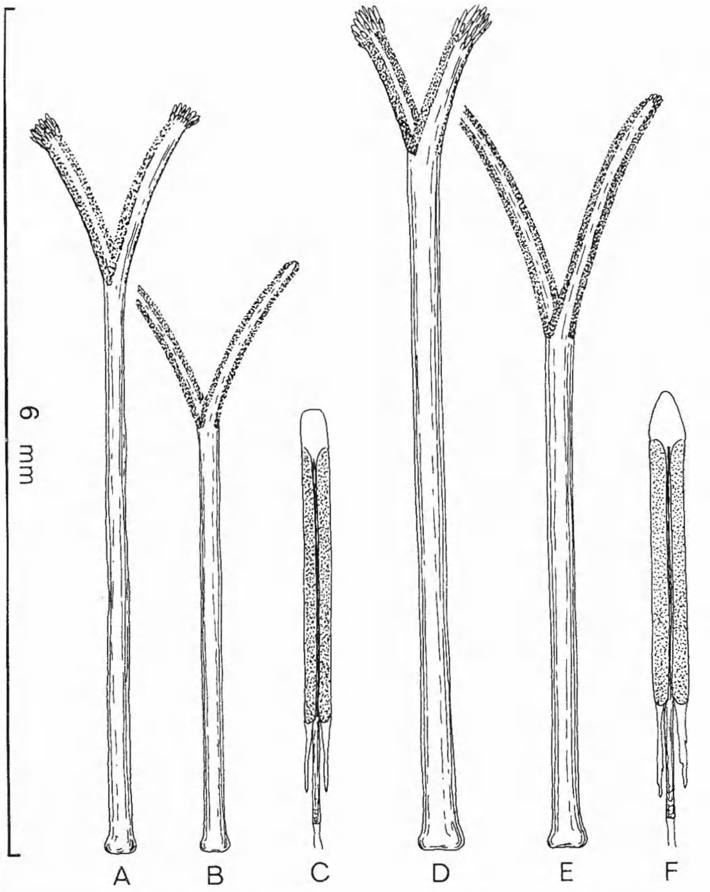

Fig. 1. – Styles and stamens of *Leysera*. – A, D: Disc-floret styles. – B, E: Ray-floret styles. – C, F: Stamens. – A–C: *L. gnaphalodes*, Bremer 167 (S). – D–F: *L. longipes*, Esterhuysen 29941 (BOL).

tion, whereas the glabrous achenes of *L. longipes* are derived.

In *L. gnaphalodes*, *L. tenella*, and *L. leyseroides* the epidermal achene cells are thickened at their upper end and somewhat imbricated (Fig. 2 B), whereas the achene surface of *L. longipes* is smooth.

Pappus. In Inuleae-Athrixiinae most genera have a pappus of many bristles. In *Leysera* there are a few bristles in the disc-florets only and a crown of inner scales, possibly reduced bristles or perhaps outgrowths from the apical rim of the achene. The pappus bristles may be barbellate or plumose (see Figs. 2 C–D and 6–9). It is difficult to say which condition is primitive and derived, respectively, but since the bristles are barbellate in the related genera, I believe that the plumose bristles of *L. gnaphalodes*, *L. tenella*, and *L. leyseroides* are derived. Apart from bristles the pappus consists of many, subulate scales in *L. gnaphalodes* and *L. longipes* and fewer, wider, flat scales in *L. tenella* (Fig. 2 C) and *L. leyseroides*.

Pollen. The pollen is similar to that of *Relhania*, *Rosenia*, and *Antithrixa* species. It has been investigated by Besold (1971 p. 18) and the description will not be repeated here.

Chromosome number. Nordenstam (1967) reported $2n=8$ for *L. gnaphalodes* and I have found the same number in both *L. gnaphalodes* and *L. tenella*. It is a remarkably low number in the tribe Inuleae, where $x=7$ and $x=10$ are prevailing. In the related genus *Relhania* $2n=14$ and $2n=10$ are known (Bremer 1976 a). The chromosome counts were made from squashed root-tips fixed in Carnoy and stained in aceto-orcein.

Primitive and derived conditions. These are outlined in Table 1, and will form a foundation for the phylogenetic reconstruction presented below.

Chemistry

Bohlmann and collaborators have investigated a great number of Compositae species, including *L. gnaphalodes* and *L. tenella*. From these two species they have reported pentaynene, a polyacetylene common in the Inuleae (Harborne 1977 p. 617) and a unique benzofurane derivative, named Leysseral-angelicate (Bohlmann & Zdero 1972). It is not known from the 9 investigated species of the related genera *Relhania* and *Rosenia* (Bohlmann pers. comm.).

Phytogeography and phylogeny

The Inuleae-Athrixiinae is essentially a southern African group. Only a few species of *Athrixia*, *Macowania*, and *Stoebe* occur in tropical Africa and Madagascar. Apart from the Mediterranean genus *Phagnalon*, treated as an "informal appendix" to the Inuleae-Athrixiinae by Merxmüller et al. (1977 p. 598), *Leysera* is the only genus which reaches further north across Sahara. The approximate total range of the genus is outlined in Fig. 3. Three of the four species occur in southern Africa, whereas *L. leyseroides* has a wide, northern distribution. No doubt the ancestor of the genus *Leysera* belonged to what is now the S African flora and the recent, wide distribution of the genus was probably achieved during the evolution of the species, to be discussed below.

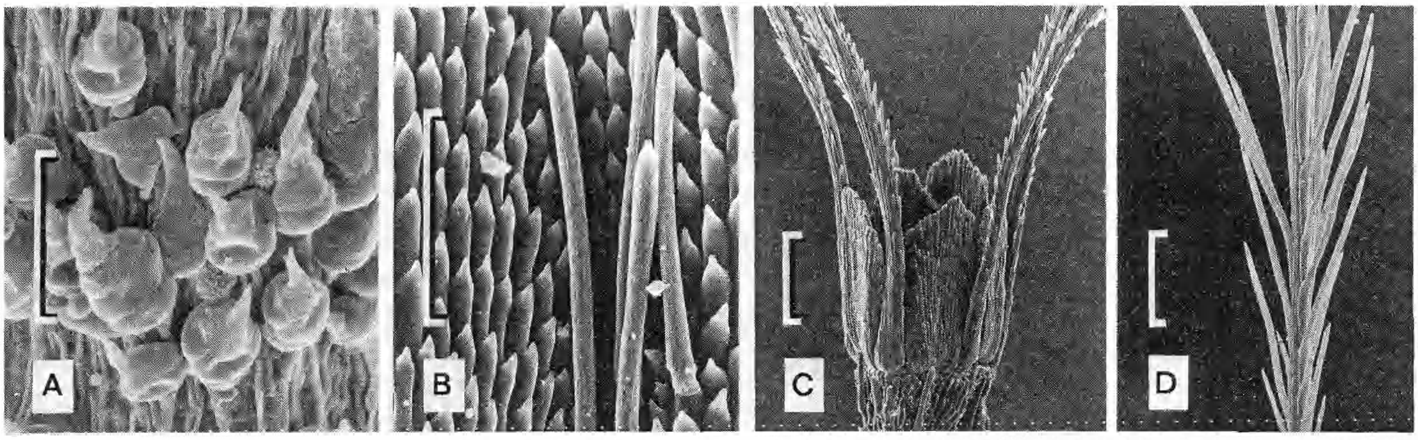

Fig. 2. Electroscan photomicrographs of floret tube hairs and achenes of *Leysera*. The length of the scales is 0.1 mm. – A: Floret tube hairs (and two pollen grains) of *L. gnaphalodes*. Similar hairs occur in *L. tenella* and *L. leyseroides*. – B: Achene surface with imbricated cells and hairs of *L. leyseroides*. *L. gnaphalodes* and *L. tenella* are similar. – C: Basal part of pappus of *L. tenella*. – D: Middle part of pappus bristle of *L. tenella* showing the transition from the barbellate to the plumose part. The pappus of *L. leyseroides* is similar. – A: Marloth 11542 (PRE). – B: Rechinger 9456 (M). – C–D: Leistner 2096 (NBG).

The phylogeny of the *Leysera* species (Fig. 4) is reconstructed with the method developed by Hennig (1966). Its application to botany is outlined by Bremer & Wanntorp (1978). The cladogram in Fig. 4 shows *L. tenella* and *L. leyseroides* as sister species, together forming a monophyletic unit, the sister group of *L. gnaphalodes*. These three species make a larger monophyletic group, the sister group of *L. longipes*. All four species constitute the monophyletic genus *Leysera*. Monophyletic groups are established by the joint possession of uniquely derived conditions, synapomorphies. In the cladogram these synapomorphies are indicated by bars with letters corresponding to the derived conditions in Table 1. The sister group relationships are supported by the vicarious distributions shown by the southern *L. tenella* and the northern *L. leyseroides* and, although with some overlapping, *L. gnaphalodes* mainly distributed in the southwestern and southern Cape (Fig. 6) and *L. tenella* + *L. leyseroides* mainly distributed in the Karoo region and SW Africa (Fig. 7) + the Mediterranean–SW Asian region.

One early branch of the genus *Leysera* is now represented by the aberrant *L. longipes,* which grows in a few mountain localities in the southwestern Cape. Another branch led to the homogeneous group of *L. gnaphalodes, L. tenella,* and *L. leyseroides*. The ancestor of this group was a perennial, which split into a perennial species, possibly occuring in the Cape,

Table 1. Primitive and derived conditions in *Leysera*.

Primitive		Derived	
A	Perennial	a	Annual
B	Shrublet	b	Suffrutex with woody rhizomes
C	Leaves ventrally furrowed and tomentose	c	Leaves ventrally flat and glabrous
D	Leaf glands with short stalks	d	Leaf glands with long stalks
E	Capitula sessile	e	Capitula on long peduncles
F	Receptacle ± smooth	f	Receptacle with scale-like outgrowths
G	Ray-floret lamina exserted	g	Ray-floret lamina not exceeding involucre
H	Floret tubes with glands	h	Floret tubes with hairs
I	Achenes pubescent	i	Achenes glabrous
J	Achene surface smooth	j	Achene surface with cells imbricated
K	Disc-floret pappus of bristles only	k	Disc-floret pappus of bristles and scales
L	Pappus bristles barbellate	l	Pappus bristles plumose
M	Pappus scales subulate	m	Pappus scales wide, flat

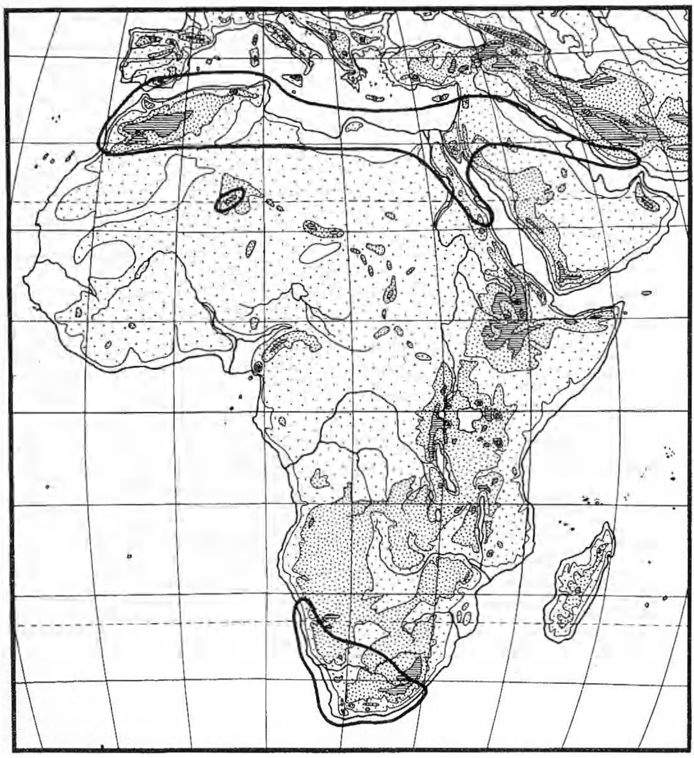

Fig. 3. The approximate total range of *Leysera*.

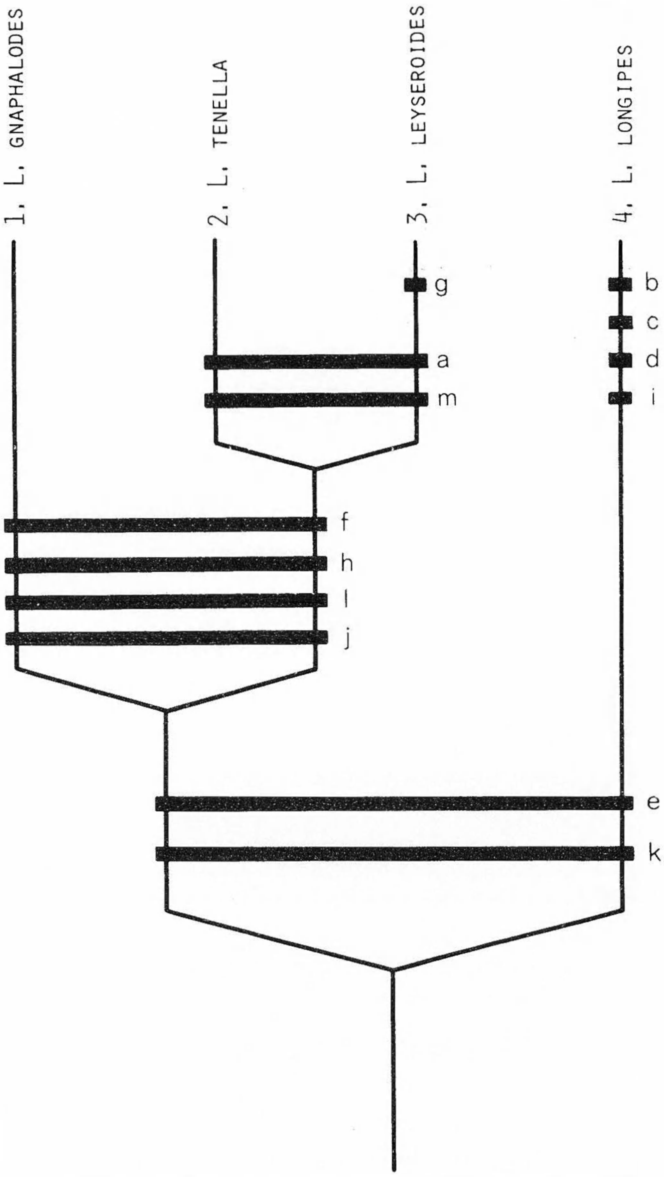

Fig. 4. Cladogram of the *Leysera* species. Bars indicate synapomorphies and letters correspond to the derived conditions in Table 1.

and an annual species, adapted to the dry conditions of the inner areas. The branch of the perennial species is now represented by *L. gnaphalodes,* whereas the annual species became the ancestor of *L. tenella* and *L. leyseroides*. During a period of drier climate this annual ancestor expanded from S Africa to N Africa and the Mediterranean–SW Asian region. Following climatic change it split and developed into the southern *L. tenella* and the northern *L. leyseroides*.

Obviously not only vicariance but also dispersal is responsible for the phytogeography of the *Leysera* species. This is illustrated in Fig. 5 with dispersal and vicariance models (Platnick & Nelson 1978 p. 2) for the monophyletic group of *L. gnaphalodes, L. tenella,* and *L. leyseroides.* A traditional dispersal model postulates a centre of origin (in this case C = roughly the Cape region), from where the ancestor is dispersed (to K = roughly the Karoo region and subsequently to N = roughly N Africa) and developed into new species. A vicariance model explains the recent distributions (C, K, and N) as fragmentation of an initial, continuous area (C + K + N). In the actual case I suggest the combined vicariance and dispersal explanation at the bottom of Fig. 5, according to which the annual ancestor of *L. tenella* and *L. leyseroides* expanded from the Karoo region (K) of S Africa to N Africa (N). Subsequently it split into the two sister species, yet another example of the well-known floristic links between the arid areas of N and S Africa. The subject has been reviewed by e.g. de Winter (1971) and Werger (1978 p. 240).

TAXONOMY

Leysera L.

Linnaeus 1763 a p. 1249, 1763 b p. 104, 1764 p. 431. – *"Leyseria"* Necker 1790 p. 11. – *"Leyssera"* auct. mult. – Type species: *L. gnaphalodes* (L.) L.

Callisia Linnaeus 1760 p. 23 (non Loefling 1758 p. 305). – Type species: *C. gnaphalodes* L. =*Leysera gnaphalodes* (L.) L.

Asteropterus (Vaillant 1722 p. 313), Adanson 1763 p. 124. – Type species: *A. Callicornia* (L.) Gaertn. =*Leysera gnaphalodes* (L.) L.

Callicornia Burman fil. 1768 p. 24. – Type species: *C. gnaphaloides* Burm. f. =*Leysera gnaphalodes* (L.) L.

Longchampia Willdenow 1811 p. 159. – Type species: *L. capillifolia* Willd. =*Leysera leyseroides* (Desf.) Maire

Leptophytus Cassini 1817 p. 11. – Type species: *L. leyseroides* (Desf.) Cass. =*Leysera leyseroides* (Desf.) Maire

Pseudocrupina Velenovský 1923 p. 6. – Type species: *P. arabica* Velen. =*Leysera leyseroides* (Desf.) Maire

Annual or perennial herbs, suffrutices or shrublets. *Leaves* alternate or occasionally opposite, seldom crowded on lateral brachyblasts, sessile, entire, linear or sometimes narrowly elliptic–lanceolate, acute–obtuse, mid-ribbed, glabrous or pubescent, glandular. *Capitula* solitary on long peduncles, heterogamous. *Involucre* urceolate–cyathiform–campanulate. Involucral bracts in several rows, imbricated, smooth and glabrous or sometimes laxly tomentose or glandular dorsally, yellowish brown. *Receptacle* epaleate, flat–convex, almost smooth or with projections or scale-like outgrowths. *Ray-florets* female, fertile. Tube cylindrical–somewhat triquetrous, glabrous or with scattered glands or multiceullular hairs. Lamina elliptic–elliptic-oblong, yellow, occasionally with a dorsal brownish stripe, 4- or seldom up to 8-veined, apically 3-lobed. Style terete, bifid, somewhat swollen at base; style-branches semiterete, obtuse, 1/4–1/2 of the style length. *Achenes* as in disc-florets but with more dense pubescence and pappus without bristles. *Disc-florets* perfect or sometimes possibly ♀-sterile. Corolla divided into a lower, cylindrical tube and an upper, narrowly cyathiform limb, yellow, 5-lobed; tube glabrous or with scattered glands or multicellular hairs; corolla lobes ovate-triangular, dorsally often gland-dotted. Anthers linear, with a sterile, flat, acute–obtuse–truncate apical appendage and sterile, subulate, entire or sometimes slightly branched, minute tails, <1/4 of the anther length. Style terete, bifid, somewhat swollen at base, slightly longer than corolla; style-branches semiterete, narrowly oblong, apically penicillate, rounded–truncate; stigmatic areas in two discrete lines. *Achenes* somewhat angular–terete, linear in outline, glabrous or with scattered, tricellular hairs (twin hairs), brown. Pappus of free–somewhat connate inner scales and 5 or often only 2–4 outer, barbellate or plumose bristles.

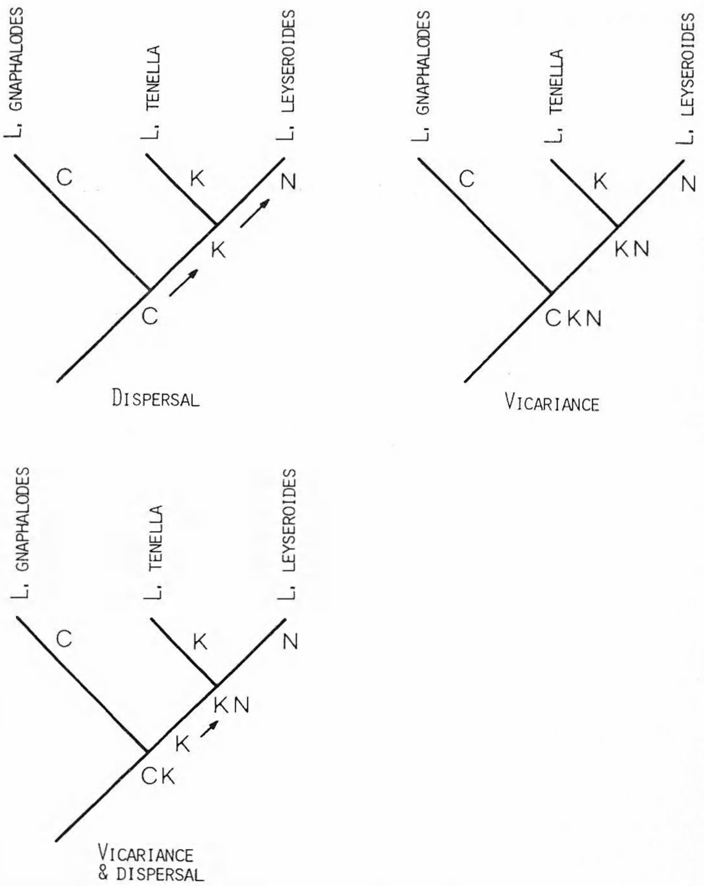

Fig. 5. Dispersal and vicariance models for *Leysera gnaphalodes, L. tenella,* and *L. leyseroides.* Letters indicate geographic regions, C = roughly the Cape region, K = roughly the Karoo region, and N = roughly N Africa. Arrows indicate dispersal.

Key to the species

1. Suffrutex with few-branched stems from woody rhizomes and always with conspicuously glandular leaves; disc-floret pappus bristles barbellate but not plumose . . . . 4. *L. longipes*
– Annual–perennial, branched herbs or shrublets with a normal primary root and more or less, often inconspicuously glandular leaves; disc-floret pappus bristles at least apically distinctly plumose 2
2. Perennial shrublet; disc-floret pappus bristles distinctly plumose all the way except at the extreme base . . . . 1. *L. gnaphalodes*
– Annual herbs; disc-floret pappus bristles basally barbellate and distinctly plumose only above the middle 3

3. Ray-floret lamina exserted, spreading (southern Africa) .... 2. *L. tenella*
– Ray-floret lamina not exceeding involucre, straight (N Africa, S Spain and SW Asia) ...... 3. *L. leyseroides*

1. **Leysera gnaphalodes** (L.) L.

Linnaeus 1763 a p. 1249, 1763 b p. 104. – *Callisia gnaphalodes* Linnaeus 1760 p. 23. –*Leysera tenuifolia* Salisbury 1796 p. 202, nom. superfl. – *Asteropterus gnaphalodes* (L.) Rothmaler 1944 p. 4. –Type: Herb. Oldenland, not traced. See under History and nomenclature.

Callicornia gnaphaloides Burman fil. 1768 p. 24, excl. syn. –*Leysera Callicornia* Linnaeus 1771 p. 286. –*Asteropterus Callicornia* (L.)Gaertner 1791 p. 460. – Lectotype: Herb. Burman (G).

Leysera incana Thunberg 1800 p. 160. –*Asteropterus incanus* (Thunb.) Rothmaler 1944 p. 4. – Lectotype: Herb. Thunberg 20080 (UPS-THUNB).

Leyssera gnaphaloides (L.) L. var. *β. glandulosa* E. Mey. ex De Candolle 1838 a p. 278. – Lectotype: Karoo, Drège (G-DC, seen in microfiche only).

Leyssera gnaphalioides (L.) L. var. *β. gracilis* Harvey 1865 p. 294. –Type: Herb. Thunberg, not traced. There is a paratype collected by Drège and determined by Harvey in S.

Asteropterus Dinteri Rothmaler 1944 p. 4. –Holotype: Dinter 4155 (B). Isotypes in G, M, PRE, S, and Z.

Asteropterus gracilis Rothmaler 1944 p. 5. –Holotype: Capland, Cathcart, Kuntze (B), not traced, probably destroyed. Isotypes in G, K, and Z.

A tomentose–glabrescent and glandular shrublet, c. 0.2–0.5 m high. *Leaves* laxly–densely set, sometimes crowded on short, lateral branchlets (brachyblasts), linear, 2–25 mm long, 0.5–1 or occasionally 1.5 mm wide, greyish-tomentose to green and glabrescent, ventrally furrowed and somewhat tomentose, glandular. *Peduncles* smooth or seldom laxly tomentose, 15–70 mm long or occasionally only 5–15 mm long. *Involucre* cyathiform–campanulate, 4–20 but usually >8 mm wide. Involucral bracts 20–110, smooth or occasionally laxly tomentose dorsally, acute–obtuse–rounded; outer small and ovate; inner gradually longer and oblong–somewhat spatulate with a scarious and often marginally brown apical limb, 6–11 × 0.8–2.4 mm. *Receptacle* flat–convex, scabrid with small projections or occasionally shortly squamose, furnished with a distal row of acute or apically laciniate, 1–5.5 mm long, persistent scales. *Ray-florets* 8–45. Tube cylindrical, glabrous or with scattered, subulate–conical, multicellular hairs. Lamina elliptic-oblong, 4–12 × 1–3 mm. *Achenes* 2.8–5 mm long, with laxly–densely scattered, slender, tricellular hairs (twin hairs) and often with a basal tuft of similar hairs, remaining clasped between the spreading, receptacular scales and the innermost involucral bracts. Pappus of short, flat, acute–obtuse, white scales but with no bristles. *Disc-florets* 35–450, perfect. Corolla 3.8–6.5 mm long; tube with scattered, subulate–conical, multicellular hairs and often with a collar of similar, densely set hairs just below the limb. Anthers 1.8–3.5 mm long, with a truncate apical appendage. *Achenes* 2.8–5 mm long, glabrous or with few, scattered, slender, tricellular hairs (twin hairs) and often with a basal tuft of similar hairs. Pappus of short, flat, acute–obtuse, white scales and 5 or occasionally 3–4 outer, evenly plumose (except for the extreme base), white bristles.

Flowering period mainly September–November but flowering specimens seen from the whole year.

Chromosome number 2n = 8. Voucher specimens: Bremer 167 (S) and Nordenstam 3291 (S). My own count confirms the first report, made by Nordenstam (1967 p. 222). The plant collected by Nordenstam is of the "*L. incana*-type", discussed below.

Distribution. *L. gnaphalodes* is a not uncommon species on flats and lower mountain slopes of the southwestern Cape. It has a rather wide distribution, extending through the Karoo, to Namaqualand and southern SW Africa in the north and to the Winterberg and Stormberg in the eastern Cape, where it grows in grassland. The distribution shown in Fig. 6 is based on the c. 220 collections examined.

Discussion. This perennial species is variable in habit, foliage, capitula, and involucre. The leaves may be laxly to densely set, greyish-tomentose to green and almost glabrous, and narrow and needle-shaped to more flat and linear. As a result there is a considerable variation in habit between the collections of *L. gnaphalodes*. Furthermore, there are rather small capitula as well as wide, many-flowered capitula, and the involucral bracts may be acute, obtuse, or rounded at apex. Even if some of the variation is due to modification, *L. gnaphalodes* is a polymorphic species consisting of populations with different genetic constitution. In the Malmesbury–Hopefield area on the flats N of

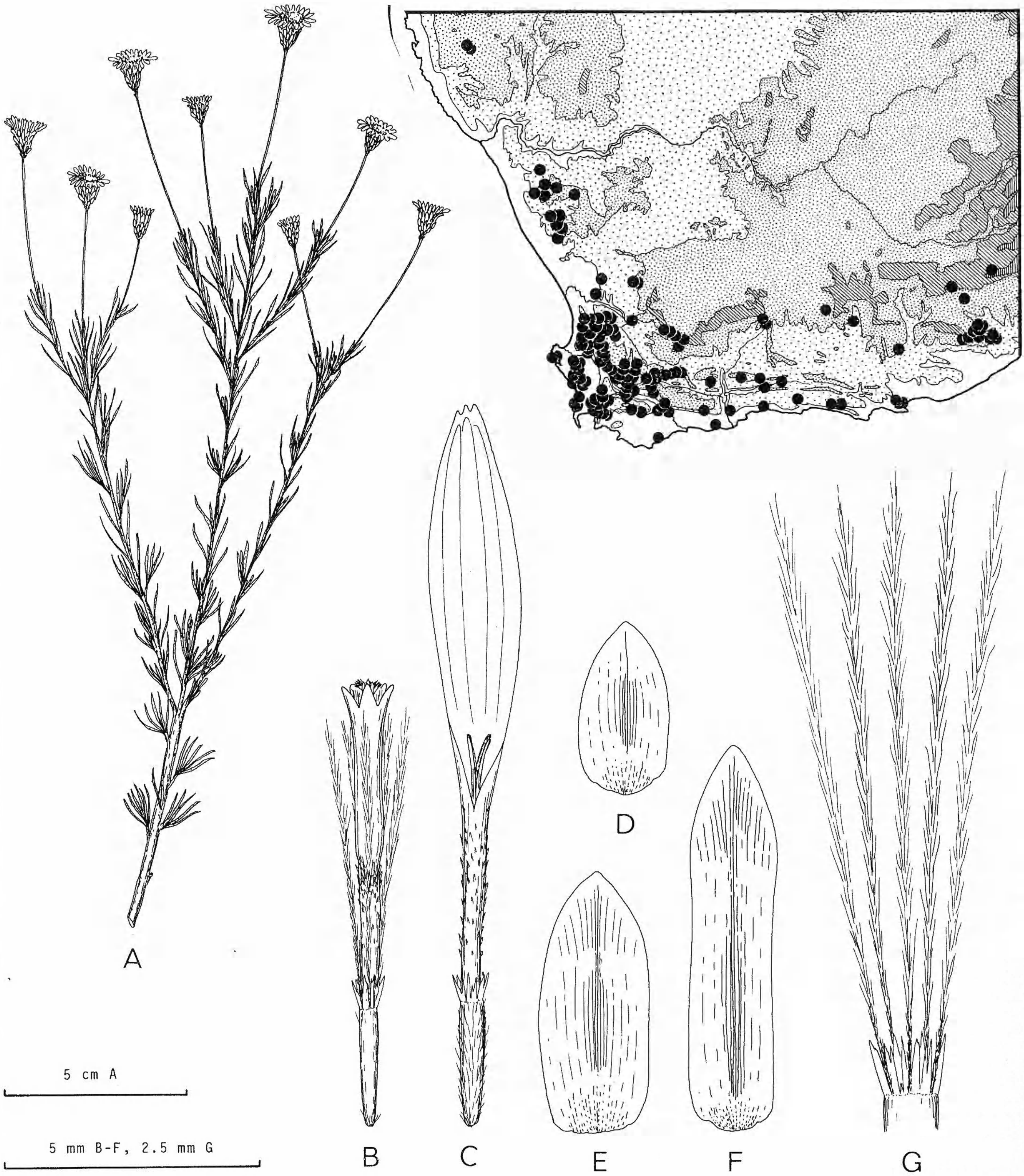

Fig. 6. Distribution and plant parts of *Leysera gnaphalodes*. – A: Portion of plant. – B: Disc-floret. – C: Ray-floret. – D–F: Outer–inner involucral bracts. – G: Pappus of disc-floret achene. – A–G: Goldblatt 3281 (S).

Cape Town the plants are usually greyish-tomentose with capitula on short peduncles and with acute involucral bracts. These are the plants described by Thunberg as *L. incana*. In the eastern Cape there are populations of plants with densely set, needle-shaped, greyish-tomentose leaves and somewhat smaller capitula. These were described by Rothmaler as *Asteropterus gracilis*. Rothmaler also described another new species, *A. dinteri,* with small capitula and

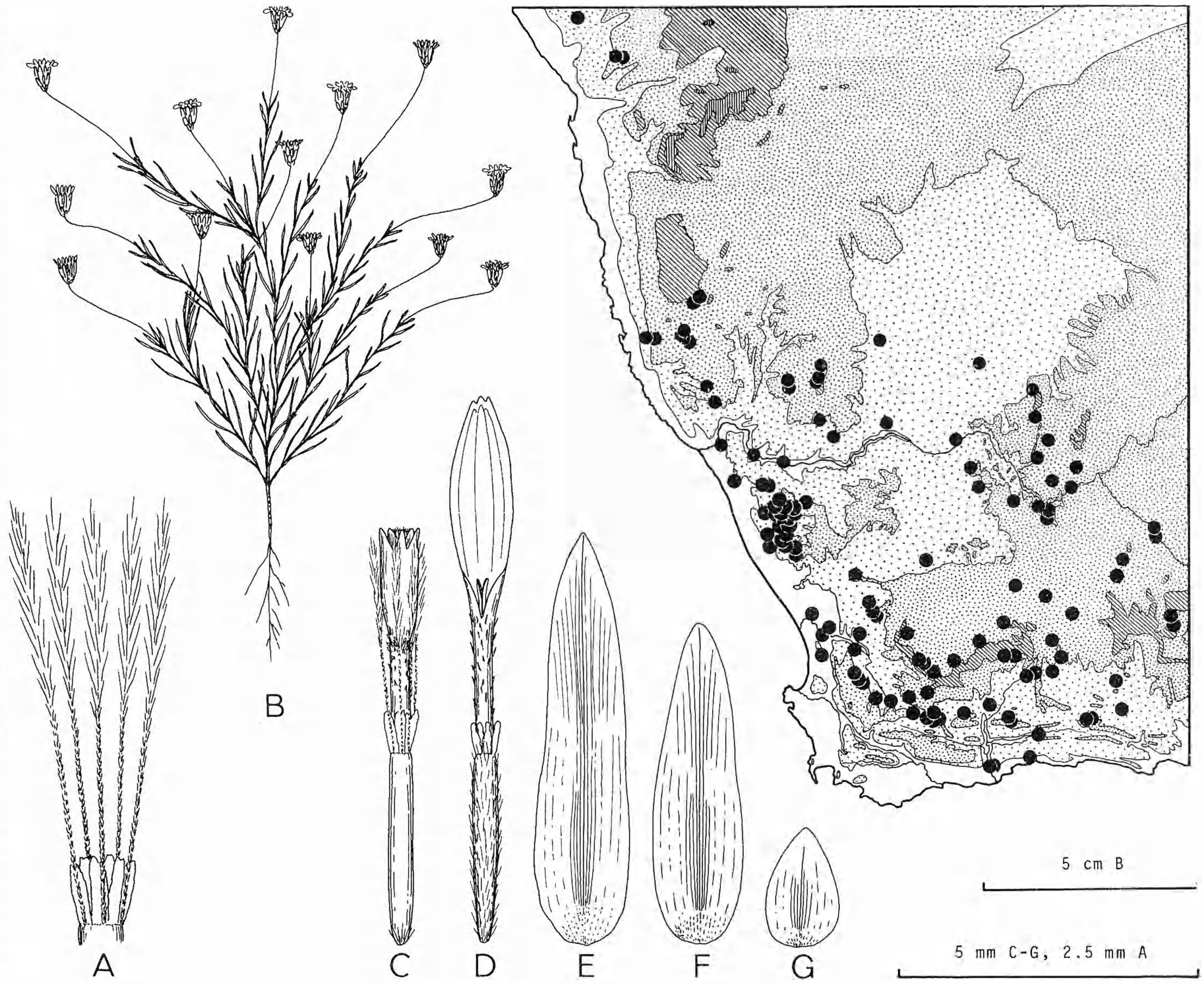

Fig. 7. Distribution and plant parts of *Leysera tenella*. – A: Pappus of disc-floret achene. – B: Habit. – C: Disc-floret. – D: Ray-floret. – E–G: Inner–outer involucral bracts. – A–G: Bremer 250 (S).

glabrous leaves from SW Africa. When the whole range of variation within *L. gnaphalodes* is considered, however, it is obvious that these species cannot be maintained and I have reduced them to synonymy. Except for the above mentioned examples it is difficult to correlate the variation with distribution and consequently I have not recognized any subspecies.

Robust specimens of *L. tenella* are similar to small-flowered plants of *L. gnaphalodes* but they can always be distinguished by the different pappus bristles (see key and Figs.).

2. **Leysera tenella** DC.

De Candolle 1838 a p. 279. – *Leyssera tenella* DC. var. *α. subcanescens* De Candolle l.c. – *Asteropterus tenellus* (DC.) Rothmaler 1944 p. 5. – Lectotype: Cedarberg, Drège (G-DC, seen in microfiche only).

Leyssera tenella DC. var. *β. glabriuscula* De Candolle 1838 a p. 279. – Lectotype: Silverfontein, Drège (G-DC, seen in microfiche only).

A tomentose–glabrescent and glandular annual herb (or occasionally perennial), small and delicate or often more vigorous and branched mainly from the base. *Leaves* laxly–densely set, sometimes almost crowded on short, lateral branchlets (brachyblasts), linear, 2–25 mm × c. 0.5 mm, greyish-tomentose to green and glabrescent, ventrally furrowed and somewhat tomentose, glandular. *Peduncles* smooth, 10–60 mm long. *Involucre* cyathiform–campanulate, 4–12 mm wide. Involucral bracts 15–50, smooth, acute–obtuse; outer small and ovate; inner gradually longer and oblong with a scarious and often brown apical limb, 5–9 × 0.7–1.6 mm. *Receptac-*

le flat–convex, scabrid with small projections and furnished with a distal row of acute or apically laciniate, 0.8–4 mm long, persistent scales. *Ray-florets* 8–35. Tube cylindrical, glabrous or with scattered, subulate–conical, multicellular hairs. Lamina elliptic, 2–9 × 0.7–3 mm. *Achenes* 2.5–3.8 mm long, with laxly–densely scattered, slender, tricellular hairs (twin hairs) and often with a basal tuft of similar hairs, remaining clasped between the spreading receptacular scales and the innermost involucral bracts. Pappus of short, flat, obtuse–truncate, white scales but with no bristles. *Disc-florets* 20–175, perfect. Corolla 2.6–4 mm long; tube with scattered, subulate–conical, multicellular hairs and often with a collar of similar, densely set hairs just below the limb. Anthers 1.2–2.5 mm long, with a truncate apical appendage. *Achenes* 2.5–3.8 mm long, glabrous or with few, scattered, slender, tricellular hairs (twin hairs) and often with a basal tuft of similar hairs. Pappus of short, flat, obtuse–truncate, white scales and 2–5 outer, basally barbellate and only apically plumose, white bristles.

Flowering period mainly August–October but flowering specimens seen from the whole year.

Chromosome number 2n = 8. Voucher specimen: Bremer 271 (S).

Distribution. L. tenella is a rather common karoo species and I have examined c. 150 collections, showing the distribution in Fig. 7. The species is widespread in southern SW Africa, Namaqualand, and the Great Karoo. The northernmost locality is an outlier on Brandberg in northern SW Africa (Nordenstam 2823, see Nordenstam 1974 pp. 44, 59).

Discussion. This annual species is rather variable in size and habit. Most of the variation is probably due to environmental modification. There are all types from small and delicate specimens to robust and vigorous plants, resembling the perennial *L. gnaphalodes*. The capitula are generally much smaller in *L. tenella* than in *L. gnaphalodes,* however, and the different pappus bristles (see key and Figs.) is a reliable diagnostic character.

3. **Leysera leyseroides** (Desf.) Maire

Maire 1929 p. 186. – *Gnaphalium leyseroides* Desfontaines 1799 p. 267. – *Leyssera discoidea* Sprengel 1815 p. 78, nom. superfl. – *Pectis discoidea* (Spr.) Hornemann 1819 p. 100. – *Leptophytus leyseroides* (Desf.) Cassini 1823 p. 78. – *Asteropterus leyseroides* (Desf.) Rothmaler 1944 p. 5. Lectotype: Herb. Desfontaines (P, seen in microfiche only).

Longchampia capillifolia Willdenow 1811 p. 160. – *Leyssera capillifolia* (Willd.) Sprengel 1819 p. 25. – Lectotype: Herb. Willdenow 15216 (B, seen in microfiche only).

Pseudocrupina arabica Velenovský 1923 p. 6. – Lectotype: El Misma, Musil (PRC?), not seen.

A tomentose–glabrescent and glandular annual herb (or occasionally perennial). *Leaves* linear, 5–25 × c. 0.5 mm, greyish green–green, laxly tomentose–glabrescent, ventrally furrowed and somewhat tomentose, glandular. *Peduncles* smooth, 15–60 mm long. *Involucre* cyathiform–campanulate, 4–9 mm wide. Involucral bracts 15–45, smooth, acute–obtuse; outer small and ovate; inner gradually longer and oblong–linear, straight, 6–9 × 0.6–1.5 mm. *Receptacle* flat–convex, scabrid with small projections and furnished with a distal row of acute or apically laciniate, 0.6–2 mm long, persistent scales. *Ray-florets* 8–30. Tube cylindrical, glabrous or with scattered, subulate–conical, multicellular hairs. Lamina elliptic-oblong, 1.5–2.5 × 0.5–0.8 mm, not exceeding involucre; the capitula thus being seemingly discoid. *Achenes* 2.8–4.5 mm long, with laxly–densely scattered, slender, tricellular hairs (twin hairs) and often with a basal tuft of similar hairs, remaining clasped between the spreading receptacular scales and the innermost involucral bracts. Pappus of short, flat, acute–obtuse, white scales but with no bristles. *Disc-florets* 20–100, perfect. Corolla 2.8–4 mm long; tube with scattered, subulate–conical, multicellular hairs and often with a collar of similar, densely set hairs just below the limb. Anthers 0.8–2 mm long, with a truncate apical appendage. *Achenes* 2.8–4.5 mm long, glabrous or with few, scattered, slender, tricellular hairs (twin hairs) and often with a basal tuft of similar hairs. Pappus of short, flat, acute–obtuse, white scales and 2–5 outer, basally barbellate and only apically plumose, white bristles.

Flowering period March–June.

Distribution. L. leyseroides has a wide distribution in the deserts or semi-deserts of N Africa and SW Asia. The known distribution is shown in Fig. 8, based on c. 105 examined collections. In Africa it occurs along the Atlas mountains in Morocco, Algeria, and Tunisia. It has been collected at the Hoggar mountains in central

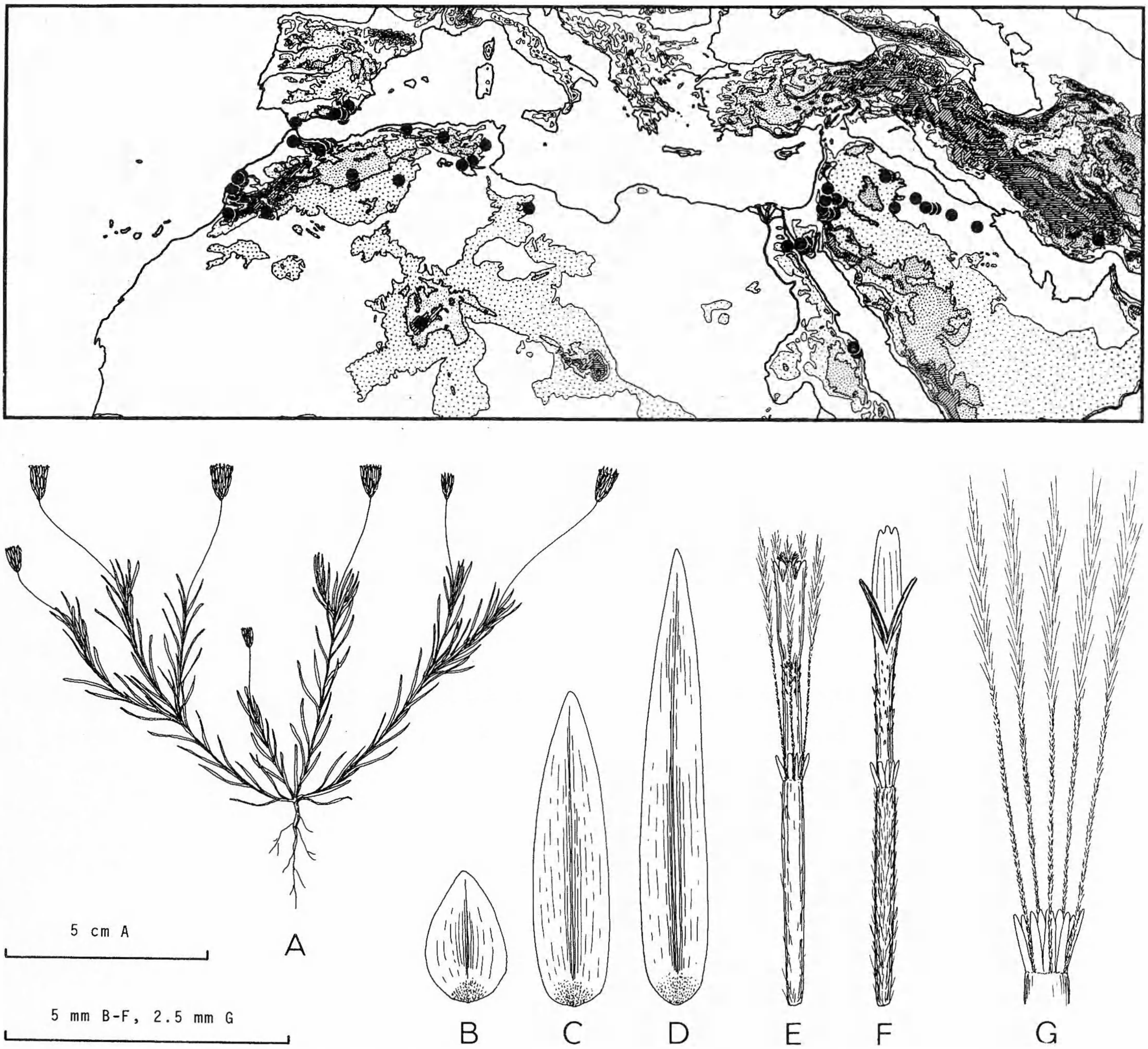

Fig. 8. Distribution and plant parts of *Leysera leyseroides*. – A: Habit. – B–D: Outer–inner involucral bracts. – E: Disc-floret. – F: Ray-floret. – G: Pappus of disc-floret achene. – A–G: Samuelsson 6634 (S).

Sahara (Meinertzhagen 155) and there are a few collections from Libya, S Egypt and N Sudan. In Asia it is known from Sinai, Israel, Jordan, S Syria, N Saudi Arabia, and Iraq, and the easternmost locality is in S Iran (Rechinger 3189). It occurs also in Europe, viz. in S and SE Spain.

Discussion. This species is closely related to *L. tenella* and the only reliable distinguishing character is the reduced, not exserted ray-floret lamina in *L. leyseroides*. As long as there is no biosystematic information on interfertility between the two I have thought it best to retain their specific status rather than reduce them to subspecies. *L. leyseroides* is a constant species compared to the much more variable *L. tenella*. They had a joint ancestor, a northern fraction of which developed into *L. leyseroides* (see Phytogeography and phylogeny). One might speculate that the immediate ancestor of *L. leyseroides* switched to a safe reproduction such as autogamy and that subsequently the ray-floret laminas became reduced. Since I have seen no living material of this species, the presence of autogamy in *L. leyseroides* remains to be shown, however.

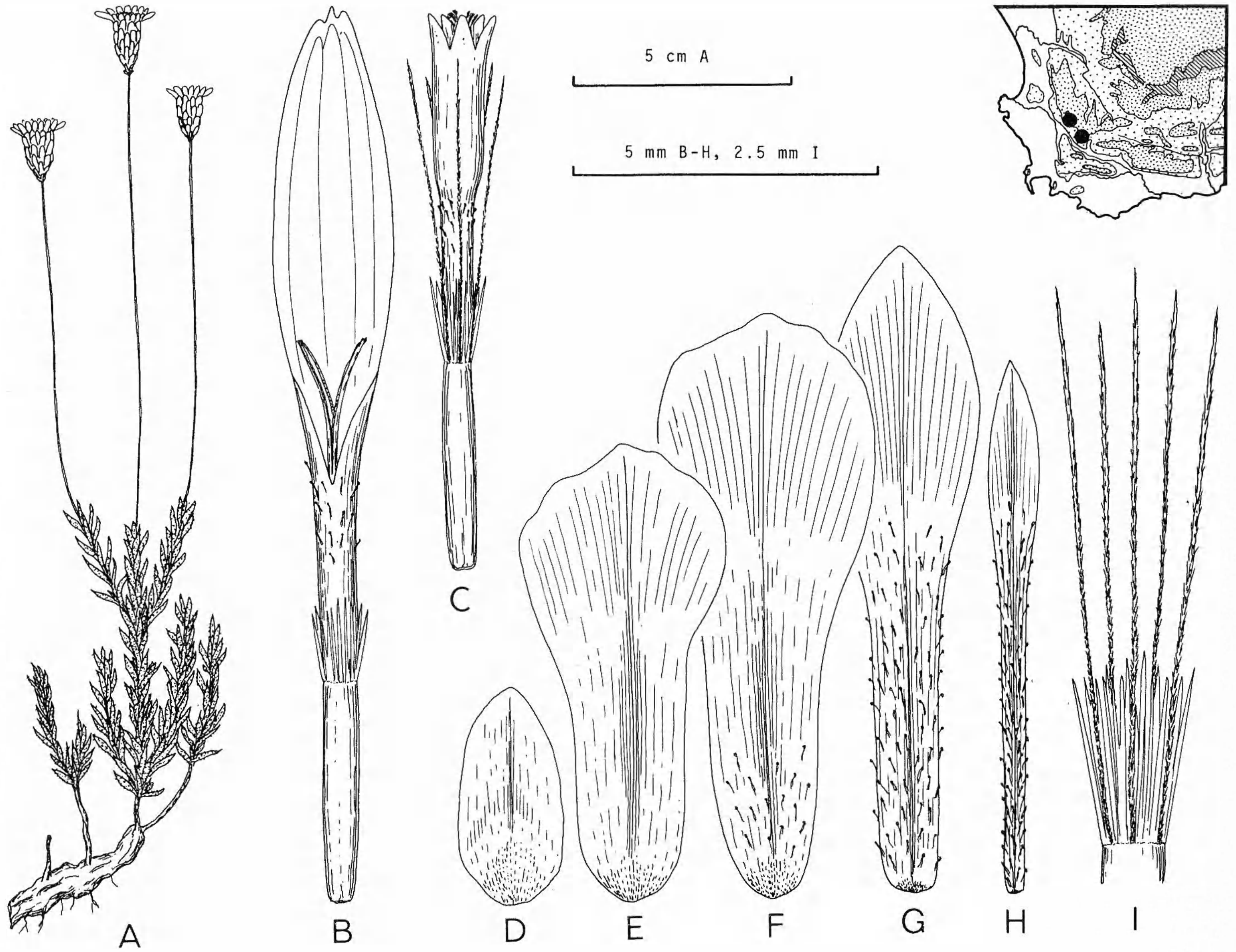

Fig. 9. Distribution and plant parts of *Leysera longipes*. – A: Habit. – B: Ray-floret. – C: Disc-floret. – D–H: Outer–inner–innermost involucral bracts. – I: Pappus of disc-floret achene. – A–I: Esterhuysen 30022 (BOL).

4. **Leysera longipes** Bremer, sp. nov.

Holotype: Esterhuysen 30022 (BOL). Isotype in S.

Suffrutex subramosus, usque ad c. 0.3 m altus, glandulosus, caudicibus subterraneis, lignosis. *Folia* alterna vel interdum opposita, linearia vel anguste elliptica–lanceolata, 3–10 mm longa, 0.5–2 mm lata, laxe puberula, marginaliter dorsoque distincte glandulosa glandulis longistipitatis, ventraliter plana glabraque, acuta–obtusa. *Pedunculi* laxe puberuli, glandulosi, vetustiores glabri, 40–170 mm longi. *Involucrum* urceolatum–cyathiforme, 5–9 mm latum. Bracteae involucri 40–65, pluriseriatae, imbricatae, laeves sed interiores basaliter dorsoque glandulis stipitatis, acutae (intimae)–obtusae–rotundatae, interdum mucronatae; interiores gradatim longiores et obovatae–spathulatae limbo apicali scarioso, ad 4 mm lato; intimae gradatim angustiores et obovato-oblongae–lineares, 8–12 mm longae. *Receptaculum* epaleaceum, planum, sublaeve–parum alveolatum. *Flores radii* 10–18, feminei, fertiles. Tubus cylindricus–parum triquetrus, glaber vel glandulis stipitatis, sparsis. Lamina elliptico-oblonga, 5–9 mm longa, 1.2–2.5 mm lata. Stylus bifidus; rami styli longitudine 1/4–1/2 styli partes aequantes. *Achaenia* linearia, 4–5.5 mm longa, glabra. Pappus squamis multis, subdistinctis, subulatis, sed setis nullis. *Flores disci* 30–60, hermaphroditi, probabiliter ♀-steriles. Corolla 5–6.5 mm longa, tubo cylindrico et limbo anguste cyathiformi; tubus glandulis stipitatis, sparsis. Antherae lineares, 2.6–3.4 mm longae, appendice apicali acuta–obtusa et caudis sterilibus longitudine 1/4 antherae partes brevioribus. Stylus bifidus, corollam aliquantum superans; rami styli apice penicillati, rotundati–truncati. *Achaenia* linearia, 3.5–4.5 mm longa, glabra, ut videtur non maturescentia. Pappus squamis multis, subdistinctis, subulatis, et setis 4–5 vel interdum 2–3, barbellatis.

A sparsely branched, up to c. 0.3 m high, glandular suffrutex with subterranean, woody rhizomes. *Leaves* linear or narrowly elliptic–lanceolate, 3–10 × 0.5–2 mm, laxly puberulous and distinctly glandular with long–stalked glands dorsally and marginally, ventrally flat and glabrous. *Peduncles* laxly puberulous and glandular with small glands, becoming glabrous, 40–170 mm long. *Involucre* urceolate–cyathiform, 5–9 mm wide. Involucral bracts 40–65, smooth but inner with stalked glands dorsally and basally, acute (innermost)–obtuse–rounded, sometimes mucronate; outer small and ovate; inner gradually longer and obovate–spatulate with a scarious, up to 4 mm wide, apical limb; innermost gradually narrower and obovate-oblong–linear, 8–12 mm long. *Receptacle* flat, almost smooth–shallowly pitted. Ray-florets 10–18. Tube cylindrical–somewhat triquetrous, glabrous or with scattered, stalked glands. Lamina elliptic-oblong, 5–9 × 1.2–2.5 mm. *Achenes* 4–5.5 mm long, glabrous. Pappus of many, almost free, subulate scales but with no bristles. *Disc-florets* 30–60, hermaphrodite, probably ♀-sterile. Corolla 5–6.5 mm long; tube with scattered, stalked glands mainly towards the base of the limb. Anthers 2.6–3.4 mm long, with an acute–obtuse apical appendage. *Achenes* 3.5–4.5 mm long, glabrous, apparently not ripening. Pappus of many, almost free, subulate scales and 4–5 or occasionally 2–3 outer, barbellate bristles.

Flowering specimens collected in December and January.

Distribution. I have examined 3 collections of this species. The localities are along the path up to the Sneeugat in the Great Winterhoek mountains N of Tulbagh (Esterhuysen 29941 and 30022) and along the path up steep sides of kloof to the Waaihoek Hut on Waaihoek Peak in the western part of the Hex River mountains N of Worcester (Esterhuysen 31068). The distribution is shown in Fig. 9.

Discussion. This new species differs from the former three species in many characters. It has very long peduncles, hence the specific epithet, and it is furthermore distinguished by e.g. its few-branched habit and distinctly glandular leaves. The achenes are glabrous and the pappus bristles are barbellate but not plumose as in the other species. In the only fruiting collection examined (Esterhuysen 31068) the ray-floret achenes are mature and fully developed, whereas apparently the disc-florets are ♀-sterile, with empty, not developed achenes. The disc-floret styles are bifid with normal stigmatic areas, however. *L. longipes* has subterranean, woody rhizomes, wherefrom new stems may regenerate after veld fires.

Taxa to be excluded

Callicornia tenuifolia and *Callicornia triflora* Burman fil. 1768 p. 24 = ? There are no specimens with these names filed under *Leysera* in Herb. Burman in G. Their systematic position is unknown to me.

Leysera arctotoides Thunberg 1800 p. 160 = *Heterolepis aliena* (L. fil.) Druce

Leysera caroliniana Walter 1788 p. 211 = ? This species is based on North American material and it certainly does not belong in the genus *Leysera*. It is probably a forgotten name, since it is not cited in modern American floras.

Leysera ciliata Thunberg 1800 p. 160 = *Mairia taxifolia* (L.) DC.

Leysera ericoides Bergius 1767 p. 294 = *Relhania fruticosa* (L.) Bremer

Leysera gnaphaloides sensu Thunberg 1800 p. 160 = *Helipterum gnaphaloides* (L.) DC.

Leyssera montana Bolus 1905 p. 138 = a new genus to be described in this journal. See Delimitation and systematic position.

"*Leysera muscoides* (Desf.) DC." Quézel & Santa 1963 p. 939, sphalm.? = *Lasiopogon muscoides* (Desf.) DC.

Leysera odorata Ruiz & Pav. ex De Candolle 1838 b p. 34, pro syn. = *Onoseris odorata* Hook. & Arn.

Leysera ovata Thunberg 1800 p. 160 = *Felicia ovata* (Thunb.) Compt.

Leysera paleacea Linnaeus 1767 p. 561 = *Relhania fruticosa* (L.) Bremer

Leysera picta Thunberg 1800 p. 160 = *Dicoma picta* (Thunb.) Druce

Leysera pilosella Thunberg 1800 p. 160 = *Aster bakeranus* Burtt Davy ex C. A. Smith

Leysera polifolia Thunberg 1800 p. 161 = *Printzia polifolia* (L.) Hutchinson

Leysera squarrosa Thunberg 1800 p. 160 = *Helipterum gnaphaloides* (L.) DC.

Leysera tridactyla E. Mey. ex De Candolle 1836 p. 215, pro syn. = *Amellus tridactylus* DC.

Acknowledgements. I am grateful to Miss I. Eriksson for technical assistance and to Dr B. Nordenstam and Mr H.-E. Wanntorp for valuable criticism of an earlier draft of the manuscript. Miss E. Esterhuysen kindly provided me with material of *L. longipes*. I am also indebted to the directors and curators of the herbaria (listed in the introduction), where I have been working or from where I have obtained herbarium material on loan.

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