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Taxonomy, phylogeny and biogeography of Kickxia and Nanorrhinum (Scrophulariaceae)

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Phylogenetic studies in *Kickxia* sensu lato, using morphological characters, show that two groups of species appear as distinct clades, one corresponding to sect. *Kickxia* and the other corresponding to sect. *Valvatae*. The differences between the two sections are of the same magnitude as those used to separate other closely related genera in the tribe. Therefore, the treatment of sect. *Valvatae* as a separate genus, *Nanorrhinum*, is proposed. Results from a dispersal-vicariance analysis indicate that the area of origin for *Nanorrhinum* is Arabia, whereas for *Kickxia* sensu stricto it is either Macaronesia, the Mediterranean Region or both these areas combined. The taxonomy of *Nanorrhinum* is revised in detail, whereas for *Kickxia* a synoptical treatment is given, mainly based on previous literature. The results indicate that the plasticity of the species of *Nanorrhinum*, as well as the variation within populations in the field, is often much greater than previously thought, and that, therefore, far too many species have been described. In the present study ten species are recognized in *Nanorrhinum*. New combinations are *N. azraqensis, N. stenanthum, N. hastatum, N. elegans, N. kuriensis, N. asparagoides, N. heterophyllum* and *N. woodii*. Three lectotypes are selected. Keys to all taxa are given, and new information on chromosome numbers and sexual systems are provided for several species.

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Introduction

Kickxia Dumort. (Dumortier 1827), in its current sense (Sutton 1988), is a genus of 46 species of dwarf shrubs or herbs distributed in Europe, South-Central and South-Western Asia, North Africa and Macaronesia. Some of the species, notably *K. elatine* ("Sharp-leaved Fluellen") and *K. spuria* ("Round-leaved Fluellen"), are weedy and widely naturalized in temperate regions. Both these species were known to Linnaeus, who placed them in his widely circumscribed *Antirrhinum* (Linnaeus 1753).

Already Chavannes (1833) realized that some species of *Kickxia* (treated by him as *Linaria* sect. *Elatinoides*), including the two species mentioned above, have operculate dehiscence of the capsule, whereas others have valvate dehiscence, and proposed that the species therefore should be placed in two distinct groups. However, he did not propose any formal names for these groups.

Wettstein (1891) introduced the names "*Operculatae*" and "*Valvatae*" for the two groups, as sections within the genus *Elatinoides*. Janchen (1933) published the combination *Kickxia* sect. *Valvatae*. Smith (1973) treated this group as a subgenus, but failed to validly publish the new combination.

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Betsche (1984) treated sect. *Kickxia* as a genus of its own and subdivided sect. *Valvatae* into two separate genera, *Pogonorrhinum* and *Nanorrhinum*, but this taxonomy was rejected by Sutton (1988), who instead returned to a taxonomy with one genus with two sections. Also, in a paper on the phylogenetic relationships within the Antirrhineae by Ghebrehiwet et al. (2000), the monophyly of the genus *Kickxia* in a wide sense was demonstrated. Thirteen new species were described by Sutton (1988) in sect. *Valvatae*, ten of them from the Arabian Peninsula and several of them indicated to be endemic to specific regions there. Still, many herbarium specimens were said to be difficult to place and Sutton proposed further studies of this group in this part of the world. Since Sutton's work many more specimens, not least of Arabian *Kickxia*, have accumulated and led to increasing problems with identifications.

The aim of the present study are (1) to revise the taxonomy at species level in *Kickxia* sensu lato, particularly the species currently classified in sect. *Valvatae*, (2) to study the phylogenetic relationships within the group and evaluate their biogeographical implications, and (3) to decide whether one, two or more genera should be recognized within the group.

Material and methods

This study is mainly based on herbarium material obtained on loan from or studied in the following herbaria: BM, C, E, ETH, FT, GB, HBG, HUJ, K, MJG, P, S, and UPS. The herbarium studies have also been supplemented by studies of living populations during field work in Yemen in November 1995 and in Eritrea and Ethiopia in August to October in both 1996 and 1997. Many plants have been grown in the greenhouses of the Botanical Garden at Uppsala University from seeds collected during the field work. The plants raised in the garden were used for studies of phenotypic behaviour and reproductive biology, and to obtain chromosome numbers.

Whether the plants are self-compatible or not was studied by isolation experiments. Crossing experiments were carried out on some of the cultivated plants. Artificial pollination was done by hand always using self-incompatible plants as females to avoid the need for emasculation of flowers. Crosses were made up to the F2 generation and viability of pollen was checked by studying stainability of pollen grains by lactic blue under a light microscope (Dafni 1992).

Chromosome counts were made in root-tip sections prepared from one or two plants from each collection. In all cases the numbers have been counted in at least two different cells. Navashin-Karpechenko was used as fixative and crystal violet as stain.

Plant parts were measured with a hand ruler or, for the finer details, under a dissection microscope. Flowers were softened in hot water before dissection. Pollen grains were studied under a light microscope. Most observations on the external morphology of seeds were made using a dissecting microscope. The terminology generally follows Sutton (1988). A scanning electron microscope (SEM) was used in a few cases. The seeds were then put on double-sided adhesive tape on stubs, and coated with gold-palladium.

Since this study is mainly based on herbarium material and morphology, a morphological species concept has been applied. Phylogenetic relationships among the species were analysed cladistically using a morphological data set. The computer parsimony program PAUP 3.1.1 (Swofford 1993) was used for the analysis and MacClade 3.01 (Maddison & Maddison 1992) for character optimization. All characters were weighted equally and treated as unordered. Trees were generated using heuristic search with TBR branch swapping, MULPARS on, steepest descent off and random addition sequences with 100 entry replicate searches. To assess the relative support for the clades a bootstrap analysis (Felsenstein 1985) with 1000 replicates was performed. Bremer support values were also calculated (Bremer 1994).

Ancestral distributions were reconstructed with the computer program DIVA 1.0 (Ronquist 1996), according to the dispersal-vicariance optimization method proposed by Ronquist (1997). The distribution maps are computer drawn using Versamap version 2.02.

Taxonomic history

In his Species Plantarum, Linnaeus (1753) described 28 species in the genus *Antirrhinum*. Three of the species were *A. elatine*, *A. spurium*, and *A. aegyptiacum*, which today are all placed in the genus *Kickxia*. The circumscription of *Antirrhinum* used by Linnaeus corresponds to the tribe *Antirrhineae* of today. In this genus he included various other genera that had been described by earlier authors, and subsequent authors sought to reinstate some of them. Thus Miller (1754), as the first author after 1753, recognized the pre-Linnaean genus *Linaria* in order to accommodate all spurred species.

Chavannes (1833) in his monograph of the tribe *Antirrhineae* divided *Linaria* into four sections,

Elatinoides, Chaenorhinum, Cymbalaria, and *Linariastrum.* The section *Elatinoides,* with its then fourteen species, corresponds to the genus *Kickxia* sensu lato of today. Chavannes (1833) was also the first to propose the division of this group into two subgroups on the basis of the dehiscence of the capsule, which is either operculate or valvate.

Bentham (1846) recognized Chavannes' four sections of *Linaria* and further described several new species from Afghanistan, East Africa and Sinai within the section *Elatinoides.* Bentham further divided the species with operculate dehiscence into two groups on the basis of whether they have a reticulate or a tuberculate testa.

Wettstein (1891) raised *Elatinoides* and the other three sections of *Linaria* to the generic level. He divided the genus *Elatinoides,* following Chavannes, into two sections named *Operculatae* and *Valvatae.* The generic name *Elatinoides* was then used by subsequent authors until Janchen (1933) recognised that *Kickxia* Dumortier (1827) had priority. Dumortier (1827) also made the two combinations *K. elatine* and *K. spuria.* Janchen (1933) transferred several species of *Elatinoides* to *Kickxia* and treated Wettstein's sections as *K.* sect. *Kickxia* (as sect. "*Operculatae*") and *K.* sect. *Valvatae.* Smith (1973) instead treated these two groups as subgenera, but failed to validly publish the new combinations.

Betsche (1984) treated section *Kickxia* as a genus of its own and subdivided section *Valvatae* into two separate genera, *Pogonorrhinum* and *Nanorrhinum,* on the basis of differences mainly in flower size, spur length, and palate structure.

Sutton (1988) argued that much of the variation in the genus was not studied in Betsche's work and preferred to return to a wider view of *Kickxia* with the operculate and valvate species in two different sections. He recognised nine species in section *Kickxia* and 37 in section *Valvatae.* Thirteen new species were described mainly from the Arabian Peninsula and the Horn of Africa, all in section *Valvatae.* Since then Danin (1991) has described one further species in section *Valvatae* based on material from Jordan.

Phylogenetic relationships

A phylogenetic analysis of the tribe *Antirrhineae* by Ghebrehiwet et al. (2000), using morphological and molecular data sets, indicates that the two sections of *Kickxia* are sister groups with *Anarrhinum* as sister to both of them together. This clade, the "*Anarrhinum* clade", is in its turn sister to the rest of the *Antirrhineae.* The clade is characterised by the synapomorphy of having connate anthers forming a ring. In the present work the phylogenetic

Table 1. Characters and character states used in the cladistic analysis of *Kickxia* sensu lato.

1. Stems herbaceous (0), ± woody (1)
2. Duration annual (0), perennial (1)
3. Length of hairs on stem up to 1.5 mm (0), 2-3 mm (1)
4. Leaves heteromorphic (0), homomorphic (1)
5. Shape of upper cauline leaves elongate (0), isodiametric (1)
6. Incision of upper cauline leaves palmatisect (0), entire (1)
7. Leaf base hastate or sagittate (0), not hastate or sagittate (1)
8. Corolla length excluding spur = 5 mm (0), > 5 mm (1)
9. Corolla tube width ≤ 5 mm (0), > 5 mm (1)
10. Palate glabrous to pubescent (0), lanate (1)
11. Spur length ≤ 5 mm (0), > 5 mm (1)
12. Spur as long as or shorter than rest of corolla (0), longer than rest of corolla (1)
13. Spur forming obtuse angle with the corolla (0), continuing with tube (1)
14. Anthers ciliate (0), glabrous (1)
15. Capsule shape subglobose to globose (0), ovoid to oblong-ovoid (1)
16. Capsule loculi equal (0), unequal (1)
17. Capsule wall thin (0), thick (1)
18. Loculi dehiscing by a single ligulate valve (0), a circumscissile split (1), several valves (2)
19. Seed external surface with columnar to conical tubercles (0), laterally elongated tubercles (1), reticulate ridges (2)
20. Seed length ≤ 0.6 mm (0), > 0. 6 mm (1)
21. Seed shape oblong-ovoid (0), oblong-ellipsoid (1), reniform (2)

Table 2. Data matrix assembled using the characters in Table 1 for the outgroup and *Kickxia* sensu lato. Polymorphic states are represented by letters as follows P = 0/1, q = 1/2. Unknown and inapplicable states are coded "?".

Taxa	1 1 2 3 4 5 6 7 8 9 0	2 1 2 3 4 5 6 7 8 9 0 1
Anarrhinum	P 1 0 0 0 0 1 P 0 0	0 0 0 0 0 0 P 0 0 1 0
Kickxia aegyptiaca	1 1 0 1 1 1 0 0 0 0	1 1 1 0 0 1 1 1 P 1 P
Kickxia cirrhosa	0 0 1 0 0 1 0 0 0 0	0 1 0 0 0 0 ? 1 1 1 0
Kickxia commutata	0 P 1 0 1 1 0 0 p 0	1 1 0 0 0 0 1 1 1 1 0
Kickxia dentata	0 1 1 1 1 1 1 1 1 1	1 0 1 0 0 1 1 1 P 1 1
Kickxia elatine	0 0 1 0 1 1 0 0 0 0	1 0 0 0 0 0 0 1 2 1 1
Kickxia elatinoides	0 1 0 1 1 1 1 1 P 1	1 1 1 0 0 1 1 1 2 1 1
Kickxia floribunda	1 1 1 1 0 1 1 1 1 0	1 0 1 0 0 1 1 1 1 1 1
Kickxia lanigera	0 0 1 1 1 1 1 0 0 0	P 0 0 0 0 0 0 1 2 1 0
Kickxia spuria	0 0 1 1 1 1 1 1 0 1	1 0 1 0 0 0 ? 1 2 1 0
Kickxia asparagoides	1 1 0 0 0 1 0 1 0 1	0 0 1 1 1 0 0 2 0 P 1
Kickxia azraqensis	1 1 0 0 0 1 0 1 0 0	1 1 0 1 1 1 0 2 0 0 2
Kickxia elegans	P P 0 1 1 1 0 0 0 0	0 0 0 1 1 1 0 2 0 0 1
Kickxia hastata	0 0 0 0 0 1 0 0 0 1	0 0 0 1 1 0 0 2 0 0 q
Kickxia heterophylla	1 1 0 0 0 1 0 1 P 1	1 1 1 1 1 0 0 2 0 P 1
Kickxia kuriensis	0 0 0 1 1 1 1 0 0 0	0 0 0 1 1 0 0 2 0 0 1
Kickxia macilenta	P 1 0 1 1 1 0 0 0 0	0 0 0 1 1 1 0 2 0 0 1
Kickxia ramosissima	1 1 0 0 1 1 0 P 0 0	P 0 0 1 1 0 0 2 0 0 P
Kickxia stenantha	1 1 ? 1 0 1 1 0 0 1	1 1 1 1 1 0 0 2 0 0 2
Kickxia woodii	1 1 0 P P 1 0 1 1 1	1 0 0 1 1 0 0 2 0 1 1

relationships within *Kickxia* sensu lato are examined cladistically by using morphological data. Twenty-one characters (Table 1) are used for the 19 taxa recognized under Taxonomy, and a data matrix of the characters is given in Table 2. Based on the results of the previous study *Anarrhinum* is used as outgroup.

Morphological characters

Several of the species in *Kickxia* sensu lato are highly polymorphic with a high plasticity in morphological characters. In the present analysis polymorphic characters are coded following Weins (1995), i.e. the widely common state is used when absolute majority is observed for it. Unknown character states are coded with a question mark. Coding of quantitative characters was done following Thiele (1993), who supports the view that overlapping morphometric data can be used in phylogenetic analyses. In order to detect discontinuities transformable into character states, mean values were calculated and plotted on a diagram. character states were delimited from the resulting graphs. The following characters and codings require some additional comments.

Stems and duration

The species of *Kickxia* sensu lato are herbs, subshrubs or dwarf shrubs with herbaceous to more or less woody stems. Among the herbaceous species, both perennials and annuals are represented.

Indumentum

The distribution and structure of the hairs in members of *Kickxia* sensu lato are highly variable. In most species both glandular and eglandular hairs are present on stems and leaves, the only exceptions being *K. azraqensis* and *K. kuriensis*, in which only glandular hairs have been seen. In the members of section *Kickxia* the indumentum is generally dense, whereas in section *Valvatae* the density of the indumentum is more variable or the indumentum may be confined to the lower part of the plant only. Plants may also be entirely glabrous. The character used in the analysis is hair length, where two distinct states are generally found, either the hairs are up to about 1.5 mm long or they are about 2-3 mm long. *K. stenantha*, which is glabrous, is here coded with a query.

Leaves

In *Kickxia* sensu lato the leaves vary tremendously in shape and size. The leaves are referred to as homomorphic when they are of similar shape and size in all parts of the plant, and as heteromorphic when the basal leaves differ markedly in shape and/or size from the upper cauline leaves. The character is coded in the analysis as two states, homomorphic and heteromorphic. In addition to the variation in shape plants can have leaves that grade in size from minute scale-like structures to full sized leaves or, as in some species of section *Valvatae,* older plants can be without leaves. The variation in shape of the upper cauline leaves is coded in two states, elongate or isodiametric. The elongate category includes leaves with a filiform, linear or lanceolate shape, whereas the isodimetric category includes leaves with a deltate, ovate or orbiculate shape.

Incision of leaf

The upper cauline leaves in *Kickxia* sensu lato are sometimes lobed, but they are never incised. In *Anarrhinum,* the outgroup, on the other hand, most species have palmately divided cauline leaves. The character is coded as two states, palmatisect or entire.

Leaf base

The base of the leaf is variable and in several species all or some of the leaves are hastate or sagittate. However, in some species the leaf base is never hastate or sagittate. In the analysis the character is coded as two states, with or without hastate or sagittate leaf base.

Corolla

The corolla is tubular and bilabiate with the abaxial lip having three lobes and the adaxial lip two lobes. The length of the corolla and the width of the corolla-tube are coded as binary characters. The measurements for the corolla length are taken from the tip of the upper lip to the base of the tube excluding the spur. The tube width is measured at the mouth opening.

Palate indumentum

The abaxial lip of the corolla is raised to form a convex structure termed the 'palate' which, to various degree, closes the mouth of the tube. When the palate is glabrous or covered by relatively short hairs it is coded as glabrous to pubescent and when the hairs are longer it is coded as lanate.

Spur

The lower abaxial part of the tube is modified to form the 'spur', a hollow, slender sac-like appendage where nectar is stored. The spur length is measured from the base of the corolla-tube to the tip of the spur. The length is also compared with the rest of the corolla and coded as two states, shorter or longer than rest of corolla. In its position the spur can form an angle with the corolla or form a continuation of the corolla tube.

Stamens

The stamens are didynamous and all four anthers are connate, forming a ring-like structure. The abaxial filament is densely lanate and the adaxial is normally glabrous. The anthers can be glabrous or have a ciliate margin.

Capsule

The shape of the capsules varies from globose to ovoid or oblong-ovoid. In most species the loculi are equal in size but a few species have unequal loculi. The capsule wall can be thin and papery or thick and more leathery.

Dehiscence

The fruit in *Kickxia* sensu lato is a dry poricidal capsule. Two types of dehiscence, opercular with a circumscissile split and valvate dehiscence with several valves are recognized in *Kickxia* sensu lato. A third type, dehiscence by a single ligulate valve is found in *Anarrhinum,* and the character is therefore treated as multistate.

Seed

The seeds in *Kickxia* sensu lato vary from 0.3 mm to 1.3 mm in size, and they have an oblong-ovoid, oblong-ellipsoid or sometimes reniform shape. The external surface of the seeds in *Kickxia* sensu lato is variously tuberculate or ridged. The character is coded as multistate with columnar to conical tubercles, laterally elongated tubercles and reticulate ridges.

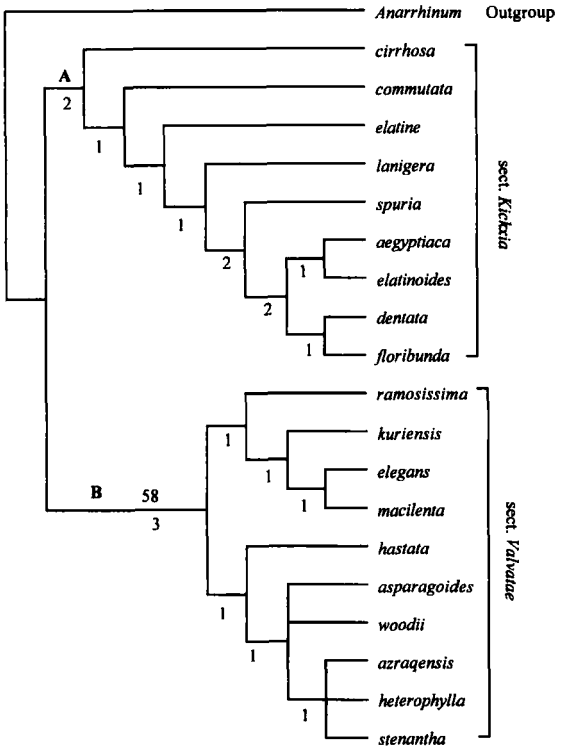


Fig. 1. The strict consensus tree of the three equally most parsimonious trees from the cladistic analysis of *Kickxia* sensu lato, 61 steps long, based on morphological characters in Table 1. The number above node B is the only bootstrap value above 50%. Numbers below nodes are Bremer support values, i.e. number of extra steps required to collapse that particular node.

Results and taxonomic conclusions

The cladistic analysis of the morphological data with 21 characters and 20 taxa (including outgroup) generated three most parsimonious trees, 61 steps long, with the consistency index 0.393 and the retention index 0.706. The strict consensus tree is presented in Fig. 1, and one of the most equally parsimonious trees is presented in Fig. 2. In the analysis the two sections, *Kickxia* sect. *Kickxia* and *K.* sect. *Valvatae,* appeared as distinct clades, represented as "A" and "B" in Fig. 1. The two clades have Bremer support values of 2 and 3 respectively. However, only clade "B" has a bootstrap value above 50.

Anarrhinum, the outgroup, has been continuously recognized as a genus since its erection in 1798. It differs clearly from both sections of *Kickxia* by it mostly palmatisect upper leaves and its capsules dehiscing by a single, ligulate valve. The palmatisect upper leaves (character 6) is a unique character not found in other member of the tribe. It therefore is a strong indication for monophyly for *Anarrhinum.*

Clade "A", with all species of sect. *Kickxia,* is supported by four characters, three synapomorphies and a parallelism. One of the characters, i.e. capsules dehiscing by a circumscissile split (character 18), is a synapomorphy without reversal or change. The other two synapomorphies, i.e. hairs 2-3 mm long (character 3) and seeds with elongate tubercles (character 19) either show a reversal higher up in the clade (character 3), or change to another state (character 19).

The valvate type of dehiscence is the commonest form in the Old World *Antirrhineae,* whereas the operculate type is unique to *Kickxia* sect. *Kickxia.* Sutton (1988) suggested that the operculate dehiscence is basically similar to the type of dehiscence with a single split found in *Anarrhinum, Albraunia, Epixiphium,* and *Neogaerrhinum.* Probably it has evolved from the dehiscence by a single ligulate valve as seen in the outgroup, *Anarrhinum.* Capsule dehiscence is an important character in the *Antirrhineae* in general and is used to distinguish

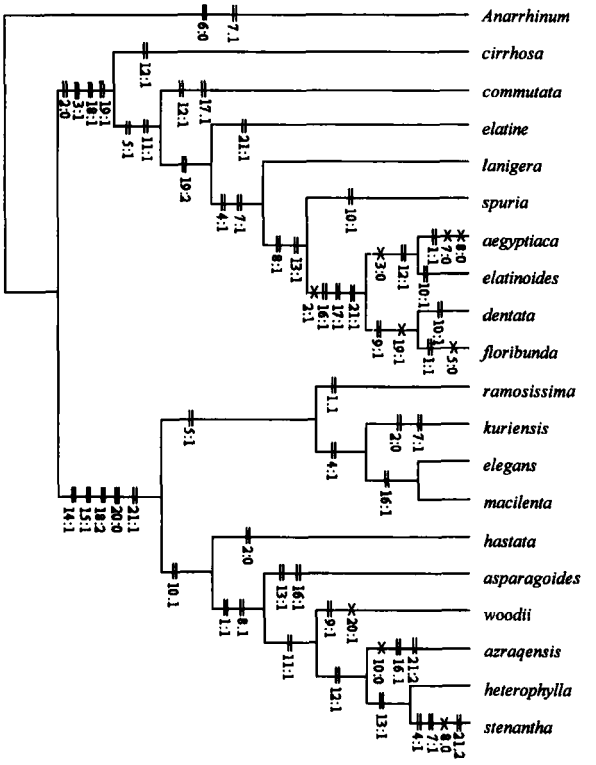


Fig. 2. Morphological characters optimised on one of the three most parsimonious trees. Black bars indicate synapomorphies, open bars indicate homoplastic characters with subsequent changes, crosses indicate reversals, and double bars indicate parallelisms.

several genera from each other, e.g. *Albraunia* from *Chaenorhinum*, and *Epixiphium* from *Maurandya*.

Clade "B" with all species of section *Valvatae* is also supported by five characters, three of which are synapomorphies without reversals. Two of the synapomorphies, i.e. glabrous anthers (character 14) and loculi dehiscing by several valves (character 18) are strong, whereas oblong to oblong-ovoid capsules (character 15) may be regarded as a weaker synapomorphy since the difference here is more gradual. The clade is also supported by a synapomorphy with a reversal, i.e. seed size less than 0.6 mm (character 20) and a parallelism, i.e. oblong-ellipsoid seed shape (character 21). Betsche's subdivision of section *Valvatae* into two genera, *Nanorrhinum* and *Pogonorrhinum* (Betsche 1984), was based on differences mainly in flower size, spur length and palate structure, but this subdivision finds no support in this analysis.

The two sections of *Kickxia* are both better supported and morphologically more well circumscribed clades than is *Kickxia* sensu lato. The characters supporting them are very clear-cut, even if features such as anther indumentum, capsule dehiscence and testa structures are not always the most easy ones to see. The differences between these two sections are certainly of equal magnitude to the differences used to separate other genera in the *Antirrhineae*, and therefore the status of the two sections is raised to generic level in the present work. For section *Valvatae* the simultaneously published generic names *Pogonorrhinum* and *Nanorrhinum* are available. Of these names *Nanorrhinum* is selected here for convenience, as its adoption necessitates a lower number of new combinations.

Biogeography

Kickxia sensu stricto has a mainly temperate area of distribution. Its species are commonly found in the Mediterranean region, central Europe and northern Africa. Most of its species, and particularly *K. elatine* and *K. spuria*, are weedy and easily dispersed and therefore occur naturalized in many parts of the world, such as North America and Australia. *K. cirrhosa*, *K. floribunda* and *K. lanigera* are mainly distributed in the Mediterranean region extending to some extent to Macaronesia and North Africa. *K. aegyptiaca* is a species of the Saharo-Sindian region occurring in North Africa, the east Mediterranean region and in South-West Asia. Two of the species, *K. elatinoides* and *K. dentata*, are local endemics in the Mediterranean part of Algeria and Tunisia respectively.

The genus *Nanorrhinum* is distributed in northern and north-eastern Africa, the Canary Islands, the Cape Verde Islands, the Arabian Peninsula, Iran, Afghanistan, Pakistan, northern India, Nepal, Bhutan, Tibet and Burma. The genus has a subtropical and tropical distribution. Two of the species, *N. heterophyllum* and *N. ramosissimum*, are widespread. *N. heterophyllum* extends from Arabia westwards to North Africa and the Canary Islands (Fig. 3). It is mainly distributed in the Somalia-Masai and the Saharo-Sindian regions (White & Léonard 1991). *N. ramosissimum* is a mainly Asiatic species with a distribution that extends from Burma westwards to India, Nepal, Pakistan, Afghanistan, Iran, Arabia and north-eastern Africa (Fig. 3). In north-east Africa, *N. ramosissimum* has somewhat isolated occurrences in north-east Somalia, north-east Kenya, north-west Ethiopia and on Jebel Marra in western Sudan.

Five of the species, *N. hastatum*, *N. asparagoides*, *N. woodii*, *N. stenanthum*, and *N. kuriensis*, belong to the Somalia-Masai region (White & Léonard 1991). *N. hastatum* and *N. asparagoides* occur in both Arabia and north-east Africa. The remaining three are local endemics, *N. woodii* with a restricted distribution in Yemen, *N. stenanthum* in north-east Somalia, and *N. kuriensis* endemic to the Abd-al-Kuri Island in the Socotra archipelago (Figs 4 & 5).

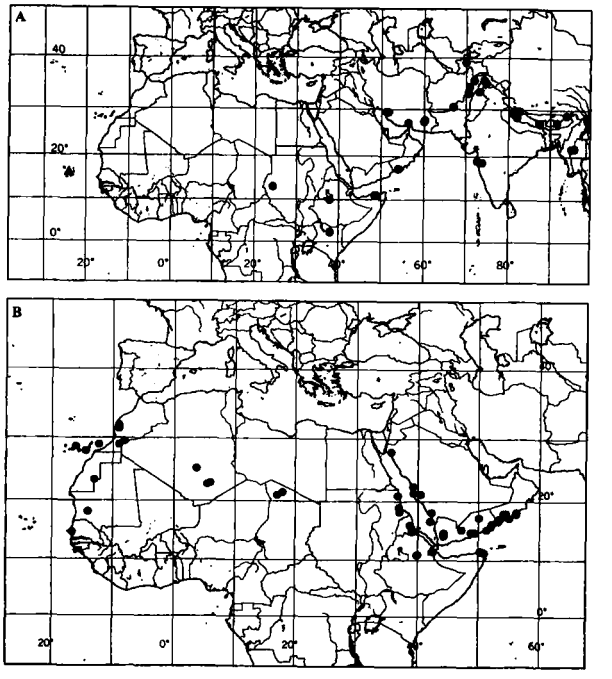


Fig. 3. A: Known distributions of *Nanorrhinum ramosissimum* (●) and *N. elegans* (▲). B: Known distribution of *N. heterophyllum* (●).

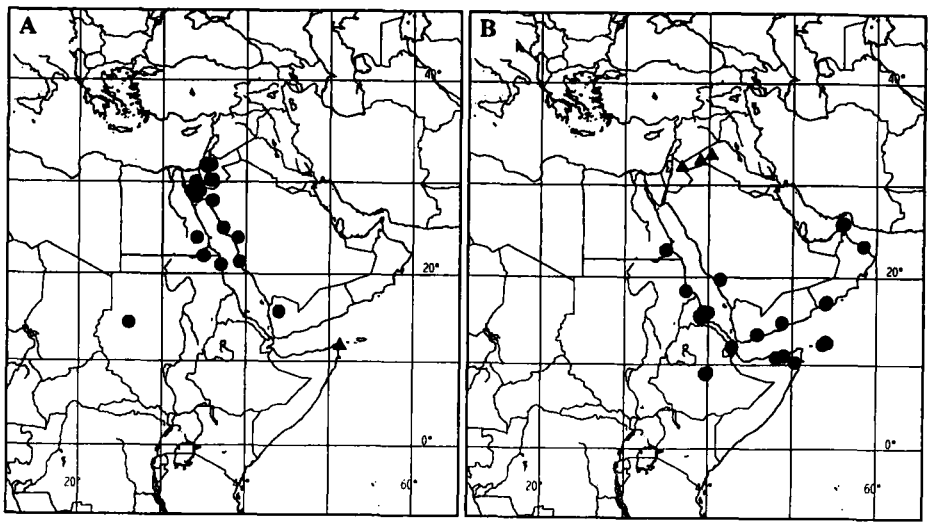


Fig. 4. A: Known distributions of *Nanorrhinum macilentum* (●) and *N. stenanthum* (▲). B: Known distributions of *N. hastatum* (●) and *N. azraqensis* (▲).

Two of the species, *N. macilentum* and *N. azraqensis* (Fig. 4), belong to the Saharo-Arabian area which is part of the Saharo-Sindian region (White & Léonard 1991). *N. macilentum* has a relatively wider distribution with occurrences in Egypt, north-east Sudan, Sinai, Israel, Jordan, Saudi Arabia and Yemen. *N. azraqensis* is a local endemic of the Syrian desert in eastern Jordan and western Iraq.

N. elegans belongs to the Macaronesian region and is endemic to the Cape Verde Islands, where it is known to occur in all of the islands.

Vicariance biogeography

In cladistic biogeography, an area of endemism can be defined by the presence of at least one endemic taxon (Harold & Mooi 1994). With this definition the following four areas of endemism for *Kickxia* sensu lato may be proposed: the Arabian Peninsula (A), the Horn of Africa (B), Macaronesia (C), and the Mediterranean region including the north-western tip of Africa (D). A matrix based on presence or absence of species in these areas was optimised on a phylogenetic tree of *Kickxia* sensu lato using the DIVA program (Ronquist 1996). DIVA, dispersal-vicariance analyses, optimises areas of endemism onto a taxon cladogram based on vicariance, and minimizes dispersal and extinction. The costs for speciation by vicariance and for speciation within an area is zero, whereas costs for dispersal and extinction is one (Ronquist 1997). The program demands fully resolved cladograms and therefore one of the

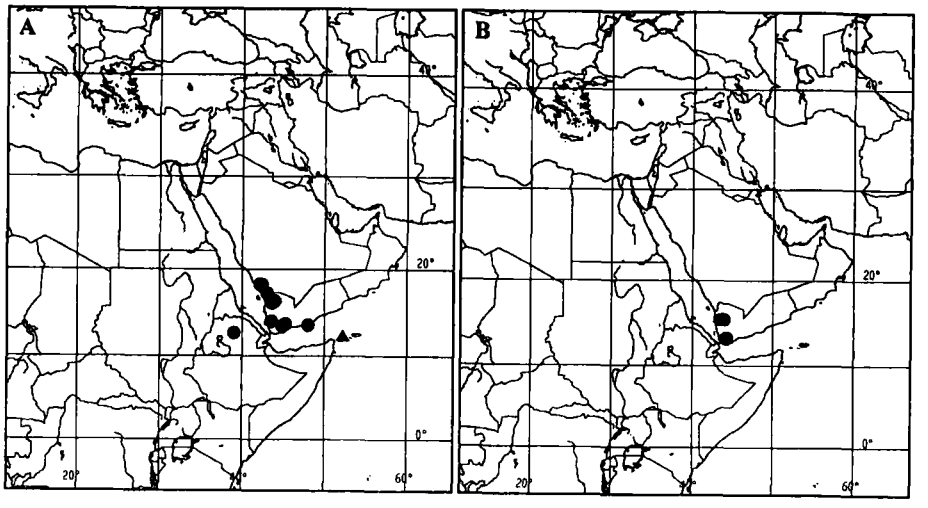


Fig. 5. A: Known distributions of *Nanorrhinum asparagoides* (●) and *N. kuriensis* (▲). B: Known distribution of *N. woodii* (●).

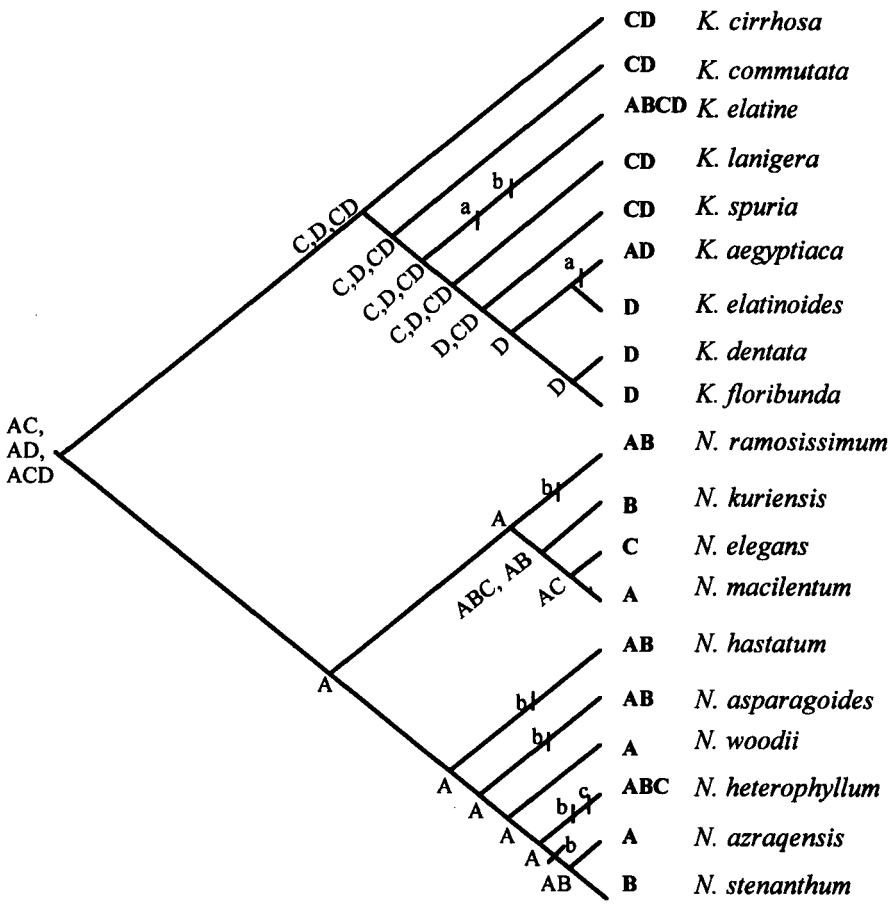


Fig. 6. Summary of the twenty optimal reconstructions of the ancestral distribution of *Kickxia* and *Nanorrhinum* using dispersal-vicariance analysis. At each node the optimal distribution prior to vicariance is given; alternative equally optimal distributions are separated with comma. The lower-case letters correspond to the areas of the upper-case letters and represent dispersal to the areas. A=Arabia, B= Horn of Africa, C=Macaronesia, and D= Mediterranean region.

trees out of the three equally most parsimonious trees resulting from the cladistic analysis of *Kickxia* sensu lato is used in the analysis.

An exact search with DIVA resulted in 20 alternative reconstructions of the distribution history each requiring 18 dispersals between areas. A summary of the optimal distributions at each ancestral node is given in Fig. 6. In all cases the results suggest the center of origin for *Nanorrhinum* to be the Arabian Peninsula. On the other hand, there is no single solution for the origin of *Kickxia* sensu stricto. For this clade the reconstructions postulate either the existence of a more or less widespread ancestor or, alternatively, Macaronesia or the Mediterranean region as the center of origin. The results also gave alternative solutions for the basal node, all suggesting a more or less widespread ancestor (Fig. 6). As for the question of centre of origin of *Nanorrhinum* and *Kickxia*, the result will be the same using any of the other equally parsimonious trees.

The first vicariance event was probably associated with the formation of vast barriers of arid zones, such as the Sahara, Sinai and Syrian deserts, between the Mediterranean region and the remaining areas of distribution. The formation of barriers followed by speciation then lead to the evolution of two lineages of species, the temperate *Kickxia* lineage and the tropical *Nanorrhinum* lineage.

Chromosome numbers

Kickxia. Previous counts of chromosome numbers in species of *Kickxia* s. str. were summed up by Sutton (1988). Five of the species investigated, *K. spuria, K. lanigera, K. commutata, K. cirrhosa,* and *K. aegyptiaca*, are diploids with 2n=18, whereas *K. elatine* is tetraploid with 2n=36. The chromosome number of *K. elatine* was confirmed in this study based on counts on material from Eritrea (see Table 3).

Nanorrhinum. The chromosome number 2n=18 has previously been reported for three of the species recognized here: *N. ramosissimum* (Verma & Dillon 1967: 217, as *Kickxia ramosissima*), *N. elegans* (Bor-

gen 1980: 70, as *Kickxia brunneri*), and *N. heterophyllum* (Reese 1957: 610, as *Linaria sagittata*; Borgen 1970: 158, as *Kickxia scoparia*). Bramwell et al. (1972: 148) also reported 2n=40 for *N. heterophyllum* (as *K. pendula*), but this number seems unlikely and needs confirmation.

In this study chromosome numbers have been counted in the progeny of eight collections representing four taxa (*N. asparagoides, N. heterophyllum, N. ramosissimum*, and *N. woodii*). All counts have given the somatic chromosome number 2n=18 (Table 3). These results indicate that the great infraspecific variation found in some of the species in the genus is not due to the occurrence of polyploid races.

Reproductive biology and crossing experiments

The flowers in *Kickxia* and *Nanorrhinum,* as in many other *Antirrhineae,* are specialised for bee pollination (Kampany 1995). The corolla is personate, where the tube is more or less closed at the mouth by a palate, an arching structure of the abaxial lip. It is usually yellow with an occasional purple tint on the palate. At the abaxial end the tube continues to form the spur, a structure for storage of nectar. The four stamens and the style are strategically placed in the tube against the ceiling, with the stigma resting at the centre of the ring of anthers just inside the mouth.

In the present study one species of *Kickxia* and six species of *Nanorrhinum* were investigated in cultivation for their sexual systems. The observations reveal that *N. heterophyllum, N. woodii* and *N. asparagoides* are self-incompatible and only produced seeds after artificial cross-pollination.This was observed in the progenies of Bremer 3844, 3845 and Ghebrehiwet 205 (all *N. heterophyllum*) and Thulin, Ghebrehiwet & Gifri 9303 (*N. woodii*), and Thulin, Ghebrehiwet & Gifri 9258 (*N. asparagoides*). In contrast, *N. hastatum, N. elegans* and *N. ramosissimum*, as well as *Kickxia elatine*, are self-compatible. This was studied in the progeny of Thulin & Gifri 9735 (*N. hastatum*), Leyens cv-95-265 (*N. elegans*), Thulin et al. 9217 (*N. ramosissimum*), and Ryding 1210 (*Kickxia elatine*).

There seems to be a correlation between sexual system and flower size, as the allogamous *N. heterophyllum* and *N. woodii* are large-flowered, whereas the autogamous *N. hastatum, N. elegans, N. ramosissimum*, and *Kickxia elatine*, are more or less small-flowered. However, the relatively small-flowered but yet allogamous *N. asparagoides* is an exception. Also, the information on sexual system of *N. hastatum is* derived from a small-flowered strain. It is quite possible that the large-flowered forms of this species found in certain areas (see under the species) are allogamous.

Artificial pollination trials were also made to investigate crossability between different forms of *N. heterophyllum,* previously treated by various workers as separate species. The crosses resulted in viable seeds that produced progenies up to the F2 generation and with a pollen stainability at 96% and above in all cases. The crosses carried out were as follows:

Bremer 3844, "*scoparia* form" (Canary Is.) × Bremer 3845 "*urbanii* form" (Canary Is.)

Ghebrehiwet 205 "*gracilis* form" (Eritrea) × Bremer 3844 "*scoparia* form" (Canary Is.)

Ghebrehiwet 205 "*gracilis* form" (Eritrea) × Bremer 3845 "*urbanii* form" (Canary Is.)

These results indicate that there are no reproductive barriers between these three "forms" of *N. heterophyllum*. Also, the plants obtained in the F1 and F2 generations are vigorous and agree well with specimens collected in the field in various parts of the area of distribution of *N. heterophyllum*.

Table 3. Chromosome numbers counted in *Kickxia* and *Nanorrhinum*.

Taxon	2n	Origin	Voucher
K. elatine	36	Eritrea	Ryding 1210
N. asparagoides	18	Yemen	Thulin, Ghebrehiwet & Gifri 9258
N. heterophyllum	18	Yemen	Thulin et al. 8135 ("*pseudoscoparia* form")
N. heterophyllum	18	Yemen	Thulin, Ghebrehiwet & Gifri 9391 ("*sabarum* form")
N. heterophyllum	18	Canary Is.	Bremer 3844 ("*scoparia* form")
N. heterophyllum	18	Canary Is.	Bremer 3845 ("*urbanii* form")
N. heterophyllum	18	Eritrea	Ghebrehiwet 205, ("*gracilis* form")
N. ramosissimum	18	Somalia	Thulin, Dahir & Hassan 9127
N. woodii	18	Yemen	Thulin, Ghebrehiwet & Gifri 9303

Taxonomy

Kickxia Dumort.

Dumortier 1827: 35; Betsche 1984: 131; Sutton 1988: 174. - *Elatine* Hill 1756: 113, nom. illeg., non L. (1753). - *Linaria* sect. *Elatinoides* Chavannes 1833: 103; Bentham 1876: 922. - *L.* subgen. *Elatinoides* (Chavannes) Nyman 1881: 542; Rouy 1909: 64. - *Elatinoides* (Chavannes) Wettstein 1891: 57. - *Elatinoides* sect. *Operculatae* Wettstein 1891: 58, nom. invalid. - *Kickxia* sect. *Operculatae* (Wettst.) Janchen 1933: 152 comb. invalid. - Type: *Kickxia elatine* (L.) Dumort. (see Pennell 1935: 313).

Dwarf shrubs, perennial or annual herbs, usually glandular-pubescent or pilose; stems prostrate to ascending or climbing by petioles. Leaves mostly alternate, simple, linear-lanceolate to suborbicular, entire, dentate or lobed, hastate or sagittate, acuminate, palmately veined, subsessile to petiolate, the petioles occasionally twining. Flowers zygomorphic, pedicellate, solitary in leaf-axils or in bracteate racemes; pedicels not cirrhose or reflexed. Calyx deeply divided, 5-lobed, the lobes entire, ± equal, imbricate, usually shorter than corolla tube. Corolla yellow, tube ± cylindrical or somewhat campanulate, calcarate abaxially at base; limb 2-lipped, the lips conspicuously unequal or subequal, the adaxial lip 2-lobed or emarginate, shorter than abaxial, erecto-patent to patent, the abaxial lip 3-lobed usually broad and spreading with low basal palate partially occluding mouth of tube; palate pubescent to lanate internally. Fertile stamens didynamous, included, the anthers marginally cohe-rent, forming a ring-like structure, ciliate, the connective not dilated above anther; staminode minute. Style simple, erect; stigma capitate, positioned through the centre of the ring of anthers. Capsule ovoid to subglobose, the walls thick leathery or thin papery, the septum erect, more or less straight, loculi equal, many-seeded, with simultaneous dehiscence or occasionally unequal with abaxial loculus few-seeded, smaller and dehiscing after the adaxial loculus, or rarely indehiscent. Capsule dehiscence operculate, with a detachable lid produced by a circumscissile split. Seeds bilaterally symmetrical, reniform to ellipsoid, testa reticulate-alveolate or tuberculate, usually papillate; tubercles broad, conical or rounded, closely spaced, sometimes laterally compressed and ridge-like; hilum median or rarely basal; epicuticular wax absent.

Mainly north temperate genus with nine, often weedy species distributed in Europe, northern Africa and western Asia, and widely introduced elsewhere.

The treatment of *Kickxia* presented here is a synopsis based on Sutton (1988), where many more synonyms can be found. In general only a limited amount of material has been seen of the taxa, and only in the Horn of Africa region a more detailed study has been made. No infraspecific taxa are recognized here, and more work on this genus is certainly needed.

Key to the species

1. Seeds tuberculate 2
1. Seeds reticulate-alveolate or with frequently anastomosed ridges 9

2. Capsules with distinctly unequal loculi 3
2. Capsules with more or less equal loculi 4

3. Pedicels 2.5-20 mm long; corolla-tube 3.5-4 mm broad at mouth. ..... 6. *K. aegyptiaca*
3. Pedicels 1-2.5 mm long; corolla-tube 5-6 mm broad at mouth. ..... 9. *K. floribunda*
4. Some or all of the upper leaves hastate or sagittate at base 5
4. Upper leaves attenuate or cuneate at base, never hastate or sagittate 7

5. Corolla 4-6 mm long ..... 1. *K. cirrhosa*
5. Corolla 7-17 mm long 6

6. Pedicels 5-30 × 0.08-0.3 mm, filiform, flexible. ... . 2. *K. commutata*
6. Pedicels 6-10 × 0.4-0.7 mm, rigid, spinescent..... ..... 6. *K. aegyptiaca*

7. Calyx-lobes 2-3 mm broad, almost entirely scarious ..... 8. *K. dentata*
7. Calyx-lobes 1-1.4 mm broad, only the margins scarious 8

8. Pedicels (4-)9-20 × 0.15-0.3 mm; calyx-lobes (0.5-)0.7-1.1 mm broad; corolla- tube 3.5-4 mm broad at mouth ..... 6. *K. aegyptiaca*
8. Pedicels 3-8 × 0.5-0.9 mm; calyx-lobes 1-1.4 mm broad; corolla-tube 4.5-6.5 mm broad at mouth ... . 7. *K. elatinoides*

9. Some or all of the upper leaves hastate or sagittate at base ..... 3. *K. elatine*
9. Upper leaves rounded or cordate at the base, never hastate or sagittate 10

10. Calyx-lobes not accrescent, 0.5-1.2 mm broad in fruit; corolla 7-11 mm long ..... 4. *K. lanigera*
10. Calyx-lobes accrescent, 2-4 mm broad in fruit; corolla 10-18 mm long ..... 5. *K. spuria*

1. Kickxia cirrhosa (L.) Fritsch

Fritsch 1897: 492; Sutton 1988: 180, Fig. 44.3,4. - *Antirrhinum cirrhosum* Linnaeus 1767: 249. - *Linaria cirrhosa* (L.) Chazelles 1790: 37; Chavannes 1833: 109; Walpers 1844: 194; Boissier 1879: 368. - *Elatinoides cirrhosa* (L.) Wettstein 1891: 58. – Type: "Linaria supina villosa, folio sagittato" (Tilli 1723: tab. 38(2), syntype).

Distribution: Western Mediterranean region, south-western Europe and the Azores.

Remarks: Kickxia cirrhosa is a weedy species that often grows in sandy soils near the sea. It is distinguished from other species in the genus by its narrow upper leaves and its small flowers with a 4-6 mm long corolla.

2. Kickxia commutata (Bernh. ex Reichenb.) Fritsch

Fritsch 1897: 492; Sutton 1988: 179, Fig. 43.1-5. - *Linaria commutata* Bernh. ex Reichenbach 1831: 373; Walpers 1844: 194. - *L. elatine* var. *commutata* (Bernh. ex Reichenb.) Visiani 1847: 161. - *Cymbalaria commutata* (Bernh. ex Reichenb.) Schur 1853: 54. - *Elatinoides commutata* (Bernh. ex Reichenb.) Wettstein 1891: 58. – Type: Yugoslavia, Istria, ex insula Cherso, Bartling s.n. (syntype, not located).

Antirrhinum graecum Bory & Chaubard in Bory 1832: 175, tab. 21. - *Linaria graeca* (Bory & Chaub.) Chavannes 1833: 108; Walpers 1844: 194; Bentham 1846: 268. - *Elatinoides graeca* (Bory & Chaub.) Wettstein 1891: 58. - *Kickxia commutata* subsp. *graeca* (Bory & Chaub.) Fernandes 1971: 74; Sutton 1988: 180. – Type: Greece, "E Scardamula et Chimova", Bory de Saint-Vincent (holotype ?, not located).

Distribution: Mediterranean Europe, northern Africa, Canary Islands.

Remarks: The species is common in the Mediterranean region and is widely naturalized elsewhere. Sutton (1988) recognised subsp. *graeca* from the eastern part of the range, but intermediates are also reported. Subsp. *graeca* has often been confused with *K. cirrhosa,* but differs in its curved (not straight) spur.

3. Kickxia elatine (L.) Dumort.

Dumortier 1827: 35; Sutton 1988: 174, Fig. 42.1,2. - *Antirrhinum elatine* Linnaeus 1753: 612. - *Linaria elatine* (L.) Miller 1768: no 16; Chavannes 1833: 107; Walpers 1844: 195; Boissier 1879: 367. - *Cymbalaria elatine* (L.) Gaertner, Meyer & Scherbius 1800: 398. - *Tursitis elatine* (L.) Rafinesque 1840: 156. *Elatinoides elatine* (L.) Wettstein 1891: 58. – Type: "*elatine*" (LINN-767.2, syntype, see Pennell 1935:313).

Linaria crinita Mabille 1867: 30. - *L. elatine* subsp. *crinita* (Mabille) Bolós & Vigo 1983: 97. - *Kickxia elatine* subsp. *crinita* (Mabille) Greuter 1967: 108; Täckholm 1974: 491; Sutton 1988: 176, Fig. 42.5, 6. – Type: Corsica, Furiani near Bastia, 8 Jul. 1866, Mabille 161 (BM isosyntype).

Distribution: Europe, northern Africa, south-western Asia, and widely introduced and naturalized elsewhere in temperate regions.

Remarks. Kickxia elatine is a weedy species that mostly grows in cultivated and waste land. It is highly variable and widespread species, and Sutton (1988) recognised two fairly distinct subspecies, the mainly European subsp. *elatine* with slender and sparsely villous stems, and the more widespread, robust and densely villous subsp. *crinita. K. elatine* resembles *K. commutata* in many ways, but can be readily identified by the reticulate-alveolate (not tuberculate) seeds.

4. Kickxia lanigera (Desf.) Freih & Hand.-Mazz.

Freih & Handel-Mazzetti 1913: 403; Sutton 1988: 178, Fig. 43.6-8. - *Linaria lanigera* Desfontaines 1798: 130; Walpers 1844: 193; Boissier 1879: 366. - *Antirrhinum lanigerum* (Desf.) Willdenow 1800: 233. - *Elatinoides lanigera* (Desf.) Coutinho 1906: 124. – Type: Tunisia: " in arvis cultis prope veterem Carthaginem", Desfontaines s. n. (P-DESF, holotype).

Distribution: South-western Europe, northern Africa, eastern Mediterranean region, south-western Asia.

Remarks: *Kickxia lanigera* is commonly found on cultivated ground and in waste places. It is very similar to and can be easily confused with *K. elatine* and *K. spuria*. However, the non-accrescent calyx with narrow lobes and the small capsules are characteristic.

5. Kickxia spuria (L.) Dumort.

Dumortier 1827: 35; Sutton 1988: 177, Fig. 42.3-8. - *Antirrhinum spurium* Linnaeus 1753: 613. - *Linaria spuria* (L.) Miller 1768: 15; Walpers 1844: 193; Chavannes 1833: 105; Boissier 1879: 366. - *Elatine spuria* (L.) Moench 1794: 525. - *Cymbalaria spuria*

(L.) Gaertner, Meyer & Scherbius 1800: 398. - *Elatinoides spuria* (L.) Wettstein 1891:58. – Type: "spurium" (LINN-767.3, syntype, see Pennell 1935: 313).

Antirrhinum spurium var. *integrifolium* Brotero 1827: 119, tab. 128. - *Kickxia spuria* subsp. *integrifolia* (Brot.) Fernandes 1971: 74; Sutton 1988: 178. – Type: Portugal, circa Olisiponema, Conimbricam et alibi in Extremadura et Beira (syntype, not located).

Distribution: Europe, northern Africa, south-western Asia, Macaronesia, naturalized elsewhere in temperate regions. The species has spread far beyond its original range and is widely naturalized on the American and Australian continents.

Remarks: This is a widespread and weedy species. Sutton (1988) recognized two "rather poorly defined subspecies", subsp. *spuria* mainly in northern and central Europe and subsp. *integrifolia* in other areas. *K. spuria* is distinguished from all other species of the genus by its entire leaves and conspicuously accrescent calyx-lobes.

6. Kickxia aegyptiaca (L.) Nábelek

Nábelek 1926: 31; Täckholm 1974: 490, Pl. 171; Sutton 1988: 185, Fig. 45.1-8. - *Antirrhinum aegyptiacum* Linnaeus 1753: 613. - *Linaria aegyptiaca* (L.) Chazelles 1790: 38; Chavannes 1833: 110; Walpers 1844: 195; Boissier 1879: 369. - *Cymbalaria aegyptiaca* (L.) Rafinesque 1840: 20. - *Tursitis aegyptiaca* (L.) Rafinesque 1840: 157. - *Elatinoides aegyptiaca* (L.) Wettstein 1891: 58. – Type: "aegyptiacum" (LINN 767.7, syntype).

Linaria fruticosa Desfontaines 1798: 39, tab. 133. - *Antirrhinum fruticosum* (Desf.) Willdenow 1800: 137. - *L. aegyptiaca* subsp. *fruticosa* (Desf.) Maire 1939: 294. - *Kickxia fruticosa* (Desf.) Rothmaler 1956: 114. – Type: Tunisia, near Gafsa, without collector (P holotype).

Linaria aegyptiaca subsp. *palaestina* Bornmüller 1909: 131; Post 1933: 285. - *Kickxia aegyptiaca* subsp. *palaestina* (Bornm.) Wickens 1975: 14; Sutton 1988: 186. – Types: Israel, Nazareth, 1895, Post s. n. (B syntype); montis Carmel, 3 May 1897, Bornmüller 1198 (B syntype, JE isosyntype); Jordan, Judea, 1897, Bornmüller 1197 (B syntype, K isosyntype); Jericho, Ain-i-Sultan et Wadi Kilt, 30 Mar. 1897, Bornmüller 1199 (B syntype, BM, JE isosyntypes).

Linaria aegyptiaca subsp. *battandieri* Maire 1925: 95. - *Kickxia aegyptiaca.* subsp. *battandieri* (Maire) Podlech 1981: 476; Sutton 1988: 188. – Type: Morocco, Figuig, Battandier s. n. (AL lectotype, selected by Wickens 1975).

Kickxia aegyptiaca subsp. *tibestica* Quézel ex Wickens 1975: 14. – Type: Chad, Tibesti, Emi Koussi, Sep. - Nov. 1956, Quézel s. n. (MARSSJ holotype, K isotype).

Distribution: Northern Africa, eastern Mediterranean region, south-western Asia.

Remarks: *Kickxia aegyptiaca* is a dwarf shrub or suffrutescent perennial characterized by its unequal capsule loculi and seed dimorphism. It is a very variable species which is usually divided into a number of infraspecific taxa on the basis of, among other things, indumentum characters, flower size and length of pedicel. Six subspecies are recognized by Sutton (1988) following Wickens (1975). However, Sutton also points to the presence of intermediate specimens and considerable variation within each taxon that makes the subspecies rather ill-defined.

7. Kickxia elatinoides (Desf.) Rothm.

Rothmaler 1956: 113; Sutton 1988: 182, Fig. 44.1,2. - *Linaria elatinoides* Desfontaines 1798: 39, tab. 132; Walpers 1844: 192. - *Antirrhinum elatinoides* (Desf.) Willdenow 1800: 235. – Type: Algeria, "in arvis pr. Mascar", Desfontaines s. n. (P-DESF, ? holotype).

Distribution: Only known from Algeria.

Remarks: *Kickxia elatinoides* is a perennial herb that grows in clay soils. It is very similar to *K. dentata,* but differs in its indumentum with shorter, more appressed hairs, narrower calyx-tube, narrower corolla-tube, and relatively longer spur. The seeds have a testa with thin ridges and are intermediate in form between seeds with tubercles and seeds with anastomosed ridges.

8. Kickxia dentata (Vahl) D. A. Sutton

Sutton 1988: 184, Fig. 44.5,6. - *Antirrhinum dentatum* Vahl 1791: 66, tab. 37. - *Linaria dentata* (Vahl) Dietrich 1818: 393. – Type: Tunisia, "legi Tuneti in glareosis", Forsskål s.n. ex herb. Vahlii (C holotype).

Distribution: Known only from Algeria and Tunisia.

Remarks: *Kickxia dentata* is readily distinguished by its calyx-lobes with broad scarious margins. It resembles *K. elatinodes* (seee above) and also grows in clay soils.

9. Kickxia floribunda (Boiss.) Täckh. & Boulos

Täckholm & Boulos 1974: 97; Täckholm 1974: 491; Sutton 1988: 184, Fig. 44.7,8. - *Linaria floribunda* Boissier 1853: 40. – Types: Jordan, "Palaestine. Pays du Amalcitis", Apr-May 1846 Boissier s. n. (G-BOIS syntype, BM photo.); "Arab. petr. ad finis Amalicitorum", Mar 1846, Boissier s. n. (G-BOIS syntype, BM photo., JE isosyntype?).

Distribution: South-eastern Mediterranean region with collections from Jordan, Israel and Sinai.

Remarks: *Kickxia floribunda* is distinguished by its procumbent and densely leafy stems and relatively large, broad, pale yellow flowers. It agrees with *K. aegyptiaca* in its capsule with unequal loculi, but can be distinguished by the shorter pedicels and wider corolla-tube.

Nanorrhinum Betsche

Betsche 1984: 131. – Type: *N. acerbianum* (Boiss.) Betsche.

Elatinoides sect. *Valvatae* Wettstein 1891: 58. - *Kickxia* sect. *Valvatae* (Wettst.) Janchen 1933: 152; Sutton 1988: 190. – Type: *K. ramosissima* (Wall.) Janchen.

Pogonorrhinum Betsche 1984: 128. – Type: *P. scoparium* (Brouss. ex Spreng.) Betsche.

Dwarf shrubs perennial or annual herbs; glabrous or glandular or eglandular pubescent; stems prostrate to erect or climbing by means of twining petioles. Leaves mostly alternate, simple or sometimes deeply divided, linear to suborbicular, entire, dentate or lobed, hastate or sagittate, generally palmately veined, petiolate to subsessile, the petioles frequently twining. Flowers zygomorphic, pedicellate, solitary in leaf-axils or in bracteate racemes; pedicels not cirrhose or reflexed. Calyx deeply divided, 5-lobed, the lobes entire, ± equal, imbricate, usually shorter than corolla tube. Corolla yellow, tube ± cylindrical or somewhat campanulate, calcarate or rarely saccate abaxially at base; limb 2-lipped, the lips conspicuously unequal or subequal, the adaxial lip 2-lobed or emarginate, shorter than abaxial, erecto-patent to patent, the abaxial lip 3-lobed usually broad and spreading with low basal palate partially occluding mouth of tube; palate glabrous to lanate internally. Fertile stamens didynamous, included, the anthers marginally coherent forming a ring-like structure, glabrous, the connective not dilated above anther; staminode minute. Style simple, erect; stigma capitate, positioned through the centre of the ring of anthers. Capsule subglobose, ovoid to oblong-ovoid, the walls coriaceous or papyraceous, the septum erect, ± straight, loculi equal, many-seeded, with simultaneous dehiscence or occasionally unequal with abaxial loculus few-seeded, smaller and dehiscing after the adaxial loculus, or rarely indehiscent. Capsule dehiscence valvate, dehiscence initiated from apex producing 1-3(-6) teeth. Seeds bilaterally symmetrical, oblong-ovoid, ellipsoid, or rarely reniform, tuberculate, the tubercles rounded to columnar, usually widely spaced, frequently papillate; hilum median or rarely basal; epicuticular wax absent.

A tropical and subtropical Afro-Asiatic genus of 10 species.

Key to the species

1. Capsule loculi unequal, the adaxial loculus larger and usually dehiscing before the abaxial loculus 2
1. Capsule loculi equal in size, both usually dehiscing at the same time 4

2. Spur 6-10 mm long, longer than rest of corolla .... 8. *N. azraqensis*
2. Spur up to 5 mm long, shorter than rest of corolla 3

3. Corolla including spur 3.5-7.5 mm long, the tube 1-2 mm broad at mouth ..... 2. *N. elegans*
3. Corolla including spur 7.5-11 mm long, the tube 2.5-3.5 mm broad at mouth ..... 4. *N. macilentum*

4. Spur longer than rest of corolla 5
4. Spur equalling or shorter than rest of corolla..... 6

5. Corolla-tube 4-9 mm broad at mouth; corolla including spur (13-)15-28 mm long .... 9. *N. heterophyllum*
5. Corolla-tube c. 1.2 mm broad at mouth; corolla including spur 11.5-13 mm long .... 10. *N. stenanthum*
6. Upper cauline leaves filiform or linear 7
6. Upper cauline leaves lanceolate, deltate or suborbicular 8

7. Plant annual; spur at right angle with the tube; basal leaves ovate to orbicular, entire or shallowly dentate ..... 5. *N. hastatum*
7. Plant perennial; spur straight or somewhat curved forming an obtuse angle with the tube; basal leaves obovate or elliptic, entire .... 6. *N. asparagoides*

8. Plant annual; leaves ovate to orbicular, not hastate ..... 3. *N. kuriensis*

8. Plant perennial; leaves lanceolate or deltate, some often hastate 9

9. Corolla-tube 1.5-3 mm wide at mouth; corolla including spur 3.5-11 mm long. ..... 1. *N. ramosissimum*

9. Corolla-tube 3.5-9 mm wide at mouth; corolla including spur 10-19 mm long ..... 7. *N. woodii*

1. Nanorrhinum ramosissimum (Wall.) Betsche

Betsche 1984 :132. - *Linaria ramosissima* Wallich 1831: 43, tab. 153; Walpers 1844: 196; Boissier 1879: 368; Hooker 1884: 251. - *Elatinoides ramosissima* (Wall.) Wettstein 1891: 58. - *Kickxia ramosissima* (Wall.) Janchen 1933: 152; Pennell 1943: 59; Sutton 1988: 190, Fig. 46. – Type: India, Uttar Pradesh, "prope Mirzapur ad ripam Ganges", 1820, Wallich 3911c (K-W lectotype, selected by Sutton 1988, BM isolectotype).

Linaria incana Wallich 1831: 43; Walpers 1844: 196; Hooker 1884: 252. - *Kickxia incana* (Wall.) Pennell 1943: 59; Sutton 1988: 195. - *Nanorrhinum incanum* (Wall.) Betsche 1984: 132. – Type: Nepal, "Nepalia" Apr 1821, Wallich 3910 (K-W holotype).

Linaria roylei Chavannes 1833: 112. – Type: India, "in provincia Delhi", Royle s.n. (not located).

Linaria ramosissima var. *pubescens* Stocks ex Hooker 1884: 251. - *L. cabulica* Bentham 1846: 270; Boissier 1879: 368. - *Kickxia cabulica* (Benth.) D.A. Sutton 1988: 196, Fig. 48. – Type: Pakistan, "Beebee Nanee" (SE Quetta, near Bolan pass), 10 Mar 1839, Griffith 215 (K holotype).

Linaria ramosissima var. *ovata* Bentham 1846: 270. - *L. ovata* (Benth.) Boissier 1879: 369. - *Kickxia ovata* (Benth.) Kitamura 1960: 355; Sutton 1988: 197, Fig. 48. – Type: Afghanistan, 1 Nov 1839, Griffith 612 (K lectotype, selected by Sutton 1988).

Linaria somalensis Vatke 1875: 305; Norman 1924: 138. - *Kicksia somalensis* (Vatke) Cufodontis 1963: 890; Sutton 1988: 199, Fig. 49. - *Pogonorrhinum somalense* Betsche 1984: 129. – Type: Somalia, Sanaag region, near "Meid" in the "Ahl" mountains, Apr 1875, Hildebrandt 1409 (BM, K isotypes).

Linaria campyloceras Rechinger & Esfandiari 1950: 90; *Kickxia campyloceras* (Rech. & Esfand.) Speta 1979: 4. – Type: Iran, Makran, "in angustiis Tang-e Sarkeh inter Transhahr et Cah Bahar", 24 Mar 1949, Sharif 292 (E not seen).

Kickxia dibolophylla Wickens 1971: 377, Fig. 1; Wickens 1976: 146; Sutton 1988: 200, Fig. 49. - *Nanorrhinum dibolophyllum* (Wickens) Betsche 1984: 132. – Type: Sudan, Darfur, Jebel Marra, 12 Dec 1962, Pettet 188 (K holotype).

Kickxia chasmophytica Wendelbo 1980: 109; Sutton 1988: 195 Fig. 48. – Type: Iran, Bandar-Abbas, Khu-e Genou, 3 Apr 1975, Wendelbo & Foroughi 15400 (GB holotype, E isotype).

Kickxia membranacea D.A. Sutton 1988: 191 Figs 46.6, 47. – Type: Bhutan, Punakha- Lobeysa, 18 Jun 1975, Grierson & Long 515 (E holotype).

Kickxia adpressa D.A. Sutton 1988: 200, Fig. 50. – Type: Kenya, N Frontier Province, Marsabit Distr., Gof Choba, 1 Mar 1963, Bally 12569 (K holotype).

Perennial herb or subshrub, glabrous, sparsely pubescent or tomentose all over with glandular or eglandular hairs up to 1.5 mm long. Stem up to 60 (-90) cm long, prostrate, scandent or ascending to erect, diffusely branched throughout. Leaves heteromorphic, basal leaves (3-)6-20 (-25) × 4-12(-25) mm, ovate to elliptic, obtuse or truncate at the apex, coarsely serrate or entire, rounded at the base, petioles 4-12 mm long, not cirrhose; upper leaves (3-)7-25 × (1.5-)3-15 mm, ovate, deltate or lanceolate, acute or subacute at the apex, entire, lobed, or rarely with few teeth near the base, hastate, sagittate or rounded to cordate at the base; petioles (2-)4-14 mm long, not or slightly cirrhose. Pedicels 7-21(-26) × 0.1-0.2 mm, erect or patent, filiform, straight, except for deflexed or recurved distal end. Calyx-lobes 3-5 × 0.4-1.4 mm, linear-subulate to lanceolate, acuminate, the margin narrowly to somewhat broadly scarious below, glabrous, glandular- or eglandular-pubescent or villous. Corolla including spur 3.5-11 mm long, yellow, glandular- or eglandular-pubescent externally; tube 1.5-3 mm broad at the mouth; adaxial lip sinus 0.3-1.2 mm; abaxial lip sinus 0.7-2.2 mm; palate glabrous or sparsely pubescent internally; spur 1.2-6.5 mm long, slender, acute, straight, patent or forming obtuse angle with tube, shorter or subequalling rest of corolla. Abaxial filaments pubescent. Capsule 2.5-5 mm long, ovoid, oblong-ovoid or subglobose, glabrous or sparsely glandular-puberulent at apex; loculi equal, many-seeded, dehiscent. Seeds 0.3-0.6 mm long, oblong-ovoid to oblong ellipsoid, practically always tuberculate, blackish- to reddish-brown; tubercles columnar, subacute or obtuse, papillate, or shortly acute, entire; papillae mostly confined to tubercle-apices, patent, slender, straight or recurved. – Figs 7A, 8.

Distribution and habitat. Nanorrhinum ramosissimum is a widespread taxon with a distribution in South-Centeral Asia, Arabia and the Horn of Africa. It is known from Burma, N India, Bhutan, Nepal, China (Tibet), Pakistan, Afghanistan, Iran, Oman, Somalia, Kenya, Ethiopia and W Sudan. The species occurs on rocky outcrops and cliffs usually in

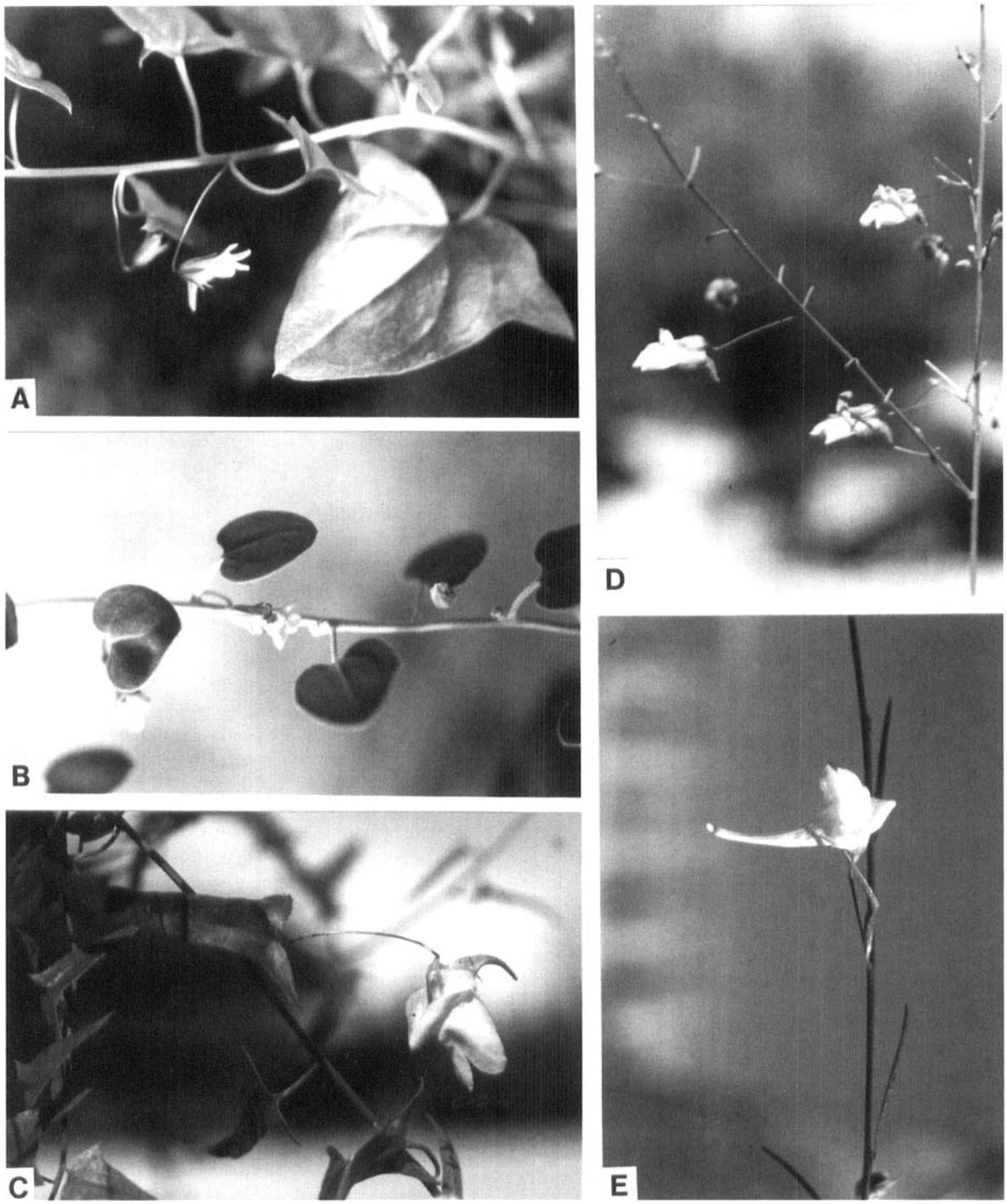


Fig. 7. Photographs of species of *Nanorrhinum*. – A: *N. ramosissimum*, grown from seeds of Thulin 9128. – B: *N. elegans*, grown from seeds of Leyens cv-95-265. – C: *N. woodii*, grown from seeds of Thulin et al. 9303. – D: *N. asparagoides*, growing on rocky slopes in Yaffa, Yemen (Thulin et al. 9257) – E: *N. heterophyllum*, grown from seeds of Bremer 3844. – A, C–E, photo by M. Thulin; B, photo by Ghebrehiwet M.

crevices of limestone rocks at 800-2400 m altitudes.

Taxonomic remarks. Kickxia ramosissima was treated by Sutton (1988) as a species restricted to South-Central Asia (India, Burma and Nepal). Of the synonyms listed above *K. incana* (central and eastern Himalaya), *K. cabulica* and *K. ovata* (both Afghanistan, India and Pakistan), *K. membranacea* (Bhutan), *K. somalensis* (Somalia), *K. dibolophylla* (Sudan), and *K. adpressa* (Kenya), were names of taxa treated as distinct species.

The oldest of these names from Africa is *K. somalensis*, of which only the type collection was available to Sutton, who noted the similarity to *K. ramosissima*. However, it was said to differ from *K. ramosissima* in its small, entire, homomorphic leaves, glabrous (not pubescent to subglabrous) palate, straight (not curved) spur, and by its seeds with more shortly papillate or entire tubercles. Today several collections from near the type locality of *K. somalensis* in northern Somalia are available, which display a wide variation in, for example, indumentum, leaf shape and seed ornamentation. Thulin, Dahir & Hassan 9127 is glabrous with ovate, entire, apically rounded leaves, and tuberculate, papillate seeds, and fits the original description of *K. somalensis* very well. However, plants grown in the greenhouse from seeds of this collection were observed to have large, hastate, cauline leaves, similar to the leaves normally found in *K. ramosissima* (Fig. 7A). All the other collections from Somalia have hastate leaves. It seems obvious that the leaf shape here is to a large extent environmentally conditioned.

Of the other collections Thulin & Warfa 6188 is glabrous except at the base, Lavranos & Carter 24825 is tomentose with short glandular and eglandular hairs, and Thulin 4349 and Thulin, Dahir & Hassan 9149 are villous with glandular and eglandular hairs up to 1.5 mm long. In the field hairy and glabrous forms have been observed growing side by side (Thulin, pers. comm.).

Also, the ornamentation of the seeds varies considerably in the material from Somalia (Fig. 8). The seeds mostly have distinct columnar tubercles with recurved papillae at the tip, although the size of the tubercles may vary. The seeds of Thulin & Warfa 6188 are extreme in that both tubercles and papillae are obsolete.

Of the other two synonyms from Africa *K. dibolophylla* was said to differ from *K. somalensis* in its hastate leaves, shorter pedicels, larger corollas with relatively longer spur, and in its seeds with entire tubercles (Sutton 1988). With the material now available from Somalia these differences do not hold true. *K. adpressa* from Kenya, on the other hand, was said to differ from *K. ramosissima* in its glandular-pubescent indumentum, smaller leaves, flowers and capsules, and by its seeds with shorter tubercles.

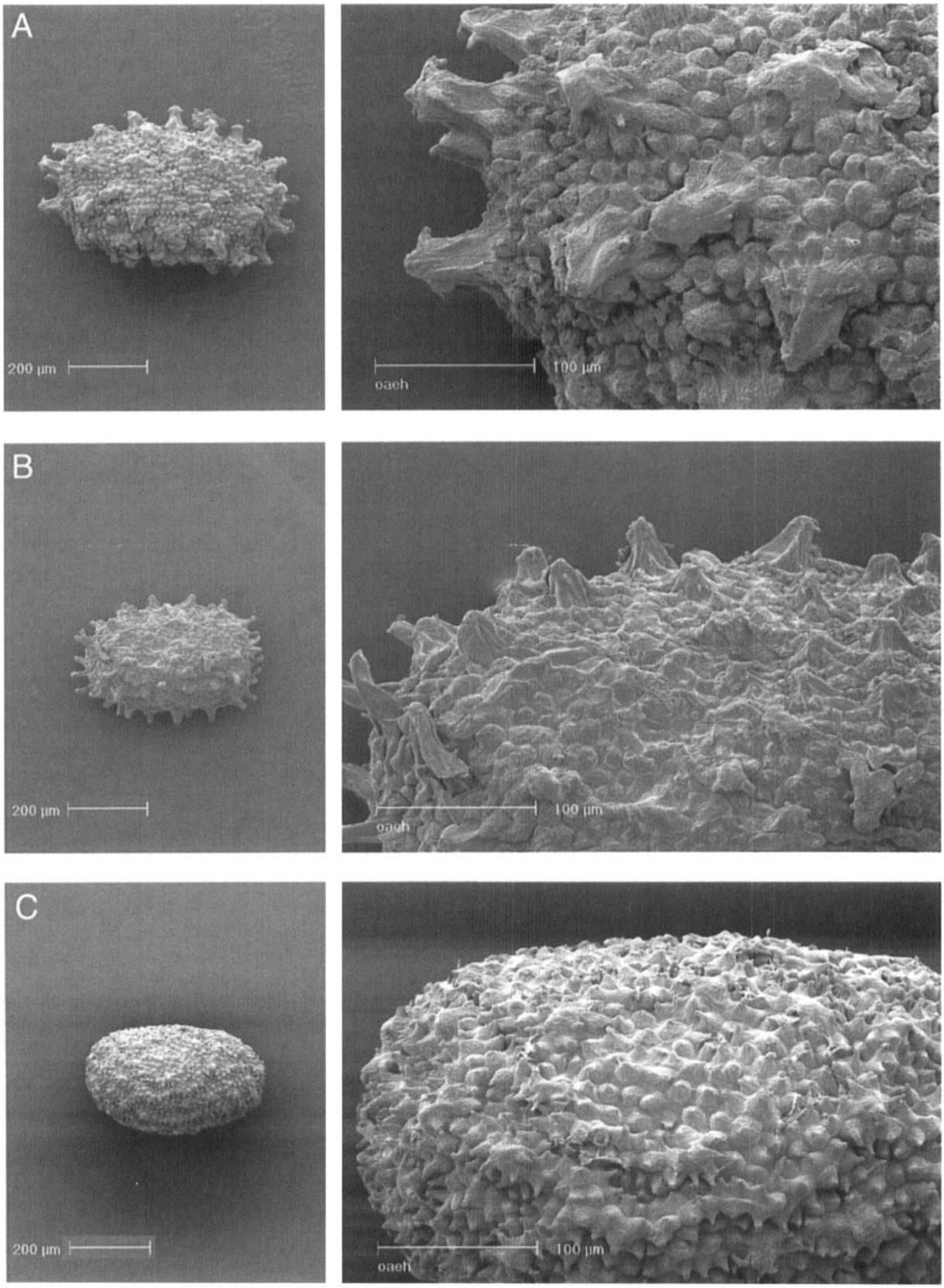
In Asia there has been much confusion concerning the circumscription of *K. ramosissima* and Sutton (1988) pointed out that "the taxonomic delimitation of *K. ramosissima, K. ovata, K. incana* and *K. cabulica* is far from clear in most accounts of this area and names on herbarium specimens should be treated with caution".

K. ovata, first described as *Linaria ramosissima* var. *ovata* by Bentham (1846), owing to its ovate-cordate leaves, but Hooker (1884) considered that it "passes so insensibly into the type that it cannot be retained". Sutton (1988) stated that *K. ovata* differs from *K. ramosissima* in its entirely glabrous stems and leaves and in its longer pedicels. He also pointed to similarities between *K. ovata* and *K. cabulica* and suggested that these two taxa may be conspecific. Pennell (1943), on the other hand, treated *K. cabulica* as conspecific with *K. incana*.

Kickxia chasmophytica, described from southern Iran, was by Sutton (1988) keyed out from *K. ramosissima* by its non-hastate leaves, but the existence of plants with hastate leaves in southern Iran was also pointed out. These were regarded as being of uncertain taxonomic status along with two specimens from adjacent parts of Oman. In my opinion these specimens all fall within the variation of a more broadly circumscribed *K. ramosissima*. Also, the type of *K. campyloceras* from Iran, with glabrous stems and minute leaves, belongs here. Other specimens from Oman are Rubens 55, 56 and 59. They were originally identified as *K. ramosissima*, but annotated by Sutton as cf. *K. somalensis*.

K. membranacea was described by Sutton (1988) on the basis of a single collection from Bhutan. It was said to differ from *K. ramosissima* mainly by its seeds with relatively larger tubercles lacking recurved papillae and by having usually sagittate leaves and calyx-lobes with a broad and irregularly lobed scarious margin. A second collection from Bhutan, Griffith 505, with rounded or hastate leaf-bases, was said to be either referable to *K. ramosissima* or represent a distinct taxon.

In my view *Nanorrhinum ramosissimum* is a fairly variable species extending from south-central Asia over the southern part of the Arabian Peninsula into north-east tropical Africa and including the types of all the synonyms mentioned above. The variation is only to a small extent geographically correlated and the erection of infraspecific taxa therefore seems not advisable.


A
200 µm
100 µm
oaeh
B
200 µm
100 µm
oaeh
C
200 µm
100 µm
oaeh

Nanorrhimum ramosissimum resembles *N. hastatum* in being small-flowered and having hastate leaves. For differences between these species, see under *N. hastatum*.

Additional specimens examined. Burma. Ava, Wallich 3911D (BM, K); Banks of Irrawady, Ridley s.n. (BM).

India. W Bengal, Calcutta, Clarke 21485b (BM); Bellary rock, Gamble 17742 (BM, K); Punjab, Drummond 20439 (K); Dehra Dun, Jubbul state, below Chaupal, Parkinson 7399 (E); Poona, Maharashtra, Saplashring hill, Narasimhan 165258 (K); Hazara, NW Himalaya, Duthie 19978 (C).

China. SE Tibet, Ludlow, Sherriff & Tailor 6299 (BM).

Bhutan. Angduphorang, Cooper 4862 (BM); cliffs near Benka, Griffith 505 (BM).

Nepal. Lapha, Karnali valley, Polunin, Sykes & Williams 3987 (BM, UPS); Bheri valley, near Dunahi, Polunin, Sykes & Williams 2476 (BM, UPS); Arun valley, Kundale Ghat, W Chainpur, Stainton 94 (BM, UPS).

Afghanistan. Nuristan, Nishei, Edelberg 817 (C); Kunar valley, near Chunki, Carter 294 (K).

Pakistan. Thal-Kurram, Aitchison 318 (BM); Kashmir, Astor, Astor valley near Ramghat, Duthie 12283 (BM); Baluchistan, Quetta, Crookshank 293 (K); Punjab, Rawal Pindi, Toji park, Stewart 7107 (S); NW Frontier Province, 4 miles S Chitral, Stainton 2215 (BM).

Iran. Baluchistan, 10-18 km from Bazman, Rechinger 55033 (E, S); 8-10 km NW of Kazerun, Davis & Bokhari 56611 (E, K); Bandar-Abbas, Kuhe Genom, Wendelbo & Foroughi 15400 (E).

Oman. Muscat, Tanuf 175 km SW Muscat, between Nawah and Bahlah, Rubens 55, 56, 59 (E); Dhofar, Jebel Qara, Wadi Urman NE of Salalah, Miller 6084 (K); Jebel al-Akhdar, Wadi Sahtan, Mandville 6181 (BM); Wadi Saiq Jebel Abhdat, Lawton 2440 (K); Sayq, Whitecomb 846 (E).

Sudan. Darfur, Jebel Mara, Steele 12 (K); Darfur, Jebel Mara, Lynes 139a (BM).

Ethiopia. Gojam Region, Debremarkos Awraja, 20 km S of Dejen, Mesfin & Kagnew 1578 (ETH, K).

Somalia. Sanaag Region: escarpment between Mait and Erigavo, Thulin 4349 (K, UPS); escarpment SE of Laasqoray, near Markat, Thulin, Dahir and Hassan 9127 (UPS); escarpment SE of Laasqoray, near Moon, Thulin, Dahir & Hassan 9149 (K, UPS). Bari Region: Galgala, Thulin & Warfa 6188 (K, UPS).

Kenya. Marsabit District: near Lake Marsabit, Delamere s. n. (BM); Mt Kulal, Gatab, Hepper & Jaeger 6890 (K).

2. Nanorrhinum elegans (G. Forst.) Ghebrehiwet comb. nov.

Antirrhinum elegans G. Forster 1787: 60. - *Kickxia elegans* (G. Forst.) D. A. Sutton 1988: 211, Figs 54.1-2; Brochmann et al. 1997: 279, Fig. 162a. – Type: Cape Verde Islands, S. Tiago, "ad portum, Praya dictum in Sti. Iacobi insula", Aug 1772, Forster s.n. (K holotype).

Linaria brunneri Bentham 1846: 270. - *L. brunneri* var. *vera* Webb 1849: 166, nom. invalid. - *Elatinoides brunneri* (Benth.) Wettstein 1891: 58. - *Kickxia brunneri* (Benth.) Janchen 1933: 152; Rustan & Brochmann 1988: 67. - *Nanorrhinum brunneri* (Benth.) Betsche 1984: 132. – Type: Cape Verde Islands, S. Tiago, "Senegambia", 1840, Brunner s.n. (K lectotype, selected by Sutton 1988).

Linaria dichondrifolia Bentham 1846: 270. - *Elatinoides dichondrifolia* (Benth.) Wettstein 1891: 58. - *Kickxia dichondrifolia* (Benth.) Janchen 1933: 152; Sutton 1988: 214, Fig. 54.3-4. - *Nanorrhinum dichondrifolia* (Benth.) Betsche 1984: 132. - *Kickxia brunneri* subsp. *dichondrifolia* (Benth.) Rustan & Brochmann 1988: 70. - *Kickxia elegans* subsp. *dichondrifolia* (Benth.) Rustan & Brochmann 1997: 284, Fig. 165. – Type: Cape Verde Islands, S. Nicolão, Forbes s.n. (K holotype).

Linaria brunneri var. *parietariifolia* Webb 1849: 166. - *Elatinoides brunneri* var. *parietariifolia* (Webb) Couthino 1914: 310. - *Kickxia brunneri* var. *parietariifolia* (Webb) A. Hansen & Sunding 1979: 92. – Type: not designated.

Linaria brunneri var. *glaberrima* J. A. Schmidt 1852: 242. - *Kickxia brunneri* var. *glaberrima* (J. A. Schmidt) Sunding 1974: 21. - *Kickxia glaberrima* (J. A. Schmidt) D. A. Sutton 1988: 215, Figs 54.5-6. – Type: Cape Verde Islands, S. Vicente, 1851, Schmidt s.n. (HBG holotype, not seen).

Linaria webbiana J. A. Schmidt 1852: 240, nom. illeg. non Visiani (1842). - *Kickxia webbiana* Sunding 1974: 21; Sutton 1988: 215, Fig. 54.7-8. - *Kickxia schmidtii* A. Hansen & Sunding 1979: iv, nom. illeg. superfl. - *Nanorrhinum webbianum* (Sunding) Betsche 1984: 132. - *Kickxia brunneri* subsp. *webbiana* (Sunding) Rustan & Brochmann 1988: 71, Fig. 3. -

Fig. 8. Scanning electron micrographs of seeds of *Nanorrhinum ramosissimum* showing variation in testa-structures in populations in Sanaag region in Somalia. Note the absence of prominent tubercles in 'C'. – A: from Thulin 4349 (UPS). B: from Thulin, Dahir & Hassan 9127 (UPS). C: from Thulin & Warfa 6188 (UPS).

Kickxia elegans subsp. *webbiana* (Sunding) Rustan & Brochmann in Brochmann et al. 1997: 286, Fig 162 b. – Type: Cape Verde Island, S. Antão "in rupibus basalticus et in locis lapidosis vallium ins. S. Antonii, praecipue pr. Ribir. grand.", Mar 1851, Schmidt s.n. (HBG holotype, not seen, BM photo.).

Perennial herb or subshrub, glabrous, puberulent, pubescent, or whitish tomentose with hairs up to 0.5 mm long. Stem up to 40(-85) cm long, pendent or prostrate, slender to somewhat stout, straight or often flexuose, moderately branched, the angle of branching wide. Leaves 2.5-14(-20) × 2.5-12(-24) mm, ovate to cordate-orbicular, reniform, elliptical, oblong, or rhomboid, entire or irregularly dentate at the margin, with subcordate to cordate or occasionally hastate-sagittate base and apiculate to acuminate or rounded apex, glabrous, pubescent or whitish tomentose; petioles 1-12(-16) mm long, not cirrhose. Pedicels 3-12 × 0.1-0.3 mm, more or less patent, straight or distally reflexed. Calyx-lobes 2.2-3 × 0.5-1 mm, linear-lanceolate, subacute to acuminate, the margins green or very narrowly scarious, densely eglandular-pubescent. Corolla including spur 3.5-7.5 mm long, pale yellow, more or less densely covered with patent eglandular hairs externally; tube 1-2 mm broad at mouth; adaxial lip sinus 0.5-1.2 mm; abaxial lip sinus 1-1.5 mm; palate subglabrous; spur 1.2-3.5 mm long, patent, slender strongly curved forwards, shorter than the rest of corolla. Abaxial filaments subglabrous. Capsule 2.5-5 mm long, oblong-ovoid, obliquely truncate, densely covered with patent eglandular hairs towards apex, loculi somewhat unequal, many-seeded, dehiscent. Seeds 0.2-0.5 mm long, oblong-ovoid, tuberculate, dark brown; tubercles conical, entire. – Fig. 7B.

Distribution and habitat. Nanorrhinum elegans is endemic to the Cape Verde Islands, where it occurs in all the main islands: Santa Antão, São Vicente, Santa Luzia, São Nicolau, Sal, Boa Vista, Maio, Santiago, Fogo, and Brava. It is distributed between sea-level and 950 m altitude, and grows on cliffs, in crevices, and on gravelly slopes.

*Taxonomic remarks.*This Cape Verdean species has for a long time been generally known as *K. brunneri.* The type of *K. elegans* was long believed to be from Madeira, but the confusion of locality information on herbarium material collected by Forster from Madeira and the Cape Verde Islands was discussed and clarified by Sutton (1988).

N. elegans is a very variable species. (Fig. 7B). It has been treated by various workers either as a single variable species divided into subspecies (Bentham 1846, Brochmann et al. 1997) or as up to four separate species (Betsche 1984, Sutton 1988). Rustan & Brochmann (1988), after intensive field studies, recognised a single species with three subspecies. The same treatment was followed by Brochmann et al. (1997), where it was further noted that the variation within *N. elegans* is more or less continuous along complex and parallel ecogeographic gradients and that the subspecies represent ecotypes, which are partly bridged by ecoclinal variation. In the present study a similar wide view is adopted and a single species is recognised, but without any subdivision into subspecies. Though extreme forms can be easily identified, there are many intermediates, and the acceptance of infraspecific taxa in this case would, in order to obtain a consistent taxonomy, necessitate a subdivision also of other variable species, such as *N. macilentum, N. ramosissimum* and *N. heterophyllum.*

N. elegans resembles *N. ramosissimum* in its habit, leaf shape and subglabrous palate, but can be readily identified by its capsules with somewhat unequal loculi and its seeds with entire tubercles.

Additional specimens examined. Cape Verde Islands. S. Antão: Rib. Grande, Lowe s.n. (BM); Morossos, Leyens cv-95-265 (UPS). S. Vicente: Martinho de Bella Vista, Monsanto, Bolle s.n. (BM, K); Moseley s.n. (BM, K); Mt. Verde, Leyens cv-95-228 (UPS). S. Nicolau: camo. da caldeira, Lowe s.n. (BM); Monte Gardo, Lowe s.n. (K); in montibus, Bolle s.n. (C, K, S); Terra-fal, Forbes s.n. (K). Fogo: Acha da Furna, Chevalier 44997 (K); S. Filipe, Lowe s.n. (BM); near S. Filipe, Chevalier 44805 (K). Boa Vista: Praia Derrubada, Lobin 688 (BM); Cardos 25, 85, 160 (K). Brava, above Pov. de S. João, Lowe s.n. (BM, K).

3. Nanorrhinum kuriensis (A. R.-Sm.) Ghebrehiwet comb. nov.

Kickxia kuriensis A.R.-Smith 1971: 37, tab. 3689; Sutton 1988: 202, Fig. 49.5-7. – Type: Yemen, Abd-al-Kuri, 12°14'N, 52°15'E, lower N facing slopes of Jebel Hassala (Qarat Saleh), 7 May 1967, Smith & Lavranos 665 (K holotype).

Annual herb, glandular-pubescent all over, with hairs up to 0.3 mm long. Stem up to 15 cm long, erect to ascending, slender, sparingly branched from the base, angle of branching wide. Leaves homomorphic, 2-10 × 2-8 mm, ovate to elliptic or suborbicular, obtuse to subacute and often apiculate at the apex, entire with a minute basal tooth, truncate, rounded or subcordate at the base; petioles 5-8(-10) mm long, not cirrhose. Pedicels 10-18 × 0.1-

0.18 mm, erecto-patent, filiform, straight. Calyx lobes 3-4.5 × 0.7-1 mm, oblong-lanceolate to oblong, with green margins, somewhat sparsely glandular-pubescent. Corolla including spur 6-7 mm long, yellowish-white, glabrous externally; tube 2-3 mm broad at mouth; adaxial lip sinus 0.7-0.8 mm; abaxial lip sinus 0.9-1.2 mm; palate sparsely pubescent; spur 2.5-3 mm long, slender, straight forming obtuse angle with the tube, shorter than the rest of the corolla. Abaxial filaments sparsely pubescent. Capsule 2.5-4 mm long, ovoid to subglobose, obtuse, glabrous; loculi ± equal, many-seeded, dehiscent. Seeds 0.45-0.55 mm long, oblong ovoid to oblong-ellipsoid, minutely tuberculate, yellowish brown to light brown; tubercles broadly conical, obtuse or rounded, subentire to papillate towards base; papillae of tubercles hemispherical to broadly conical.

Distribution and habitat. Nanorrhinum kuriensis is known only from the type collection from the island of Abd-al-Kuri in the Socotra archipelago. It grows in the shade of limestone boulders at an altitude of c. 90 m.

Taxonomic remarks. Nanorrhinum kuriensis, with its annual habit, nearest resembles *N. hastatum,*but can be easily identified by its indumentum of only glandular hairs, and by its ovate to elliptic or suborbicular leaves with a truncate, rounded or subcordate base. In *N. hastatum* the indumentum, at least partially, consists of eglandular hairs, and at least the upper leaves are linear to lanceolate and usually have a hastate or sagittate base.

4. Nanorrhinum macilentum (Decne.) Betsche

Betsche 1984: 132. - *Linaria macilenta* Decaisne 1834: 252; Walpers 1844: 195; Bentham 1846: 271; Boissier 1879: 369. - *Kickxia macilenta* (Decne.) Danin & Hedges 1973: 265; Sutton 1988: 210, Fig. 52. – Type: Egypt, "Dégaiga Arab, desert du Sinai", Jun 1832, Bové 75 (P lectotype, selected here, P, G, K isolectotypes).

Linaria acerbiana Boissier 1879: 366; Bornmüller 1913: 79. - *Kickxia acerbiana* (Boiss.) Täckholm & Boulos 1974: 98; Täckholm 1974: 491; Feinbrun-Dothan 1977: tab. 307, 1978: 185; Sutton 1988: 204, Fig. 51; Wood 1997: 261. - *Nanorrhinum acerbianum* (Boiss.) Betsche 1984: 132. – Types: Egypt, "Aegyptische Küste zwichen Kosser und Ras-Benass, Wady Etit bei Wady Lechuma," 9 Apr 1864, Schweinfurth 230 (G-BOIS lectotype, seen in photo., selected here, BM isolectotype).

Nanorrhinum acerbianum subsp. *montanum* Betsche 1984: 132. – Type: "Cultus ex semine in horto botanico moguntino", 2 Sep 1982, Betsche g 3152 (MJG holotype).

Linaria kneuckeri Bornmüller 1909: 130. - *Kickxia kneuckeri* (Bornm.) Täckholm & Boulos 1974: 97; Täckholm 1974: 491. – Types: Egypt, "in deserto arabico prope Suez, in montis Ataka arids apricis ad basin rupium specimen unicum multicaule", 18 May 1908, Mons Sinai (in "Wadi Timan"), 21 Apr 1904, and "Wadi Mossagawit", 26 Apr 1904, Kneucker s.n. (JE, KH syntypes, not seen).

Linaria bentii Skan 1906: 289. - *Kickxia bentii* (Skan) Dandy 1956: 138. *Nanorrhinum bentii* (Skan) Betsche 1984: 132. – Type: Sudan, Nubia, about 21° North lat., "near Mohammad Qol", 0-4000 ft, Bent s.n. (K holotype).

Linaria nubica Skan 1906: 290. - *Kickxia nubica* (Skan) Dandy 1956: 137; Täckholm 1974: 491. – Type: Sudan, Nubia, about 21° N, "near Mohammad Qol" 0-4000 ft, Bent s.n. (K holotype).

Kickxia scariosepala Täckholm & Boulos 1974: 98; Täckholm 1974: 491. – Type: Sinai, in the mountains of Feiran Oasis, Täckholm 187 (CAI holotype, not seen).

Kickxia collenetteana D. A. Sutton 1988: 208, Figs 52, 53. – Type: Saudi Arabia, Jabal Dabagh, 85 km SW Tabuk, 5100ft, 23 Apr 1983, Collenette 4389 (BM holotype, E, K isotypes).

Kickxia judaica Danin 1977: 23; Feinbrun-Dothan 1978: 185; D. A. Sutton 1988: 210, Fig. 52. – Type: Jordan, Judean desert Wadi el Quilt, 14 Mar 1975, Danin s.n. (HUJ holotype, E, G, K isotypes).

Kickxia petrana Danin 1991: 181. – Type: Jordan, Petra, Künne 3488 (HUJ holotype, B isotype).

Nomenclatural notes. Sutton (1988) cited Bové 74 (P) as syntype of *Linaria macilenta*, but Decaisne (1834) in the protologue, cited only Bové 75. In Paris there are two duplicates of Bové 75, one labelled as type and the other as isotype. Other duplicates of Bové 75 are found in K and G. The Paris material that has a sketch diagram of a flower on it (the one labelled as type) is selected here as the lectotype.

In the protologue of *Linaria acerbiana* Boissier (1879) cited collections of both Acerbi and Schweinfurth. Acerbi's material was probably housed in B, where it is no longer extant (W. Lack, pers. comm.). However, the two specimens Schweinfurth 230 and 381 are present in G-BOIS. Schweinfurth 230 is selected here as the lectotype.

Perennial herb or subshrub, glabrous to tomentose all over, with glandular or eglandular hairs up to 1

mm long. Stem up to 60 cm long, sometimes practically without or with very minute leaves, erect or ascending, somewhat slender, much branched below and sparingly branched above. Leaves (2-)5-20(-27) × 1-17(-21) mm, ovate to orbicular, acute and often apiculate at the apex, entire or shallowly denticulate, with cordate, truncate or hastate base; petiole 3-17(-35) mm long, rarely cirrhose, often sinuate. Pedicel 1.5-3 × 0.2-0.4 mm, erect, straight or curved, rigid. Calyx-lobes glandular pubescent 3-4.5 × 0.5-1(-1.6) mm, linear-lanceolate to ovate, acute or acuminate, the margin broadly scarious below. Corolla including spur 7.5-11 mm long, densely eglandular- or glandular-pubescent, yellow with red-spotted palate; tube 2.5-3.5 mm broad at mouth; adaxial lip sinus 0.6-1.1 mm; abaxial lip sinus 1.1-1.6 mm; palate sparsely pubescent; spur 3-5 mm long, forming obtuse angle with tube, slender, straight or somewhat curved, acute, shorter than or subequalling rest of corolla. Abaxial filaments pubescent towards base. Capsule (2-)2.5-3.5 mm long, broadly ovoid and obtuse to rarely subglobose and emarginate or bilobed, glandular-puberulous or glabrous; loculi unequal, dehiscent, the adaxial loculus many-seeded and larger than the abaxial loculus. Seeds 0.35-0.5(-0.55) mm long, oblong-ovoid to oblong-ellipsoid, tuberculate, yellowish to blackish brown, tubercles conical to subglobose, truncate or rounded, subentire to shortly papillate.

Distribution and habitat. Nanorrhinum macilentum is known from Egypt, Sudan, Israel, Jordan, Saudi Arabia, and Yemen (Fig. 4A). It occurs in sandy wadis, on rocky slopes and limestone cliffs, in fissures of granite rocks or crevices of lava, from sea level up to 2640 m altitude.

*Taxonomic remarks.*This taxon is treated here in a wider sense than by previous authors. It was first described as *Linaria macilenta* by Decaisne (1834), but its epithet has been either misapplied or very narrowly used. Instead, *L. acerbiana* Boissier (1879) has been the most widely used name for this common and variable species (Sutton 1988). The reasons for the misapplication of the name *L. macilenta* were explained in detail by Danin (1973), who clarified the nomenclatural confusion that had existed for a long time between *Linaria macilenta* and *L. spartioides.* Still, he treated *K. macilenta* as an endemic species in southern Sinai, different from *K. acerbiana.*

Danin (1977) used differences in indumentum, corolla size and colour, pedicel length, shape of capsule, and surface of seed, to differentiate *K. macilenta, K. acerbiana* and his new species *K. judaica.*

The distributions of *K. macilenta* and *K. judaica,* as shown by Danin (1977), are within the range of distribution of the more widespread *K. acerbiana,* with *K. macilenta* located at the southern and *K. judaica* at the northern periphery of the distribution of *K. acerbiana* in Sinai. Moreover, within this area Danin (1991) described yet another new species, *K. petrana,* but admitting that this has a somewhat intermediate position between *K. macilenta, K. judaica* and *K. acerbiana.*

Sutton (1988) accepted *K. judaica* as different from *K. macilenta* and *K. acerbiana*, and also added the new species *K. collenetteana* from Saudi Arabia. This was said to differ from *K. macilenta* by its prostrate stems with short glandular hairs at the base, and its subsucculent leaves with a thicker texture.

The major differences between *K. macilenta, K. acerbiana, K. judaica, K. collenetteana* and *K. petrana* given by Danin (1977, 1991) and Sutton (1988) are in indumentum and habit characters, but *K. judaica* also differs in having capsules with less unequal loculi. However, with the extensive material available today it does not seem possible to make any clear distinction between any of these taxa. All characters used to separate them are highly plastic and all delimitations of taxa are actually arbitrary. My conclusion is that only a single variable species is involved and for this the combination *Nanorrhinum macilentum* is already available.

N. macilentum is closely realated to *N. azraqensis*, another species with asymmetrical capsules with a larger adaxial loculus. The placenta of the adaxial loculus in both these species also grows upwards from the base of the septum, projecting into the loculus cavity, and with seeds developing around its periphery, thus giving the impression of free-central placentation (Sutton 1988). For differences between *N. macilentum* and *N. azraqensis*, see under the latter.

Additional specimens examined. Egypt. Sinai: Kaiser 559 (S); Wadi Feiran, Drar 188 (S); N of Iqna near Bir el Main, Tadmor S-4774 (BM, E); Gebel Serbal, Danin S-4766 (E); Jebel Katarina, Kinrose s. n.(E); Wadi Abar, Gabal Ataqa, near Suez, Drar 48 (S).

Sudan. Darfur, 40-80 km NE of Fasher, Lynes 336 (BM); Darfur, Lynes 401 (BM).

Israel. desert SW of Eilath near coast, Lyshede s. n. (C).

Jordan. Wadi Yutum, Boulos, Jallad, Lahham & Humaidan 7540 (S); Ma'an, 5 km NW Rum station, Frey & Kürschner 5030 (E); Dead Sea, Shingle at mouth of Arnon, Davis 3753 (E); Wadi Quelt, below monastry of St. George, Davis 3652 (E); Jerusalem, Dinsmore 1238 (E).

Saudi Arabia. North Hijaz, Wadi Aswawin, Collenette 417 (K); Wadi Ulalahile, 40km NW of Najram, Collenette 2077 (E); Unat Khaybar, Collenette 3847 (E); Wadi Kharar, Jiddah - Taif road, Collenette 3338 (E); Najarana, Collenette 3308 (E); Jebel Anagayn, 95 km S of Madinah, Collenette 5972 (E); road from Umm Lajj to Al Ays, Collenette 7065 (E).

Yemen. South of Hawiri near Mamer N of Sanaa, Wood Y/74/357 (BM).

5. Nanorrhinum hastatum (Benth.) Ghebrehiwet comb. nov.

Linaria hastata R. Br. ex Bentham 1846: 269; Skan 1906: 290. - *Kickxia hastata* (R. Br. ex Benth.) Dandy 1956: 137; Cufodontis 1963: 889; Täckholm 1974: 490; Sutton 1988: 248, Fig. 68; El Husseini & Zareh 1994: 319, Pl. III Fig. 2. – Type: Eritrea, "Abyssinia", Salt s.n. (BM lectotype, selected by Sutton 1988).

Linaria indecora Franchet 1882: 55; Skan 1906: 292. – Type: Somalia, without precise locality, Révoil 105 (P holotype).

Linaria capillipes Hochst. ex. Bentham 1846: 269. – Type: Eritrea, Modat near Ailet, Schimper 1042 (K holotype, BM, S isotypes).

Annual herb, glabrous, ± villous at the base and glabrous above or ± villous all over with glandular- or eglandular-hairs up to 1.5 mm long. Stem up to 65(-140) cm long, erect or ascending, very slender, trailing to somewhat scandent, simple or branched, the angle of branching somewhat narrow to wide. Leaves heteromorphic; basal leaves 4-10 × 1.5-4.5 mm, lanceolate to suborbicular, acute or obtuse at the apex, entire or shallowly dentate, attenuate at the base, caducous, petiole 3-8 mm long, not cirrhose; upper leaves (3-)8-32 × (0.2-)3-5 mm, linear to lanceolate, acute at the apex, entire except for the basal lobes, hastate to sagittate or the uppermost with attenuate base, petiole 0.5-8 mm long, sometimes cirrhose. Pedicels (7-)15-30 × 0.07-0.15 mm, erecto-patent, filiform, ± straight. Calyx lobes 2.5-3.5 × 0.5-0.8 mm, linear-lanceolate or lanceolate, acute, the margins narrowly to somewhat broadly scarious, glandular-puberulent to glabrous. Corolla including 3.5-7(-12) mm, yellow with darker palate, with sparse eglandular or glandular hairs externally; tube 1.6-2.5(-4.5) mm broad at mouth; adaxial lip sinus 0.3-0.7 mm, abaxial lip sinus 0.5-1 mm; palate lanate; spur 1.5-4(-7.5) mm, almost at right angle with the rest of corolla, straight ± curved, somewhat slender, shorter than rest of corolla. Abaxial filaments sparsely villous. Capsule 2.5-3.5 mm long, ovoid, obtuse, glandular puberulent at the apex or glabrescent. Seeds 0.4-0.6 mm long, oblong or reniform, tuberculate, reddish to dark-brown; tubercles columnar to conical, obtuse to subacute, entire. – Fig. 9.

Distribution and habitat. Nanorrhinum hastatum is distributed in the Horn of Africa and the Arabian peninsula. It is known from Sudan, Eritrea, Ethiopia, Djibouti, Somalia, Saudi Arabia, Yemen, Socotra, Oman, and Arab Emirates. Its presence in Gebel Elba, Egypt was reported by El Husseini & Zareh (1994) from collections deposited in CAI and CAIM but in the present study no specimens of *N. hastatum* from Egypt was examined. *N. hastatum* is reported to grow along wadis, on cliffs and gravelly slopes of granite or limestone rocks, on boulders, and on alluvial open plains, at an altitude between sea level and 1450 m.

Taxonomic remarks. The flowers of *N. hastatum* are very variable in size. Specimens collected from Eritrea, Yemen, Socotra and Somalia within an

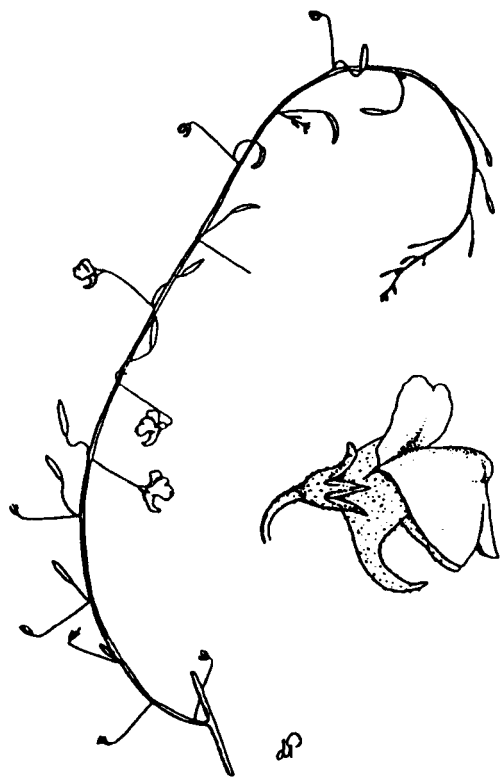


Fig. 9. A relatively large-flowered form of *Nanorrhinum hastatum* from Yemen, unusual in having a curved spur, habit × 0.75 and flower × 4.5, from Thulin et al. 8476.

altitudinal range of 0-1000 m are small-flowered, with corolla length including spur up to 3.5-7 mm and with the tube 1.6-2.5 mm wide at the mouth. In contrast, specimens collected from 1100 m and above in Ethiopia, Yemen and Somalia generally have larger flowers, with corolla up to 12 mm long and tube width up to 4.5 mm (Fig. 9)

Nanorrhinum hastatum resembles *N. ramosissimum* in many ways, such as in indumentum and size and shape of the leaves. However, the two species can be readily differentiated by the somewhat campanulate floral tube, with lanate palate in *N. hastatum,* and the more or less cylindrical floral tube with pubescent to subglabrous or glabrous palate in *N. ramosissimum*. Also, in *N. hastatum* the seed tubercles are without papillae and the pedicels are usually longer than 20 mm, whereas in *N. ramosissimum* the seed tubercles are usually papillate and the pedicels are generally shorter than 20 mm. Moreover, *N. hastatum* is annual, whereas *N. ramosissimum* is perennial.

Additional specimens examined. Eritrea. Dahlak Islands, Hotha, Terraciano, 408 (FT); ibid, Harat, Pappi 4501 (FT); Mont Maraifa near Saati, Schweinfurth & Riva 551 (K, FT); Hirgigo, Stower, Smith& Gilliland 4097 (BM, K); Wokiro, Greathead 158 (BM); Mt. Ghedem, Terracciano & Pappi 5 (FT); Ghatelai, Ryding & Sileshi 1764 (ETH, UPS); Semhar, Dogali, Garetti 11, 13 (FT); Ghinda, Baldrati 3587 (FT); Habab, Melchet-Tzaroba, 1909, Pappi 8225 (FT); Mensa, Messeb valley, Fiori 1607 (FT).

Ethiopia. Shewa Province: Mt. Fantale, Gilbert 526 (ETH, K); 28 km E of Metahara on road to Nazaret, Gilbert, Sebsebe & Vollesen 7411 (ETH, K, UPS); Yerer and Kereyu Awraja, 162 km from Addis, Ensermu 820913-2/14 (ETH, UPS).

Sudan: Hatatera, Red Sea hills, Jackson 2810 (K).

Djibouti. SE end of Bara Wein, Orta hill, Lavranos 11260 (E).

Somalia. Somaliland, Wagga Mt., Lort Phillips s.n. (BM, K); Galgallo, 64 km SW of Bosaso, Bally & Melville 15727 (K); Bari region, 35 km on Iscusciuban-Gardo road, near Pichi well, Thulin & Warfa 5487 (K, UPS); Sanaag, escarpment S of Laasqoray, along the road to Geldora pass, Thulin, Dahir & Hassan 9180 (UPS).

Saudi Arabia. Foot of Jebel Sharda, Jiddah-Jizan road, Collenette 3257 (E).

Yemen. Abyan: Jabal al-Arays, Thulin, Eriksson, Gifri & Långström 8476 (UPS); 26 km from Shuqrah on road towards Lawdar, Thulin, Beier & Hussein 9513 (UPS). Hadramout: Mola Matar area, Kawr Sayban, Thulin, Eriksson, Gifri & Långström 8155 (UPS); Al Misnah, 33 km from W of Thilah al Ulya, Thulin, Beier & Hussein 9904 (UPS). Socotra: c. 6 km SE of Qalansiyah, Miller, Guarino, Obadi, Hassan & Mohammed 8409a (E); 1 km SW of Hadibu, Thulin & Gifri 8506 (E); Deishel, Thulin & Gifri 8512 (UPS); Nuged plain, 1 km N of Magahe, Thulin & Gifri 8547 (UPS); Mumi area, Thulin & Gifri 8637 (UPS).

Oman. Muscat: al-Hajar track, Mandaville 3398 (BM); Ar Rustag, Rubens 103a (E). Dhofar: ravine below Ras Hamar, 15 km from Salalah, Miller 7524 (E, K, UPS); between Qusuf and Ghazayn, Whitecombe 777 (E); Jabal Qara, Wadi 'Urman NE of Salalah, Miller 6084 (E, K, UPS); Lansab industrial area, Gallagher 7876 (E).

United Arab Emirates. Fujairah Emirates, between Khatt and Dibba, Western 170 (E); Ras al Khaimah Emirate, Western 513 (E); Masafi, 10 km N of Masafi town, Western 1155 (E); 35 km N of Al Fujairah, between Ras Dibba and Dibba, Thulin & Al-Gifri 9987 (UPS).

6. Nanorrhinum asparagoides (Schweinf.) Ghebrehiwet comb. nov.

Linaria asparagoides Schweinfurth 1867: 99; Skan 1906: 291; Schwartz 1939: 242. - *Kickxia asparagoides* (Schweinf.) Cufodontis 1963: 889; Sutton 1988: 248, Fig. 68.6-8; Wood 1997: 261. – Type: Ethiopia, Agew, Bellagas valley, Abbaherruké, 7 Aug 1852, Schimper 442 (P lectotype, selected here, K, P isolectotypes).

Kickxia abhaica D.A. Sutton 1988: 241, Fig. 65; Collenette 1985: 445. – Type: Saudi Arabia, Asir, Abha pass, 25 Oct 1971, Popov 71/267 (BM holotype, BM isotype).

Kickxia petiolata D.A. Sutton 1988: 244, Fig. 66; Wood 1997: 261. – Type: Yemen, NE of Taiz, 8 Feb 1978, Wood 2223 (BM holotype; E, K isotypes).

Kickxia saccata D. A. Sutton 1988: 246, Fig. 67; Wood 1997: 261. – Type: Yemen, Jebel Ras, 15 km NE of Hays, 8 Apr 1981, Miller & Long 3493 (E holotype, BM isotype).

Nomenclatural notes. Nanorrhinum asparagoides was collected twice by Schimper from Bellegas and Gageros in W Agew, Ethiopia in 1852 and 1854 respectively (Gillett 1972). Duplicates of the Bellegas material, labelled as Schimper 442, are now in Paris and Kew, and of the Gageros material, Schimper 41 is present in Florence. In his description Schweinfurth made no mention of these specimens and it is therefore not possible to know which material he used. Cufodontis (1963) suggested that it was probably Schimper 41, whereas Sutton (1988) cites Schimper 442 in Paris as holotype. Here one of

the three duplicates of Schimper 442 in Paris is chosen as a lectotype.

Perennial herb or subshrub, glabrous or somewhat sparsely glandular- or eglandular-pubescent, with hairs up to 0.3 mm long. Stem up to 65 cm long, ascending to erect or sometimes prostrate or hanging, usually much branched from the base and, more sparsely so above, the angle of branching narrow to wide. Basal leaves 5-35 × 3-15 mm, obovate or elliptic, rounded or obtuse at the apex, entire with cuneate base, sparsely pilose, caducous, petiole 3-9 mm long, not twining; upper leaves 5-55 × 0.2-5 mm, filiform, linear or linear-lanceolate, acute, entire, with hastate, attenuate, cuneate or rounded base, glabrous, petiole 0-20 mm long, sometimes twining. Pedicel 3-17 × 0.1-0.2 mm, erecto-patent, usually curved at distal end. Calyx-lobes glabrous or glandular-puberulent, 2.5-3.5 × 0.5-1 mm, linear-lanceolate to lanceolate, acuminate, the margin narrowly to somewhat broadly scarious. Corolla including spur 6-9(-13) mm long, sparsely glandular- or eglandular-pubescent, yellow sometimes with purple tinge; tube 2-4(-5) mm broad at mouth; adaxial lip sinus 0.5-1.5 mm; abaxial lip sinus 1-2.5 mm; palate lanate internally; spur (1-)3-7 mm long, occasionally gibbous or conical, straight or somewhat curved and forming an obtuse angle with the tube. Abaxial filaments tomentose or sparsely villous. Ovary ovoid, 1 × 0.5 mm; style 2.5-3 mm long. Capsule 2-4 mm long, subglobose or oblong-ovoid, the apex obtuse or truncate to shallowly emarginate, glandular-puberulent or glabrous; loculi equal, many-seeded, dehiscent. Seeds 0.5-0.9 mm long, oblong- ovoid to oblong-reniform, tuberculate, blackish-brown; tubercles narrowly conical, acute, papillate or entire; papillae of tubercles patent, slender, straight or recurved. – Figs 7D, 10.

Distribution and habitat. Nanorrhinum asparagoides has a limited distribution in the Horn of Africa and the Arabian Peninsula. It is known from Ethiopia, Yemen and Saudi Arabia. In the Horn of Africa it is known only from the Agew area in the north-central part of Ethiopia, and in the Arabian Peninsula its distribution is limited to the south-western part. The species occurs on rocky slopes, in rock crevices or on terrace walls at altitudes between 700 and 2000 m.

Taxonomic remarks. Nanorrhinum asparagoides (as *Linaria asparagoides*) was described on the basis of material collected by Schimper in the Agew area in northern Ethiopia in the 1850's (Schweinfurth 1867). Apparently no other material has been collected from Ethiopia or elsewhere in Africa until in 1997, when the species was recollected by the author in the same area more than 140 years later. Schwartz (1939) cited a collection (Schweinfurth 115) from Schugra in southern Yemen, but this has not been seen and is probably no longer extant.

Sutton (1988) based his description of *N. asparagoides* (as *Kickxia asparagoides*) largely on material from northern Yemen believed by him to be conspecific with Schimper's material. Seeds, for example, were not available in the original material from Ethiopia, but on the basis of Yemeni material they were described as having papillate tubercles. However, the seeds from the recent Ethiopian material have tubercles without papillae (Fig. 10).

Sutton (1988) also described the new species *K. abhaica* from Saudi Arabia and *K. petiolata* and *K. saccata* from northern Yemen, all placed close to *K. asparagoides* in his revision. *K. abhaica* was described from the vicinity of Abha in the Asir mountains. It was characterized by its more or less sessile, linear, upper leaves, small, densely pubescent corolla with the spur shorter than the rest of the corolla, and its seeds with elongate, entire tubercles. It was said to differ from *K. asparagoides* in its longer pedicels and narrower corolla tube, and in its seeds with non-papillate tubercles.

Kickxia petiolata was described from south-western Yemen and was said to differ from *K. asparagoides* in its leaves with mostly 3–20 mm long petioles (leaves not sessile or subsessile), and in its seeds with non-papillate tubercles, and from *K. abhaica* in its petiolate leaves, longer spur, and mostly larger seeds with longer tubercles. However, for example Collenette 4611 and 4469, collected from near the type locality of *K. abhaica*, have upper leaves with up to 11.5 mm long petioles, i.e. well inside the range of *K. petiolata*.

Kickxia saccata was described from a single collection from the isolated mountain Jebel Ras in south-western Yemen. This collection was said to be remarkable for its lack of a spur and to be the only ecalcarate species described in the genus. It was said to be superficially similar to *K. petiolata*, but differing, in addition to the lack of a spur, also in its subsessile leaves, shorter pedicels, glabrous capsules, and smaller seeds with papillate tubercles.

At a visit to Jebel Ras in November 1995 I had the opportunity to study some large populations of plants from the type locality of *K. saccata*. Within these populations there was a variation not only in spur length, but also in petiole and pedicel length. So, for example, Thulin, Ghebrehiwet & Gifri 9362 and 9367 represent plants with a distinct spur and long twining petioles, Thulin, Ghebrehiwet & Gifri 9361 and 9371 have more or less saccate corollas without spur, and Thulin, Ghebrehiwet & Gifri 9360 and 9364 have spurs of intermediate length. In the

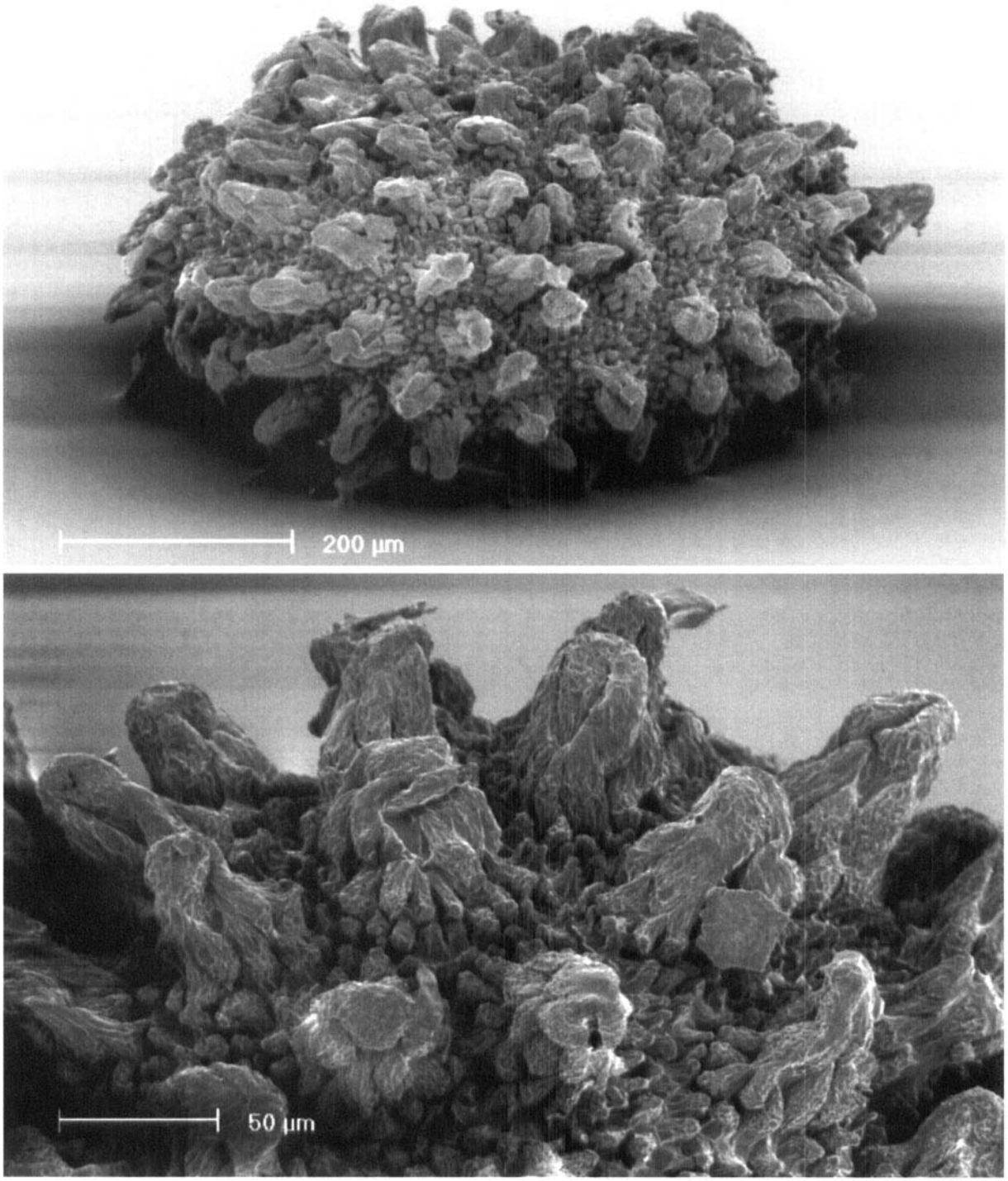


Fig. 10. *Nanorrhinum asparagoides*, scanning electron micrographs of seed from Ghebrehiwet 410 (UPS).

material there is also a considerable variation in pedicel length and some individuals have puberulous capsules. A similar range of variation was found in another population studied in the field in the Lahij Region (Thulin, Ghebrehiwet & Gifri 9257-9260).

These field studies clearly show that the recognition of *K. saccata* and *K. petiolata* are untenable. The variation within populations is much greater than previously thought, and the types of these names are just more or less extreme forms within a continuous range of variation. Both *K. saccata* and *K. petiolata* therefore are here placed in the synonymy of *Nanorrhinum asparagoides*. Also *K. abhaica* clearly falls within the variation of *N. asparagoides*.

Nanorrhinum asparagoides is characteristic with its very narrow upper leaves and its relatively small flowers with a short spur (Fig. 7D). It is similar to to some forms of *N. hastatum*, but differs from this in being a perennial herb or subshrub and in its seeds with often papillate tubercles. *N. hastatum*, on the other hand, is an annual herb with seeds with non-papillate tubercles.

Additional specimens examined. Ethiopia. Agew, Gageros, Schimper 41 (FI); Agew, 55 km NW of Sokota, near Tsiska, Ghebrehiwet 410 (UPS).

Saudi Arabia. Abha Mts, S of Abha, Khattab 517 (BM); Asir, foot of Dila pass, Thesiger 115 (BM); Ad Dharb to Abha road, Chaudhary 3907 (E); 15 km S of Abha, Jizan road, Collenette 4469 (E); Wadi Uss SW of Jebel Sawdah, Collenette 4468 (BM, E); Jebel Fayfa, 100 km NE of Jizan, Collenette 3539 (BM).

Yemen. Merkez Hoquail, Maqbaneh, Wood Y/74/336 (BM); Shaharah, Wood 2509 (BM, E); on the track to Shaharah, Wood 3380 (BM, K); Jebel Ras, Thulin, Ghebrehiwet & Gifri 9360-9364 (UPS); Lahij ,Wadi Yahar near Harada, Thulin, Ghebrehiwet & Gifri 9257-9260 (UPS).

7. Nanorrhinum woodii (D. A. Sutton) Ghebrehiwet comb. nov.

Kickxia woodii Sutton 1988: 239, Figs 62.1-3, 64a-e; Wood 1997: 261. – Type: Yemen, Rubaisa near Turba, 26 Oct 1974, Wood Y/74/133 (BM holotype and isotype).

Kickxia scalarum Sutton 1988: 237, Figs 61.1, 2, 64f; Wood 1997: 261. – Type: Yemen, "Uossil", 1 Feb 1889, Schweinfurth 1149 (BM holotype, F, K isotypes).

Perennial herb or subhrub, glabrous to villous throughout with glandular or eglandular hairs up to 0.5 mm long. Stems up to 45 cm long, prostrate, ascending or scandent, slender, flexuose, sparingly branched, the angle of branching narrow to wide. Basal leaves caducous, 4-27 × 2-26 mm, ovate to elliptic or orbicular, obtuse, entire, with rounded to cuneate base, petiole 1.5-5 mm long not twining; upper leaves (3.5-)8-33 × (1.3)3-18 mm, lanceolate to ovate or deltate, acute or acuminate, entire or often dentate, with hastate to sagittate base, petiole 1-11 mm long, not twining. Pedicels 7-27 × 0.15-0.25 mm, patent or erecto-patent, straight, curved at the end, slender. Calyx-lobes glabrous to sparsely glandular pubescent, 2.5-5 × 0.9-1.7 mm, lanceolate to ovate, long-acuminate, margins broadly scarious, especially below. Corolla including spur 10-19 mm long, somewhat sparsely to densely glandular-pubescent externally, yellow sometimes with purple tinge, or occasionally almost white, tube (3.5-)5-9 mm broad at mouth; adaxial lip sinus 1-3 mm; abaxial lip sinus 1.6-4.5 mm; palate lanate internally; spur 5-9 (-11) mm long, abruptly attenuate, slender, straight or curved, forming an obtuse angle with tube more or less equalling or shorter than rest of corolla. Abaxial filament villous. Capsule 3.5-5 mm long, oblong-ovoid, truncate, sparsely glandular-puberulent at apex; loculi equal, many-seeded, dehiscent. Seeds 0.65-0.8 mm long, oblong-ovoid, tuberculate, blackish brown; tubercles conical, subentire or papillate, acute; papillae of tubercles absent or short, patent to slender, ± straight, the apex rounded to acute. – Fig. 7C.

Distribution and habitat. Nanorrhinum woodii is known only from Yemen. It has a discontinuous distribution with one group of populations around Haraz in the north, with drier habitat, and another in the south on the Gaheli escarpment near Turba, in an area with relatively wetter conditions. It grows on cliffs and rocky slopes between c. 1200 and 2500 m altitude.

Taxonomic remarks. Sutton (1988) treated the northern and southern populations of *N. woodii* as distinct species (*K. scalarum* and *K. woodii* respectively). *K. scalarum* was said to differ from *K. woodii* in its less stiff and more flexuous stems, its glandular to scabrid or glandular-pubescent (not eglandular-villous) stems, its heteromorphic (not homomorphic) and relatively narrower leaves, its smaller corolla with a narrower tube, and in its seeds with conical, acute, subentire or papillate (not narrowly conical or columnar, more or less acute and entire) tubercles.

However, more or less stiff stems are also found in specimens from the northern area, such as King 301, 302 and 303. These specimens also have a variable indumentum, where King 303 is scabrid, King 302 is subvillous, and King 301 is villous. Progeny of King 302 cultivated in the greenhouse had glabrous to minutely papillate stems. This is a clear indication that the indumentum may be highly variable even within a single population.

From progeny of Thulin, Ghebrehiwet & Gifri

9303, cultivated in the greenhouse, as well as from field observations, it is evident that also the southern population has distinct basal leaves. The corolla length and tube width in the material studied by me is 10-18 mm respectively 4.5-7 mm in the northern population and 14-16.5 mm respectively 5.5-7.5 mm in the southern population. Thus there is a complete overlap in the variation of these characters between the two areas. Finally, the examination of seeds from Thulin, Ghebrehiwet & Gifri 9303 showed the presence of broadly conical, acute tubercles also in a population from the southern area. These seeds are actually very similar to those of King 301, 302 and 303 from the northern area. My conclusion is that no clear distinction can be made between the northern and the southern populations. The two names involved, *K. scalarum* and *K. woodii*, were published simultanously, and for the combined taxon I choose to use the epithet *woodii*.

Both *K. woodii* and *K. scalarum* were described to have yellow flowers by Sutton (1988), and this certainly is the normal colour. However, the progeny of King 302, grown in the greenhouse, had almost white flowers.

Sutton (1988) mentioned Popov 531 (BM, K) from southern Yemen as probably a form of *K. scalarum* with very narrow, entire leaves. However, this specimen represents the large-flowered form of *Nanorrhinum hastatum* occurring in Hadramout (see under *N. hastatum*).

Nanorrhinum woodii in many ways resembles *N. heterophyllum*, but can be readily identified by its spur that is more or less equalling or shorter than the rest of the corolla (Fig. 7C). In *N. heterophyllum* the spur is clearly longer than the rest of the corolla.

Additional specimens examined. Yemen. Al Hajarah, c. 2 km from Menacha, King 301, 302, 303 (E); Bait Al Bashari -Towila, c. 30 km SW of Amran, Miller 238 (E, K); W Mahawit, Wood 3103 (BM, E); Haraz near Bayt Shamran, Jabel Masar, Wood 3350 (E, K); below Ribat, Jebbal Safan, Haraz, Wood 3359 (BM); near Maghratah on the pass between Jebel Hafash and J. Milhan, Wood 3446 (BM, K); Rahidah road to Hayfan, Clissold & Wood 3475 (BM); Juheli hills 100 km NW of Aden, Wahab s.n. (E); Taizz Region, near Turba, Gaheli, Thulin, Ghebrehiwet & Gifri 9303 (UPS).

8. Nanorrhinum azraqensis (Boulos & Lahham) Ghebrehiwet comb. nov.

Kickxia azraqensis Boulos & Lahham 1977: 277; Sutton 1988: 211, Figs 52.4, 52.8. –Type: Jordan, Wadi 35km W of Azraq Oasis, 14 Apr 1976, Täckholm, Hadidi, Lahham & Boulos 8981 (HUJ holotype, not seen, BM, K, S isotypes).

Perennial herb or shrub, glandular pubescent all over, hairs up to 0.5 mm long. Stems up to 30 cm long, decumbent, somewhat stout, much branched throughout, the angle of branching wide. Leaves heteromorphic; basal leaves 9-17 × 5-11 mm, lanceolate-elliptic to suborbicular, obtuse at the apex, attenuate-truncate at the base, petiole 7-20 mm long, not twining; upper leaves 2.5-15 × 3-13 mm, ovate to deltate, acute to obtuse and often mucronate at the apex, entire, hastate, or sometime sagittate, petiole 1-4(-8) mm long, not twining. Pedicels 6-16 × 0.3-0.6 mm, erecto-patent, usually curved at distal end. Calyx-lobes 3.5-4.5 × 1-1.5 mm, linear-lanceolate, acuminate, the margin broadly to narrowly scarious at base, densely glandular-pubescent. Corolla including spur 11-17 mm long, yellow, glandular pubescent externally; tube 4-4.5 mm broad at mouth; adaxial lip sinus 1-1.5 mm; abaxial lip sinus 1.5-2 mm; palate pubescent towards base; spur 6-10 mm long, forming obtuse angle with tube, very slender, acute, exceeding rest of corolla. Abaxial filaments sparsely pubescent at base. Capsule 4-5 mm long, ovoid to suborbicular, oblique, glandular puberulent at apex; loculi very unequal, dehiscent, adaxial loculus exceeding abaxial, many-seeded. Seeds 0.5-0.65 mm long, reniform, tuberculate, greyish- or yellowish-brown; tubercles ± hemispherical, papillate.

Distribution and habitat. Nanorrhinum azraquensis is known to occur in east-central Jordan and eastern Iraq, but it is likely to occur also in adjacent parts of Syria and Saudi Arabia. The species occurs in desert oases at about 300-800 m altitude.

Taxonomic remarks. Nanorrhinum azraquensis, like *N. macilentum*, has capsules with unequal loculi, but differs in its 6-10 mm long spur that exceeds the rest of the corolla. In *N. macilentum* the spur is 3-5 mm long and is clearly shorter than to almost as long as the rest of the corolla. *N. azraqensis* is often confused in herbaria with *Kickxia aegyptiaca*, which also has capsules with unequal loculi, but *K. aegyptiaca* differs in having opercular and not valvate dehiscence. In the absence of capsules, *N. azraqensis* can be easily distinguished from *K. aegyptiaca* by its glabrous anthers, a diagonistic character of *Nanorrhinum* as compared to the ciliate anthers in *Kickxia* .

Additional specimens examined. Iraq. Wadi Al-Walaj about 75 km SW of Rutba, Rechinger 9935 (K, UPS);

H3 - Jordan Border, Allizi & Omar 36197 (K).

Jordan. Wadi Shaumari, 40 km NE of El-Jafir, Boulos & Jallad 7995 (BM, K); 40 km W of Azraq desert, Dinsmore 12160 (K); Azraq Druz, Townsend 65/383 (K); 10km W of Azraq oasis, Täckholm, Hadidi, Lahham, Boulos 7135 (BM, K).

9. Nanorrhinum heterophyllum (Schousb.) Ghebrehiwet comb. nov.

Antirrhinum heterophyllum Schousboe 1800: 194; Poiret 1816: 19. - *Linaria heterophylla* (Schousb.) Steudel 1821: 482, nom. illeg. non Desf.; Sprengel 1825: 790; Chavannes 1833: 112; Walpers 1844: 196; Lowe 1861: 32. - *Kickxia heterophylla* (Schousb.) Dandy 1956: 137; Danin & Hedge 1973: 267; Sutton 1988: 219, Fig. 57.1-6. - *Pogonorrhinum heterophyllum* (Schousb.) Betsche 1984: 129, Fig. 2. - Type: Morocco, "in fruticetis provinciae Hahoe", Schousboe s.n. (C holotype).

Linaria gracilis R. Br. ex Bentham 1846: 269, nom. illeg. - *Kickxia gracilis* D. A. Sutton 1988: 221, Fig. 57.7, 8. – Type: Eritrea, "Abyssinia", Salt s.n. (BM holotype).

Antirrhinum sagittatum Poiret 1816: 19. - *Linaria sagittata* (Poir.) Steudel 1821: 483; Hooker 1873: tab. 6060; Skan 1906: 291; Jahandiez & Maire 1931: 670. - *Kickxia sagittata* (Poir.) Rothmaler 1956: 116. – Type: cultivated in the Botanical Garden of Paris (P-DESF, holotype, not seen).

Linaria scoparia Sprengel 1825: 789. - *L. spartioides* Brouss. ex L. Buch 1828: 163; Walpers 1844: 196. - *Elatinoides spartiodes* (L. Buch.) Wettstein 1891: 58. - *Kickxia spartiodes* (L. Buch.) Janchen 1933: 152, Danin and Hedge 1973: 265 pro parte. - *K. scoparia* (Sprengel) Kunkel 1972: 67; Sutton 1988: 216, Figs 55.1-3. - *Pogonorrhinum scoparium* (Sprengel) Betsche 1984:129. – Type: Canary Islands, Tenerife, Broussonet s.n. (MPU holotype not seen).

Linaria circinata D. Don 1834: 235; Walpers 1844: 196. – Type: plate 235, based on plant grown in Chelsea Botanic Garden from seeds believed to be from North Africa.

Linaria lancerottae Delile 1837: 26. – Type: cultivated in Montpellier from seeds originating from the Canary Islands, Lanzarote (MPU holotype not seen, BM photo.)

Linaria webbiana Visiani 1842: 142; Walpers 1844: 195. – Type: cultivated in Padova from seeds originating from the Canary Islands, Lanzarote (not located).

Linaria sagittata var. *homeophylla* Battandier 1890: 638; Jahandiez & Maire 1931: 670. – Type: Figure in Webb, Phyt. can. tab. 181.

Linaria heterophylla var. *linearifolia* Battandier 1900: 252; Jahandiez & Maire 1931: 670. – Type from Algeria, Oued Inçokki and Ain Guettara (not located).

Linaria patula Baker 1895: 222; Sutton 1988: 233. – Types: Somalia, Golis range near Wadiba, Apr 1895, Cole s.n. & Lort-Phillips s.n. (K syntypes).

Linaria urbanii Pitard 1908: 290. - *Kickxia urbanii* (Pit.) Larsen 1963: 417; Sutton 1988: 218, Fig. 55.4. - *K. sagittata* var. *urbanii* (Pit.) Sunding 1970: 79. - *K. heterophylla* subsp. *urbanii* (Pit.) Kunkel 1976: 57. – Types: Canary Islands, Gran Canaria, Baia del Confital, 12 Feb 1905, Pitard 310 (P syntype); Guia, Feb 1906, Pitard 651 (P syntype).

Linaria musili Velenovsky 1912: 6; Sutton 1984: 223. – Type from Saudi Arabia (not located).

Linaria spiniflora O.Schwartz 1939: 241. - *Kickxia spiniflora* (O.Schwartz) D. A. Sutton 1988: 229, Fig. 58.6-7. – Type: Yemen, Hadramaut, Wadi Do'an, Masna'a, 1931, Wissman 1313 (HBG holotype not seen).

Linaria pendula Kunkel 1970: 8. - *Kickxia pendula* (Kunkel) Kunkel 1972: 56; Bramwell 1972: 148, Fig 3 E; Sutton 1988: 218, Fig. 55.5-7. - *Pogonorrhinum pendulum* (Kunkel) Betsche 1984: 129. – Type: Canary Islands, Gran Canaria, Aguimes-Termisas km 3, 19 Nov 1969, Kunkel 12882 (C holotype, G isotype).

Kickxia heterophylla subsp. *canariensis* V. W. Smith in D. A. Sutton 1988: 220. – Type: Canary Islands, Fuerteventura, N coast of Jandia peninsula, cliffs near Cofete, 9 May 1969, Bramwell 1584 (RNG holotype, not seen).

Kickxia heterophylla subsp. *subsucculenta* Kunkel 1976: 57; Sutton 1988: 221. – Type: Canary Islands, Lanzarote, Famara, 7 Jan 1974, Kunkel 16188 (G holotype not seen, C isotype).

Pogonorrhinum hartlii Betsche 1984: 129, tabs 1a-b, 7b. - *Kickxia hartlii* (Betsche) D. Heller in Heller & Heyn 1987: 43. – Type: Egypt, Sinai, "cultus ex semine in horto botanico moguntino", 2 Sep 1982, Betsche g 3158a (MJG holotype).

Kickxia qaraica D. A. Sutton 1988: 227, Figs 58.6-7, 59; Miller & Morris 1988: 262. – Type: Oman, Dhofar, Wadi 5 km N 'Ravens Roost', Salalah-Thamrait road, 4 Oct 1979, Miller 2505 (E holotype, BM, K isotypes).

Kickxia corallicola D. A. Sutton 1988: 225, Figs 56, 58.1. – Type: Saudi Arabia, 8 km S of Rabigh, Red Sea coast, 22 Feb 1971, Mandaville 3002 (BM holotype).

Kickxia kasalensis V.W. Smith in Sutton 1988: 223. – Type: Sudan, Tokar Distr., Karora hills, Khor Kadow, Robbie 9 (K holotype).

Kickxia pseudoscoparia V.W. Smith & D. A.

Sutton 1988: 231, Figs 60, 61.6-7. – Type: Saudi Arabia, Asir, Taif, 30 May 1971, Popov 71/160 (BM holotype).

K. sabarum D. A. Sutton 1988: 235, Figs 61.3-4, 63; Wood 1997: 261. – Type: Yemen, Jebel Dawran, 9 May 1980, Wood 3238 (BM holotype).

Perennial herb or subshrub, glabrous or scabrid, often sparsely tomentose below or densely eglandular-pubescent throughout, with hairs up to 0.5 mm long. Stem (3-)25-85(-400) cm long, varying from erect, stout, and sometimes somewhat spinescent to prostrate or scandent to ascending and more or less slender. Basal leaves 4-25 × 1.5-14 mm, elliptic, oblong to broadly ovate or lanceolate, linear to filiform, obtuse, subacute or acute at the apex, entire or occasionally dentate, cuneate or rounded at the base, caducous, petiole 1.2-11 mm long; upper leaves (1.2-)3-40 × (0.4-)1.5-12 mm, filiform, linear, lanceolate, deltate, oblong or ovate to elliptic or suborbicular, acute to obtuse at the apex, entire, attenuate, cuneate, hastate, sagittate, or round at the base, thin-textured or somewhat succulent, sometimes absent, petiole 0-16 mm long, often twining. Pedicels 4-24 × 0.1-0.6 mm, erect, erecto-patent or patent, straight except for the distal end. Calyx-lobes 2.5-6 × 0.6-1.6 mm, linear-lanceolate to ovate, acute or acuminate, margins scarious, glabrous or sparsely glandular-pubescent. Corolla including spur (13-)15-28 mm long, yellow, sometimes suffused with pink or purple spots on the palate, glabrous to sparsely eglandular- or glandular-pubescent externally; tube 4-9 mm broad at mouth; adaxial lip sinus (0.5-)1-2 mm; abaxial lip sinus (1-)1.5-3.5 mm; palate lanate; spur (8-)10-22 mm long, more or less continuing line of tube, stout at the base, straight or curved, exceeding rest of corolla. Abaxial filaments lanate. Ovary ovoid 1.3-1.5 × 1 mm; style 2.2-3.2 mm long. Capsule 2.5-6 mm long, oblong-ovoid or subglobose, the apex truncate or emarginate, sometimes glandular-puberulent; loculi equal, many-seeded, dehiscent. Seeds 0.5-0.7(-1) mm long, oblong-ovoid to oblong-reniform, echinate-tuberculate, reddish-brown; tubercles subglobose or conical, rounded, obtuse or acute, entire, subentire or papillate. – Fig. 7E.

Distribution and habitat. *Nanorrhinum heterophyllum* is distributed from the Canary Islands and the Cape Verde Peninsula in the West across the interior parts of northern Africa to North-East Africa and the Arabian Peninsula in the East. It is known from the Canary Islands, Morocco, Algeria, Mauritania, Senegal, Chad, Egypt, Sudan, Eritrea, Ethiopia, Djibouti, Somalia, Jordan, Saudi Arabia, Yemen and Oman. No material from Djibouti has been seen, but two collections from there were cited by Lebrun, Audru & Cesar (1989). *N. heterophyllum* grows in a wide range of habitats such as on coastal sand-dunes, along wadis, on rocky slopes of basalt, granite and limestone, from sea level up to 2600 m.

Taxonomic remarks. The circumscription of *N. heterophyllum* (= *Kickxia heterophylla*) has varied greatly between different authors. Danin & Hedge (1973) took a comparatively broad view of the species and included material from the Canary Islands in the west to the Arabian Peninsula and the Horn of Africa in the east. They also recognized *K. spartioides* as a closely related species with more or less the same area of distribution. The two species were said to differ in leaf width, petiole length and habit, but several specimens from Arabia and North Africa were listed as atypical or intermediate.

Sutton (1988) took a much narrower view of *K. heterophylla* and restricted it to material from the Canary Islands and North Africa. *K. spartioides* was also recognized, under the earlier name *K. scoparia*, but was restricted to material from the the Canary Islands only. Sutton (1988) also recognized the previously described *K. pendula* and *K. urbanii* as endemics to the Canary Islands. The material from the Arabian Peninsula and north-eastern Africa treated by Danin & Hedge as either *K. heterophylla* or *K. spartioides* was by Sutton referred to a series of new species: *K. gracilis* (a new name for *Linaria gracilis* R.Br. ex Benth.) from Egypt, Eritrea, Ethiopia, Sudan and Somalia, *K. kasalensis* from Sudan, *K. corallicola* and *K. pseudoscoparia* from Saudi Arabia, *K. qaraica* from Oman, and *K. sabarum* from northern Yemen. He also recognized the previously described but little-known *K. spiniflora* from southern Yemen. Another previously described species, *Linaria patula* from Somalia, was included in *K. heterophylla* by Danin & Hedge (1973), who stated it to be "intermediate between *K. heterophylla* and *K. spartioides*", whereas Sutton (1988) left it with the comment that it "may form part of the variation of *K. gracilis* or a distinct species".

The many species recognized by Sutton were said to differ in characters such as corolla and spur length, width of the corolla-tube at the mouth, indumentum, rigidness of the stem, petiole length, angle of branching, leaf shape and whether the leaves are homomorphic or heteromorphic, size of calyx-lobes, and size and shape of the tubercles on the seeds.

Today much more material is available, particularly from the Arabian Peninsula, and several forms have come to light that cannot easily be accomodated in any of the taxa recognized by Sutton. Thulin,

Beier & Hussein 9751 from escarpment rocks in the Hauf area in Yemen, near the border of Oman, is tomentose all over and has orbicular leaves, whereas Thulin, Beier & Hussein 9771 from the same area has a variable indumentum and ovate to deltoid leaves. Thulin, Beier & Hussein 9607, 9663 and 9714 from Ras Fartak in southern Yemen represent another very variable form series with great variation in habit, leaf shape and indumentum.

Cultivation experiments (see under Reproductive biology and crossing experiments) show that the variation to some extent is genetically based and many of the forms keep their characteristic indumentum and leaf shape also under greenhouse conditions. However, the subdivision into taxa with heteromorphic respectively homomorphic leaves made by Sutton (1988) is not supported by the cultivation experiments. In all cases when progeny from plants with apparently homomorphic leaves was grown in the greenhouse, a more or less basal rosette of leaves very different from the other cauline leaves was produced. However, this rosette eventually often disappear giving the impression of a plant with homomorphic leaves. A striking example is the collection Thulin et al. 8135 from southern Yemen with stout rigid stems with a few, minute, subsessile, linear leaves. Progeny grown from seeds of this collection showed slender, flexuous stems with distinctive basal leaves, and with many hastate or sagittate cauline leaves with distinct petioles.

Crossing experiments (see under Reproductive biology and crossing experiments) involving forms referable to respectively "*K. scoparia*" (Fig. 7E) and "*K. urbanii*" from the Canary Islands and to "*K. gracilis*" from Eritrea showed that these "taxa" are interfertile in all combinations and give a progeny with all kinds of combinations of characters.

My conclusion is that far too many taxa were recognized in this group by Sutton (1988) and that also the subdivision into two major taxa as proposed by Danin & Hedge (1973) is untenable. In my opinion only one variable taxon can be recognized when all material and other evidence available today are taken into consideration. At the same time it is clear that, in some parts of the area of distribution, more than one form of the species may be present and locally give the impression of different taxa.

Additional specimens examined. Spain. Canary Islands. *Lanzarote*: Famara, Bourgeau 317 (K); San Joseph los Palmos, Bourgeau 377 (E, K); San Jose, Bourgeau 1460 (E, UPS). *Fuerteventura*: Puerto de Cabras, Pitard 308 (S); Hansen 353 (C). *Gran Canaria*: Tirajana valley near Fortaleza, Stearn 1148 (BM); Guayadegua, Kunkel 19345 (C); Aguimes, Bremer 3844 (UPS); Arinaga punta de los Cuervistas, Bremer 3845 (UPS); Urbani pit, Stork s.n. (K, S); Asplund 1367 (K, S, UPS). *Tenerife*: Guimar, Montanas des los Guirres, Bolle s. n. (E, UPS); ibid, Asplund 446 (UPS). *Gomera*: road from San Sebastian to Benchyigua, Aldridge 1177 (BM).

Morocco. Djebel Amistten, Lindberg 2175 (S); Sid pr. Safi, Samuelsson 6390 (S); N of Tamari, Davis D.48433 (BM, E); above Sidi Mousa, near Tiznit, Davis 53562 (BM, E); 3 km from Marakech to Chemaia, Davis 54210 (BM, E); Schonkak, Balls B2490 (BM, E, S); Moyen Atlas, Bin-el-Quidane S of Beni-Mellal, Jonsell 5410 (UPS).

Algeria. Arak, Meinertzhagen s.n. (BM); Central Sahara, Oued Tamarasset, Meinertzhagen 102 (BM, K); ibid., Haggar Mts, Meinertzhagen 173 (K).

Mauritania. Nr. Atar, Ifan, Popov 47 (BM); Nouakchott, Arvidsson 79, 80, 81 (K).

Senegal. Cape Verde peninsula, N of Dakar, Quakam, Dunnet 64 (K).

Chad. Tibesti, 125 km Zouar-Bardai, Guichard KG/Tib/31 (BM); Tronan Natron, Tibesti, Hinchnisbrooke 35 (K).

Egypt. Gebel Elba: Khattab 6288 (K), Wadi Rabdeit, Shabetai F1702 bis (K), Wadi Seranti, Newberry 218 (BM). Ras el Naqb, Drar 830 (S); Gebel Hamra Dom, Drar 191 (S); Gebel Hadarba, Murray 3823 (K).

Sudan. Suakin, Uaratab, Schweinfurth 237 (BM, K); Red Sea Hills, Lugard s.n. (BM); ibid, Erkowit-Sinkat, Aylmer 254 (BM, K); Kassala, Nubia, Bent s.n. (K); ibid, Gedian pass, Jackson 2939 (K).

Eritrea. Hebo-Acrur, Baldrati 2345 (FT); near Adi Caieh, 80 km SE of Asmera, Hagos 158 (ETH, K); Assaorta, in the Haddas Valley, Pappi 5150 (FT, S); Adi Hadid, 17 Km S of Segeneiti, Ghebrehiwet 205 (UPS); Keren, river Anseba, Tellini 825 (FT); Messhalit pass, Bally B6685 (K).

Ethiopia. 26 km W of Bati along Dessie road, Boulos & Getahun 11782 (UPS); near Bati, E of Kombolcha, de Wilde et al. 7351 (ETH, K); Kalu Awraja, Chleka river gorge 30 km SW of Degan, Mesfin 6433 (C, ETH).

Somalia. Bari Region: coast of Migiurtini, Puccioni & Stefanini 721 (FT); mountain pass W of Baragal c. Thulin & Warfa 5530 (K, UPS); 20 km S Dhurbo on road towards El Gal, Thulin & Warfa 5976 (K, UPS); Ras Hantara, Thulin & Warfa 5587 (K, UPS).

Jordan. 10-12 km N of Aqaba, Boulos, Al-Eiswi & Jullad 6134 (K); Marin Biology station, 6 km S of Aqaba, Hemsky s. n. (K).

Saudi Arabia. Wadi Hebran, Schimper 147 (E); Wadi Sawawin, Collenette 438 (K); 8 km S Rabigh,

Mandaville 3002 (BM); Taif, Popov 71/160 (BM); Shuaybah, 50 km S of Jedda, Collenette 3832 (E); Farasan Island off Jizan, Collenette 4171 (E); Al-Abha Region, Aquabat Al-Abna, SE Baljurashi, Fayed 1397 (E); 50 km N of Khaybar, Al-Ulva road, Collenette 5771 (E); 15 km N of Talhah SE of Abha, Lavranos & Collenette 18335 (E); wadi below Sadah, Gordon 595 (E).

Yemen. Wasit, 20 km N of Sadah, Miller 3174 (E); Manach, Müh-Ho 241 (E); Bait al Lahida E of Sanaa, Wood 2448 (BM, E, K). Jabal Dawran: Gillespie 23 (BM), Wood 3238 (K), Thulin, Ghebrehiwet & Gifri 9391 (UPS). Abyan: escarpment to the Awdillah plateau, Thulin, Eriksson, Gifri & Långström 7909 (UPS); Wadi Dheiqua, 24 km W of Al-Mahfid, Boulos 16892 (BM). Hadramaut: Aquqbet Huwere, Wissman 2987 (BM); Mola Matar area, Thulin, Eriksson, Gifri & Långström 8092 (UPS); 15 km NE of Riyan, Thulin, Beier & Hussein 9526 (UPS). Mahrah: 16 km NE of Itab, Thulin, Beier & Hussein 9558 (UPS); Ras Fartak, above Al Wadi, Thulin, Beier & Hussein 9507 (UPS); Sadfan, along road between Jadib & Damqawt, Thulin, Beier & Hussein 9714 (UPS); near Yemen/Oman border, crossing NE of Hawf, Thulin, Beier & Hussein 9751 (UPS).

Oman. Dhofar: 43 km N of Salalah on the Tamrait road, Radcliffe-Smith 5127 (K); Jebel Qara, Fitzgerald 1248/2 (BM), ibid., Miller 2257 (BM, K); Khor Gish Gish, E of Sadh, Miller 6189 (E, K); Manston to Mudhai road, Miller 6305(E); Ayun pools, c 40 km NW of Salalah, Miller & Nyberg 9071 (E, K); Ras Sawqirah c 5 km W of Sawqiraha, Miller 9452 (E K); plateau above Sharbithat, Miller and Nyberg 9440 (K); Lye water hole at base of Jebel Semhan, Miller 6208 (K).

10. Nanorrhinum stenanthum (Franch.) Ghebrehiwet comb. nov.

Linaria stenantha Franchet 1882: 55; Skan 1906: 492; Cufodontis 1963: 890; Sutton 1988: 270 (microfiche). – Type: Somalia, without precise locality, 22 July 1881, Révoil 104 (P holotype).

Perennial herb or subshrub; stems up to 12 cm long, ascending to erect, glabrous, usually woody and much branched from the base, angle of branching narrow. Leaves (3.3-)6.6-10.6(-14.8) × (0.5-)0.8-1.6(-2.5) mm, linear to oblong, entire, obtuse or apiculate at the apex and attenuate at the base; petiole 0-4.9 mm long, not twining. Pedicel 15-20 × 0.16-0.2 mm, erecto-patent, usually curved at the distal end. Calyx-lobes glabrous, 2.4-2.8 × 0.6-0.8 mm, lanceolate to ovate, acute at the apex, the margins narrowly scarious. Corolla including spur 11.5-12.5 mm long, eglandular-pubescent, yellow; tube 1.2 mm broad at the mouth; palate internally lanate; spur 7.4-7.8 mm long, exceeding rest of corolla, narrow, slender, straight and continuing with the tube. Capsule 2-3.6 mm long, oblong-ovoid, glandular puberulent at the tip; loculi equal, many-seeded, dehiscent. Seeds 0.6 × 0.5 mm, brown, reniform, with very minute tubercles.

Distribution and habitat. Nanorrhinum stenanthum is known only from north-eastern Somalia. The type collection is without precise locality, but it is very likely that it originates from north-eastern Somalia, where Révoil is known to have collected, and from where the only other known collection originates. According to Thulin & Warfa 5906 the species grows on limestone rocks at c. 200 m altitude.

Taxonomic remarks. Nanorrhinum stenanthum has, since its publication in 1882, remained obscure to taxonomists, mainly due to the poor original description and the absence of other collections than the type. Skan (1906) referred to it as an imperfectly known species, Cufodontis (1963) stated the species to be probably referable to *Kickxia somalensis*, and Sutton (1988), in his revision of the tribe *Antirrhineae*, listed it in the index under dubious and unknown species.

Today *N. stenanthum* is known from two collections, the type collection by Révoil made in 1881 and Thulin & Warfa 5906 made in 1986. Obviously it is a narrow endemic of north-eastern Somalia. *N. stenanthum* resembles *N. ramosissimum* in being a small-flowered shrublet, but differs in its longer (c. 7.5 mm versus 1.2-6.5 mm long) spur, which is continuing with the tube and exceeds the rest of the corolla. In *N. ramosissimum* the spur is shorter than to almost as long as the rest of the corolla and it forms an obtuse angle with the tube. Also, *N. stenanthum* is smaller than *N. ramosissimum* with smaller linear to oblong leaves with attenuate base (not ovate to lanceolate and with hastate, sagittate, rounded or cordate base).

Additional specimen examined. Somalia. Bari Region, Cape Guardafui, 11°50'N 51°17'E, 19 Nov 1986, Thulin & Warfa 5906 (K, UPS).

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