On anatomy, adaptations to xerophytism and taxonomy of Anabasis inclusive Esfandiaria (Chenopodiaceae)

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Morphological characters used to distinguish the monotypic genus *Esfandiaria* from *Anabasis* were found to be of little taxonomic value. The only species is transferred to *Anabasis* as *A. calcarea* (Charif & Aellen) comb. nov. and is placed in the section *Esfandiaria* (Charif & Aellen) comb. nov. The anatomy of *A. calcarea* and 4 other investigated species belonging to as many sections, shows much variation. Many structures considered to be adaptations to xerophytism have been found. Particularly remarkable is the 8–11-layered epidermis of *A. calcarea* with stomata placed at the bottom of 200 μm long oblique canals. Sections of stems, leaves and wood are described and illustrated.

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The monotypic genus *Esfandiaria* Charif & Aellen (Chenopodiaceae) was in the comments to the description considered to be closely related to the genus *Anabasis* (Aellen 1952). New material and field studies gradually have lead to doubts about the distinctness of this genus. In spite of the remarkable habit of its only species, there seems to be no clear morphological character to distinguish *Esfandiaria* from *Anabasis*. The species is thus better transferred to *Anabasis* under the name *A. calcarea* (for a formal transfer, see Conclusions).

A. calcarea grows on the border of the desert under extreme ecological conditions. It is usually found on small hills with a whitish soil, probably gypsum, hardly with any other plants around it. With the succulent, articulated, strongly glaucous stem and the cone-like inflorescences on short branches it is certainly a most remarkable plant (Fig. 1). Originally it was thought to be endemic to a small area on the NW margin of the great salt desert of Dasht-e Kavir in Iran. In recent years it has been found in several new localities, all more or less on the margin of the desert (Rechinger & Wendelbo 1976 p. 35; Wendelbo 1977 p. 163). Thus the known area has become much extended (Fig. 2). Some work has already been done on the anatomy of *Anabasis* (Metcalfe & Chalk 1950, Fahn & Arzee 1959, Fahn 1963, Fahn & Dembo 1964, Fahn & Shchori 1968). However, the anatomy of some characteristic Iranian species belonging to different sections of *Anabasis* have never been studied and such results are presented here.

It was thought that an anatomical investigation of *Anabasis calcarea* and some other characteristic members of the genus might throw more light on relationships within the genus and provide characters of taxonomic value. It was also expected that, due to the extreme habitats of these plants, interesting xeromorphic structures might be revealed.

Material and methods

This study is entirely based on fresh material which was preserved in FAA before sectioning. Hand sections of internodes of young stems, wood and leaves were placed in Eau de Javelle for 5 minutes. After washing with water sections were placed in safranin dissolved in 50 % alcohol for 5 minutes. Excess stain

Fig. 1. *Anabasis (Esfandiaria) calcarea* on the margin of the salt desert Dasht-e Kavir. Iran: Turan Protected Area, near Delbar. Photo P. W. 28.9.1975.

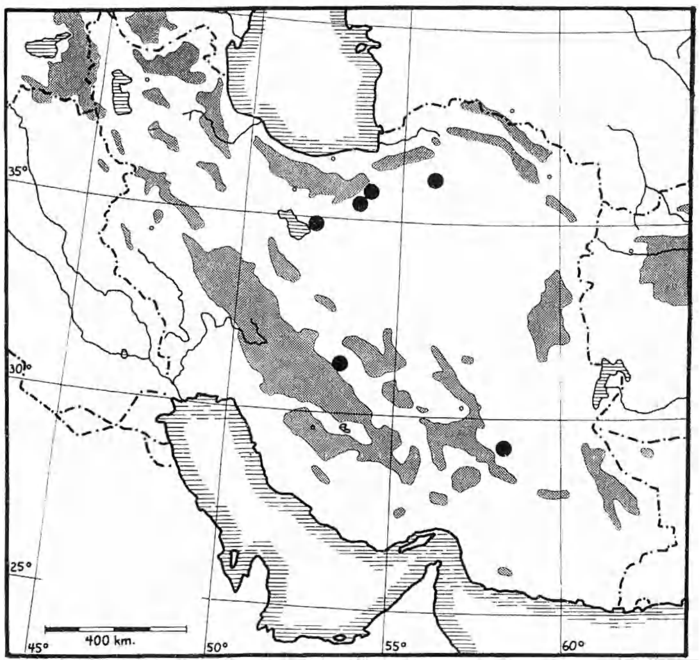


Fig. 2. Known distribution of *Anabasis calcarea*. Shaded: areas above 2400 m.

was removed with 50 % acidified alcohol and after thorough dehydration with absolute alcohol sections were mounted in euparal. Young stems were examined in transverse and longitudinal sections, wood and leaves were studied only in transverse sections. Photomicrographs and camera lucida drawings were made from the slides which are kept in the Biology Department, Pahlavi University, Shiraz, Iran. Dried voucher specimens are kept in the Herbarium of Ariamehr Botanical Garden, Tehran (TARI).

The following specimens (all from Iran) were examined:

Anabasis (sect. *Esfandiaria) calcarea* (Charif & Aellen) Bokhari & Wendelbo – Shahrud-Semnan prov.: Turan Protected Area, N of Delbar, 28.9.1975, P. Wendelbo & H. Foroughi.

A. (sect. *Adenophora*) *annua* Bge – Central prov.: Mardabad, SW of Karaj, 10.11.1975, P. Wendelbo.

A. (sect. *Anabasis*) *aphylla* L. – Shahrud-Semnan prov.: E of Shahrud, 29.9.1975, P. Wendelbo & H. Foroughi.

A. (sect. *Brachylepis*) *eriopoda* (Schrenk) Bth. – Shahrud-Semnan prov.: Turan Protected Area, N of Delbar, 28.9.1975, P. Wendelbo & H. Foroughi.

A. (sect. *Setifera*) *setifera* Moq. – Shahrud-Semnan prov.: W of Semnan, 30.9.1975, P. Wendelbo & H. Foroughi.

Anatomy

The young stem

Nodes. In all the investigated species the stems and branches are articulated and ± succulent. Elongation of the young internodes is a result of the activity of an intercalary meristem present at the constricted base of each internode. At the apex of each internode there are two opposite leaves, the connate bases of which form a cup around the constricted part of the next internode and its meristem. The inside of this sheath or cup has a dense cover of woolly hairs embedding the constricted part (Fig. 3 A, B). The epidermis of the lower part of the internode is uniseriate or biseriate even in those species where the normal stem epidermis is multiseriate. These epidermal cells are thin-walled and slightly cutinised. In the constricted region a group of sclerified parenchyma has been observed in *A. calcarea* (Fig. 3 C, D) only. In all the investigated species there is a zone of compressed parenchyma cells at the basis of the internodes. In older stems this zone of cells was found to be suberised.

Epidermis. In all investigated species the epidermis has a distinct cuticle and the cell walls beneath are strongly cutinised. In *A. annua* (Fig. 7 C) there is a single layer of epidermis and the epidermal cells are very long as seen in longitudinal section (Fig. 6 C). In *A. setifera* (Figs. 7 A, 6 D) there is also a single epidermis but the cells are short in longitudinal view. *A. setifera* is the only species where the stem has two ridges and two grooves (Fig. 8 C). The ridges and grooves are strengthened by collenchymatous cells (Fig. 7 A, B). In *A. eriopoda* (Figs. 7 D, 6 A) and *A. aphylla* (Figs. 7 E, 6 B) the epidermis is 3-layered, in *A. calcarea* (Figs. 4 A, C, 5) 8–11-layered.

In *A. eriopoda, A. aphylla* and *A. calcarea* there is a continuous single layer of hypodermis.

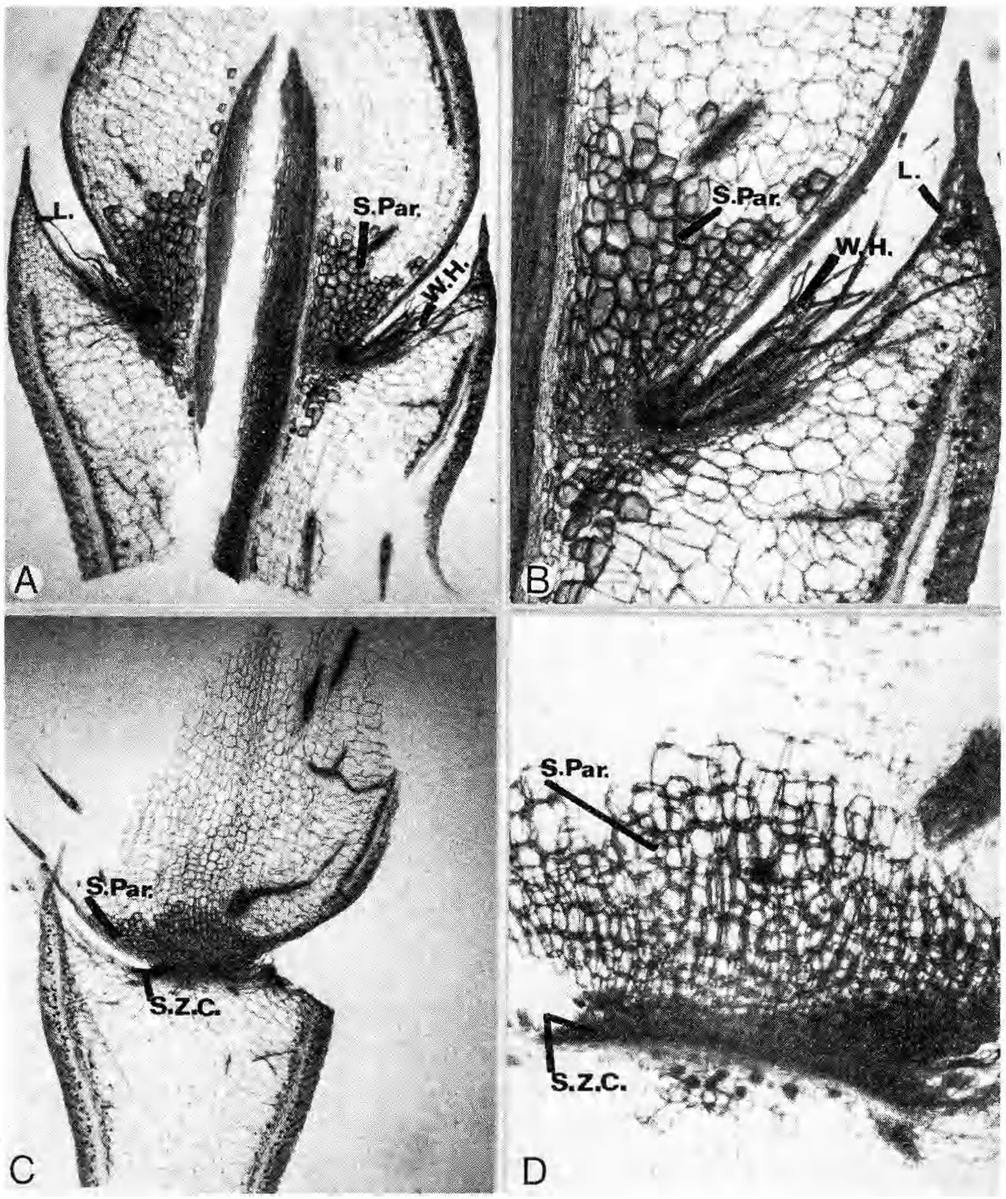


Fig. 3. *Anabasis calcarea*. Longitudinal sections of stem through node. – A, B: Sclerified parenchyma (S.Par.) in the nodal region and woolly hairs (W.H.) surrounding the joint (A × 17, B × 35). – C, D: Sclerified parenchyma and suberised zone of cells (S.Z.C.) in the joint (C × 17, D × 50). – L. leaf.

In *A. setifera* there is also a single layer of hypodermis but it is interrupted below the ridges and grooves. Crystals are usually present in the hypodermal cells. Hypodermis is lacking in *A. annua*.

Stomata. In *A. annua* stomata were not observed on the stem. (The assimilative tissues are restricted to the leaves in this species.) In the other species of *Anabasis* stomata are present all around the stem and are orientated perpendicularly to the longitudinal axis of the internode. In *A. setifera* (Figs. 7 A, 6 D) the stomata are slightly sunken below the epidermis. In *A. eriopoda* (Figs. 7 D, 6 A) and *A. aphylla* (Figs. 7 E, 6 B) stomata are deeply sunken below the epidermis and are confined to stomatal cavities. In *A. calcarea* (Figs. 4 A, 5) the stomata are deeply sunken and are present at the base of up to 200 μm deep, obliquely orientated stomatal canals which are present all around the stem. As far as we have been able to determine from the literature, such deep, obliquely orientated stomatal canals have not been reported for any plant, although Böcher & Lyshede (1968 Fig. 15) have a rather similar case in the South American *Bredemeyera collettioides* of Polygalaceae. Stomata deeply sunk in a several-layered epidermis is beautifully illustrated by Böcher (1975) in the case of *Prosopis kuntzei* of Leguminosae.

The epidermal cells lining the stomatal cavities or canals, as well as the outer edges of the guard cells are covered by a thick cuticular layer. The guard cells continue developing thick cutinised walls, and ultimately the cell lumen is very much reduced. If the cell lumen is very small, the turgor pressure no longer seems able to cause the stomatal aperture to open.

Cortex. The fleshy tissue around the vascular cylinder is the 'cortex'. It usually includes a well-developed chlorenchyma overlying an extensive water storage tissue (Fig. 8). We agree with Fahn & Arzee (1959) and Fahn (1963) who have produced convincing evidence that fleshy internodal tissue is axial in nature and is a true cortex.

In *A. annua* the cortex is present directly below the uniseriate epidermis and is made up of water storage parenchymatous cells (Fig. 7 C). In *A. calcarea* (Fig. 4 A, C), *A. eriopoda* (Fig. 7 D), *A. aphylla* (Fig. 7 E) and *A. setifera* (Fig. 7 A) further inward from the hypodermis there is a highly differentiated cortex which is quite similar in all these species. Below the hypodermis there is a chlorenchyma which is made up of an outer layer of palisade and an inner layer of short cells. In *A. calcarea, A. eriopoda* and *A. aphylla* the chlorenchymatous layers are continuous all around the stem but in *A. setifera* there is no chlorenchyma below the ridges and grooves (Fig. 8 C). Below the chlorenchyma there is a very well-developed water storage tissue made up of mostly large parenchymatous cells. Thus in these species the cortex performs the function of photosynthesis and water storage. There are a few small cortical vascular bundles present in the cortex. In *A. eriopoda* and *A. aphylla* these bundles are usually accompanied by fibres which are sometimes forming a sheath in *A. eriopoda*. Crystals are also present in some water storage cells. The innermost layers of the cortex are usually composed of much smaller cells than the middle layers. In *A. calcarea* sclereids are present in these cells (Fig. 4 A, C). In *A. eriopoda* (Fig. 7 D) and *A. setifera* (Fig. 7 A) there are groups of broad-lumened fibres in the innermost layer of the cortex. In *A. aphylla* (Fig. 7 E) there are strands of narrow-lumened fibres in the cortex, and below these strands of fibres and just outside the vascular cylinder there are 3–4 layers of cortex which are made up of radially elongated parenchyma. Such radially elongated parenchyma has not been observed in any of the other species. Cortical fibres are not present in *A. annua*.

Stele. As in other Chenopodiaceae (Metcalfe & Chalk 1950) there are two zones in the primary vascular cylinder. In *A. aphylla* (Fig. 8 E) there is a complete cylinder of phloem and xylem in the outer zone. In the inner zone there are two large and two small distinct vascular bundles. In *A. setifera* (Fig. 8 C) the outer vascular zone is similar to that of *A. aphylla* but in the inner zone there are two large and many small vascular bundles. In *A. annua, A. eriopoda* and *A. calcarea* the outer zone has a number of small phloem bundles but the xylem forms a continuous cylinder. In the inner zone there are 4–6 vascular bundles of different size in *A. annua* (Fig. 8 B), in *A. eriopoda* (Fig. 8 D) perhaps a few more, and in *A. calcarea* (Fig. 8 A) there are four vascular bundles of equal size in the inner zone. In all the species there is an excessive development of narrow-lumened fibres in the xylem of the outer and inner zones.

Pith. In *Anabasis calcarea* the pith is parenchymatous and has a number of well-developed brachysclereids (Fig. 4 B, C). Some crystals are also present in the pith. In the other species the pith is only composed of parenchyma with intercellular spaces. In *A. aphylla* there is an excessive formation of crystals in the pith (Fig. 7 E). Crystals are also present in the pith of *A. eriopoda* and *A. annua* but not in the pith of *A. setifera* (Fig. 7 A).

The old stem

The axis is remarkable for its anomalous secondary growth, whereby concentric zones of secondary tissue or distinct collateral vascular bundles are produced in the wood from a succession of cylinders or arcs of cambium. When secondary tissue is in the form of vascular bundles, there is an extensive development of conjunctive tissue, in which these bundles are embedded.

In *A. calcarea* (Fig. 9 A) the secondary tissue is in the form of a number of irregularly orientated vascular bundles. Each vascular bundle has a well-developed group of narrow-lumened fibres on the lower side. Wood parenchyma is also well-developed and occurs in the form of concentric layers around the individual vascular bundle and its associated group of narrow-lumened fibres. There are sand crystals in a number of the cells of the wood parenchyma. In

Abbreviations used in Figs. 4–11

ab. – abaxial
ad. – adaxial
b.l.f. – broad-lumened fibres
c.b. – cortical bundle
coll. – collenchyma
cr. – crystals
cu. – cuticle
e.pa. – elongated parenchyma
ep. – epidermis
f. – fibrous tissue
f.s. – fibrous strand
hy. – hypodermis
n.l.f. – narrow-lumened fibres
p. – pith
pa. – parenchyma
pal. – palisade
ph. – phloem
r. pa. – ray parenchyma
s.cr. – sand crystals
scl. – sclereid
sp. – spongy mesophyll
s.ph. – secondary phloem
s.x. – secondary xylem
st. – stomata
st.c. – stomatal canal
st. ca. – stomatal cavity
st.t. – storage tissue
v.b. – vascular bundle
w.f. – wood fibres
w.pa. – wood parenchyma
x. – xylem

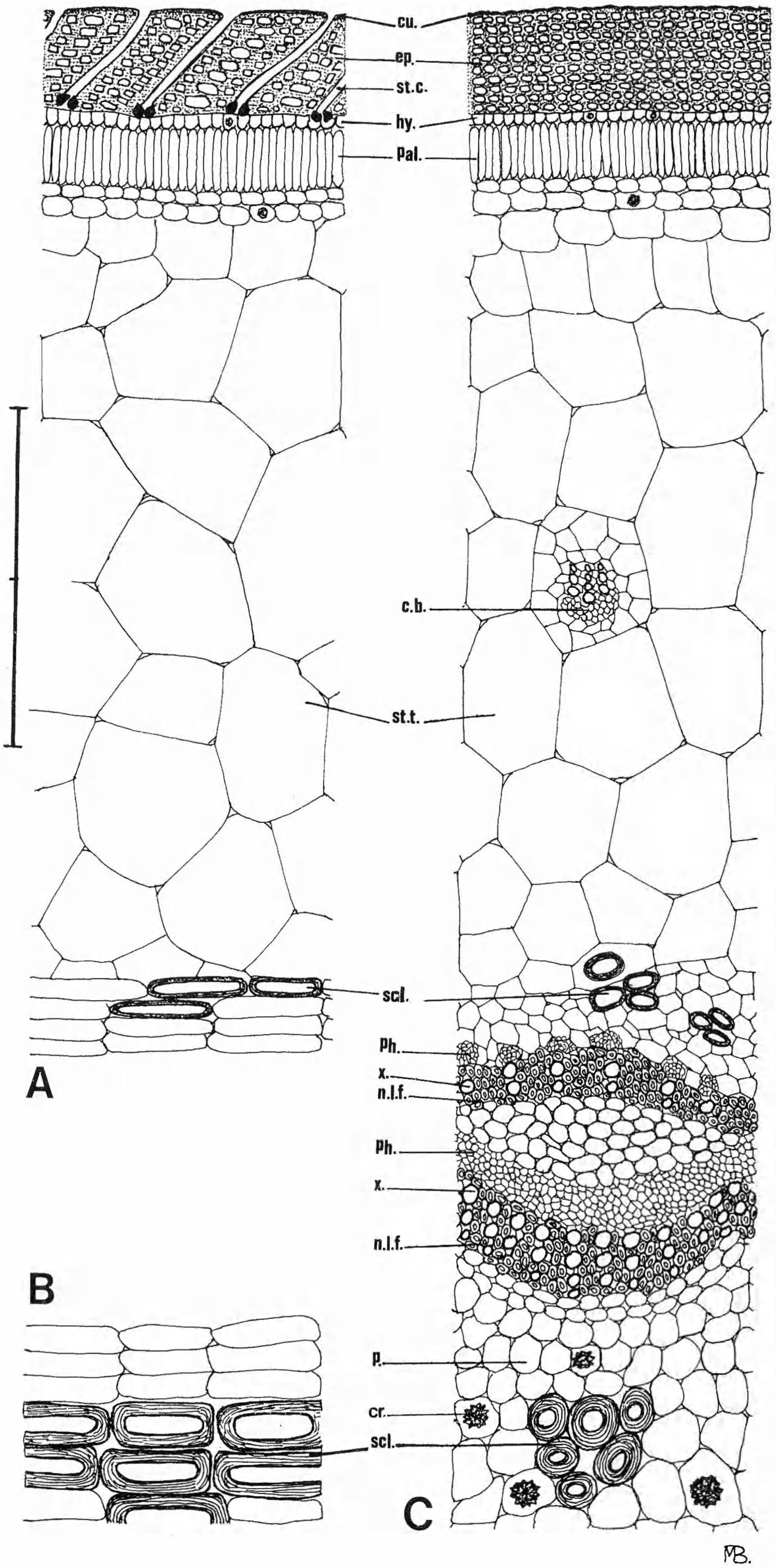


Fig. 4. *Anabasis calcarea*. – A: Longitudinal section of part of stem, vascular tissue and pith not shown. – B: L.s. of pith showing brachysclereids. – C: Transverse section of part of stem. – Scale 500 μm.

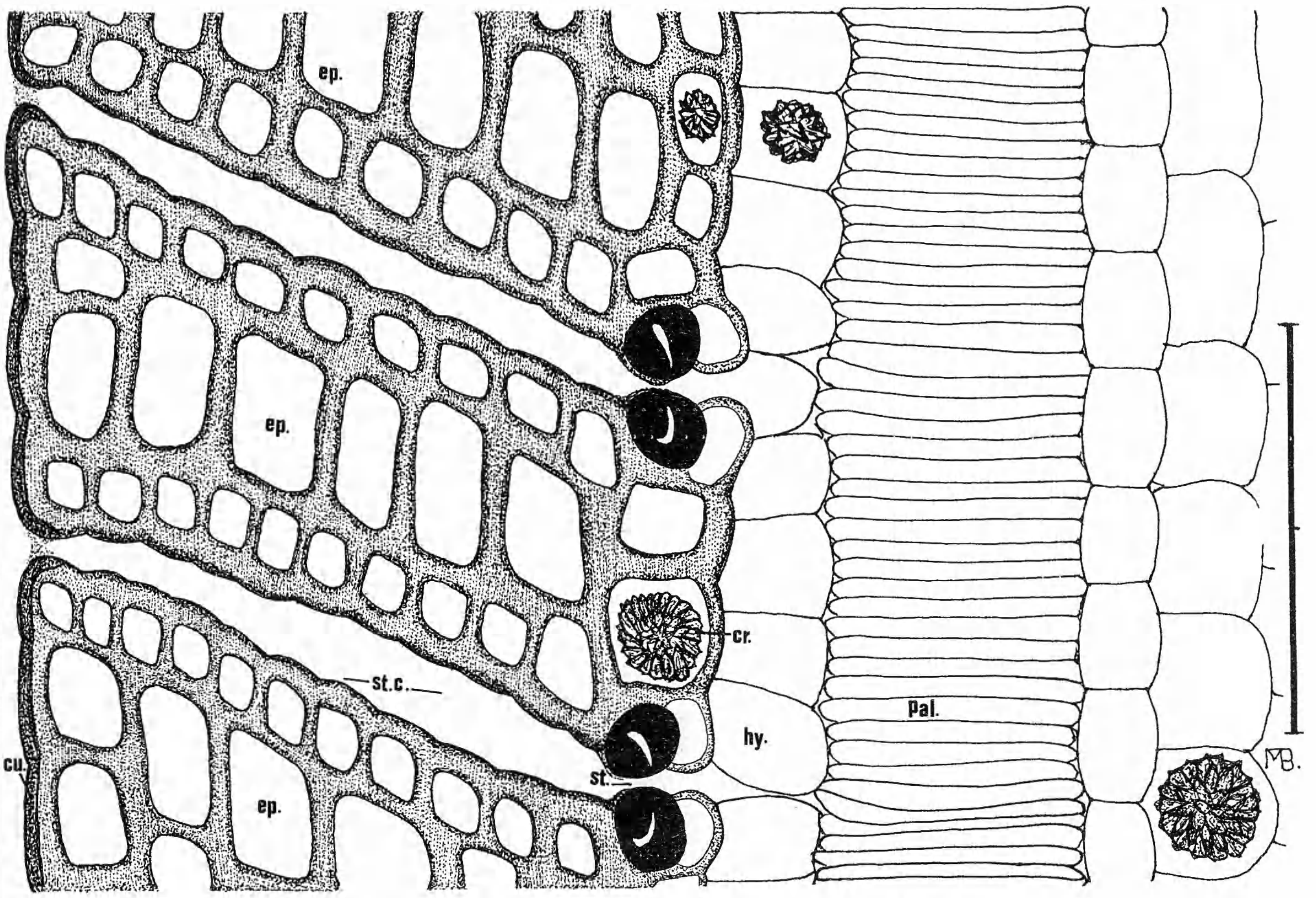


Fig. 5. *Anabasis calcarea*. Longitudinal section of part of stem. – Scale 100 μm.

A. setifera (Fig. 9 B) the transverse section of the wood exhibits alternate zones of woody fibres and thin-walled parenchyma. The zone of thin-walled parenchyma is continuous with the phloem groups of the successive rings of bundles. The individual bundles of a single woody zone tend to be separated from one another by thick-walled ray parenchyma, i.e. rays one cell wide. In *A. annua* much wood is developed at the end of the season in spite of the fact that it is an annual. The anomalous secondary growth results in the formation of wood in which there are a number of small vascular bundles occuring in concentric layers (Fig. 9 C). These bundles are embedded in an extensively developed fibrous conjunctive tissue which is made up of narrow-lumened fibres. The individual bundles are separated from one another by thick-walled ray parenchyma, i.e. rays one cell wide. In *A. aphylla* and *A. eriopoda* the basic pattern of anomalous secondary growth is the same as in *A. annua* but the vascular bundles are much larger and there is an extensive development of thin-walled ray parenchyma.

Leaf

In *Anabasis calcarea, A. aphylla* and *A. eriopoda* there are two opposite, reduced, scale-like leaves at the apex of each internode of the articulated stem. They are connate below so as to form a cup-like structure in which the base of the next internode is immersed. In these species the anatomy of the free part of the scale-like leaf was examined. In *A. setifera* and *A. annua* the leaves are well-developed, terete, fleshy, spreading or divaricate, ± cylindrical or pyriform respectively, opposite and connate at the base.

The scale-like leaves are bifacial. In *A. calcarea* (Fig. 10 A, B) and *A. aphylla* (Fig. 10 C, D) the adaxial epidermis is uniseriate. The cell lumen is small due to the highly cutinised cell walls. In *A. eriopoda* (Fig. 10 E, F) the adaxial epidermis is distinctly biseriate but also has highly cutinised cell walls and a small cell lumen. In *A. aphylla* and *A. eriopoda* the abaxial epidermis is biseriate but in *A. calcarea* it is distinctly

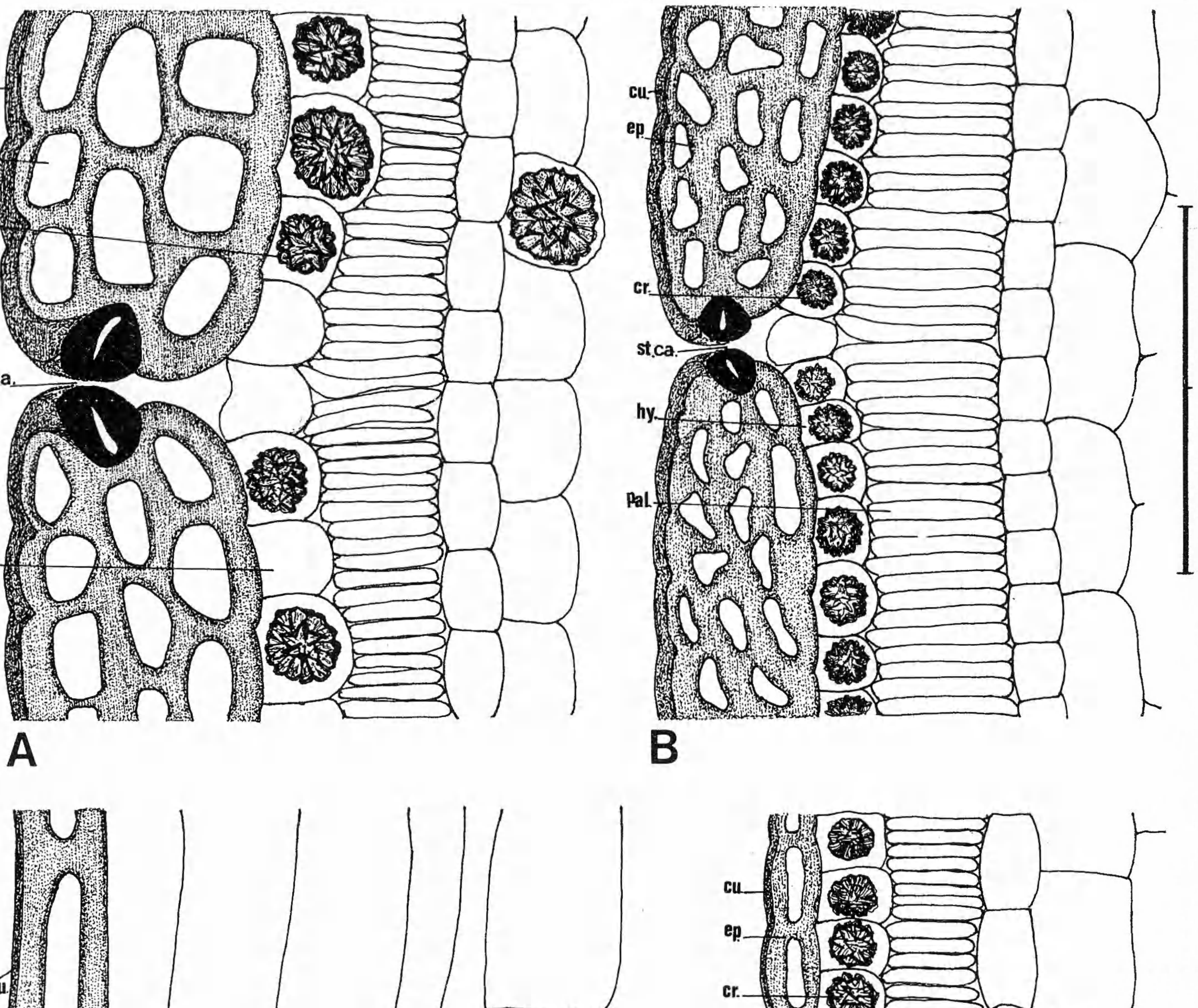


Fig. 6. Longitudinal sections of part of stem. – A: *Anabasis eriopoda*. – B: *A. aphylla*. – C: *A. annua*. – D: *A. setifera*. – Scale 100 μm.

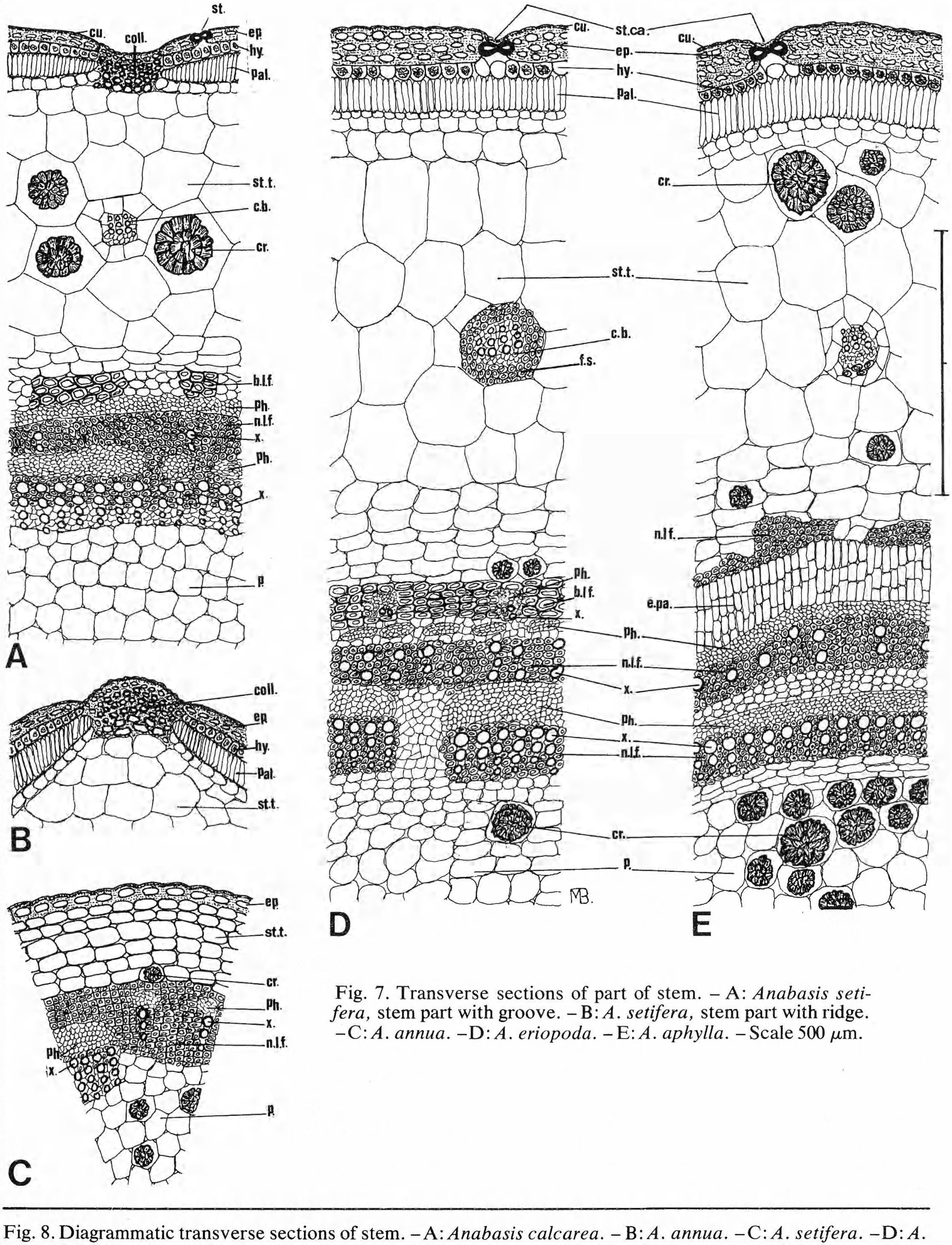
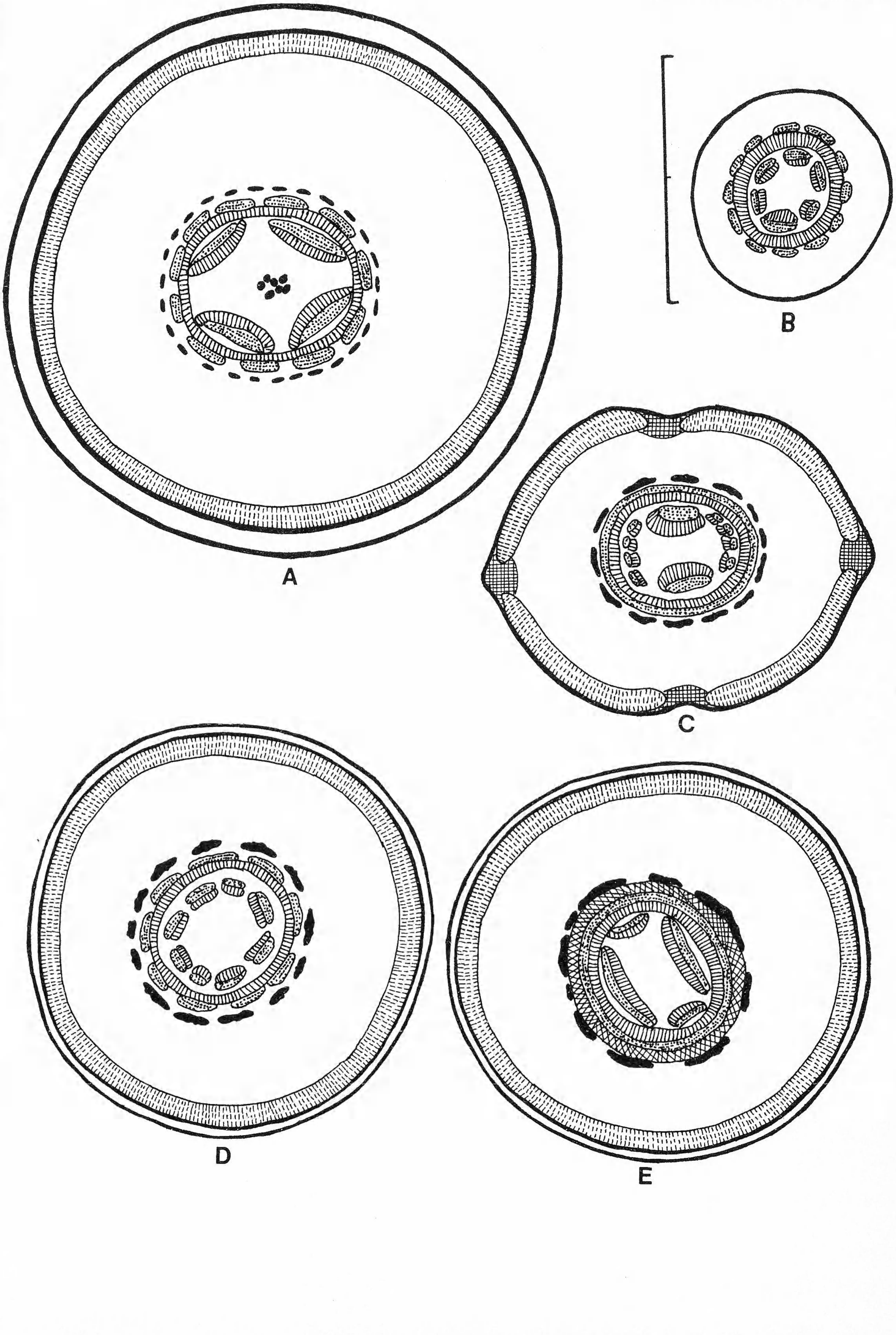


Fig. 7. Transverse sections of part of stem. – A: *Anabasis setifera,* stem part with groove. – B: *A. setifera,* stem part with ridge. – C: *A. annua.* – D: *A. eriopoda.* – E: *A. aphylla.* – Scale 500 μm.

Fig. 8. Diagrammatic transverse sections of stem. – A: *Anabasis calcarea.* – B: *A. annua.* – C: *A. setifera.* – D: *A. eriopoda.* – E: *A. aphylla.* – Cortical fibres and sclereids solid black; collenchyma cross-hatched; radially elongated parenchyma diagonally hatched; chlorenchyma ticked; xylem hatched; phloem dotted. Xylem fibres and phloem fibres not shown. – Scale 2 mm.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B
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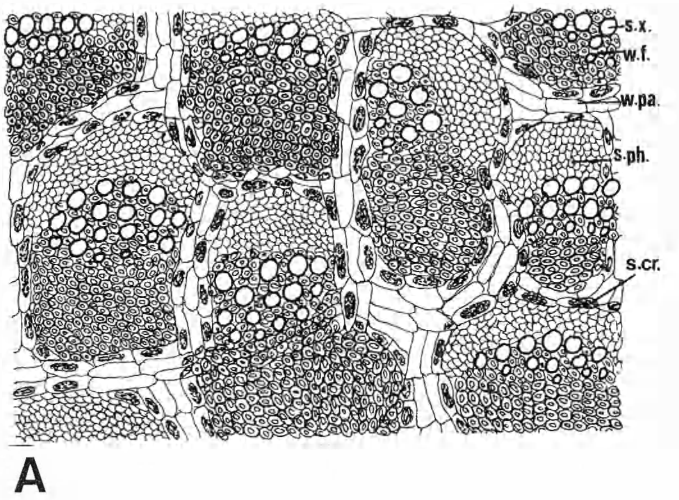
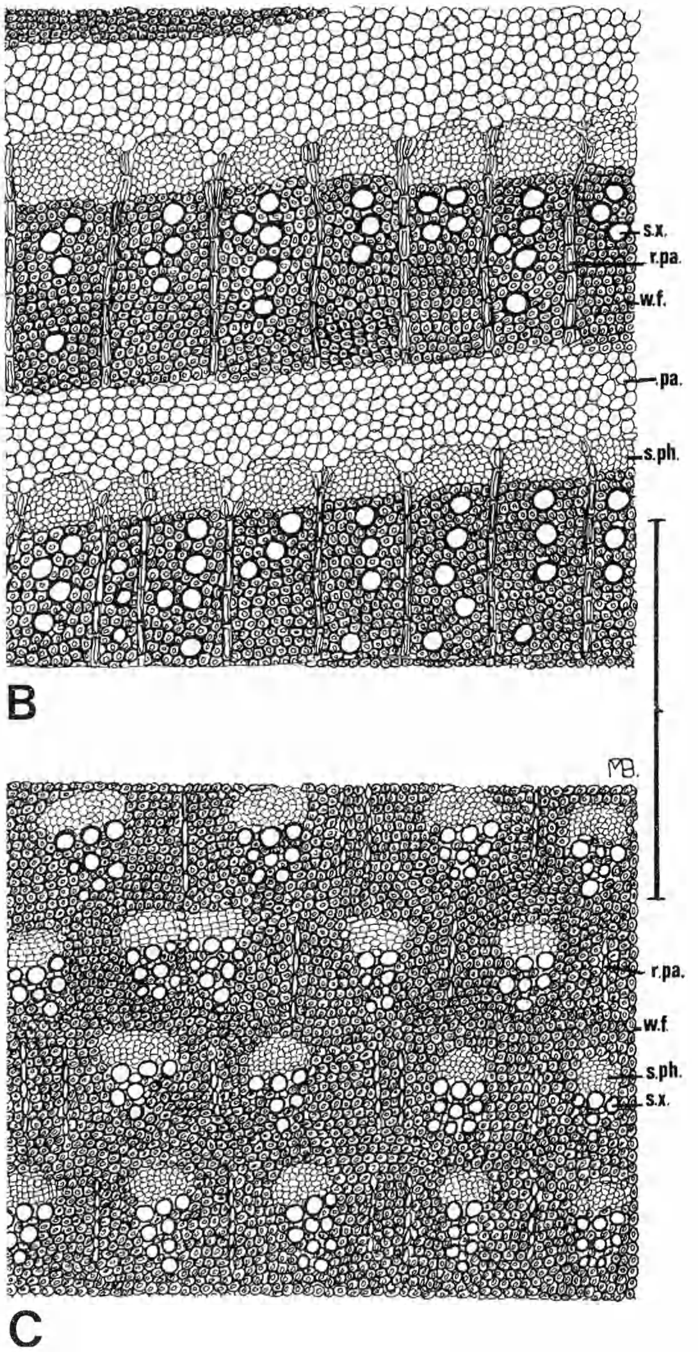


Fig. 9. Transverse sections of part of wood. – A: *Anabasis calcarea*. – B: *A. setifera*. – C: *A. annua*. – Scale 500μm.

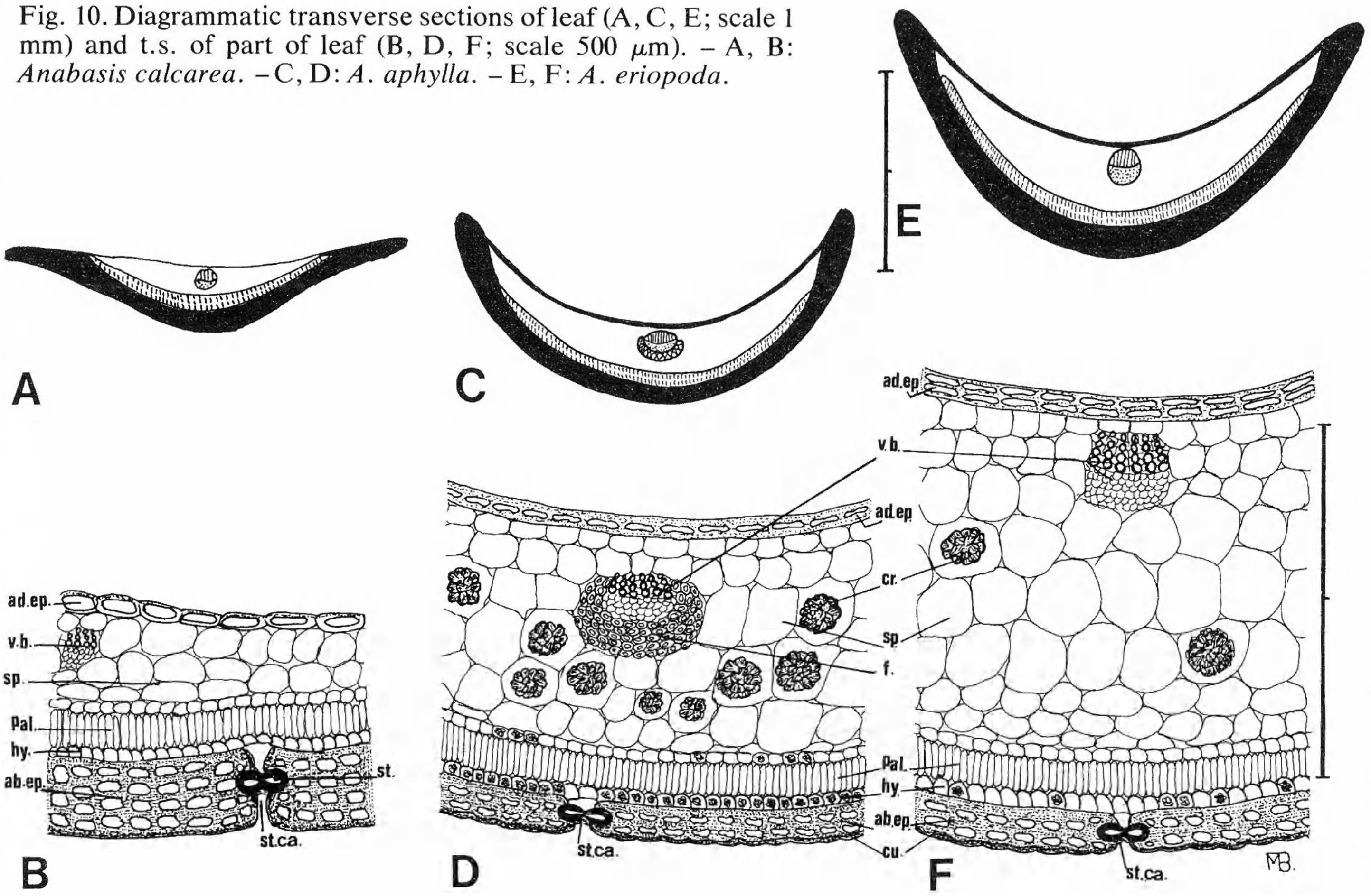


multiseriate. The cell walls of the abaxial epidermis are cutinised.

Stomata are confined to the abaxial epidermis and are orientated at a right angle to the long axis of the leaf. The epidermis produces a deep cavity or groove above the guard cells. The outer wall of the epidermis including the outer edges of the guard cells are covered by a thick cuticle. Immediately below the abaxial epidermis there is a single layer of hypodermis consisting of more or less isodiametric cells. In *A. eriopoda* many and in *A. aphylla* most of the hypodermal cells contain crystals but in *A. calcarea* crystals were not observed in these cells. Below the hypodermis there are two layers of chlorenchyma. The outer one consists of compact palisade cells and the inner of short, more or less cubical cells. In *A. aphylla* crystals were observed in some of these short cells. Further inward there is a spongy mesophyll which is made up of water storage parenchyma. Crystals are present in the spongy mesophyll of *A. aphylla* and *A. eriopoda*. There is a single main collateral vascular bundle in the centre of the leaf, with xylem adaxially and phloem abaxially. In *A. aphylla* there is a group of narrow-lumened fibres on the abaxial side of the vascular bundle (Fig. 10 C).

The terete leaf. In *A. setifera* (Fig. 11 B) and *A. annua* (Fig. 11 A) the cylindrical or pyriform leaves are well-developed, centric and are terete in cross section. The internal structure of the leaf is similar in both these species. There is a uniseriate epidermis all around, and the cells have a narrow lumen and cutinised walls. There is also a thin cuticle. Stomata are orientated at a right angle to the long axis of the leaf and are uniformly distributed all around the leaf. Below the epidermis there is a single layer of hypodermis often containing crystals. Further inward there is a circular area of chlorenchyma which has an outer compact palisade layer and an inner layer of short cells. The spongy mesophyll is very well-developed and is made up of large water-storage parenchyma all around the central main vascular bundle. Crystals are found in a few spongy mesophyll cells.

Fig. 10. Diagrammatic transverse sections of leaf (A, C, E; scale 1 mm) and t.s. of part of leaf (B, D, F; scale 500 µm). – A, B: *Anabasis calcarea*. – C, D: *A. aphylla*. – E, F: *A. eriopoda*.



Discussion

Stebbins (1952 p. 35 ff.) pointed out that one reason for rapid evolution in arid and semiarid regions is the number of different specialized structures which plants can evolve for adaptation to dry conditions, and he gave a number of examples, mainly referring to exomorphic characters. Many other cases of such xeromorphic structures will be found in the papers by Böcher & Lyshede (1968, 1972) on the anatomy of East Patagonian dry steppe plants together with references to previous research in this field. Wendelbo (1971) showed how the evolution of the mainly Afghano-Iranian genus *Dionysia* (Primulaceae) entirely could be related to gradual adaptation to more arid conditions.

Adaptations to xerophytism

The investigated species of *Anabasis* show a number of structures which must be considered as adaptations to the arid conditions under which they grow.

Water storage. Zohary (1962) has classified succulents, and our plants fall under his group: *Anabasis* type of succulents. In this group the water storage tissue is confined to the fleshy cortex around the vascular cylinder of the stem. In *A. annua* and *A. setifera* the water storage tissue is present in the fleshy cortex of the stem as well as in the fleshy mesophyll of the leaf.

These plants have a well developed mechanical tissue in their young stems and in the wood. The increasing proportion of mechanical tissue has been recognized as a general principle in the structure of plants growing in dry habitats. The extensive development of lignified fibrous tissue in the young stem and wood of *Anabasis* could protect the living tissue and keep the plant from collapsing when drying out; it could also serve as a water retaining tissue. Porsch (1926), cited by Pyykkö (1966), stated that the physiological significance of lignification ultimately lies in the high water retaining capacity of the cell wall. In fact, the lignified cell wall in a living plant is never completely dried out owing to its high water binding capacity.

Reduction of water loss. The investigated plants have a specialized epidermis which is

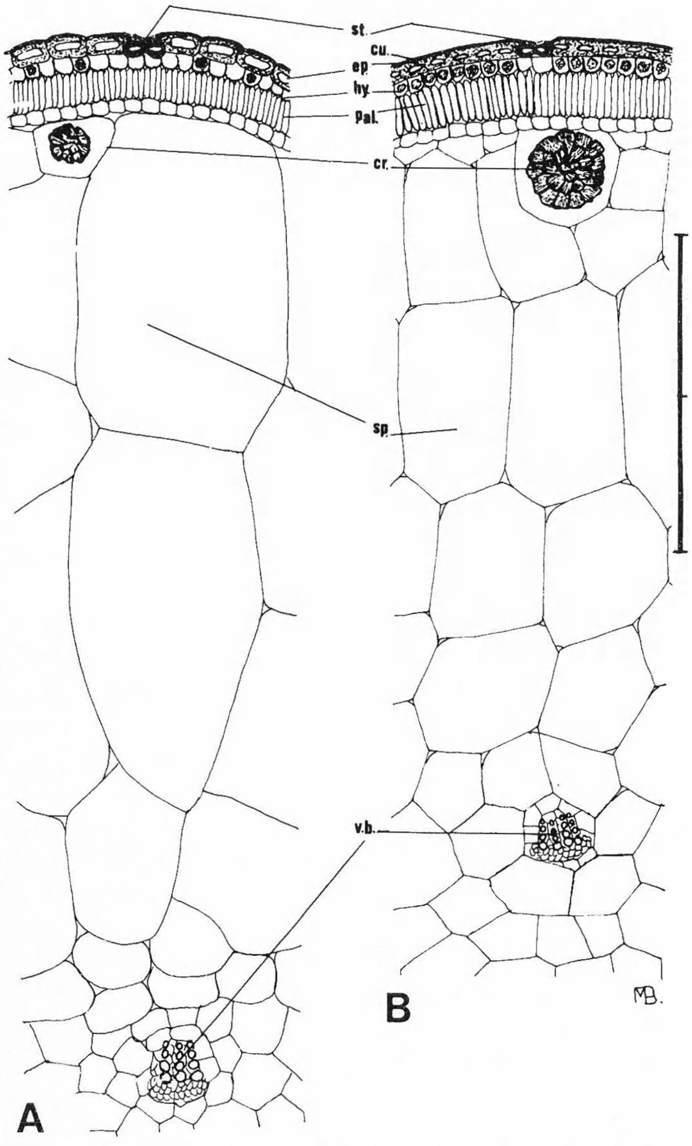


Fig. 11. Transverse sections of part of leaf. – A: *Anabasis annua*. – B: *A. setifera*. – Scale 500 μm.

cuticularised and highly cutinised. Ecological literature offers ample proof of the high efficiency of cuticular restriction in plant transpiration. According to Weaver & Clements (1938) the cuticular transpiration of xerophytes under water stress is practically nil, so it is evident that the principle of water economy in time of drought can also be achieved by the strengthening of the protective tissue (Oppenheimer 1960).

Stomata are chief organs for loss of water from the plant body, but exchange of gases which is vital for plant life takes place only through stomata. If the stomata are directly exposed to atmosphere the principle of water economy will not be achieved. So plants of dry habitats show various adaptative features which protect stomata from direct sunlight. The resistance to water vapour passing through the stomata is increased by the length of the way to the surface (cf. Böcher & Lyshede 1968, 1972, Wendelbo 1971). So either the stomata are sunken below the epidermis as in *A. annua* and *A. setifera*, or located in stomatal cavities as in *A. aphylla* and *A. eriopoda*. In *A. calcarea* stomata are present at the base of deep stomatal canals and this represents an extreme case in stomatal protection. There is a dilemma here as these extreme, long stomatal canals which reduce the water loss must be a great hindrance to the exchange of gases. The loss of water from stomata is further reduced by the cutinization of the guard cells. Eco-physiological experiments to show how the system works would be of great interest (Böcher & Lyshede 1968 p. 42).

The woolly connate leaf bases surrounding the growing zone with a weakly developed epidermis at the base of the internode, should be looked upon as a protective feature.

Reduction of surface as seen in scale-like leaves and transfer of the assimilatory function to the stem are well-known and characteristic features of xerophytes. The zone of compressed parenchyma cells found at the base of the internodes becomes suberised with age and most probably functions as an abscissal tissue. Under extremely dry conditions the internodes might be sealed off and then perhaps also 'thrown off' one by one. In this way the surface will be reduced. Dry stems or *A. calcarea* from last year lying on the ground often are divided up into the individual internodes (field observations – P.W.).

Time scale. The investigated plants seem to show xeromorphic structures in most exomorphic and endomorphic characters. For plants living under arid conditions the selection pressure for such adaptations to xerophytism must be a strong one (cf. Stebbins 1952). In fact, since the subdeserts and deserts of SW and C Asia represent a geologically young habitat, one may draw the conclusion that the evolution in *Anabasis* and other groups of Chenopodiaceae characteristic of these areas has been a rather rapid one and that the groups in question are comparatively young.

Anatomy and taxonomy

Aellen (1950 p. 264) stated in his comments to the new genus *Esfandiaria* that it undoubtedly is close to *Anabasis*. Distinguishing morphological characters from the latter are the thick, terete internodes of stem, the cone-like inflorescences and the upright tip of the root of the embryo. These characters do not seem to have much value on the generic level except, possibly, the contracted inflorescence. The perianth segments, the wings of the fruiting perianth, the red, berry-like, glandular fruit with a vertical, coiled embryo are the same as found in *Anabasis* species. The genus *Esfandiaria* is better treated as a section of *Anabasis*, judged from the exomorphic characters.

One of the aims of this work has been to find new and neglected endomorphic characters of taxonomic value and correlate them with exomorphic ones. The anatomical characters of the investigated plants show much variety, hence we might have a fresh set of characters which could be used to supplement those commonly used in classification. However, most of these characters are clearly adaptive, showing different kinds of xeromorphic features and should thus be used with great care at the generic level.

The following anatomical characters distinguish *Anabasis calcarea* from the other investigated species of the genus: (1) A 4-layered abaxial leaf epidermis; (2) A many-layered stem epidermis; (3) Presence of obliquely orientated, deep stomatal canals in the stem; (4) Presence of brachysclereids in the pith and in the innermost region of the cortex; (5) A special type of wood in which irregularly orientated vascular bundles and concentric layers of wood parenchyma containing sand crystals are present.

To check the taxonomic value of these anatomical characters one should compare them with such characters that distinguish between the different investigated species of *Anabasis*.

A. annua differs anatomically from the 3 other species as follows: (1) Absence of hypodermis and chlorenchyma from the stem; (2) Epidermal cells very long in longitudinal section; (3) Extensive development of lignified fibrous tissue in the wood.

A. setifera could be distinguished on the following anatomical characters: (1) Presence of collenchymatous cells below ridges and grooves; (2) Discontinuation of hypodermis and chlorenchyma below ridges and grooves; (3) Absence of crystals from the pith; (4) Wood exhibiting alternate zones of wood and thin-walled parenchyma.

Anatomically *A. aphylla* and *A. eriopoda* are rather similar but the former could be distinguished from the latter by the following characters: (1) Single-layered adaxial leaf epidermis; (2) Presence of fibrous tissue below the main vascular bundle of the leaf; (3) Presence of radially elongated cells in the innermost zone of cortex; (4) Presence of narrow-lumened strands of cortical fibres.

The investigated species obviously show a great deal of diversity in their anatomical characters. The differences between *A. calcarea* and the rest of the *Anabasis* species may not be so much greater than between the latter *inter se*. The many-layered epidermis with the long stomatal canals being the most striking feature in *A. calcarea* seems to represent an extreme case of adaptation to xerophytism. In *A. annua* and *A. setifera* there is a 1-layered epidermis with stomata hardly sunken below the surface, whereas in *A. eriopoda* and *A. aphylla* the epidermis is 3-layered with stomatal cavities. Other species of *Anabasis* may have a thicker epidermis and represent intermediate stages in this adaptive trend.

Conclusions

The investigated species show a wide range of anatomical characters distinguishing between them. Many more species must be checked before the phylogenetical and taxonomical value of these characters can be established, e.g. whether they can be of any help in grouping the species into sections or other infrageneric taxa.

Many endomorphic structures are found that must be considered as adaptations to xerophytism, in addition to the exomorphic ones. The most remarkable structure found is the 8–11-layered, highly cutinised epidermis of *Anabasis (Esfandiaria) calcarea* with the stomata at the bottom of 200 μm deep, obliquely orientated canals. At the base of the internodes there is a zone of compressed parenchymatic cells that gradually become suberised. This zone is interpreted as an abscissal tissue which works in the way that internodes may be sealed off and then perhaps 'thrown off' to reduce the surface under periods of extreme drought. The woolly inside of the connate leaf bases protects the meristem situated near the base of the internodes.

The genus *Esfandiaria* should be merged with

Anabasis; however, it can be upheld as a section within this genus.

Anabasis sect. **Esfandiaria** (Charif & Aellen) Bokhari & Wendelbo comb. nov.

Basionym: *Esfandiaria* Charif & Aellen, Verhandl. Naturf. Gesellsch. Basel 63: 262 (1950). – Type species: *Anabasis calcarea* (Charif & Aellen) Bokhari & Wendelbo.

Stem and branches with a many-layered epidermis and stomata at bottom of deep, obliquely orientated canals. Leaves scale-like with a 4-layered abaxial 'epidermis. Inflorescences contracted, cone-like. Perianth segments winged in fruiting stage. Fruit glandular.

Anabasis calcarea (Charif & Aellen) Bokhari & Wendelbo comb. nov.

Basionym: *Esfandiaria calcarea* Charif & Aellen, Verhandl. Naturf. Gesellsch. Basel 63: 262 (1950).

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The genus Calceolaria in NW South America

II. The sections Chasmatochila, Thamnobia, Ericoides and Lehmannina

Ulf Molau

Molau, U. 1978 09 30: The genus Calceolaria in NW South America. II. The sections Chasmatochila, Thamnobia, Ericoides and Lehmannina. *Bot. Notiser 131:* 293–316. Stockholm. ISSN 0006-8195.

Four sections of *Calceolaria* (Scrophulariaceae) in NW South America are revised, viz. sect. *Chasmatochila* (1 species in the area), *Thamnobia* (10), *Ericoides* (2) and *Lehmannina* (1). They all possess narrow, sessile or shortly petiolate leaves. *C. adenanthera, C. odontophylla* and *C. crenata* Lam. subsp. *australis,* all in sect. *Thamnobia,* are described as new. Chromosome numbers are reported for *C. crenata* (2n = 36), *C. rosmarinifolia* Lam. (2n = 36), *C. hyssopifolia* H. B. K. (2n = 32), *C. helianthemoides* H. B. K. (2n = 36) and *C. ericoides* Vahl (2n = 36).

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Sect. 2. **Chasmatochila** Pennell

Pennell 1951 p. 98 – Type species: *Calceolaria martinezii* Kränzlin.

Perennial herbs or shrubs with lanceolate leaves. Lips of corolla spreading, the orifice completely open. Thecae ascending.

A single species of central Ecuador.

1. **Calceolaria martinezii** Kränzlin

Sodiro ex Kränzlin 1905 p. 105 – Orig. coll.: Martínez s.n. (B holotype, destroyed, photograph of type at F and PH).

Calceolaria patens Kränzlin 1907 a p. 103 – Orig. coll.: Spruce 5151 (K lectotype, BM, W).

Illustrations. Fig. 1; Kränzlin 1907 a p. 103 Fig. 20 (as *C. patens*).

Scandent *subshrub* with long internodes, 1–1.5 m high. Inflorescence and all vegetative parts covered with a dense, velvety buffish pubescence; hairs eglandular. *Leaves* 6–14 × 1.2–3.2 cm, lanceolate, acute, cuneate; above olivaceous, densely sericeous; beneath lighter, lanate; margins serrulate. Petioles 2–10 mm, sericeous. *Inflorescence* terminal, comprising 2 pairs of 6–20-flowered cymes on primary peduncles (1–)2–7 cm long. Cyme bracts rudimentary or absent. Pedicels up to 2 cm long, sericeous. *Sepals* 3–4.5 × 2–3 mm, ovate, slightly acuminate, mucronate, externally densely sericeous, internally glabrous. *Corolla* pale yellow or yellowish white, externally puberulous, internally with a villous tuft below the stamens, the lips widely spreading; upper lip 8–15 mm long and about as wide, ascending, slightly arched; lower lip 13–18 mm long and 10–15 mm wide, saccate only in about 1/3 of its length, pendent, exposing the orifice. *Anthers* 2.2–2.6 mm, light brown, opening throughout; thecae ascending, ± globose, equal. *Filaments* 1.5 mm. *Style* 2.8–4.0 mm, distally curved, *Capsule* ovoid-conical, 3–5 mm long, villous with gland-tipped hairs.

Habitat. Mountain scrub at altitudes between 2700 and 3000 m.

Distribution. Fig. 2. Endemic, known only from the province of Tungurahua, Andes of central Ecuador. A rare species, collected six times on the western slopes of Cordillera Oriental.

Remarks. C. martinezii is a unique taxon with no close relatives. In leaf morphology it shows similarities with sect. *Thamnobia,* but the flowers are quite different from those of the last-named section.

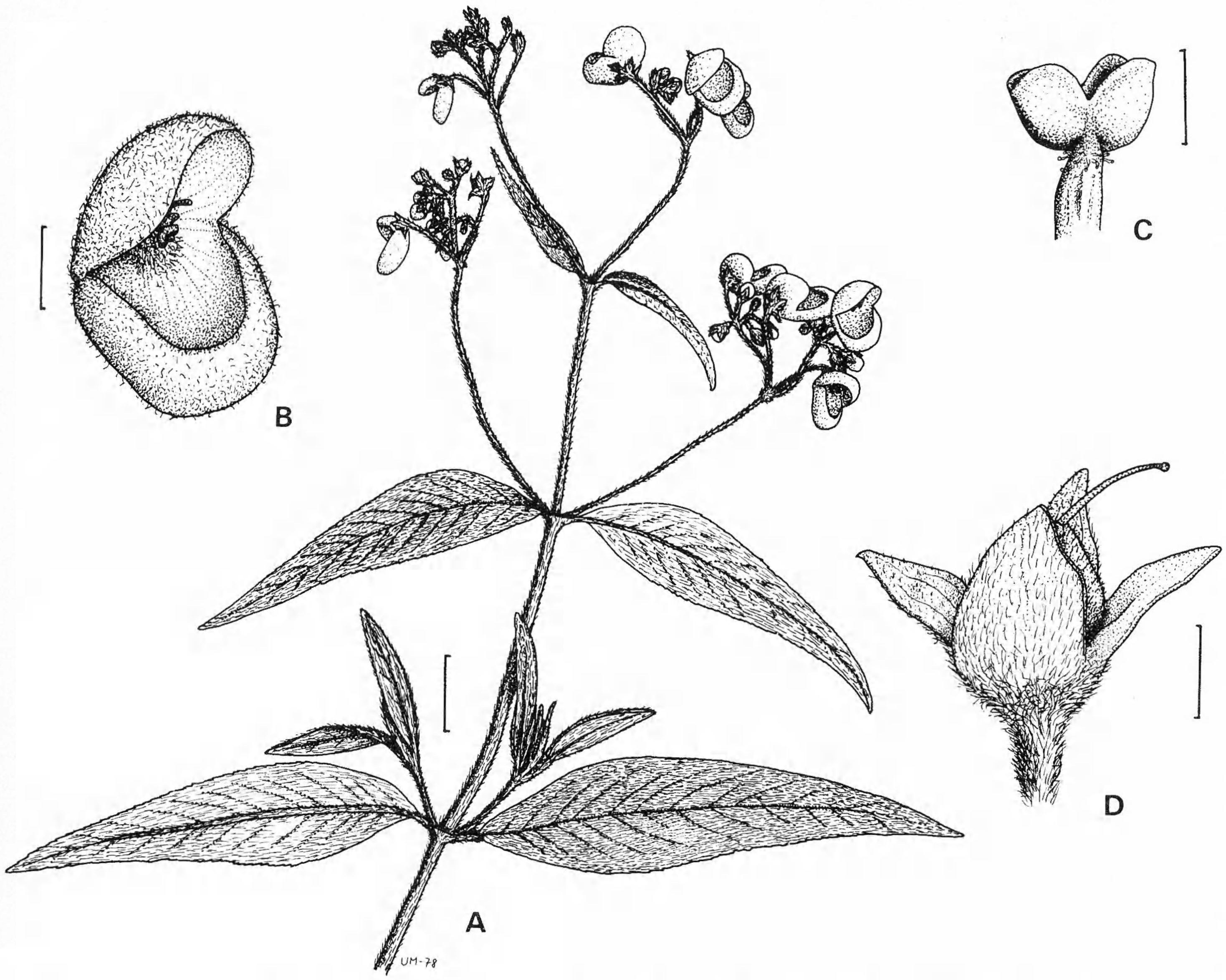

Fig. 1. *Calceolaria martinezii* (Asplund 8070) – A: Flowering branch. – B: Corolla. – C: Stamen. – D: Capsule. – All drawings made from herbarium material. – Scales: A 2 cm, B 5 mm, C 1 mm, D 2 mm.

C. patens is nothing but a small specimen of *C. martinezii*.

Specimens studied. Ecuador. Tungurahua: Between Leito and La Cima, Cordillera Oriental, 2700–3000 m, 15.XI.1944, Acosta-Solís 9032 (F) – Vicinity of Patate, Hacienda Leito, thicket, 2800 m, 5.VIII.1939, Asplund 8070 (S) – Río Loro near Guachi, S of Ambato, Martínez s.n. (B destroyed, photographs F, PH) – Cusatagua, vicinity of Ambato, III.1919, Pachano 185 (NY, US) – Sine loco 2830 m, Sodiro 115/16 (P) – In sylvis montis Tungurahua, 1800–2700 m, XI. 1857, Spruce 5151 (BM, K, W).

Sect. 3. **Thamnobia** Pennell

Pennell 1951 p. 99 – Type species: *Calceolaria rosmarinifolia* Lam.

Perennial herbs or subshrubs. Leaves narrow, usually lanceolate, herbaceous or coriaceous, sessile or short-petiolate; margins ± revolute. Corolla yellow, unspotted, internally with a villous tuft below the stamens; upper lip smaller than the lower one, hooded, concealing the anthers; lower lip projecting (upcurved in *C. hyssopifolia*), usually saccate in about half its length, the proximal part appressed against the upper lip and ± closing the orifice. Anthers 2–3 mm long, opening throughout or to connective; thecae divaricate or deflexed, elliptic, equal. Filaments shorter than the anthers.

Thamnobia is one of the most important sections of the genus in the northern Andes. It ranges from southern Colombia to Peru, but reaches its highest species diversity in Ecuador. A related group in southern Peru and Bolivia, sect. *Revolutae* Pennell, differs in having longer, exposed anthers and leaves incanous beneath. In Chile some species of sect. *Rugosae* Kränzlin resemble *Thamnobia* in growth habit, but differ in floral characters, such as very long filaments.

In all but two species of this section the anthers are opening throughout. In *C. helianthemoides* and *C. lavandulaefolia,* however, they are opening to the connective. These two species also possess fasciculate leaves, which is a similarity to sect. *Fasciculata*. However, all the basical characters of sect. *Thamnobia* are present, and the two species are most conveniently retained in this section.

Most species of sect. *Thamnobia* have very restricted distributions; some are endemic to a single valley or a couple of neighbouring mountains. They occur at altitudes between 2500 and 4500 m and are most frequently found in the lower páramo zone.

The tetraploid chromosome number 2n = 36 seems to be the ordinary one in this section. *C. hyssopifolia* has 2n = 32, reported twice independently.

As in all other sections treated in this series, leaf-shape terminology follows Stearn (1973). The term "lanceate" is used according to Baranov (1965).

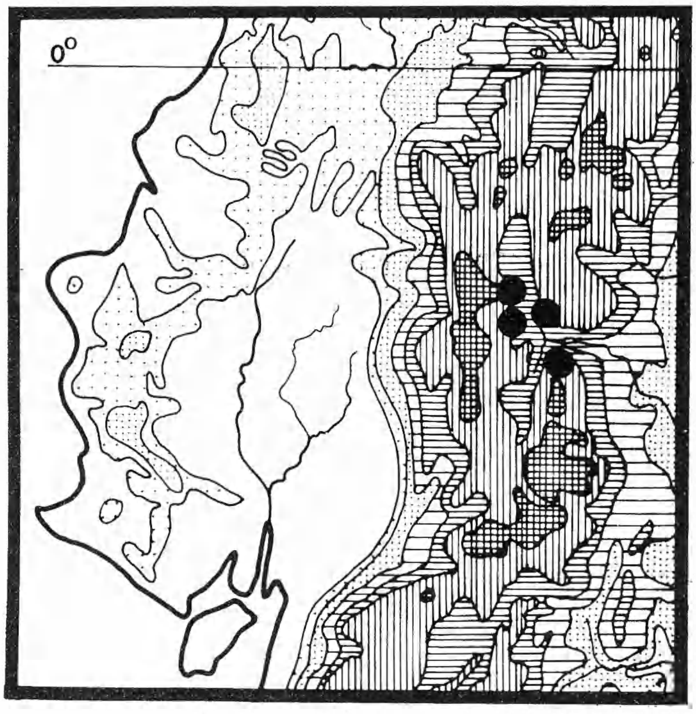

Fig. 2. Known distribution of *Calceolaria martinezii.*

Key to the species of sect. Thamnobia

1. Leaves clasping at base 2
– Leaves not clasping at base 5
2. Leaves herbaceous, beneath pilose–villous with gland-tipped hairs; margin plane or deflexed, crenate, serrate or dentate 3
– Leaves ± coriaceous, beneath lanate; margin revolute, apparently entire 4
3. Leaves cocktail-shaped (erecto-patent with deflexed apices), not jointed .... 1. *C. crenata*
– Leaves straight, slightly jointed across the nodes (sutures visible) .... 2. *C. odontophylla*
4. Leaves 6–12 cm long, olivaceous-lanate beneath; corolla entirely yellow .... 5. *C. spruceana*
– Leaves 3–5.3 cm long, white-lanate beneath; corolla yellow above, white beneath .... 4. *C. lavandulaefolia*
5. At least lower side of leaves lanate or villous 6
– The whole plant essentially glabrous 9
6. Leaves elliptic, loosely yellowish arachnoid-lanate beneath .... 7. *C. gossypina*
– Leaves lanceolate, greenish or ferrugineous-lanate with coarse hairs beneath 7
7. Pedicels glabrous or puberulous; thecae divaricate .... 4. *C. rosmarinifolia*
– Pedicels appressed hirsute; thecae deflexed 8
8. Leaves lanceolate, 5–8 cm long, petiolate .... 3. *C. adenanthera*
– Leaves narrowly lanceolate or linear, 3–5 cm long, sessile .... 6. *C. ferruginea*
9. Leaves lanceolate; sepals glabrous; anthers opening throughout .... 8. *C. hyssopifolia*
– Leaves elliptic, fasciculate; sepals internally puberulous; anthers opening to connective .... 9. *C. helianthemoides*

1. **Calceolaria crenata** Lam.

Herb or *subshrub* 0.4–1.2 m high, lower parts of stems covered with deflexed, persistent, dead leaves. Pedicels, peduncles and distal parts of stems villous with spreading gland-tipped hairs. *Leaves* 3.0–14.0 × 1.0–5.0 cm, narrowly ovate or lanceate, cocktail-shaped (erecto-patent with apices and margins deflexed), acute or obtuse, sessile, basally cordate and clasping; above hirsute or pilose with mostly gland-tipped hairs; below reticulate-venose, loosely villous or pilose; margins crenate, often with mucronulate teeth. *Inflorescence* terminal, comprising 1–3 pairs of 6–34-flowered cymes on primary peduncles 1.2–12.5 cm long. Cyme bracts sometimes present in the lower cymes. Primary pedicels 1.0–2.8 cm, subordinate pedicels shorter. *Sepals* 2.8–5.3 × 1.9–3.5 mm at anthesis, later on slightly enlarged, light green, ovate or narrowly ovate, acuminate; externally hirsute or pilose with coarse, gland-tipped hairs; internally glabrous or finely puberulous distally. *Corolla* bright yellow, externally finely puberulous with gland-tipped hairs, at least around the orifice; upper lip 3–5 mm long and somewhat wider than long; lower lip 12–24 mm long and 8–15 mm wide, saccate in 1/3–1/2 of its length. *Anthers* 1.5–3.2 mm, brownish or buffish, opening throughout; thecae divaricate or slightly deflexed. *Filaments* 0.8–1.3 mm. *Style* 1.3–3.8 mm, curved. *Ovary* glandular-pubescent. *Capsule* ovoid, 4–7 mm long, finely tomentose with spreading gland-tipped hairs.

Habitat. Mountain scrub and páramo, at altitudes between 2550 and 4000 m.

Remarks. *C. crenata* is the most widely distributed species of sect. *Thamnobia*. It is a common páramo plant in northern Ecuador and southernmost Colombia. It is morphologically very variable. Specimens from Colombia have less pubescent foliage, smaller corollas, more deflexed thecae and shorter styles than specimens from Ecuador. Penell (1951) recognized the Colombian specimens as a distinct species, *C. colombiana* Pennell. Now, when more material from the "border area" has accumulated, it is obvious that all specimens belong to the same taxon, representing a cline rather than a series of discrete subspecies. The geographically isolated population in the province of Azuay in southern Ecuador is, however, distinct in some characters and hence recognized as a different subspecies, subsp. *australis*.

Key to the subspecies

1. Leaves above green or dark green, plane or slightly rugose .... 1 A. ssp. *crenata*
– Leaves above light green or yellowish green, deeply reticulate-rugose .... 1 B. ssp. *australis*

1 A. **Calceolaria crenata** subsp. **crenata**

Calceolaria crenata Lamarck 1785 p. 556 – *Fagelia crenata* (Lam.) Kuntze 1891 p. 459 – Orig. coll.: Jussieu s.n. (P holotype).

Calceolaria amplexicaulis Humboldt, Bonpland & Kunth 1818 p. 384 – *Fagelia amplexicaulis* (H. B. K.) Kuntze 1891 p. 459 – Orig. coll.: Bonpland 3019 (B-WILLD holotype, F fragment).

Calceolaria floribunda Humboldt, Bonpland & Kunth 1818 p. 385 – *Calceolaria paniculata* Willd. ex Link 1820 p. 55 – Orig. coll.: Bonpland s.n. (B-WILLD lectotype, F fragment, P).

Calceolaria fallax Kränzlin 1907 b p. 194 – Orig. coll.: Jameson 71 (W holotype).

Calceolaria colombiana Pennell 1951 p. 110 – Orig. coll.: Olsson 5 (PH holotype, BM, F, US).

Illustrations. Fig. 3 A–D; Humboldt, Bonpland & Kunth 1818 Tab. 171 (as *C. amplexicaulis*); Pennell 1951 p. 104 Fig. 4 (as *C. colombiana*).

Leaves (4.0–)4.5–11.0(–14.0) × 1.4–3.5(–5.0) cm, above green or dark green, plane or slightly rugose. *Sepals* 2.8–5.3 × 2.0–3.5 mm, mucronate. *Corolla* as in the previous description. *Anthers* 2.0–3.2 mm. *Style* 1.3–3.8 mm.

Chromosome number. 2n = 36. – Voucher: Harling et al. (leg. Molau) 14845 (GB). – The same chromosome count has previously been reported by Srinath (1939 p. 106).

Distribution. Fig. 4. Ranging from the province of Tungurahua, central Ecuador, to the department of Cauca in southern Colombia, at altitudes between 2550 and 4000 m. *C. crenata* ssp. *crenata* is one of the most frequently collected taxa of the genus in the investigated area. In all, 204 specimens from 129 collections have been studied.

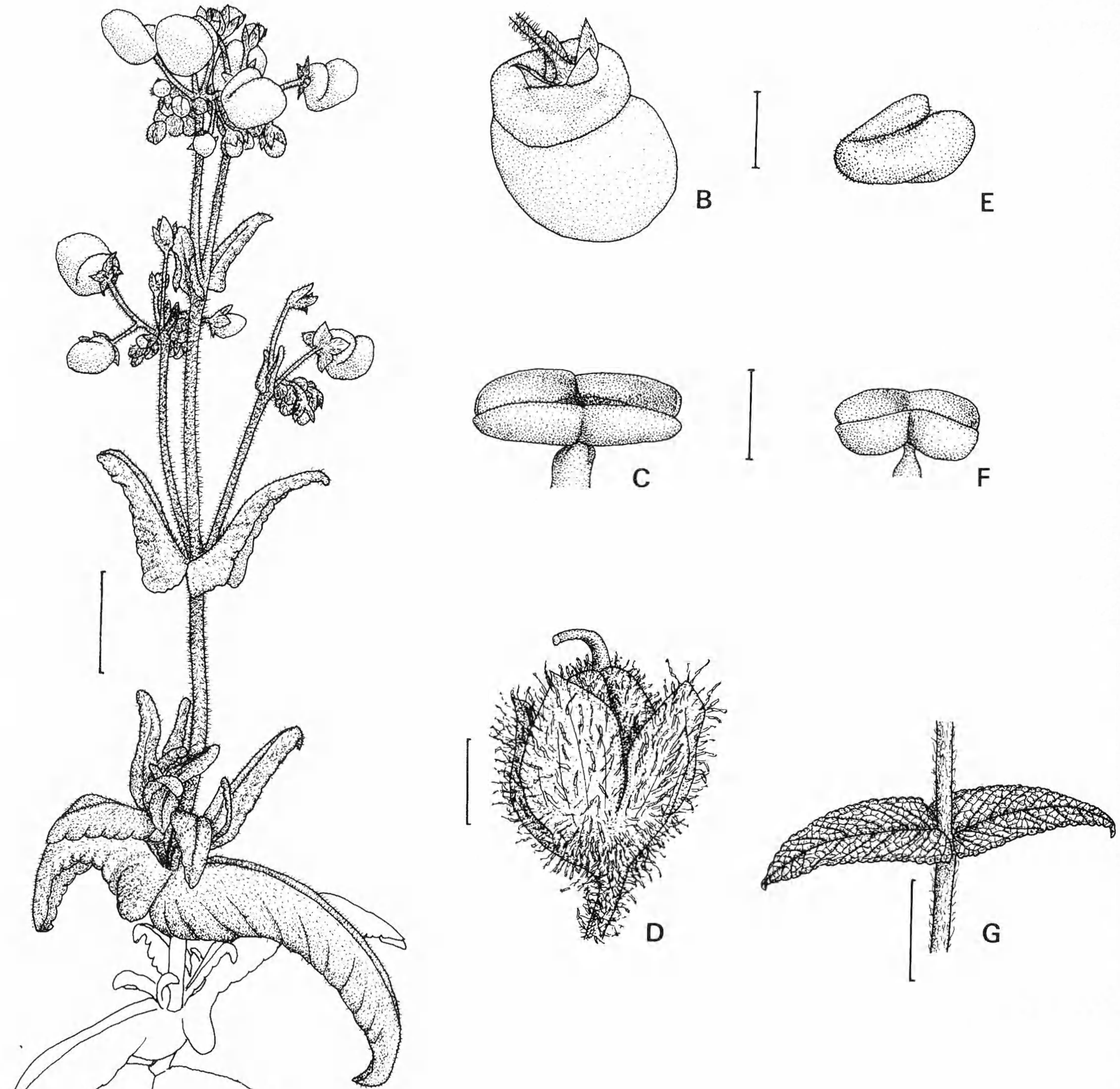

Fig. 3. *Calceolaria crenata*. – A–D: ssp. *crenata*. – A: Habit. – B: Corolla. – C: Stamen. – D: Capsule. – A–C leg. Molau; Harling et al. 14845, D Holm-Nielsen et al. 5165. – E–G: ssp. *australis*. – E: Corolla. – F: Stamen. – G: Leaves. – E, F leg. Molau; Harling et al. 15089, G Harling & Andersson 14482. – A drawn from photograph; B, C, E, F drawn from fixed material; D, G drawn from herbarium material. – Scales: A, G 2 cm, B, E 5 mm, C, F 1 mm, D 2 mm.

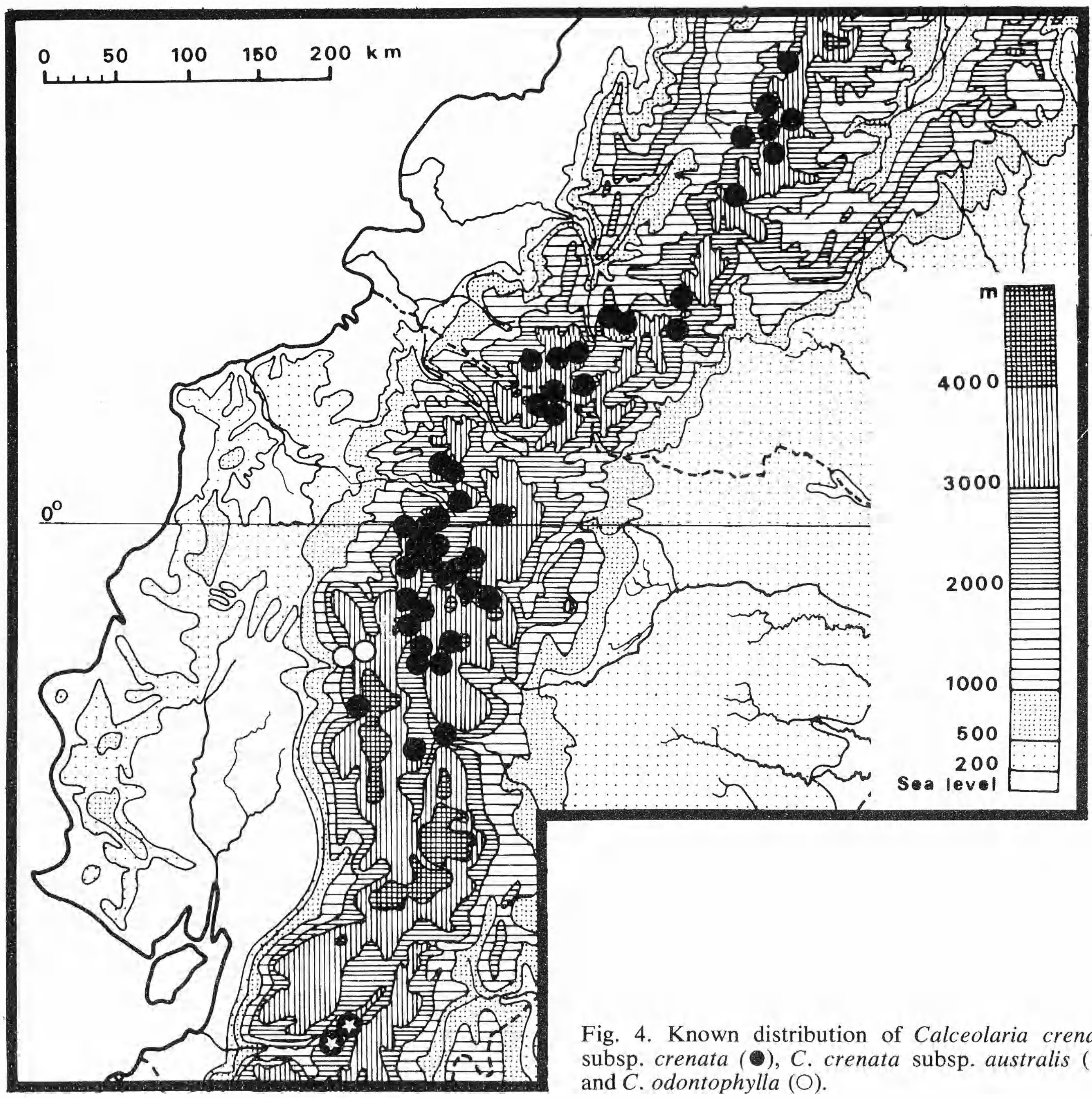

Fig. 4. Known distribution of *Calceolaria crenata* subsp. *crenata* (●), *C. crenata* subsp. *australis* (✪) and *C. odontophylla* (○).

*Remarks.*As did Pennell (1951), I consider *C. amplexicaulis* and *C. floribunda* to be synonymous with *C. crenata,* differing from the type of the latter only in minor characters quite within the variability of this taxon.

C. fallax Kränzlin was based upon a small specimen, quite within the variability of the subspecies now concerned. Pennell (1951) applied this name on a species of sect. *Dermatophylla,* a mistake that is remarkable as he obviously had in his possession a good photograph of the type specimen.

Representative specimens. Colombia. Cauca: Páramo de Las Delicias, Central Andes of Popayán, 3000–3500 m, Lehmann 4480 (GH, K, S, US) – Valle de Las Papas, 2900 m, 5.IV.1944, Olsson 5 (BM, F, PH, US). –*Nariño:* Cumbal, grassland, 3500 m, 11.II.1941, von Sneidern s.n. (S) – Tuquerres, 3000 m, Triana 2330 (G, NY, P, W). –*Putumayo:* Páramo de San Antonio, road from Pasto to Sibundoy, 2850–2930 m, 13.III.1953, Schultes & Cabrera 18905 (GH, U). – *Ecuador. Carchi:* Road Tulcán–San Gabriel, ca 20 km S of Tulcán, 3000–3100 m, 22.II.1974, Harling & Andersson 12035 (GB) – Wooded hills about 8 km S of Tulcán, 10.VIII.1923, Hitchcock 20961 (GH, NY, PH, US). – *Imbabura:* Laguna Cuicocha, crater lake 30 km W of Ibarra, 3100 m, 24.V.1973, Holm-Nielsen et al. 6327

(AAU, GB, MO) – Road Cotacachi–Apuela, 21 km from Cotacachi (Intac valley), 3300 m, 11.VIII.1976, Øllgaard & Balslev 8686 (AAU). – *Pichincha:* Cantón Quito, trail Nono–San Francisco, 3000 m, 14.IX.1935, Mexía 7690 (BM, GB, K, MO, PH, S, U, UC) – E slopes of Cerro Pichincha, 3000–4000 m, 26.I.1977, leg. Molau; Harling et al. 14845 (GB). – *Napo:* Volcán Antisana, 3200 m, 16.III.1953, Prescott 985 (NY). – *Cotopaxi:* Páramo de Cotopaxi, Latacunga to Machachi, 3000 m, 13.VII.1939, Balls 7217 (E, F, K, PH, UC). – *Tungurahua:* Near Mocha, 19.IV.1945, Camp E-2414 (PH). – *Bolívar:* Hacienda Talahua, 3300 m, 29.IV.1939, Penland 568 (F, PH).

1 B. **Calceolaria crenata** subsp. **australis** Molau subsp. nov.

Orig. coll.: Harling & Andersson 14482 (GB holotype).

Illustration. Fig. 3 E–G.

Differt a subspecie crenata foliis clarius virentibus vel etiam flavescentibus, valide rugosis, 3.0–5.5 cm longis, 1.0–1,9 cm latis; corolla et antheris minoribus, stylo 1.4–1.7 mm.

Leaves 3.0–5.5 × 1.0–1.9 cm, above bright yellowish green and deeply reticulate-rugose. *Sepals* 4.0–5.2 × 1.9–2.2 mm, not mucronate. Upper lip of *corolla* 3–5 mm long and wide; lower lip 12–18 mm long and 8–12 mm wide. *Anthers* 1.5–2.3 mm. *Style* 1.4–1.7 mm.

Distribution. Fig. 4. Endemic, restricted to Páramo de Tinajillas in the southern part of the province of Azuay, Ecuador, at altitudes of 2900–3400 m.

Specimens studied. Ecuador. Azuay: 20 km N of Oña, 2900 m, 4.VIII. 1959, Harling 6265 (S) – Southern parts of Páramo de Tinajillas, 3200 m, 9.V.1974, Harling & Andersson 14482 (GB) – Km 91 on Pan American Highway N of Loja, 79°10'W 3°25'S, 2900 m, 5.V.1973, Holm-Nielsen et al. 5056 (AAU,GB, MO) – Páramo de Tinajillas, km 68 from Cuenca, 3400 m, 6.II.1977, leg. Molau; Harling et al. 15089 (GB).

Calceolaria crenata subsp. **crenata** × **hyssopifolia**

Calceolaria quitoënsis Pennell 1951 p. 105 – Orig. coll.: Jameson 32 (NY holotype).

This hybrid arises sporadically in the province of Pichincha, northern Ecuador, where the two parental species are common and flower at the same time. It is intermediate in shape of leaves and sepals as well as in vesture. Pollen grains are irregular and unequal in size and no seeds are produced. Pennell (1951) dicussed the intermediate characters of Jameson 32 in a footnote under *C. crenata*. In the same paper, however, it was made the type specimen of a new species.

Specimens studied. Ecuador. Pichincha: Environs of Quito, rare, IV.1858, Jameson 32 (NY) – Above Quito, 2750 m, Jameson 165 (BM, E, G, K, P, PH). – *Sine loco:* Fraser s.n. (BM).

2. **Calceolaria odontophylla** Molau sp. nov.

Orig. coll.: Harling 4916 (S holotype).

Illustration. Fig. 5 A–B.

Frutex scandens, tota planta valide glutinosa. Caules glabri. Folia 5.0–7.7 cm longa, 1.7–2.3 cm lata, lanceata, ad basin cordata et admodum connata; supra vivide viridia, glabra; infra viridia, reticulato-venosa, nervis pilosis vel hispidis, pilis glanduliferis, ceterum glabra; margine aequaliter serrato dentibus mucronulatis. Inflorescentia terminalis, 2–3 paria cymarum 8–20 florum complectens; pedunculis primariis 1.7–6.5 cm longis. Bracteae cymarum adsunt, saltem in cymis inferioribus. Pedicelli 0.9–1.7 cm longi, puberulosi et glandulosi. Sepala 3.2–3.3 mm longa, 2.0–2.6 mm lata, triangularia, leviter acuminata; extra glabra, glutinosa; intus papillosa; margine breviter ciliato. Corolla flava, labio superiore 5–8 mm longo, 7–11 mm lato, arcuato; labio inferiore 10–17 mm longo, 10–16 mm lato, media fere longitudine saccato. Antherae 2.7–3.0 mm longae, fuscae, totae dehiscentes, inferiore parte subtiliter glandoso-papillosae; thecae leviter deflexae. Filamenta 1.5–2.2 mm longa, glanduloso-puberulosa. Stylus 3.1–4.0 mm longus, paene rectus. Ovarium dense puberulosum, pilis glanduliferis. Capsulam maturam non vidi.

Scandent *subshrub,* at least 0.5–1 m high; the whole plant strongly glutinose. Stems glabrous, woody below. *Leaves* 5.0–7.7 × 1.7–2.3 cm, lanceate, cordate and somewhat connate at base (connate part 2–3 mm wide on each side of node; suture between the jointed leaf-bases visible, at least beneath); above bright green, glabrous; beneath green, reticulate-venose, nerves pilose or hispid with gland-tipped hairs, tissue glabrous; margins regularly serrate with mucronulate teeth. *Inflorescence* terminal, comprising 2–3 pairs of 8–20-flowered cymes on primary peduncles 1.7–6.5 cm long. Cyme-bracts present, at least in the lower cymes. Pedicels 0.9–1.7 cm, puberulous and glandular. *Sepals* 3.2–3.3 × 2.0–2.6 mm at anthesis, triangular, slightly acuminate; externally glabrous, glutinous; internally papillose; the margin shortly ciliate. *Corolla* bright yellow, externally glandular-puberulous, at least around the orifice; upper lip 5–8 mm long and 7–11 mm wide, arched; lower lip 10–17 mm long and 10–16 mm wide, saccate in about 1/2 of its length; the orifice partially exposed. *Anthers* 2.7–3.0 mm, dark brown, opening throughout, beneath finely glandular-papillose; thecae slightly deflexed. *Filaments* 1.5–2.2 mm, glandular-puberulous. *Style* 3.1–4.0 mm, nearly straight. *Ovary* densely puberulous with gland-tipped hairs. Mature *capsule* not seen.

Habitat. Rocky places and shrubby slopes in cloud forest at altitudes between 2500 and 3300 m.

Distribution. Fig. 4. Endemic, restricted to the surroundings of Pilaló, western slopes of Cordillera Occidental in the province of Cotopaxi, Ecuador.

Remarks. C. odontophylla is easily recognized by the unusual foliage and relatively long filaments. It is most closely related to *C. crenata,* even if it in some aspects resembles *C. semiconnata* Pennell of sect. *Symplocophylla.* The species of the latter section, however, have coriaceous and more truly connate leaves.

Specimens studied. Ecuador. Cotopaxi: Pilaló, 2500–3000 m, 1–3.V.1959, Harling 4916 (S) – Quevedo-Latacunga road, above Pilaló, 78°56′W 0°58′S, 3200–3300 m, 8.IV.1973, Holm-Nielsen et al. 3277 (AAU, GB, MO).

3. **Calceolaria adenanthera** Molau sp. nov.

Orig. coll.: Asplund 9982 (S holotype).

Illustration. Fig. 5 C–E.

Frutex scandens, internodiis pro ratione longis. Folia 5.0–8.0 cm longa, 1.2–1.5 cm lata, lanceolata, acuta, ad basin cuneata, petiolata; supra chlorascentia, pilosa; infra laxe lanata vel villosa, saltem in nervis, pilis subfulvis, reticulato-venosa, textura pallide viridi; margine denticulato, revoluto. Petioli hirsuti, 3–6 mm longi. Inflorescentia terminalis, 2 paria cymarum 4–8 florum complectens, pedunculis primariis strigosis, 1.8–4.8 cm longis. Bracteae cymarum desunt. Pedicelli hirsuti, 1.0–2.3 cm longi. Sepala ovata, 2.0–3.5 mm longa, 1.6–2.3 mm lata, viridia, mucronata; extra tomentosa, intus puberulosa; margine ciliato. Corolla vitellina, extra puberulosa, pilis glanduliferis; labio superiore 4–6 mm longo, 5–7 mm lato, arcuato; labio inferiore 10–16 mm longo, 9–13 mm lato, ad tertiam partem longitudinis saccato. Antherae fulvae, 2.0–2.3 mm longae, totae dehiscentes, superficie papillosa, glandulis sessilibus vel in brevibus stipitibus sitis; thecae deflexae, singulae ca 1.5 mm longae. Filamenta 1.0–1.2 longa, glandoso-puberulosa. Ovaria dense pubescentia, pilis glanduliferis. Stylus paene rectus, 3.0–4.6 mm longus. Capsulam non vidi.

Scandent *subshrub* with relatively long internodes; stems at least 0.5–1 m long, pilose. *Leaves* petiolate, lanceolate, 5.0–8.0 × 1.2–1.5 cm, acute, cuneate at base; above dull green, pilose; beneath loosely buffish lanate or villous, at least on the nerves, reticulate-venose, tissue pale green; margins denticulate, revolute. Petioles buffish hirsute, 3–6 mm. *Inflorescence* terminal, comprising 2 pairs of 4–8-flowered cymes on strigose primary peduncles 1.8–4.8 cm long. Cyme bracts lacking. Pedicels buffish hirsute, 1.0–2.3 cm. *Sepals* ovate, 2.0–3.5 × 1.6–2.3 mm, green, mucronate; externally tomentose, internally puberulous; margin ciliate. *Corolla* deep yellow, externally puberulous with gland-tipped hairs; upper lip 4–6 mm long and 5–7 mm wide, arched; lower lip 10–16 mm long and 9–13 mm wide, saccate in 1/3 of its length. *Anthers* yellowish brown, 2.0–2.3 mm, surface papillose with sessile or short-stalked glands, opening throughout; thecae deflexed, each one ca 1.5 mm long. *Filaments* 1.0–1.2 mm, glandular-puberulous. *Ovary* densely pubescent with gland-tipped hairs. *Style* nearly straight, 3.0–4.6 mm. *Capsule* not seen.

Habitat. Mountain scrub at altitudes between 3000 and 3750 m.

Distribution. Fig. 6. Restricted to the eastern slopes of Cordillera Oriental in the provinces of Tungurahua and Chimborazo, central Ecuador. Only two collections known.

Remarks. C. adenanthera is most closely related to *C. rosmarinifolia* and *C. ferruginea* but differs in several conspicuous characters, such as the distinctly petiolate leaves, the long styles and the glandular anthers (whence name).

Very little is collected in the inaccessible parts of the high Andes where *C. adenanthera* grows. It is not unlikely that it occurs more regularly in the present area than indicated by the two known collections.

Specimens studied. Ecuador. Tungurahua: Cordillera de Llanganates, near junction of Río Golpe and Río Sangarinas (Desaguadero), 3000–3500 m, 26.XI.1939, Asplund 9982 (S). – *Chimborazo:* Páramo de Pinllillic, E of Alao, 3750 m, 14.III.1944, Acosta-Solís 7705 (F).

4. **Calceolaria rosmarinifolia** Lam.

Lamarck 1785 p. 556 – *Fagelia rosmarinifolia* (Lam.) Kuntze 1891 p. 460 – Orig. coll.: Jussieu s.n. (P holotype, C).

Calceolaria graminifolia Humboldt, Bonpland & Kunth 1818 p. 386 – *Fagelia graminifolia* (H. B. K.) Kuntze 1891 p. 459 – *Calceolaria bifida* Willd. ex Link

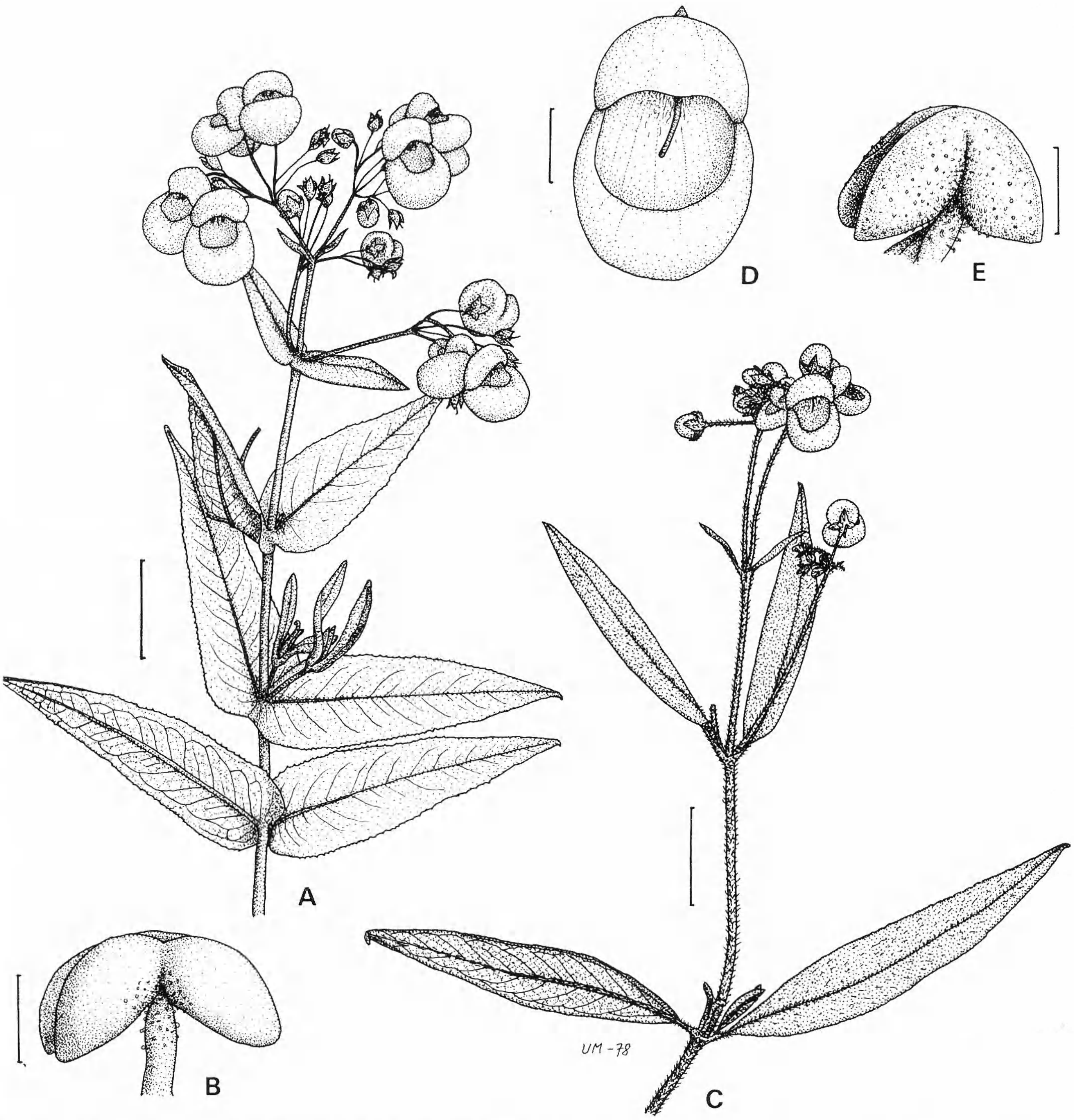

Fig. 5. A–B: *Calceolaria odontophylla* (Harling 4916). – A: Flowering branch. – B: Stamen. –C–E: *C. adenanthera* (Asplund 9982). – C: Flowering branch. – D: Corolla. – E: Stamen. – All drawings made from herbarium material. – Scales: A, C 2 cm, B, E 1 mm, D 5 mm.

1820 p. 53 – Orig. coll.: Bonpland 3284 (P lectotype, B-WILLD, F fragment).

Calceolaria hartwegii Bentham 1844 p. 147 – *Fagelia hartwegii* (Bentham) Kuntze 1891 p. 460 – Orig. coll.: Hartweg 822 (K holotype, BM, CGE, E, G, LD, LE, NY, OXF, P, W).

Calceolaria henrici Hooker 1869 Tab. 5772 – Orig. coll.: Anderson Henry s.n. cultivated in Scotland, propagated from seeds received from Jameson, Quito (K holotype).

Calceolaria stenophylla Kränzlin 1907 b p. 193 – Orig. coll.: Jameson s.n. (W holotype, S).

Illustrations. Fig. 7; Hooker 1869 Tab. 5772 (as *C. henrici*).

Scandent *subshrub,* 0.5–3 m long; stems glabrous; the whole plant strongly glutinous. *Leaves* sessile, narrowly lanceolate, (4.5–)6.0–12.0 (–14.5) × (0.4–)0.7–1.8 cm, acute, cuneate at base; above green, glabrous, ± rugose; below loosely greenish-lanate or -villous with long flexuose gland-tipped hairs; margins denticulate,

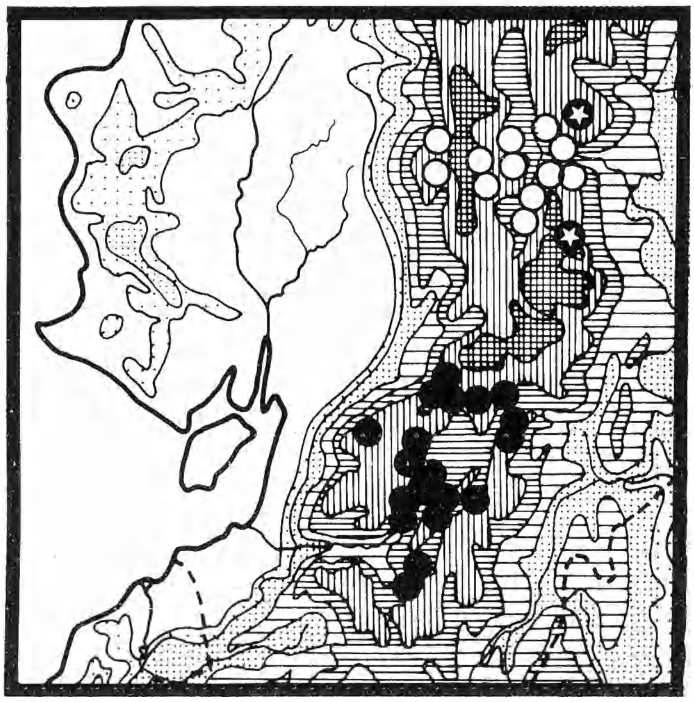

Fig. 6. Known distribution of *Calceolaria adenanthera* (✪), *C. rosmarinifolia* (●) and *C. spruceana* (○).

revolute. *Inflorescence* terminal, comprising 2–4 pairs of 4–14-flowered cymes on glabrous or puberulous primary peduncles 0.8–7.0 cm long (the uppermost shortest). Cyme bracts lacking. Pedicels 0.8–2.5 cm, glabrous or puberulous, glandular. *Sepals* triangular or ovate, 2.0–3.5 (–4.5) × 1.8–3.5(–4.5) mm, acute, glabrous, glandular. *Corolla* bright yellow; upper lip 4–6 mm long and 7–10 mm wide, hooded; lower lip 12–18 mm long and 9–14 mm wide, saccate in 1/2 of its length, inflated, its proximal part appressed against the upper lip. *Anthers* buffish, 2.0–3.0 mm, opening throughout; thecae divaricate. *Filaments* 0.8–1.0 mm. *Ovary* glandular-puberulous. *Style* 1.5–2.3 mm, curved. *Capsule* ovoid or conical, 4–6 mm long, glandular-puberulous.

Chromosome number. 2n = 36. – Voucher: Harling et al. (leg. Molau) 14969 (GB).

Habitat. Mountain scrub and open bushy slopes at altitudes between 2500 and 3600 m.

Distribution. Fig. 6. Restricted to southern Ecuador. Probably the most abundant *Calceolaria* species in the provinces of Cañar and Azuay. Outside that area only known from one collection from the adjacent part of the province of Loja. In all, 94 specimens from 39 collections have been studied.

Remarks. C. rosmarinifolia is most closely related to *C. spruceana, C. ferruginea* and *C. adenanthera* of central Ecuador; in foliage it also resembles *C. ludens* Kränzlin from southern Peru.

C. graminifolia, C. hartwegii, C. henrici and *C. stenophylla* were correctly considered synonymous to *C. rosmarinifolia* by Pennell (1951).

Representative specimens. Ecuador. Cañar: Páramo between Biblián and Cañar, 3350–3600 m, 18.IX.1944, Camp E-438 (NY, PH) – Taday–Pindilig, ca 2800 m, 4.IV.1974, Harling & Andersson 13169 (GB) – Above El Tambo, 3300 m, 29.VII.1962, Játiva & Epling 249 (GH, S, U, UC, US). – *Azuay:* 1–8 km N of Sevilla de Oro, 2500–2750 m, VII.–VIII.1945, Camp E-4550 (F, G, K, MO, NY, P, PH, U, UC) – Road Cuenca–Loja, ca 20 km S of Cumbe, 3000–3200 m, 19.III.1974, Harling & Andersson 12668 (GB) – Portete de Tarqui, road Cuenca–Girón, 2700 m, 3.II.1977, leg. Molau; Harling et al. 14969 (GB). – *Loja:* Mountains of Saraguro, Hartweg 822 (BM, E, G, K, LD, NY, OXF, P, W).

5. **Calceolaria spruceana** Kränzlin

Kränzlin 1907 a p. 104 – Orig. coll.: Spruce 6081 (K lectotype, W).

Calceolaria rosmarinifolia var. bonplandii Diels 1937 p. 142 – Orig. coll.: Bonpland 3145 (B-WILLD lectotype, F fragment, P).

Illustration. Fig. 8 D–F.

Scandent *subshrub,* 1–3 m long, the whole plant glutinous. *Leaves* 6.0–9.5(–12.0) × 1.0–2.0(–3.0) cm, sessile, lanceolate, acute, cordate and clasping at base; above dark green, rugose, ± glabrous; beneath densely light olivaceous lanate; margins revolute, denticulate but apparently entire. *Inflorescence* terminal, comprising (2–)3–4 pairs of 6–20-flowered cymes on tomentose primary peduncles 2.0–9.5 cm long (the uppermost shortest). Cyme bracts usually lacking. Pedicels tomentose, 0.3–1.8(–2.8) cm. *Sepals* 3.0–5.2 × 1.5–3.5 mm, triangular or ovate, acute or acuminate, slightly mucronate; externally puberulous or tomentose; internally glabrous. *Corolla* light yellow, externally puberulous; upper lip 4–8 mm long and about as wide, arched; lower lip 8–16 mm long and 6–12 mm wide, saccate in 2/5–1/2 of its length. *Anthers* light brown, 1.8–2.7 mm, opening throughout; thecae divaricate. *Filaments* 1.0–1.4 mm. *Style* ± straight, 2.0–3.2 mm. *Ovary* tomentose. *Capsule* conical, 4–6 mm long, villous.

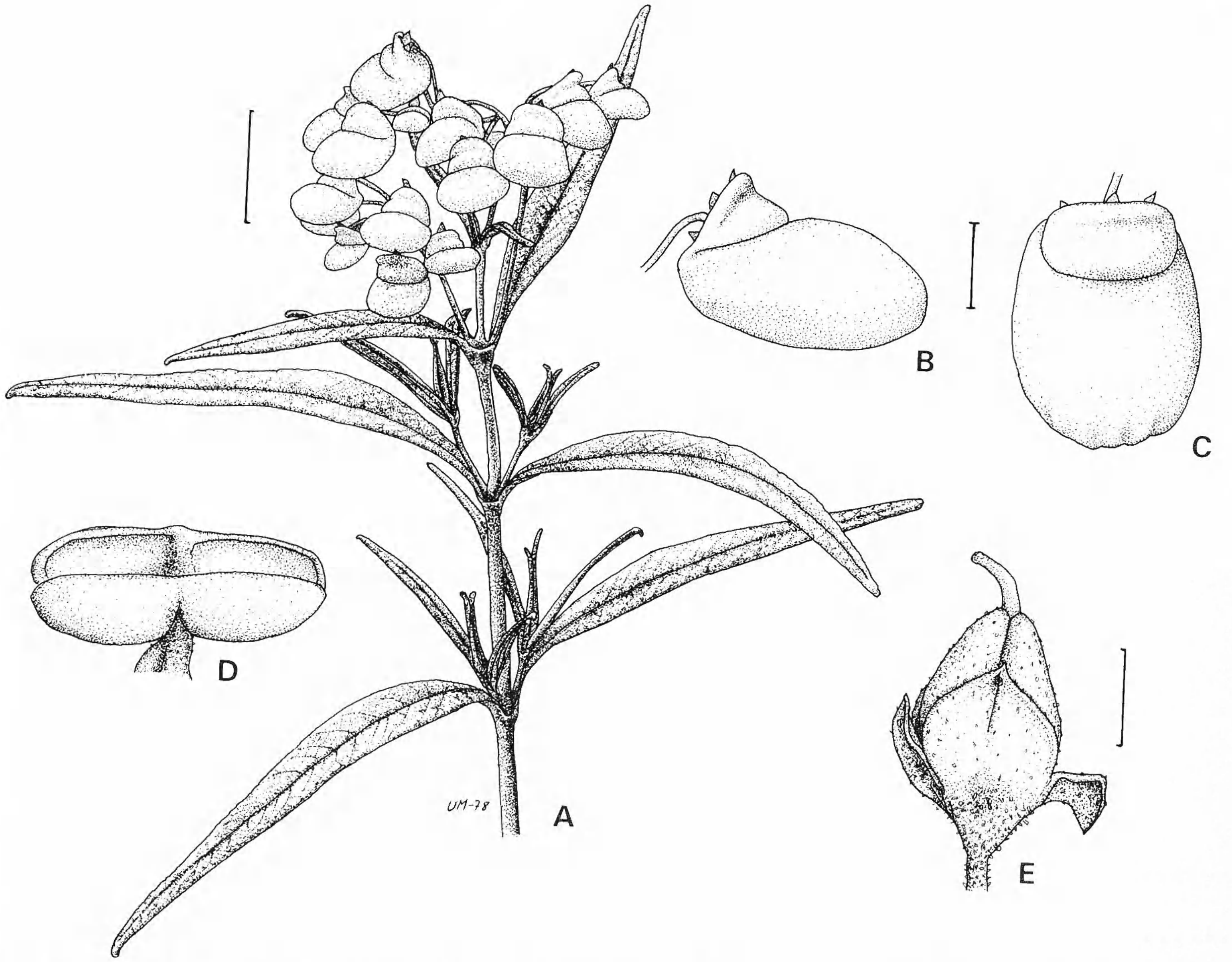

Fig. 7. *Calceolaria rosmarinifolia*. – A: Flowering branch. – B, C: Corolla. – D: Stamen. – E: Capsule. – A–D leg. Molau; Harling et al. 14969, E Harling & Andersson 13245. – A drawn from photograph, B–D drawn from fixed material, E drawn from herbarium material. – Scales: A 2 cm, B, C 5 mm, D 1 mm, E 2 mm.

Habitat. Scrub at altitudes between 1500 and 3300 m, often found in margins of forests near streams and pastures.

Distribution. Fig. 6. Restricted to the interandine basin of central Ecuador in the provinces of Tungurahua, Bolívar and Chimborazo, but abundant in many places within that area. In all, 48 specimens from 26 collections have been studied.

Remarks. This species was erroneously referred to by Pennell (1951) as *C. ferruginea* Cav. The type specimen of the latter (which Pennell evidently never saw), preserved at the Madrid herbarium, confirms that *C. ferruginea* Cav. is conspecific with *C. ledifolia* Pennell, not with *C. spruceana*.

The type specimen of *C. rosmarinifolia* var. *bonplandii* is a quite normal specimen of the species now concerned.

Representative specimens. Ecuador. Tungurahua: Between Leito and La Cima, Cordillera Oriental, 2700–3000 m, 15.XI.1944, Acosta-Solís 8990 (F); 8999 (F) – Vicinity of Patate, Hacienda Leito, 2650 m, 2.VIII.1939, Asplund 8009 (G, K, LD, P, S, UPS, US) –Mocha, near Ambato, ca 3000 m, VII.1939, Sandeman 20 (BM, K); 68 (BM, K). – *Chimborazo:* Ca 3–4 km from Puela, 10.X.1968, Lugo 560 (GB) – Between San Andrés and Quatro Esquinas, X.1952, Fagerlind & Wibom 871 (S) – East of Riobamba, 3200 m, 21.III.1934, Schimpff 876 (G, M, MO, Z). – *Bolívar:* Hacienda Talahua, 3200 m, 3.V. 1939, Penland 624 (GH, PH); 2000 m, 5.V.1939, Penland 661 (F, GH, PH).

6. **Calceolaria ferruginea** Cav.

Cavanilles 1799 p. 27 – *Fagelia ferruginea* (Cav.) Kuntze 1891 p. 459 – Orig. coll.: Nee s.n. (MA holotype, MPU).

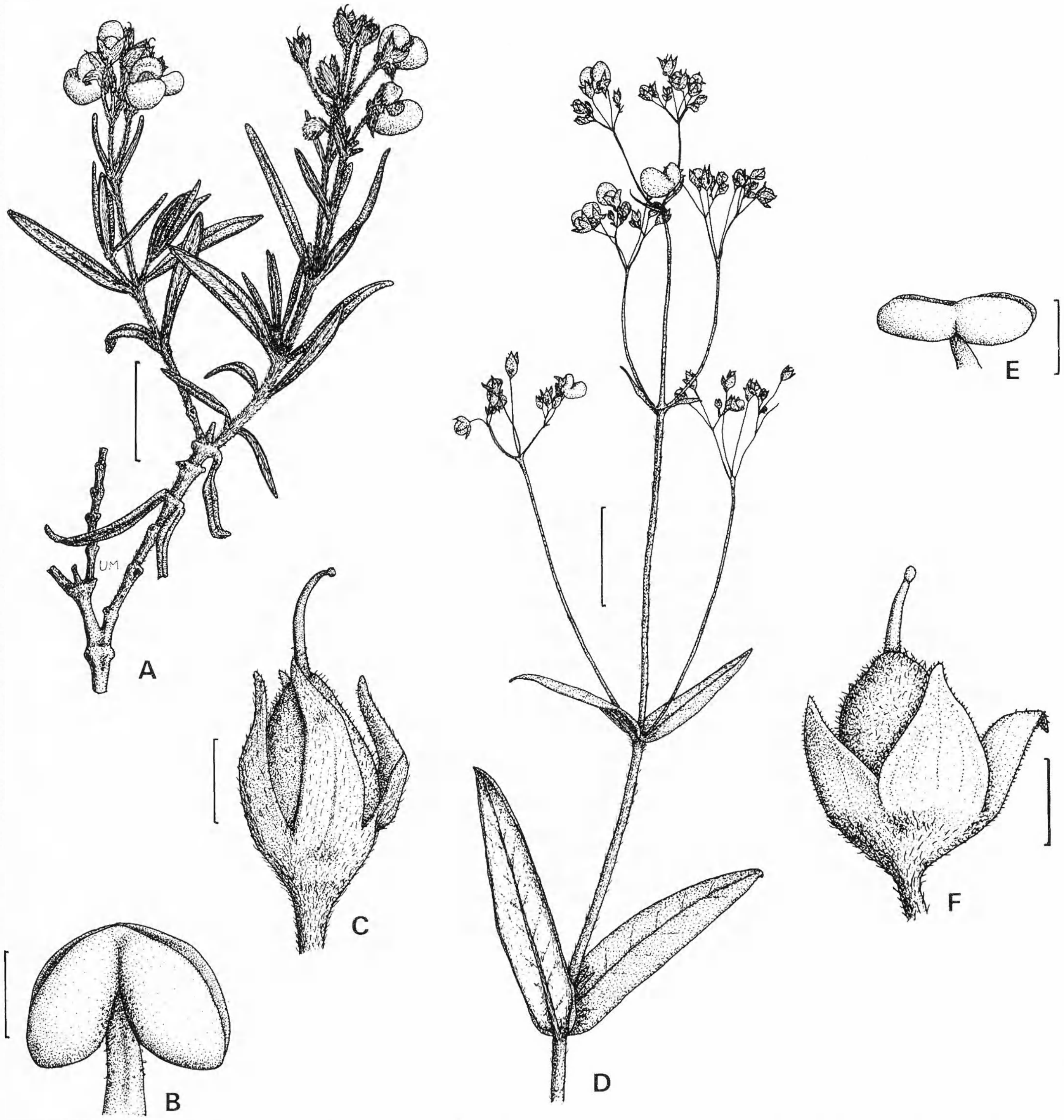

Fig. 8. A–C: *Calceolaria ferruginea*. – A: Flowering branch. – B: Stamen. – C: Capsule. – A, B Harling et al. 9633, C Penland 510. – D–F: *C. spruceana*. – D: Flowering branch. – E: Stamen. – F: Capsule. – D, E Asplund 8009, F Böcher et al. 106. – All drawings made from herbarium material. – Scales: A, D 2 cm, B, E 1 mm, C, F 2 mm.

Calceolaria ledifolia Pennell 1951 p. 102 – Orig. coll.: Pen!and 510 (PH holotype, F, GH).

Illustrations. Fig. 8 A–C; Cavanilles 1799 Tab. 445 Fig. 1; Pennell 1951 p. 97 Fig. 2 (as *C. ledifolia*).

Low *subshrub*, 0.3–1.0 m high, stems woody, knotty, distally strigose or tomentose with brownish hairs; internodes short. *Leaves* 2.0–5.0 × 0.2–1.0 cm, sessile, narrowly lanceolate, sometimes almost linear (when margins strongly revolute), coriaceous, obtuse, cuneate to rounded at base; above dark green, glutinous, ± rugose, glabrous or pilose; beneath densely brownish or olivaceous lanate with coarse hairs. *Inflorescence* terminal, comprising 2 pairs of 2–4-

flowered cymes on appressed-hirsute primary peduncles 1.5–5.0 cm long. Cyme bracts rudimentary. Pedicels hirsute with brownish hairs, 0.8–2.7 cm. *Sepals* ovate, 3.2–5.3 × 2.0–3.0 mm at anthesis, acute; externally appressed-hirsute; internally glabrous, glutinous, green with brown nerves. *Corolla* bright yellow, externally pilose with gland-tipped hairs; upper lip 5–7 mm long and about as wide, globose; lower lip 10–21 mm long and 7–17 mm wide, saccate in 2/5–1/2 of its length. *Anthers* yellow or yellowish brown, 2.0–2.8 mm, opening throughout; thecae deflexed, each one 1.4–1.8 mm. *Filaments* ca 1.0 mm. *Ovary* glandular-tomentose. *Style* 2.5–4.0 mm, curved. *Capsule* broadly ovoid, 4–7 mm long, puberulous with gland-tipped hairs.

Habitat. Open páramo at altitudes between 3250 and 4300 m.

Distribution. Fig. 9. Restricted to the higher mountain areas of the provinces of Bolívar, Tungurahua and Chimborazo, central Ecuador. In all, 40 specimens from 25 collections have been studied.

Remarks. Pennell (1951) used the name *C. ferruginea* for the wrong species. Furthermore, some of the labels of Nee's collections have been intermixed. The correct locality for the type of *C. ferruginea* is the slopes of Volcán Chimborazo above Guaranda (Pennell 1951).

C. ferruginea is a species of the high Andes. It is most closely related to *C. rosmarinifolia* and *C. spruceana*, but differs in pubescence, growth habit, anther shape and style length. Specimens from extremely high altitudes have more strongly revolute leaf-margins and denser pubescence than have specimens from lower altitudes.

Representative specimens. *Ecuador*. *Bolívar:* Western slopes of Volcán Chimborazo, ca 3500 m, 18.V.1968, Harling et al. 9633 (GB) – Sinche, 3350 m, XI.1923, Tate 466 (US). – *Chimborazo:* Cubillín, Cordillera Oriental, 3300–3400 m, 1.III.1944, Acosta-Solís 7564 (F) – Urbina, towards V. Chimborazo, ca 3700 m, 27.VII.1939, Asplund 7917 (S) – Southern slopes of V. Chimborazo, 4250 m, 18.VIII.1939, Asplund 8371 (K, S) – Calere, beyond Pueblo of San Juan toward páramo, 3300 m, 21.IV.1939, Penland 510 (F, GH, PH) – Carahuairazo, 3500–4000 m, 16.IV.1927, Rorud s.n. (F, O) – Chimborazo above Chiquipoquio, IX.1881, Sodiro 115/19 (P). – *Tungurahua:* Pilahuín, 3500 m, IV.1927, Rorud s.n. (O).

Fig. 9. Known distribution of *Calceolaria ferruginea* (●) and *C. gossypina* (○).

7. **Calceolaria gossypina** Bentham

Bentham 1846 p. 223 – *Fagelia gossypina* (Bentham) Kuntze 1891 p. 459 – Orig. coll.: Hall 7 (K holotype).

Calceolaria erioclada Bentham 1846 p. 215 – *Fagelia erioclada* (Bentham) Kuntze 1891 p. 459 – Orig. coll.: Jameson 29 (GH holotype, LA).

Calceolaria tungurahuae Pennell 1951 p. 103 – Orig. coll.: Penland 335 (PH holotype).

Illustrations. Fig. 10 A–C; Kränzlin 1907 a p. 97 Fig. 19 A–C; Pennell 1951 p. 104 Fig. 3 (as *C. tungurahuae*).

Low *subshrub,* 0.2–0.5 m tall; stems woody, knotty, much branched with short internodes. Younger parts of stems as well as inflorescences densely arachnoid-lanate with pale yellow or whitish hairs. *Leaves* narrowly elliptic, 2.0–5.2 × 0.4–1.5 cm, obtuse, cuneate, short-petiolate; above dark green, rugose, glabrous or pilose, glutinous; beneath densely arachnoid-lanate with pale yellow or whitish hairs; margins revolute, denticulate but apparently entire. Petioles 1–5 mm, densely lanate. *Inflorescence* terminal, comprising 1–2 pairs of 2–10-flowered cymes on primary peduncles (0.8–)2.0–4.8 cm long. Cyme bracts lacking. Pedicels 1.0–2.5 cm. *Sepals* 4.0–6.3 × 2.3–4.0 mm, ovate or triangular, acute or slightly acuminate, shortly mucronate; externally lanate, internally light green and glabrous. *Corolla* sulphur yellow; upper lip 4–6 mm long and usually somewhat wider than long, arched; lower lip 12–17 mm long and 10–14 mm wide, saccate in 1/3–2/5 of its length. *Anthers* 2.0–2.8 mm, yellowish brown, opening throughout; thecae ± deflexed. *Filaments* ca 1.0 mm. *Ovary* lanate. *Style* 2.0–4.0 mm, slightly curved. *Capsule* 5–6 mm long, ovoid, villous.

Habitat. Rocky places and crevices in open páramo at altitudes between 3300 and 4750 m, rarely lower.

Distribution. Fig. 9. Restricted to the provinces of Pichincha, Cotopaxi and Tungurahua in Ecuador. Not common.

Remarks. Within its distribution area *C. gossypina* occurs in small isolated populations on the highest mountains. Since the southernmost population differs in growth habit, Pennell regarded it as representing a distinct species, *C. tungurahuae*. The picture is further complicated by the morphological variation connected with altitude. *C. erioclada,* recognized by Bentham and Pennell by its larger leaves, is thus nothing but a "lowland" form of *C. gossypina*.The morphological differences between the populations are too vague to warrant taxonomic distinction between the different variants. *C. gossypina* is better considered as a single species, comprising geographically isolated populations exposed to genetic drift.

Specimens studied. Ecuador. Pichincha: Cerro Pichincha, 4250 m, Hall 7 (K); Jameson 254 (BM, E, G, K, P, W); Jameson s.n. (BM, F, G, K, LE, OXF, US); 4000 m, Jameson 67 (NY); altitude unknown, Karsten s.n. (W); Remy s.n. (P) – Vicinity of Quito, 2750 m, Jameson 29 (GH, LA); altitude unknown, Jameson 59 (BM, G, OXF), Jameson s.n. (K) – Cerro Rumiñahui, 4750 m, 15.XI.1920, Holmgren 957 (PH, S); 4250 m, Jameson s.n. (K). – *Cotopaxi:* Road Quevedo–Latacunga, Zumbagua, 3300 m, 2.V.1968, Harling et al. 8876 (GB). – *Tungurahua:* Volcán Tungurahua, northern slopes, 3800–3900 m, 10.XI.1933, Heinrichs 525 (B, G, M, Z); Minza páramo, 3800 m, 6.IV.1939, Penland 335 (PH); altitude unknown, 1857–1859, Spruce s.n. (K). –*Sine loco:* Pearce s.n. (BM).

8. **Calceolaria hyssopifolia** H. B. K.

Humboldt, Bonpland & Kunth 1818 p. 386 – *Fagelia hyssopifolia* (H. B. K.) Kuntze 1891 p. 460 –*Calceolaria linifolia* Willd. ex Link 1820 p. 54 – Orig. coll.: Bonpland 3146 (P holotype).

Calceolaria perrevoluta Pennell 1951 p. 107 – Orig. coll.: Jameson s.n. (K holotype, S, US, W).

Illustration. Fig. 10D–G.

Subshrub, 0.5–1.5 m high, sometimes climbing; stems erect or ascending, glabrous. *Leaves* sessile, narrowly lanceolate, rarely linear, (1.0–)2.5–6.7 × 0.2–1.1 cm, glabrous, ± obtuse, cuneate at base; above green, strongly glutinous; beneath pale green, pinnate-venose; margins entire or denticulate, ± revolute. *Inflorescence* terminal, comprising 2–3 pairs of (1–)4–12-flowered cymes on glabrous primary peduncles 1.0–4.7 cm long. Cyme bracts always present. Pedicels 0.5–2.5 cm long, strongly glutinous, glabrous or finely puberulous. *Sepals* triangular, 3.0–5.0 × 1.5–2.5 mm at anthesis, later slightly enlarged, acute, glabrous, green, strongly glutinous. *Corolla* sulphur or light yellow above, white beneath, sometimes the upper lip entirely white; upper lip 3–5 mm long and 5–10 mm wide, hooded, somewhat flattened; lower lip 13–23 mm long and 10–16 mm wide, saccate in about 1/2 of its lenght, inflated, upcurved. *Anthers* brown or buffish, 2.0–2.8 mm, opening throughout; thecae divaricate. *Filaments* 1.0–1.2 mm. *Ovary* glabrous. *Style* 1.5–2.6 mm, curved. *Capsule* widely conical, 5–7 mm long, glabrous, glutinous.

Chromosome number. 2n = 32. – Voucher: Harling et al. (leg. Molau) 14843 (GB). – The same chromosome count has previously been reported by Darlington & Janaki Ammal (1945).

Habitat. Mountain scrub and open grass páramo at altitudes between 2500 and 4300 m.

Distribution. Fig. 11. Andes of Ecuador; common in the provinces of Imbabura and Pichincha, scattered in Cotopaxi, Tungurahua, Bolívar, Chimborazo and Cañar, sporadic in Carchi and Azuay. In all, 151 specimens from 90 collections have been studied.

Remarks. *C hyssopifolia* is one of the most common species of the genus in northern Ecuador. It exhibits a considerable altitudinal amplitude connected with morphological adaptations. Specimens growing at 4000 m and above have fasciculate linear leaves with strongly revolute margins and very short internodes. Pennell (1951) regarded these as representing a distinct species, *C. perrevoluta*. Now, when the stock of collections available has increased, a continuous variation between the extreme forms is seen.

Hybrids between *C. hyssopifolia* and *C. crenata* ssp. *crenata* have been collected on Cerro Pichincha, province of Pichincha, Ecuador; for further description, see under *C. crenata* ssp. *crenata*.

Representative specimens. Ecuador. Carchi: Páramo de Tuza, 5.VI.1876, André K.617 (K); 2500–3200 m, 31.I.1881, Lehmann 514a (BM, G, LE, PH). – *Imba-*

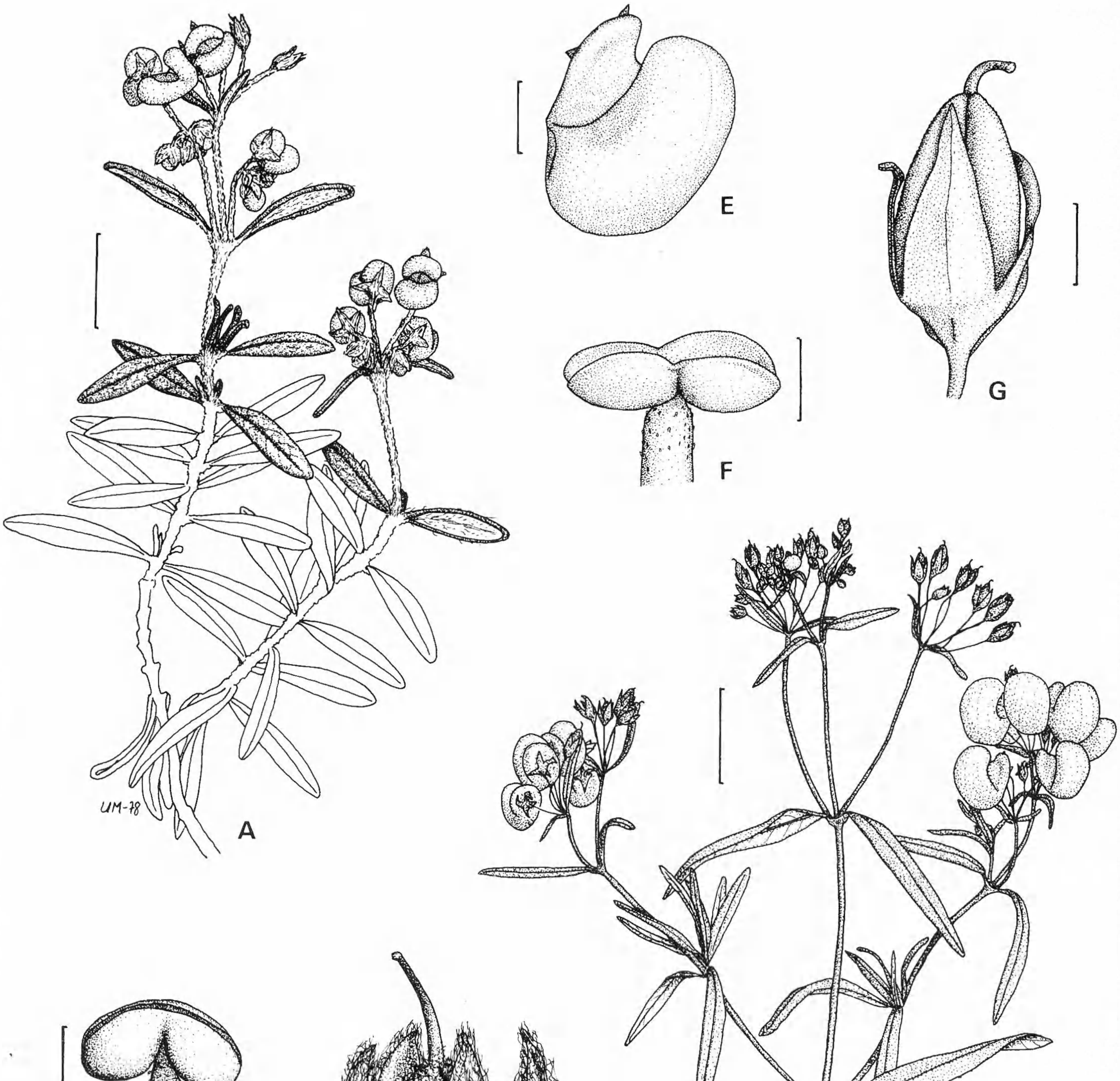

Fig. 10. A–C: *Calceolaria gossypina*. – A: Flowering branch. – B: Stamen. – C: Capsule. – A, B Jameson 254, C Holmgren 957. – D–G: *C. hyssopifolia*. – D: Flowering branch. – E: Corolla. – F: Stamen. – G: Capsule. – D, G Asplund 6967, E, F leg. Molau; Harling et al. 14843. – A–D, G drawn from herbarium material, E, F drawn from fixed material. – Scales: A, D 2 cm, B, F 1 mm, C, G 2 mm, E 5 mm.

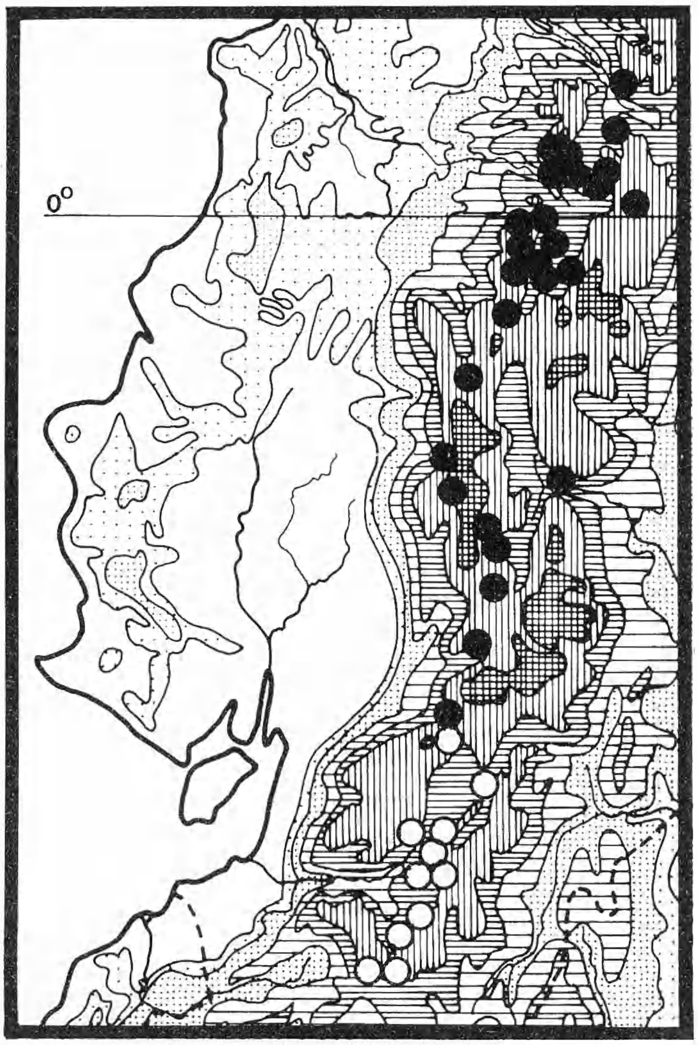

Fig. 11. Known distribution of *Calceolaria hyssopifolia* (●) and *C. helianthemoides* (○).

bura: Lago Cuicocha, 3000–3100 m, 10.IV.1956, Asplund 20214 (S); 30.V.1939, Penland 876 (GH, PH); 23.VII.1974, Plowman et al. 3784 (GH); 10.XII.1966, Sparre 13373 (S) – Road Cotacachi–Apuela, 21 km from Cotacachi (Intac valley), 3300 m, 11.VIII.1976, Øllgaard & Balslev 8685 (AAU). – *Pichincha:* 10 km E of Cayambe, 3100 m, 2–6.III.1959, Harling 4361 (S) – Cerro Pichincha, 3500 m, 16.VIII.1966, Eliasson 92 (GB); Hartweg 1273 (BM, E, G, K, LD, LE, OXF, P, W); 26.I.1977, leg. Molau; Harling et al. 14843 (GB) – Cerro Corazón, 3350 m, 15.III.1953, Prescott 854 (S). – *Cotopaxi:* Páramo on Latacunga–Tigua road, ca 4000 m, 14.XI.1939, Haught 2933 (PH). – *Tungurahua:* Baños, ca 2500 m, V.1927, Rorud s.n. (O). – *Bolívar:* Western slopes of Volcán Chimborazo, ca 3500 m, 18.V.1968, Harling et al. 9628 (GB). – *Chimborazo:* Guamote, 3100 m, 13.VI.1939, Asplund 6883 (G, K, S, UPS). – *Cañar:* Near El Tambo, 3300 m, 29.VII.1962, Játiva & Epling 250 (S, UC); ca 3000 m, 22.IV.1945, Camp E-2805 (NY, PH); 5.VII.1945, Camp E-4010 (PH, S). – *Azuay:* Páramo of Azuay, 4000 m, X.1864, Jameson s.n. (K, S, US, W).

9. **Calceolaria helianthemoides** H. B. K.

Humboldt, Bonpland & Kunth 1818 p. 387 – *Fagelia helianthemoides* (H. B. K.) Kuntze 1891 p. 460 – Orig. coll.: Bonpland 3308 (P lectotype, B-WILLD).

Illustration. Fig. 12 A–D.

Low *subshrub;* stems erect, 0.2–0.5 m high, reddish, white-puberulous, with short internodes. The whole plant glutinous. *Leaves* sessile, fasciculate, primary leaves 1.1–2.5 × 0.4–0.8 cm, elliptic or narrowly ovate, glabrous, obtuse, rounded at base; above green or dark green; beneath pale green, pinnate-venose; margins denticulate, revolute and apparently entire. *Inflorescence* terminal, few-flowered, comprising 1–2 pairs of 1–4-flowered cymes on puberulous primary peduncles 1.4–6.8 cm long. Cyme bracts present. Pedicels 0.7–2.3 cm, glandular-puberulous. *Sepals* ovate, acuminate, 3.0–4.5 × 2.0–3.5 mm at anthesis, later somewhat enlarged, yellowish green, often turning red distally; externally glabrous; internally white-puberulous. *Corolla* above light or sulphur yellow, beneath white; upper lip 3–6 mm long and 4–7 mm wide, hooded, subglobose; lower lip 14–22 mm long and 9–16 mm wide, saccate in 1/2–2/3 of its length, projecting, almost circular and somewhat flattened. *Anthers* whitish, 1.9–2.5 mm, opening to connective; thecae divaricate. *Filaments* 0.9–1.2 mm. *Ovary* glabrous. *Style* 1.2–2.5 mm, curved. *Capsule* conical, 5–6 mm long, glabrous, glutinous.

Chromosome number. 2n = 36. – Voucher: Harling et al. (leg. Molau) 15073 (GB).

Habitat. Grass páramo and clearings in mountain scrub at altitudes between 2500 and 3700 m.

Distribution. Fig. 11. Common in the Andes of southern Ecuador, restricted to the provinces of Cañar, Azuay and northern Loja. In all, 60 specimens from 26 collections have been studied.

Remarks. This elegant species is characteristic of the highlands of southern Ecuador. It is similar to *C. lavandulaefolia* in floral morphology. Arrangement of the foliage shows certain affinities to sect. *Fasciculata.*

Representative specimens. Ecuador. Cañar: Near El Tambo, 3000–3500 m, 6–9.VII.1945, Camp E-4091 (F, G, GH, K, MO, NY, P, PH, UC, US). – *Azuay:* Portete de Tarqui, road Cuenca–Girón, 2700–2900 m, 5.IV.1974, Harling & Andersson 13233 (GB) – Near Gualaceo, VIII.1864, Jameson 72 (K, PH, S, US, W) –

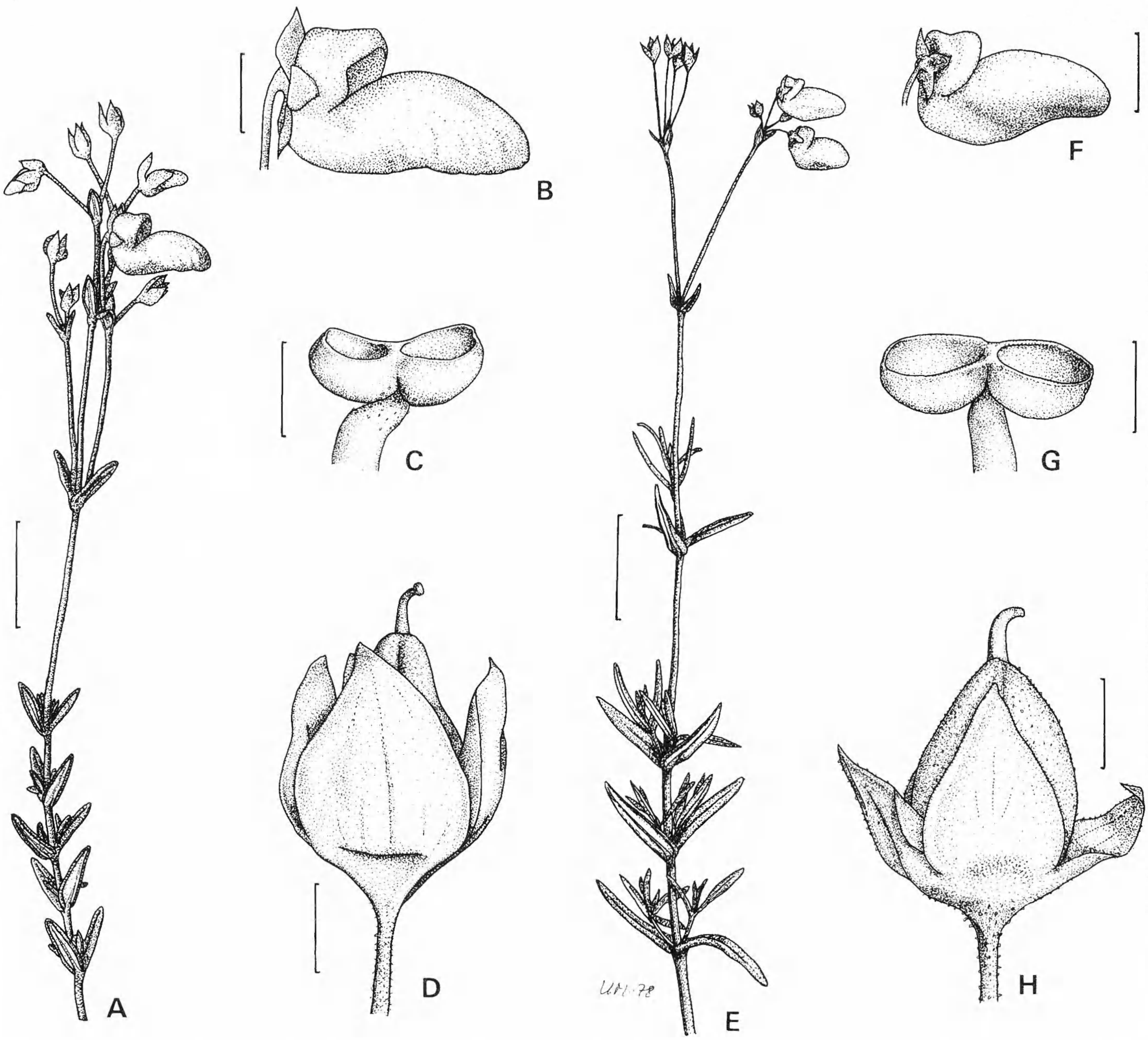

Fig. 12. A–D: *Calceolaria helianthemoides*. – A: Habit. – B: Corolla. – C: Stamen. – D: Capsule. – A–C leg. Molau; Harling et al. 15073, D Holm-Nielsen et al. 5043. – E–H: *C. lavandulaefolia*. – E: Habit. – F: Corolla. – G: Stamen. – H: Capsule. – E, H Harling & Andersson 13255, F, G leg. Molau; Harling et al. 14971. – A, B, F drawn from photographs, C, G drawn from fixed material, D, E, H drawn from herbarium material. – Scales: A, E 2 cm, B, F 5 mm, C, G 1 mm, D, H 2 mm.

Ca 35 km S of Cumbe, Páramo de Tinajillas, 3200 m, 9.V.1964, Harling & Andersson 14469 (GB); 5.II.1977, leg. Molau; Harling et al. 15073 (GB). – *Loja:* Chuquiribamba, 4.XI.1876, André K.609 (F, K, NY) – Saraguro, ca 2500 m, 10.III.1947, Espinosa E-1424 (PH); 1841–43, Hartweg 823 (BM, CGE, E, G, K, LD, LE, NY, OXF, P) – Vicinity of Las Juntas, 28.IX.1918, Rose 23186 (US).

10. **Calceolaria lavandulaefolia** H. B. K.

Humboldt, Bonpland & Kunth 1818 p. 386 – *Fagelia lavandulaefolia* (H. B. K.) Kuntze 1891 p. 460 – *Calceolaria rosmarinifolia* subsp. *lavandulaefolia* (H. B. K) Weddell 1857 p. 139 – *Calceolaria gnidifolia* Willd. ex Link 1820 p. 54 – Orig. coll.: Bonpland s.n. (P lectotype, B-WILLD, F fragment).

Calceolaria hypoleuca Bentham 1846 p. 222 (non Kränzlin) – *Fagelia hypoleuca* (Bentham) Kuntze 1891 p. 460 – Orig. coll.: Hall 5 (K holotype).

Illustration. Fig. 12 E–H.

Subshrub. 0.2–0.8 m high; stems with relatively long internodes, erect or ascending, sparsely branched, reddish-brown, distally puberulous. *Leaves* sessile, ± fasciculate. Primary leaves

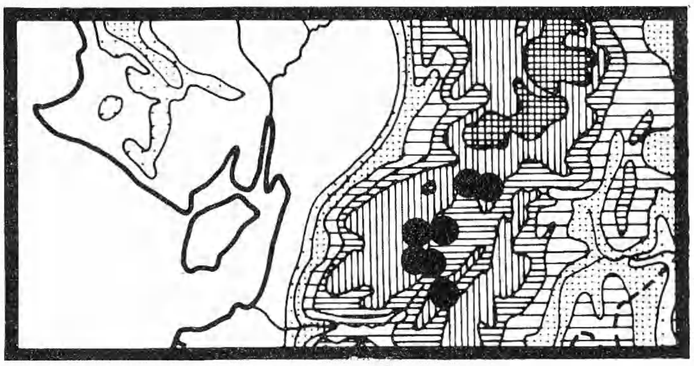

Fig. 13. Known distribution of *Calceolaria lavandulaefolia*.

3.0–5.3 × 0.5–0.9 cm, narrowly triangular, obtuse, clasping at base; above dark green, finely rugose, essentially glabrous, glutinous; beneath lanate with white or greenish-white hairs; margin revolute, entire. *Inflorescence* terminal, comprising 1(–2) pairs of 1–8-flowered cymes on primary peduncles 1.2–5.6 cm long. Cyme bracts present, when more than 4 flowers in the cymes also subordinate bracts. Pedicels 1.1–2.1 cm, puberulous and strongly glutinous. *Sepals* triangular or ovate, 3.0–5.0 × 1.7–3.8 mm, slightly acuminate, yellowish green, turning red at the margins; externally glabrous and glutinous, internally puberulous. *Corolla* pale sulphur yellow, beneath ± white; upper lip 4–5 mm long and 5–6 mm wide, hooded, globose, somewhat flattened dorsally; lower lip 13–25 mm long and 12–17 mm wide, saccate in 2/3–3/4 of its length, almost circular, slightly flattened. *Anthers* 2.2–2.6 mm, buffish, opening to connective; thecae divaricate or slightly deflexed. *Filaments* 0.8–1.2 mm. *Ovary* glabrous, glutinous. *Style* 1.3–2.0 mm, curved. *Capsule* ovoid, 4–6 mm long.

Habitat. Mountain scrubs and transition to páramo at altitudes between 2500 and 3200 m.

Distribution. Fig. 13. Scattered in the provinces of Cañar and Azuay, Ecuador. The more norhterly localities reported by Bonpland and Hall are probably erroneous. Bonpland's type specimen is labelled ''montis ignivomi Pichincha et Parami de Assuay''; only the latter locality is correct. Hall's specimen is labelled ''Quito'', a name that time used in a wider sense and often including major parts of the Ecuadorean Andes. The species has never since been reported from northern Ecuador. In all, 30 specimens from 21 collections have been studied.

Remarks. This species is similar to *C. helianthemoides* in floral characters, such as shape and colour of corolla and dehiscence of the anthers. In foliage, however, the two species differ greatly.

As Pennell (1951) stated, *C. hypoleuca* Bentham (non Kränzlin) is synonymous to *C. lavandulaefolia;* the type specimens are very similar.

Representative specimens. Ecuador. Cañar: N of Biblián, 2900–3000 m, 6.IV.1974, Harling & Andersson 13255 (GB). – *Azuay:* Road Cuenca–Loja, ca 20 km S of Cumbe, 3000–3200 m, 19.III.1974, Harling & Andersson 12664 (GB) – Portete de Tarqui, road Cuenca–Girón, 2700–2750 m, 3.II.1977, leg. Molau; Harling et al. 14971 (GB) – Cuenca, 2600 m, 16.VII.1939, Penland 1044 (F, GH, PH).

Sect. 4. **Ericoides** Pennell

Pennell 1951 p. 112 – Type species: *Calceolaria ericoides* Vahl.

Erect, sparsely branched shrubs. Leaves fasciculate on axillary short shoots, numerous, ericoid, linear with strongly revolute margins; leaves on the main stems (primary leaves) usually alternate. Synflorescence terminal or subterminal, irregular, consisting of numerous dichasial 1–8-flowered florescences. Corolla yellow; upper lip very short, 1–2 mm long, not covering the anthers; lower lip upcurved, saccate in 1/3 of its length, closing the orifice. Anthers opening throughout; thecae divaricate, elliptic, equal.

Sect. *Ericoides* comprises two species of the high Andes of Ecuador and Peru.

Key to the species of sect. Ericoides

1. Leaves and sepals externally shortly hirsute .... 1. *C. ericoides*
– Leaves and sepals externally glabrous, strongly glutinous .... 2. *C. linearis*

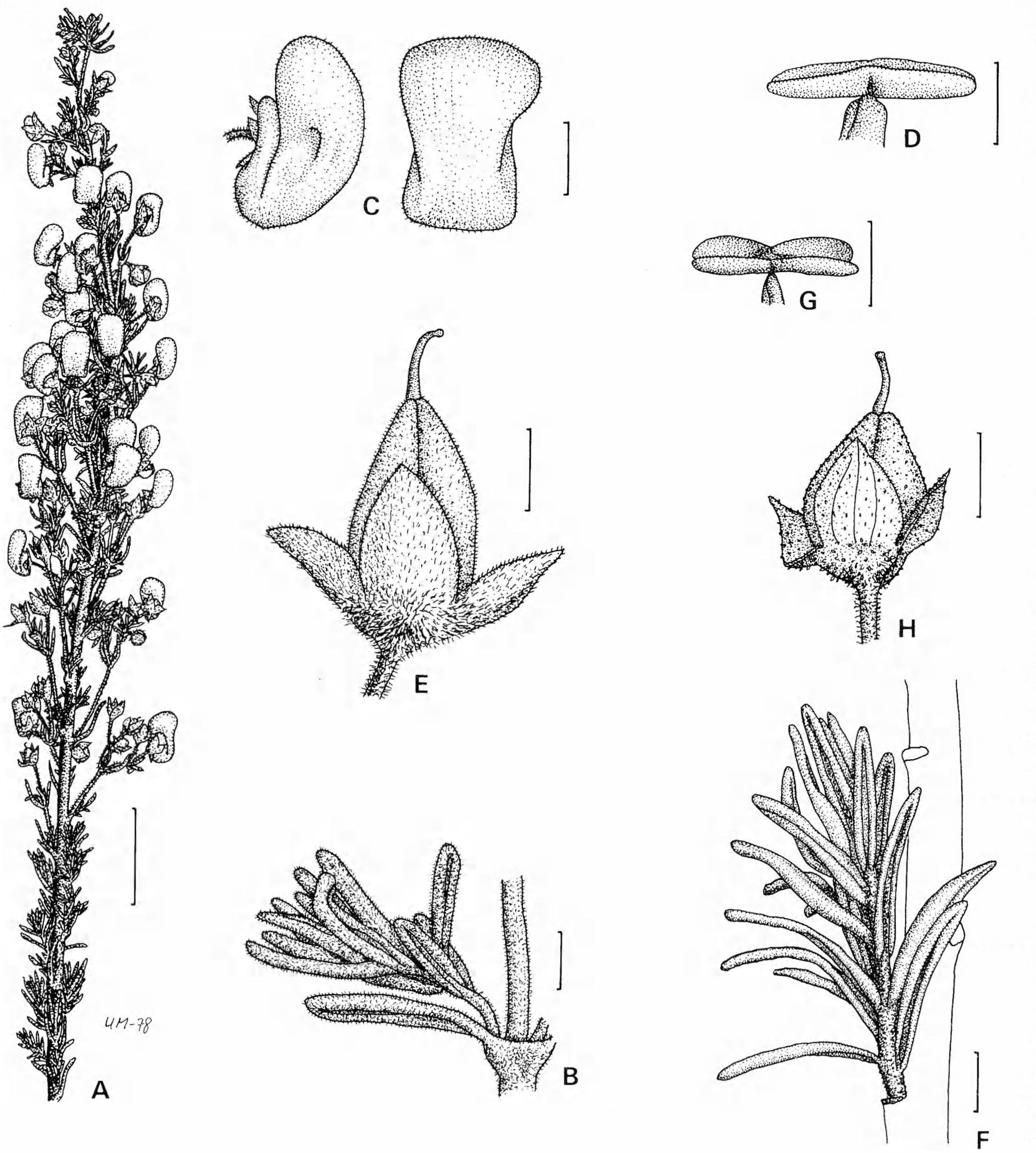

Fig. 14. A–E: *Calceolaria ericoides*. – A: Habit. – B: Leafy short shoot – C: Corolla. – D: Stamen. – E: Capsule. – A–D leg. Molau; Harling et al. 14844, E Humbles 6296. – F–H: *C. linearis* (Hutchison et al. 6287). – F: Leafy short shoot – G: Stamen. – H: Capsule. – A, B, E–H drawn from herbarium material, C, D drawn from fixed material. – Scales: A 2 cm, B, E, F, H 2 mm, C 5 mm, D, G 1 mm.

1. **Calceolaria ericoides** Vahl

Vahl 1805 p. 190 – *Fagelia ericoides* (Vahl) Kuntze 1891 p. 459 – Orig. coll.: Jussieu s.n. (P holotype, C, G.).

Calceolaria canescens Willd. ex Link 1820 p. 54 – Orig. coll.: Bonpland 3028 (B-WILLD holotype, P, W).

Illustration. Fig. 14 A–E.

Erect or ascending *shrub,* 0.3–1.5 m high; inflorescence and distal parts of stems hirsute. *Leaves* linear, straight, obtuse, sessile, green; margins strongly revolute, concealing the glabrous lower surface; externally hirsute. Primary leaves 10–14(–18) × 1.0–1.5 mm, fasciculate leaves smaller. *Sepals* pale or yellowish green, 3.0–5.5 × 1.5–3.0 mm, ovate, acute; externally shortly hirsute, internally puberulous. *Corolla* sulphur or lemon yellow, externally villous (at least proximally); upper lip ring-like, 1–2 mm long; lower lip 13–22 mm long and 5–10 mm wide. *Anthers* brown, 2.0–2.5 mm. *Filaments* very short, not exceeding 1 mm. *Ovary* glandular. *Style* 1.8–2.2(–3.0) mm. *Capsule* narrowly conical, 5–8 mm long, ± tomentose.

Chromosome number. 2n = 36. – Voucher: Harling et al. (leg. Molau) 14844 (GB).

Habitat. Grass páramo and clearings in mountain scrub, often in full exposure, at altitudes between 2800 and 4400 m.

Distribution. Fig. 15. The species is disjunct with its main distribution in Ecuador, where it is known from Pichincha to Azuay. The species also occurs in a limited area in northern Peru, south of the Piura Divide. In all, 207 specimens from 106 collections have been studied.

Remarks. C. ericoides is one of the most common species of the genus in the páramos of the provinces of Pichincha, Chimborazo and Cañar. The distribution gap between Pichincha and Chimborazo may be due to the fact that very little is collected at the small number of suitable localities present in this area.

Specimens from northern Peru are somewhat aberrant with slightly longer styles and finer hairs; occasionally they also have maroon-red spots in the neck of the lower corolla lip. However, these deviations are slight and not sufficient to support a segregation into subspecific taxa.

The type of *C. canescens* is a typical specimen of *C. ericoides*. For some abstruse reason it was separated from the latter by Willdenow. The name *C. canescens* was suggested by Bonpland on the labels of his collection 3028, and has been used for several species of Bolivia and southern Peru.

Representative specimens. Ecuador. Pichincha: Cerro Pichincha, 3300 m, 18.V.1939, Asplund 6142 (G, K, LD, NY, S, UPS, US); 3400 m, 4.IX.1928, Firmin 519 (F, US); 1843, Hartweg 1274 (BM, CGE, E, G, K, LD, LE, NY, OXF, P, W); 3600–3800 m, 3.VI.1973, Holm-Nielsen et al. 6672 (AAU, GB, MO); 3500–4000 m, 26.I.1977, leg. Molau; Harling et al. 14844 (GB) – Cerro Antisana, 3700 m, 8.VIII.1960, Grubb et al. 708 (K) – Páramo of Volcán Cayambe, 3600 m, Harling 4449 (S). – *Tungurahua:* Above Mocha, André K.1418 (K). – *Bolívar:* Western slopes of Volcán Chimborazo, ca 3500 m, 18.V.1968, Harling et al. 9626 (GB). – *Chimborazo:* Alao, Cordillera Oriental, 3200 m, 5.II.1944, Acosta-Solís 7177 (F) – Southern slope of V. Chimborazo, 3800 m, 18.VIII.1939, Asplund 8362 (G, K, LD, S, UPS, US) – Calere, beyond San Juan, 3300 m, 21.IV.1939, Penland 481 (F, GH, PH) – SE of Riobamba, 3300 m, 22.III.1934, Schimpff 892 (G, GH, M, MO, Z). – *Cañar:* Near El Tambo, 2900–3050 m, 5.VII.1945, Camp E-3972 (F, G, GH, K, MO, NY, P, PH, UC, US) – Road Taday–Azogues, 3000–3300 m, 4.II.1977, leg. Molau; Harling et al. 15020 (GB). – *Azuay:* Hacienda Pizhín on road from Cuenca to Oña, ca 2800 m, 23.IX.1955, Asplund 17774 (S) – Cerro Soldados, W of Sayausid, ca 3400 m, 25.IV.1968, Harling et al. 8764 (GB). – *Peru. Amazonas:* Eastern side of Cerro Calla-Calla, 30.V.1966, Edwin & Schunke 3631 (F, G, GH, NY, US, W) – Summit of Cerro Puma-Urco, 3100–3200 m, 3.VII.1962, Wurdack 1142 (GH, K, P, S, UC). – *Cajamarca:* Hualgayoc, 3500–4200 m, 16.XI.1948, Scolnik 1345 (PH).

2. **Calceolaria linearis** R. & P.

Ruiz & Pavón 1798 p. 19 – *Fagelia linearis* (R. & P.) Kuntze 1891 p. 460 – Orig. coll.: Pavón s.n. (MA holotype, BM, G).

Calceolaria alternifolia Cavanilles 1799 p. 28 – *Fagelia alternifolia* (Cav.) Kuntze 1891 p. 459 – Orig. coll.: Nee s.n. (MA holotype, F fragment, G).

Illustrations. Fig. 14 F–H; Cavanilles 1799 Tab. 445 Fig. 2 (as *C. alternifolia*).

Erect *shrub,* 0.4–0.9 m high; inflorescence and distal parts of stems puberulous and strongly glutinous. *Leaves* linear, straight or arcuate, sessile, apices obtuse and ± deflexed; margins strongly revolute, concealing the papillose lower surfaces; externally glabrous and strongly glutinous. Primary leaves 9–26 × 0.9–2.0 mm, fasciculate leaves smaller. *Sepals* ovate, 3.0–4.5 × 1.8–3.0 mm at anthesis, yellowish, acute, on both sides finely glandular-puberulous. *Corolla* lemon yellow, externally slightly glandular; upper lip ring-like, 2 mm long; lower lip 10–20 mm long and 5–10 mm wide. *Anthers* buffish, 1.6–3.0 mm. *Filaments* 0.8–1.0 mm. *Ovary* glandular. *Style* 1.4–2.0 mm, distally curved. *Capsule* ovoid, 4–8 mm long, glandular or puberulous with gland-tipped hairs.

Habitat. Dry, exposed grassy slopes at altitudes between 2600 and 4000 m. Often growing in colonies.

Distribution. Fig. 15. A strictly Peruvian species, only once collected north of the Piura Divide (Sandeman 4290). Ranges from the department of Piura to Lima. Not common, most frequently collected in the departments of La Libertad and Ancash. In all, 34 specimens from 12 collections have been studied.

Remarks. This species is similar to *C. ericoides* in growth habit, but differs in vesture and anther colour. No other close relatives are known at present.

C. linearis and *C. alternifolia* were described at about the same time; the type specimens of the two are almost identical.

Representative specimens. Peru. Piura: Huancabamba, 2600 m, VIII.1943, Sandeman 4290 (K, OXF, PH). – *La Libertad:* 9 km W of and below Shorey toward Trujillo, 3590 m, 11.VIII.1964, Hutchison et al. 6287 (C, F, G, GH, K, LE, M, MO, NY, P, S, UC).– *Ancash:* Beyond Lake Llanganuco, prov. Yungay, 3200 m, 31.VII.1960, Saunders 508 (BM). – *Lima:* Buenaventura, Nee s.n. (F, G, MA). –*Junín:* San José de Acobambilla, 3850 m, 1.VIII.1961, Lloyd & Marshall 284 (K).

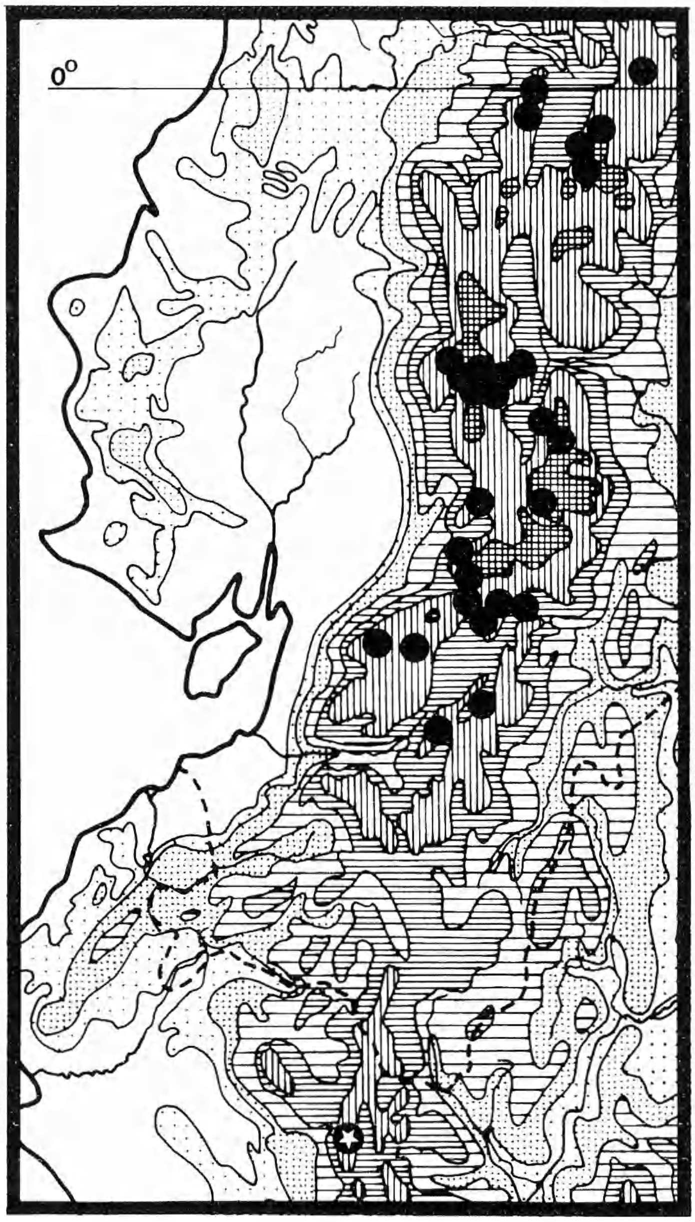

Fig. 15. Known distribution of *Calceolaria ericoides* (●) and *C. linearis* (✪) N of the Piura Divide.

Sect. 5. **Lehmannina** Pennell

Pennell 1951 p. 151 – Type species: *Calceolaria lehmanniana* Kränzlin.

Erect herbs; stems and foliage densely pubescent with coarse brownish hairs. Leaves sessile, ± elliptic. Primary peduncles very long, ascending. Corolla white, lips spreading.

A single species in north-western South America.

1. **Calceolaria lehmanniana** Kränzlin

Kränzlin 1905 p. 100 –*Fagelia lehmanniana* (Kränzlin) Pennell 1920 p. 173 – Orig. coll.: Lehmann 6134 (PH lectotype, K, LE).

Illustration. Fig. 16.

Robust, erect *herb,* 0.4–1.0 m high. Stems densely villous or lanate with ascending brownish coarse hairs; lower internodes short. *Leaves* sessile, narrowly elliptic, 6.0–12.5 × 2.3–4.2 cm, acute, cuneate at base; above yellowish green, papillose and pilose or tomentose, beneath pinnate-venose, nerves hirsute or lanate, tissue glabrous or villous with gland-tipped hairs; margins deeply serrate, plane, proximally entire. *Inflorescence* terminal, comprising 1(–2) pairs of 12–36-flowered cymes on glandular-villous primary peduncles (6.5–)9.5–27(–30) cm long. Cyme bracts present. Lateral branches of cymes long, ascending, with gradually shorter peduncles and mixed mono- and dichasial arrangement. Primary pedicels glandular-tomentose, 1.5–3.2 cm, subordinate pedicels gradually shorter. *Sepals* green, ovate or lanceate, 3.2–6.5 ×

Fig. 16. *Calceolaria lehmanniana* (Harling & Andersson 12206). – A: Habit. – B: Corolla. – C: Stamen. – D: Capsule. – A, C drawn from herbarium material, B, D drawn from photograph. – Scales: A 2 cm, B 5 mm, C 1 mm, D 2 mm.

1.9–3.6 mm at anthesis, later somewhat enlarged, acuminate or caudate, on both sides puberulous or villous with gland-tipped hairs. *Corolla* white, often turning pink or purplish distally, rarely yellow, externally finely glandular-puberulous; upper lip 4–6 mm long and 6–8 mm wide, arched over the anthers; lower lip pendent, 9–14 mm long and 7–11 mm wide, saccate in 1/3–2/5 of its length. *Anthers* brown, 1.9–2.4 mm, opening throughout; thecae divaricate, elliptic, equal. *Filaments* 0.9–1.4 mm. *Ovary* glandular-puberulous. *Style* straight, 1.8–2.7 mm. *Capsule* globose, 4–7 mm long, shortly glandular-tomentose.

Habitat. Mountain scrub at altitudes between 2200 and 3300 m.

Distribution. Fig. 17. Ranges from the department of Cauca in southern Colombia to the province of Napo in northern Ecuador, where it is restricted to the eastern cordillera. This species has not previously been reported from Ecuador.

Remarks. C. lehmanniana is an aberrant species with no close relatives in north-western South America. Some species of southern Peru (viz. *C. heterophylla* R.& P. and *C. vulpina* Kränzlin) may belong to the section, but differ in characters of corolla and anthers.

The white colour of the corolla is a unique feature in the investigated area. However, one specimen with yellow flowers has been collected in Ecuador (Harling & Andersson 12507).

Specimens studied. Colombia. Cauca: Volcán Sotará, Páramo de Barbillas, 3000–3300 m, Lehmann 6134 (K, PH). – *Huila:* E of San Antonio, upper Magdalena, 4.IV.1944, Olsson 3 (F, G, PH). – *Nariño:* E of Aponte, Río Majinsanoy, 2700 m, 29.VI.1963, Bristol 1176 (GH) – Cerro Tablón, above Las Mesas on W slope of Volcán Doña Juana, 2700–2800 m, 15.XII.1944, Ewan 16584 (PH, US) – 5 km E of Volcán Doña Juana, 3000 m, 20.X.1943, Fosberg 21272 (NY, P, S, UC, US) – Puruquí, prov. de Tuquerres, 2800 m, V. 1853, Triana s.n. (BM, G, NY, P, W). – *Putumayo:* Sibundoy, 2225 m, 30.VIII.1963, Bristol 1357 (GH) – Valle de Sibundoy, San Francisco, 2300 m, 11.VIII.1965, Uribe 5391 (F, NY). – *Ecuador. Carchi:* Above El Pun towards Tulcán, ca 3050 m, 14.VII.1955, Asplund 16872 (S); 3100–3200 m, 26.II.1974, Harling & Andersson 12206 (GB). – *Napo:* Valley of Río Papallacta, Cuyuja, 2400–2500 m, 23.IX.1939, Asplund 8798 (LD, S, UPS, US) – Ca 5 km E of Santa Bárbara, 2700 m, 4.III.1974, Harling & Andersson 12457 (GB) – Road Santa Bárbara–La Bonita, ca 2600 m, Harling & Andersson 12507 (GB).

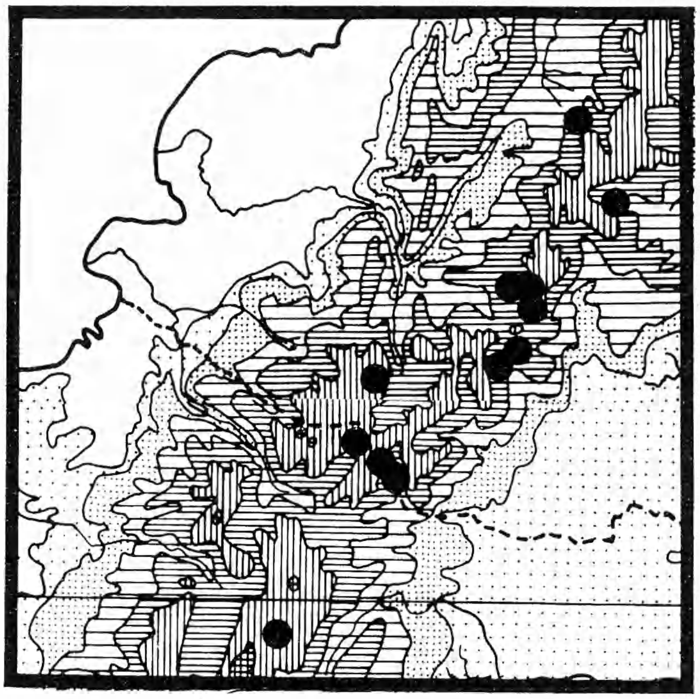

Fig. 17. Known distribution of *Calceolaria lehmanniana*.

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New subspecies of Ranunculus auricomus from Västmanland, Sweden

Erik Julin

Julin, E. 1978 09 30: New subspecies of Ranunculus auricomus from Västmanland, Sweden. *Bot. Notiser 131:* 317–348. Stockholm. ISSN 0006-8195.

The following new subspecies of *Ranunculus auricomus* L. are described and illustrated: *almquistii, amoenoviridis, caespitosulus, dissimilifolius, erectus, expansus, hallstaënsis, inconcinnus, inconspectiflorus, longimammus, rectiangulus, robusticaulis, sublaetevirens* and *sundinii*. Distribution maps are given for the subspecies *almquistii, amoenoviridis, erectus, longimammus, rectiangulus* and *sundinii*.

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This paper is preparatory to the new *Flora of Västmanland* now being prepared by Ulf Malmgren. The subspecies described are not closely related; the only reason for treating them in the same paper is that they occur in the province of Västmanland.

The terminology used is the same as that in a previous paper (Julin 1977). In the illustrations of the series of basal leaves the oldest leaf is shown at the top left-hand side and the youngest at the bottom right-hand side. Since a complete leaf series is rarely present on a single specimen, the leaves drawn have been taken from several plants in the type collection.

A complete list of all the localities for the subspecies mapped has been deposited at the Museum of Natural History, Section for Botany, S-104 05 Stockholm 50, Sweden, and copies will be sent on request. The abbreviations of the names of provinces follow Hylander (1953), except that 'Klm' has been included in 'Sm' and 'Gbg' in 'Vg'.

R. auricomus L. ssp. **almquistii** Julin ssp. nov.

Holotypus: Suecia, Sudermannia, Åker, Åkers styckebruk, in hortis 13.5.1964 Julin (UPS).

Planta mediocriter alta. *Caules* erecti vel curvati, ramos sub angulo sat lato emittentes, intra reliquias foliorum rosulariorum anni proximi vaginis aphyllis 1–3 instructi. *Folia rosularia* plerumque magna, ambitu reniformia vel paene orbicularia, sinu basali 0° ad fere 90°. Folia exteriora lata, trilobata ad tripartita, lobo (segmento) medio rotundato vel cuneato, obtruncate crenato, lobis (segmentis) lateralibus obtruncate crenatis, indivisis vel leviter incisis. Folia intermedia tripartita, segmento medio cuneato, rotundate mammiformiter dentato, segmentis lateralibus ± profunde lobulatis, lobulis rotundate mammiformiter dentatis. Folia sequentia multipartita, segmentis lanceolatis, mammiformiter vel acute dentatis. Folia interiora foliis intermediis similia sed acutius dentata. Folia aestivalia utrimque pilosa, inaequaliter triangulariter mammiformiter dentata, trilobata, lobo medio cuneato, lobis lateralibus latis, incisura levi una alterave praeditis, incisuris inter lobos angustis. *Laciniae foliorum caulinorum* sat longae, lanceolati-lineares, obtusae, integerrimae vel – validiores – saepe dente vel lacinula aperta una alterave instructae. *Flores* vel perfecti, petalis omnibus bene evolutis, ad 30 mm diametro, laete lutei, vel imperfecti, petalis nonnullis vel omnibus abortivis. Sepala interdum 6, apice nigro-violacea. Stamina numerosa apicem capituli pistillorum fere aequantia. Carpella sat magna. Torus magnus, c. 6 mm longus, ovatus, pilosus. Carpellophora mediocriter longa. Intervallum nullum. Androclinium sursum crassius.

Ssp. *almquistii* could perhaps be classified under *R. fallax*. The occurrence of leafless sheaths, the relatively large size of the flowers and of the basal leaves and, to a certain extent, the configuration of the latter, point in this direction. Nevertheless, the almost linear form of the segments of the cauline leaves and their sparsity of toothing are in my opinion of greater classificatory significance.

Young, tender plants of ssp. *almquistii* and

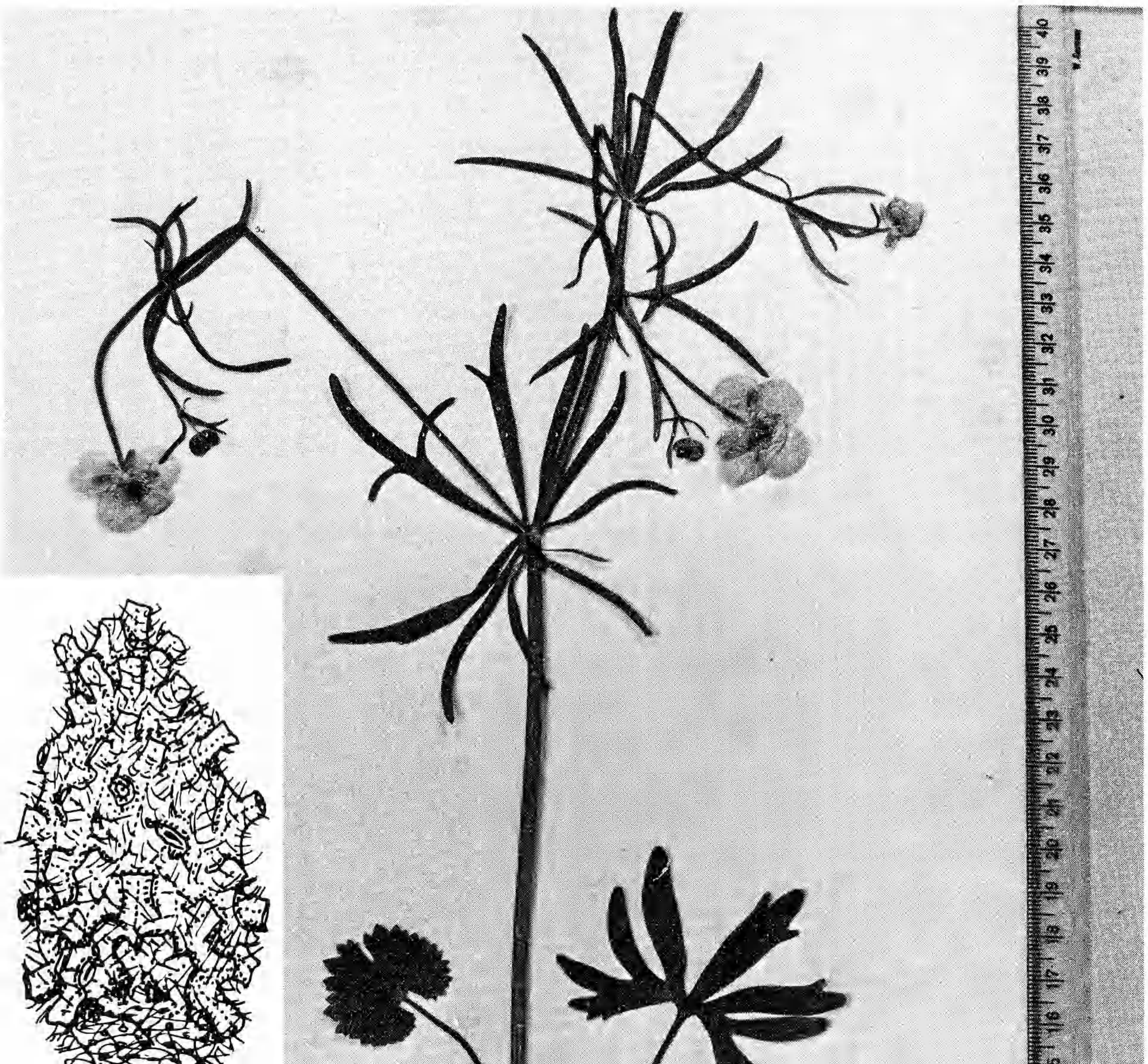


Fig. 1. *R. auricomus* ssp. *almquistii*. Holotype. – Left: Receptacle, × c. 10.

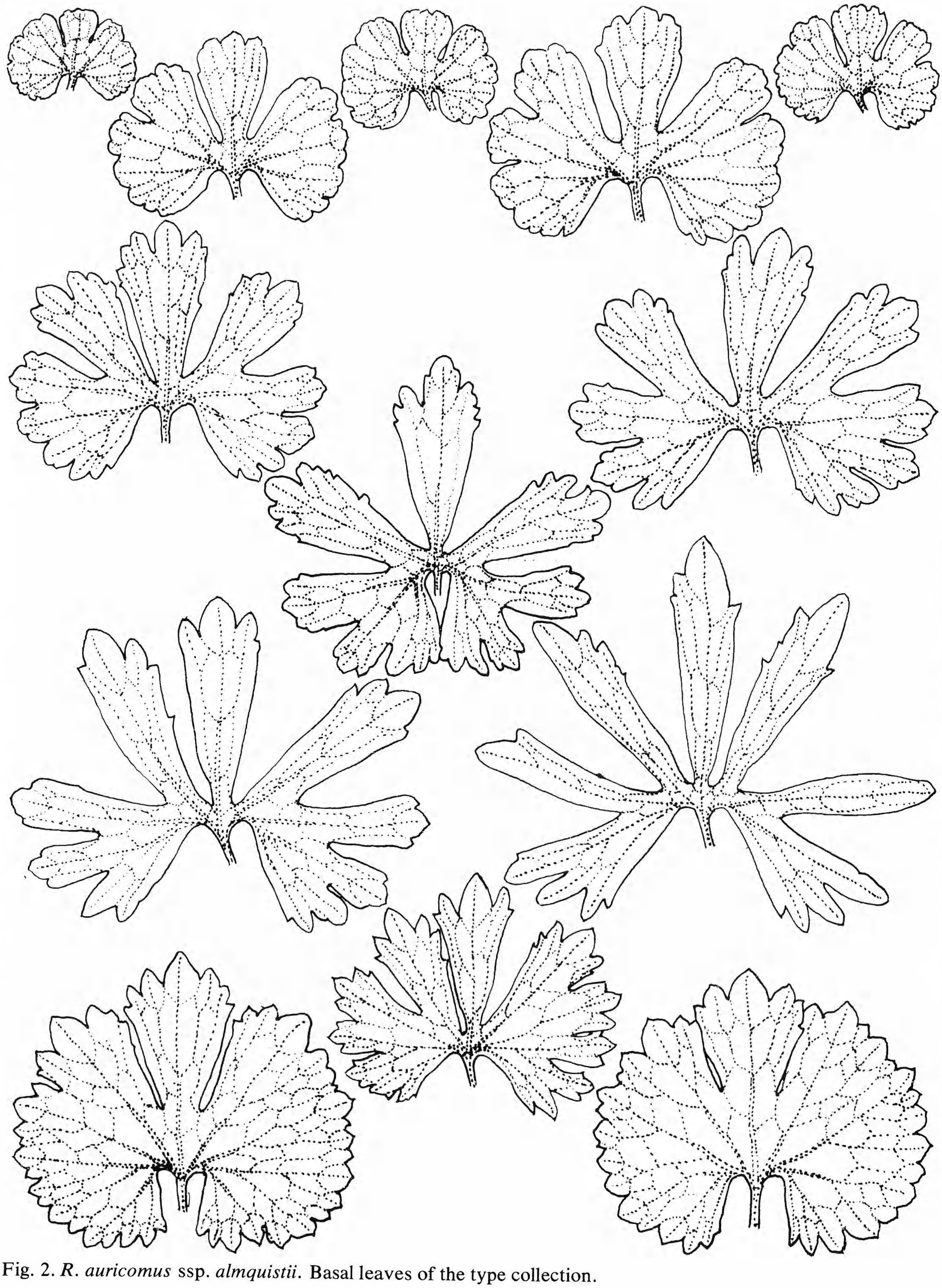


Fig. 2. *R. auricomus* ssp. *almquistii.* Basal leaves of the type collection.

Fig. 3. Known distribution of *R. auricomus* ssp. *almquistii.*

ssp. *marklundii* Nannf. & Julin may appear very similar, but can be distinguished from each other most easily by the receptacles; those of ssp. *marklundii* are more rounded and much more densely pubescent than those of ssp. *almquistii.* Before I had seen ssp. *almquistii* growing in nature I myself confused it with ssp. *marklundii* and some incorrect identifications exist in Julin (1965). In this paper they have been included in the locality list under their correct name and marked with an asterisk.

The subspecies is named in honour of Professor Erik Almquist (1892–1974) who has collected it many times.

Ecology: Most of the habitats are in the grounds of mansions, palaces and church-yards in the country, and in gardens and parks in towns and other built-up areas. The remaining localities can often be interpreted as secondary in relation to the first-mentioned kinds. The distribution of ssp. *almquistii* seems to be connected in some way with the garden and park culture of former times.

Localities (Fig. 3): Sweden: Srm 31, Nrk 1, Upl 3, Vsm 6.

R. auricomus L. ssp. **amoenoviridis** Julin ssp. nov.

Holotypus: Suecia, Dalecarlia, Sundborn, Skuggarvet 20.6.1965 R. Morander (UPS).

Planta mediocris vel sat alta. *Caules* plerumque erecti, subtus violacei, ramos sub angulo acuto emittentes. *Folia rosularia* amoene viridia, ambitu ± reniformia, sinu basali ± aperto. Folia exteriora parte adversa ± rubro-violacea, crenata, indivisa ad trilobata, lobo medio cuneato, lobis lateralibus indivisis vel leviter lobulatis. Folia intermedia ± acute mammiformi-dentata, multipartita, segmentis ± angustis, rotundate cuneatis, apice dilatatis, vel cuneatis vel lanceolatis, saepe petiolulatis. Folia interiora serrata, tripartita vel trilobata, segmento (lobo) medio cuneato, lateribus saepe inaequaliter dentatis, segmentis (lobis) lateralibus leviter lobulatis vel indivisis, marginibus lateralibus segmentorum (loborum) concavis, sinibus inter segmenta (lobos) saepe profunde inaequaliter incisis. Folia aestivalia ambitu fere quinquangularia, leviter trilobata, lobis latis, triangulariter vel mammiformiter dentatis. *Laciniae foliorum caulinorum* mediocres ad sat longae, lineares, obtusulae, integerrimae vel dentibus vel lacinulis patulis praeditae, saepe sat numerosae; vaginae basales foliorum caulinorum extra rubellae. *Flores* plerumque perfecti, petalis omnibus evolutis, ad 20 mm diametro. Sepala apice plerumque rubroviolacea. Stamina numerosa apicem capituli pistillorum superantia. Styli breves, sat erecti. Torus obovatus; gynoclinium glabrum vel paene glabrum, carpellophoris apice mediocribus, basi brevioribus; intervallum glabrum, androclinio dense piloso longius.

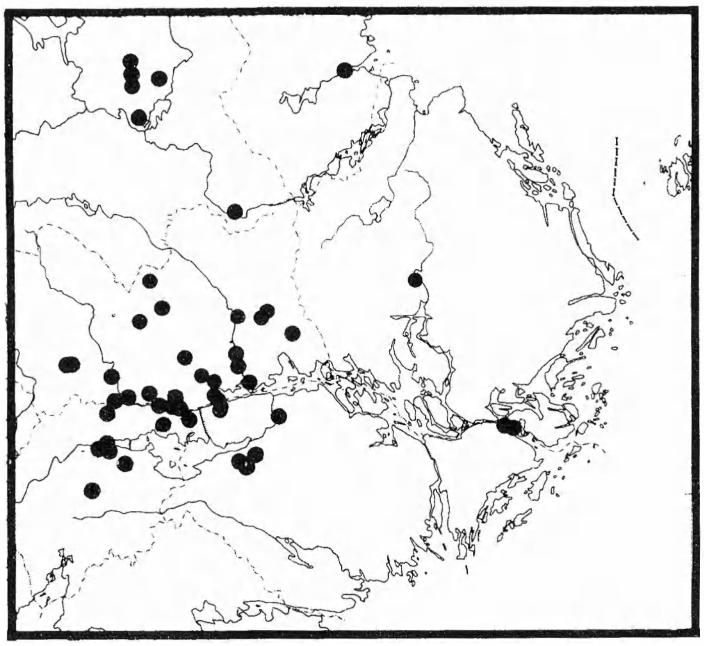


Fig. 4. Known distribution of *R. auricomus* ssp. *amoenoviridis.*

Ecology: This subspecies occurs on lawns and other grassy areas in gardens and parks, on roadsides, in ditches, on pastures, margins of man-made habitats, dry or damp meadows, forest meadows, edges of woods or thickets, in aspen or alder groves, in mixed deciduous and coniferous forests, on drained woodland marshes, and on river and lake shores.

Localities (Fig. 4): Malmgren 1970 (nom. nud.). – *New localities:* Sweden: Srm 8, Nrk 11, Upl 1, Vsm 28, Gstr 1, Dlr 6.

R. auricomus L. ssp. **caespitosulus** Julin ssp. nov.

Holotypus: Suecia, Vestmannia, Malma, in querceto sicco juxta viam 1 km a NW parte templi 28.5.1977 Julin (UPS).

Planta parva, caespitosa. *Caules* saepe arcuatim curvati. Folia laete et amoene viridia. *Folia rosularia* ambitu reniformia ad fere orbicularia. Folia exteriora tripartita, segmento medio late cuneato, apice crena apicali lata et dentibus lateralibus parvis uno alterove instructo, segmentis lateralibus bilobatis, lobo anteriore segmento medio simili, lobo posteriore lobulato, lobulis integerrimis. Folia intermedia foliis exterioribus similia, sed crena apicalis segmenti medii in dentem longum mammiformem mutata et segmenta saepe paulum petiolulata. Folia aestivalia ± acute mammiformiter vel triangulariter dentata, partita, lobata vel leviter solum incisa. *Laciniae foliorum caulinorum* breves, lineari-lanceolatae, obtusulae, integerrimae vel – in folio infimo – apicem versus dilatatae et saepe breviter dentatae. *Flores* valde imperfecti, petalis omnibus vel plurimis abortivis. Sepala apice rubroviolacea. Stamina sat numerosa apicem capituli pistillorum parvi, globosi superantia. Torus acute ovatus, c. 4 mm longitudine. Gynoclinium glabrum, carpellophoris mediocriter longis. Intervallum nullum. Androclinium rare breviter pilosum.

Sweden: Västmanland. Malma, dry slope with oaks at the main road 1 km NW of the church 1977 E. Julin (holotype).

R. auricomus L. ssp. **dissimilifolius** Julin ssp. nov.

Holotypus: Suecia, Vestmannia, Kärrbo, juxta templum 4.6.1977 Julin (UPS).

Planta mediocris ad sat alta. *Caules* erecti, inferne violacei, ramos sub angulo sat acuto emittentes. Diversa genera foliorum rosulariorum et figurae marginum eorum maximas dissimilitudines praebent. *Folia* exteriora trilobata, lobo medio rotundate cuneato, lobis lateralibus incisis, lobis crenatis. Folia sequentia tripartita, segmento medio longo, lanceolato vel cuneato, segmentis lateralibus profunde lobulatis; dentes apicales et apices segmentorum, loborum lobulorumque foliorum illorum et sequentium obtusi vel rotundati, dentes laterales parvi, plerumque acuti. Folia intermedia quinque- vel septempartita, segmentis longis, lanceolatis, ± petiolulatis, sinu basali peraperto. Folia interiora tripartita, sinu basali angusto, segmento medio cuneato vel sat late lanceolato, petiolulato, segmentis lateralibus iterim partitis, segmentulis lobulatis vel dentatis. Folia aestivalia tripartita, segmento medio lanceolato, segmentis lateralibus latis, ± profunde lobulatis, sinu basali marginibus paene parallelis, denique foliis exterioribus magis magisque similia. *Laciniae foliorum caulinorum* mediocres ad sat longae, lineari-lanceolatae, obtusulae, integerrimae vel interdum dente vel lacinula una alterave praeditae. *Flores* sat perfecti, petalis plurimis bene evolutis, ad 16 mm diametro. Sepala apice rubroviolacea. Stamina sat pauca, apicem capituli pistillorum fere aequantia. Styli fere recta. Torus ovatus, c. 4 mm longitudine. Gynoclinium prasinulum, modice pilosum, carpellophoris mediocriter longis, pilosis. Intervallum nullum. Androclinium dense pilosum.

Sweden: Västmanland. Kärrbo, at the church 1977 E. Julin (holotype). – Kungs-Barkarö, Norra Kungsladugården, damp depression in deciduous forest 1972 T. Sundin.

R. auricomus L. ssp. **erectus** Julin ssp. nov.

Holotypus: Suecia, Ostrogothia, Kärna, margine viae publicae a SW parte templi 800 m 20.5.1964 Julin (UPS).

Planta mediocriter alta. *Caules* saepe plurimi, sat crassi, erecti, ramos sub angulo acuto emittentes. *Folia rosularia* exteriora ambitu orbicularia, multipartita, segmentis sese partim obtegentibus, late rotundatis, basi angustis, crenatis, sinu basali marginibus parallelis. Folia intermedia ambitu reniformia, multipartita, segmentis petiolulatis, cuneatis, rotundate vel acute mammiformiter dentatis, sinu basali aperto. Interdum folium sequens valde dissectum, segmentis segmentulisque cuneatis vel lanceolatis, acute dentatis, longe petiolulatis. Folia interiora foliis intermediis similia, segmentis tamen angustioribus et acutius dentatis. Folia aestivalia utrimque passim parce pilosa, tripartita, segmento medio ± late lanceolate cuneato, dente apicali triangulari, acuto, magno et dentibus lateralibus similibus minoribus instructo, segmentis lateralibus iterim partitis vel lobatis, acute dentatis. *Laciniae foliorum caulinorum* plurimae mediocriter longae, lineari-lanceolatae, apice dilatatae, integerrimae vel – saepe in folio infimo – dentibus vel lacinulis reflexis nonnullis praeditae. *Flores* vel perfecti, ad 20 mm diametro, vel imperfecti, petalo uno alterove abortivo, petalis prae ceteris subspeciebus angustis. Sepala sat magna, luteoviridia. Stamina numerosa, capitulo pistillorum magno mox breviora. Torus magnus, c. 6 mm longitudine, oblongus, glaber. Carpellophora mediocriter longa. Intervallum 0,7 mm, androclinium 0,5 mm longitudine.

Ecology: In Sweden the moderately hemerophilous ssp. *erectus* is common in the central parts of northern Götaland, especially on and around Mt Omberg, in Falbygden and at the south end of the lake Vättern. It is also present in the neighbourhood of Gothenburg and – in Norway – several localities exist near the Oslo fjord. In Sweden the northern boundary runs along the lakes Hjälmaren and Mälaren. It is remarkable that this subspecies seems to be entirely absent from southern Götaland. It is clear that this goldilocks thrives on the calcareous soils of the Cambro-Silurian areas, but these are also districts with ancient cultural traditions, and historical factors have probably been more important in producing the present

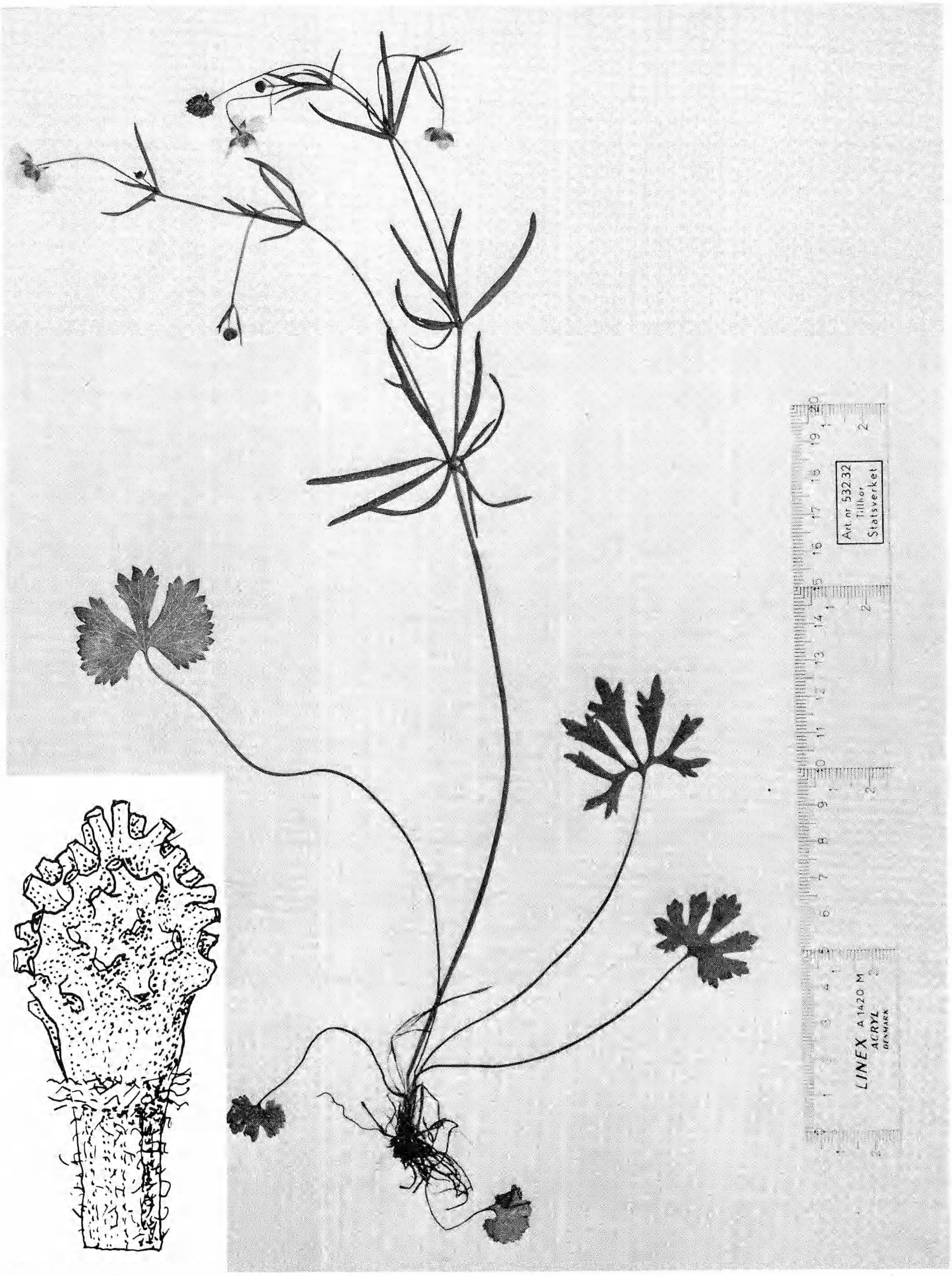


Fig. 5. *R. auricomus* ssp. *amoenoviridis*. Holotype. – Below left: Receptacle, × 10.

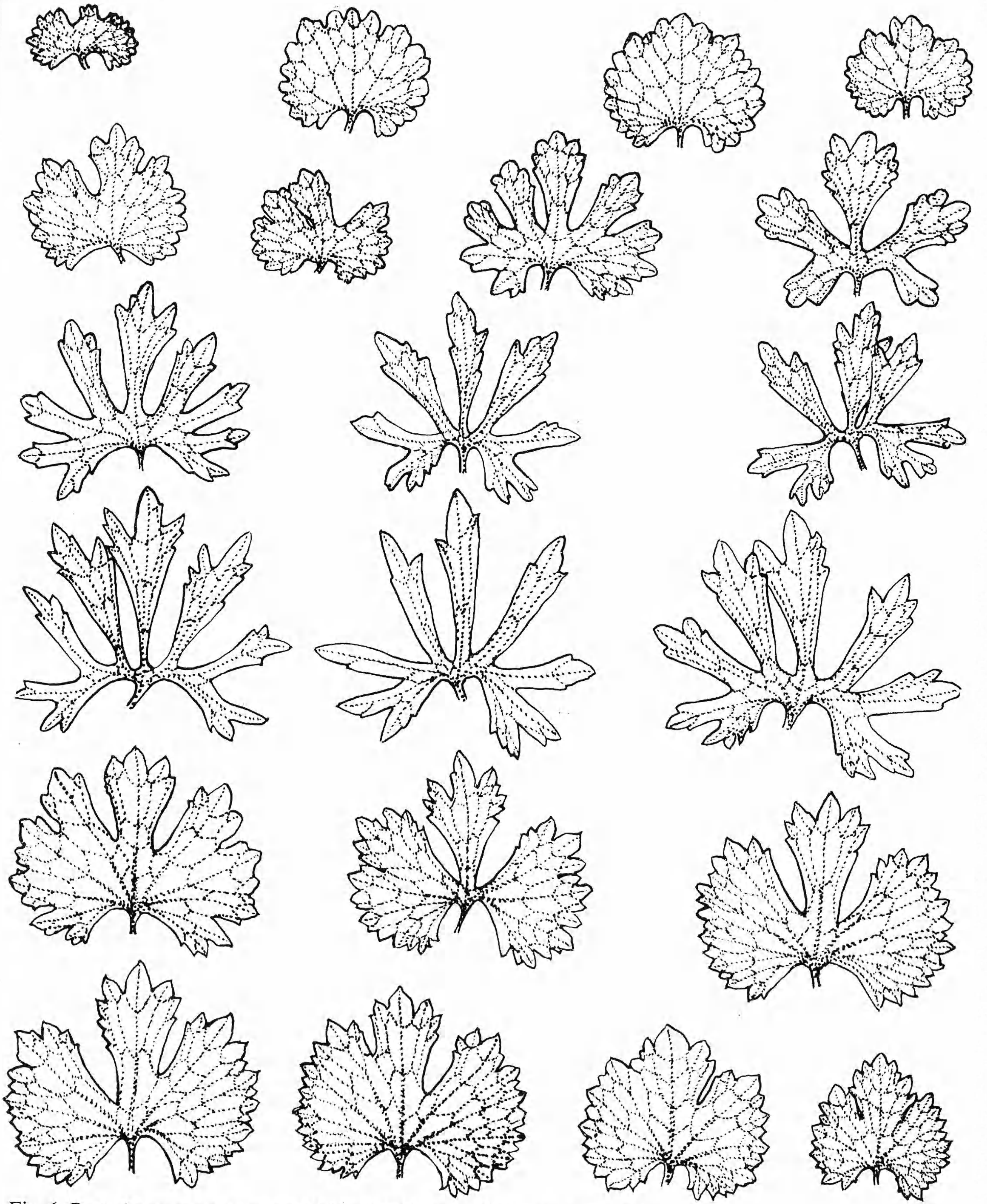


Fig. 6. *R. auricomus* ssp. *amoenoviridis*. Basal leaves of the type collection.

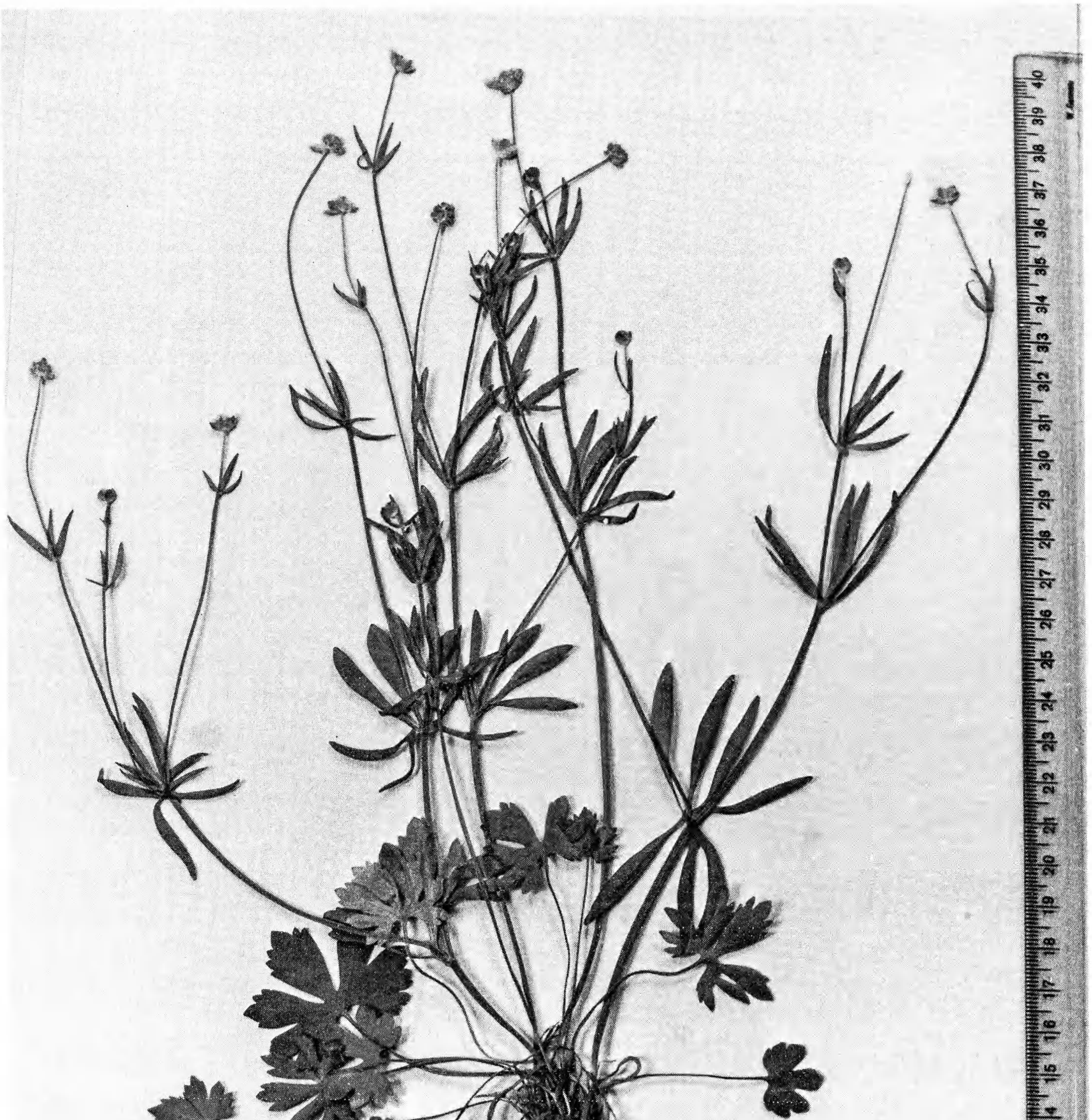


Fig. 7. *R. auricomus* ssp. *caespitosulus*. Holotype.

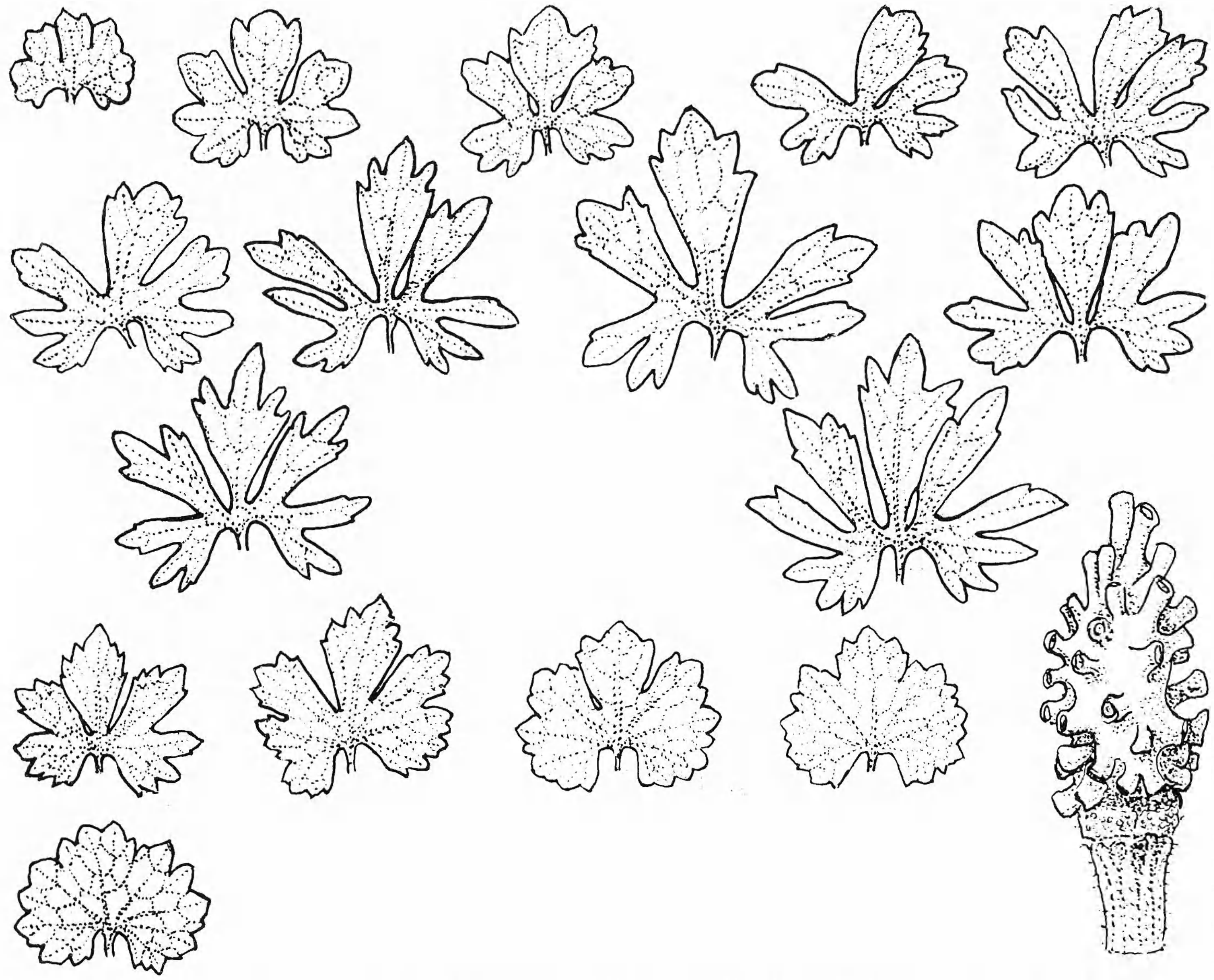


Fig. 8. *R. auricomus ssp. caespitosulus.* Basal leaves of the type collection. – Below right: Receptacle, × 10.

disjunct distribution of the subspecies than edaphic factors.

Localities (Fig. 13): Denmark: Jl 1. Sweden: Gtl 1, Sm 12, Hl 1, Ög 13, Vg 28, Bh 1, Nrk 2, Vsm 3. Norway: Östf 2, Vestf 2, Akh 5.

R. auricomus L. ssp. **expansus** Julin ssp. nov.

Holotypus: Suecia, Vestmannia, Berg, Åsby, in pascuo consaepto 11.6.1969 U. Malmgren 29 (UPS).

Planta mediocriter alta, saepe sat robusta, foliis obscure viridibus. *Caules* vel erecti vel curvati. *Folia rosularia* exteriora ambitu semiorbicularia ad reniformia, late triangulariter vel rotundate dentata vel lobata. Folia intermedia reniformia, sinu basali aperto, tripartita, segmento medio cuneato vel rotundate cuneato, segmentis lateralibus ± profunde lobatis, segmentis sese partim obtegentibus, late triangulariter vel rotundate dentatis, interdum petiolulatis. Folia aestivalia ambitu orbicularia, sinu basali marginibus parallelis, ± profunde multilobata, incisuris inter lobos

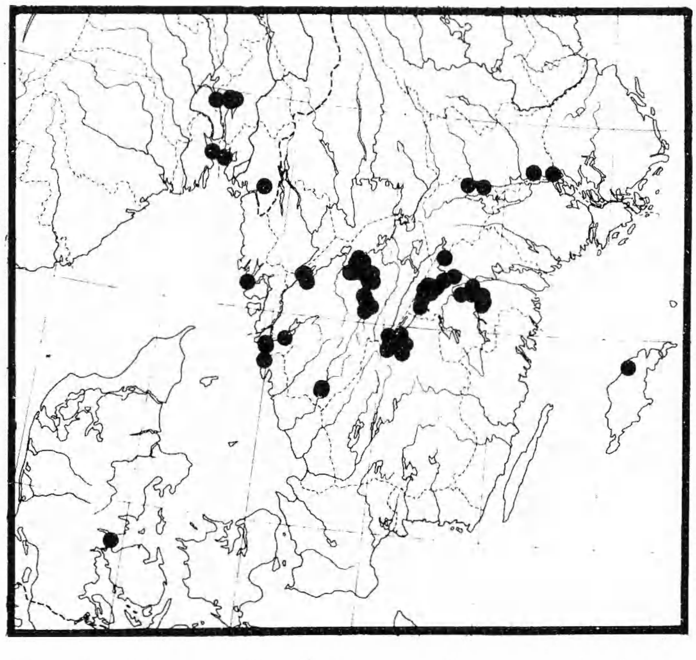


Fig. 13. Known distribution of *R. auricomus* ssp. *erectus.*

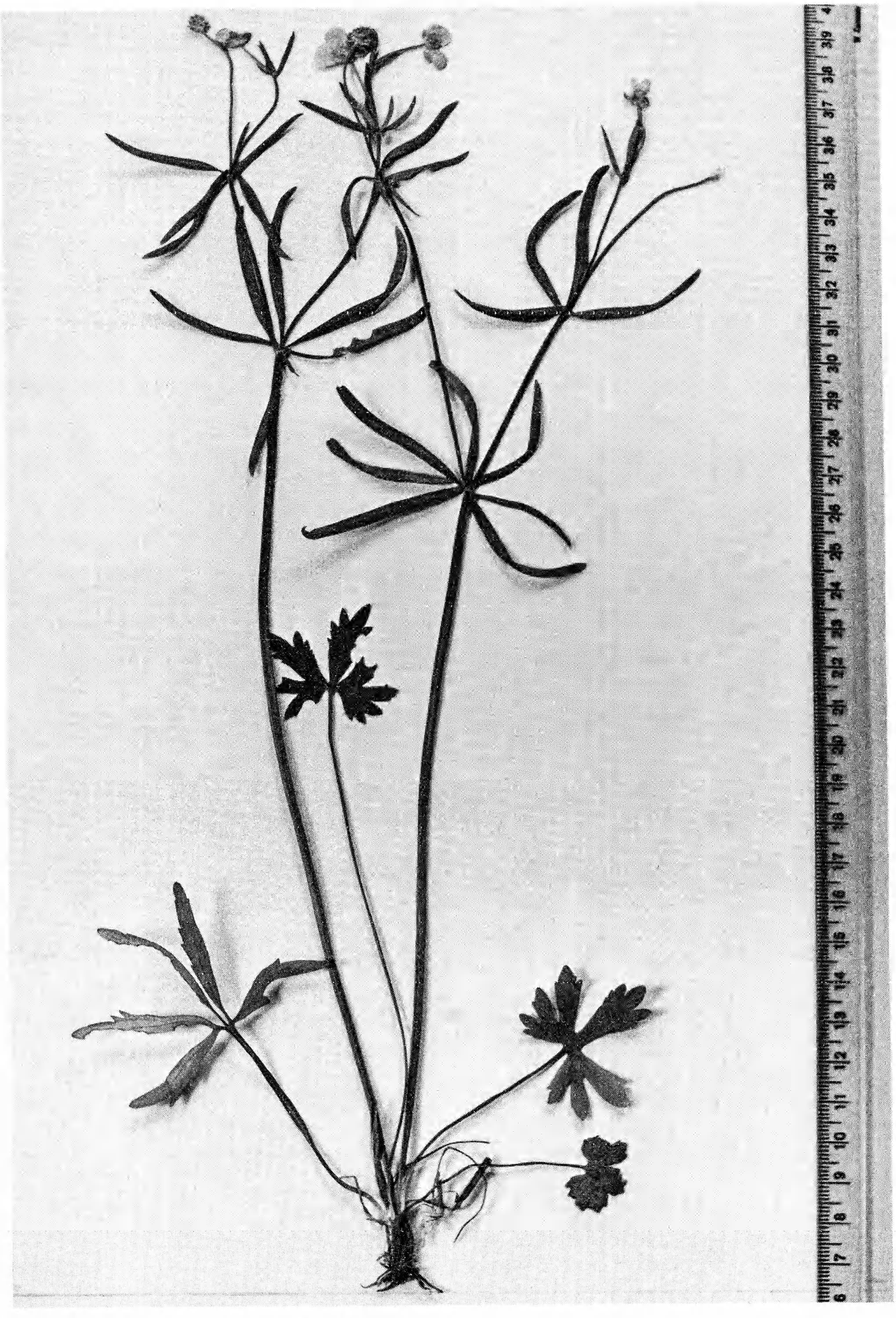


Fig. 9. *R. auricomus* ssp. *dissimilifolius*. Holotype.

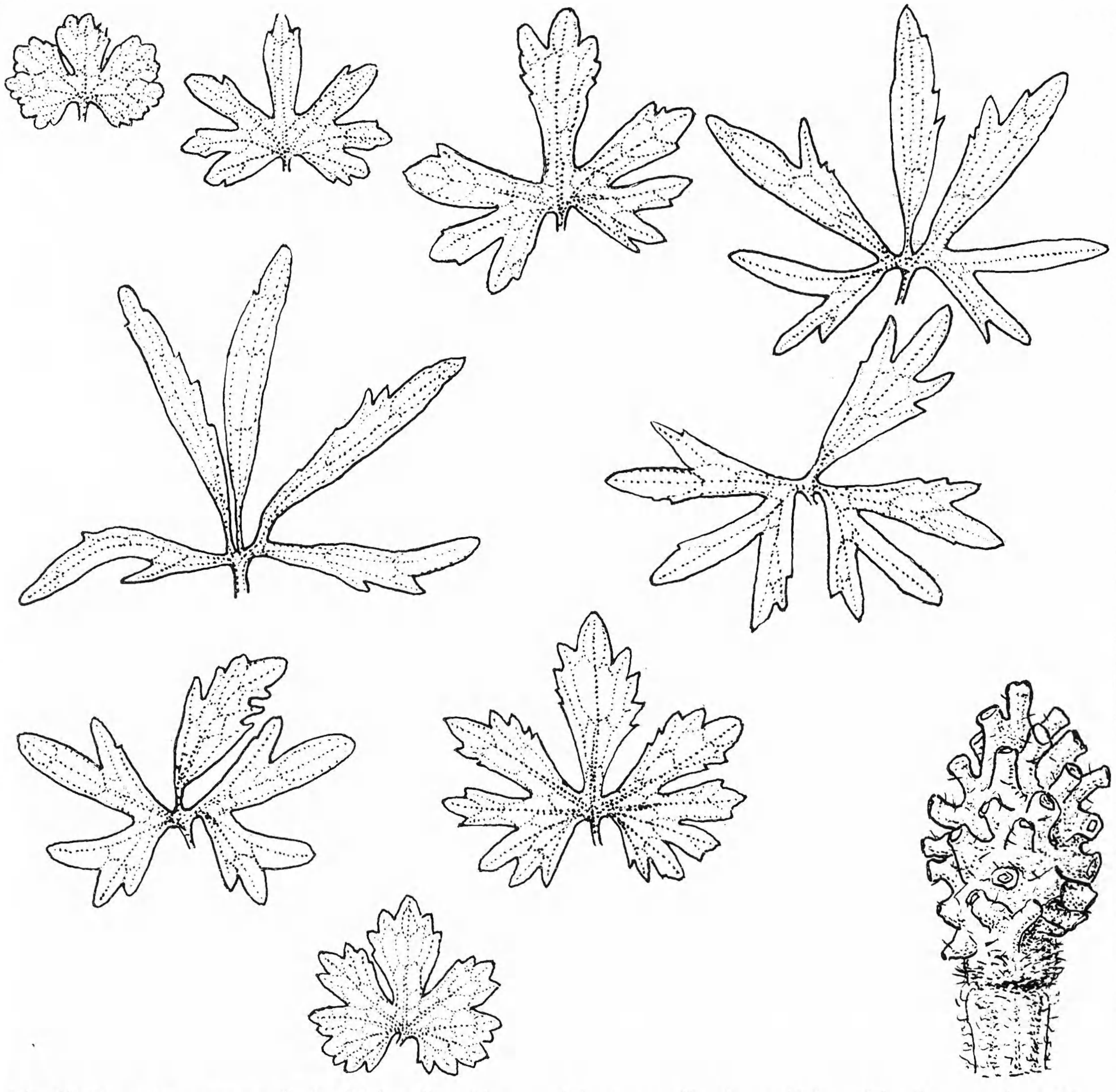


Fig. 10. *R. auricomus* ssp. *dissimilifolius*. Basal leaves of the type collection. – Below right: Receptacle, × 10.

angustis, lobis triangulariter dentatis, dente apicali magno, dentibus lateralibus minoribus. *Laciniae foliorum caulinorum* mediocriter longae, ± late lineari-lanceolatae, obtusulae, integerrimae vel interdum dente lato brevique uno alterove praeditae. *Flores* vel perfecti, petalis omnibus bene evolutis, ad 17 mm diametro, vel imperfecti, petalis plurimis vel omnibus abortivis. Sepala pallida, apice obscure fulva. Stamina sat numerosa apicem capituli pistillorum fere aequantia. Torus acute ovatus, 4 ad 6 mm longitudine. Gynoclinium glabrum. Carpellophora brevia vel mediocriter longa. Intervallum nullum. Androclinium pilosum.

Sweden: Västmanland. Berg, brook-side pasture 1969 U. Malmgren 40, 41; Jolsterhagen (previously a paddock) 1969 U. Malmgren 51; Norrby, a former paddock 1969 U. Malmgren 48; Åsby, enclosed pasture 1969 U. Malmgren (holotype). – Dingtuna, pasture near the church 1977 U. Malmgren 377. – Viker, hillock at the road fork to Norra Viker 1970 T. Sundin.

R. auricomus L. ssp. **hallstaënsis** Julin ssp. nov.

Holotypus: Suecia, Vestmannia, Berg, Skansön ad Hallstahammar, in ripa fluminis 10.6.1969 U. Malmgren 20 (UPS).

Planta mediocris ad sat alta. *Caules* erecti vel subtus aliquanto curvati. *Folia rosularia* ambitu reniformia vel paene semiorbicularia, sinu basali aperto vel peraperto. Folia exteriora trilobata, lobo medio cuneato, apice tridentato, lobis lateralibus latis, rotundate lobulatis

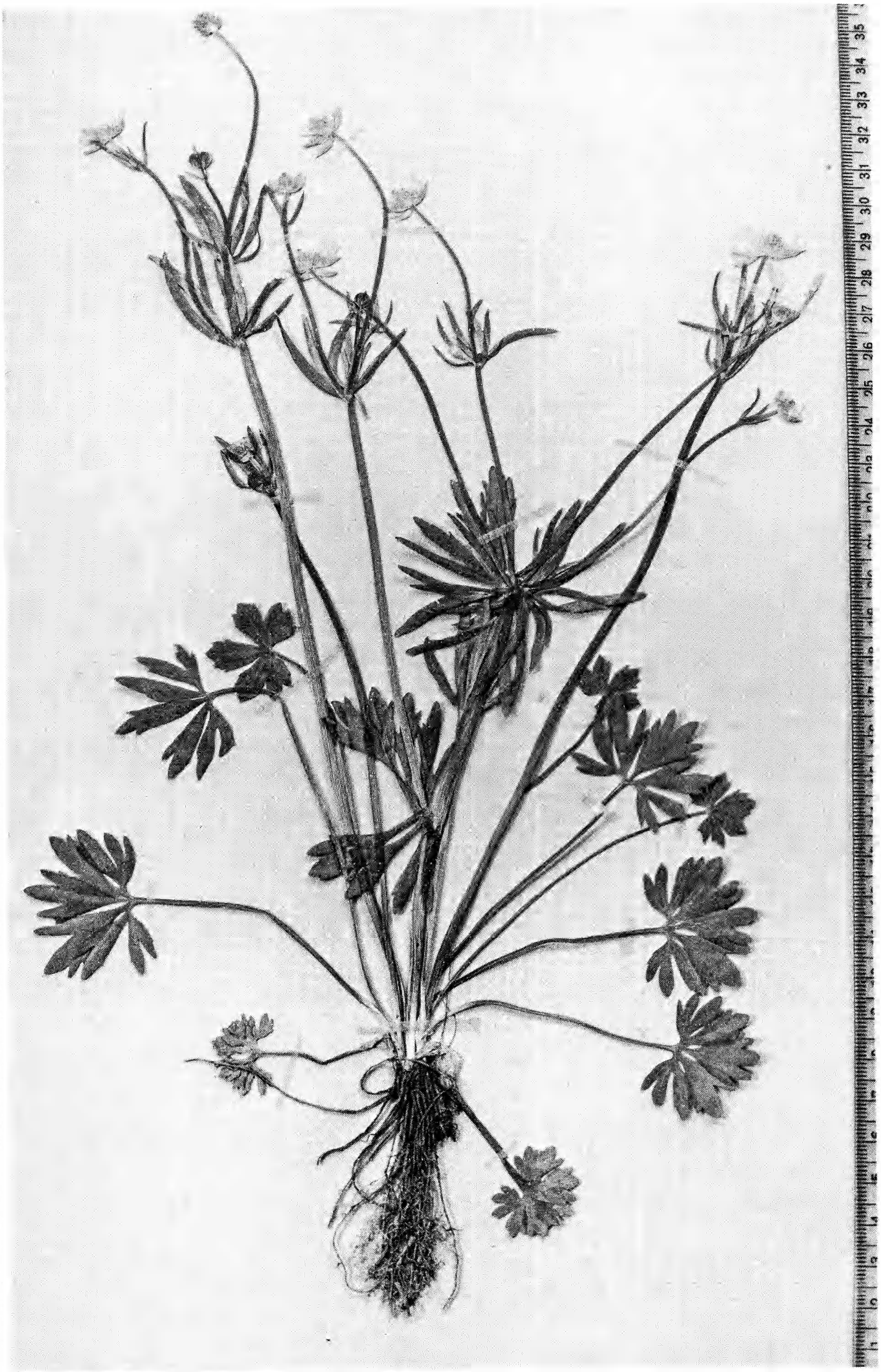


Fig. 11. *R. auricomus* ssp. *erectus*. Holotype.

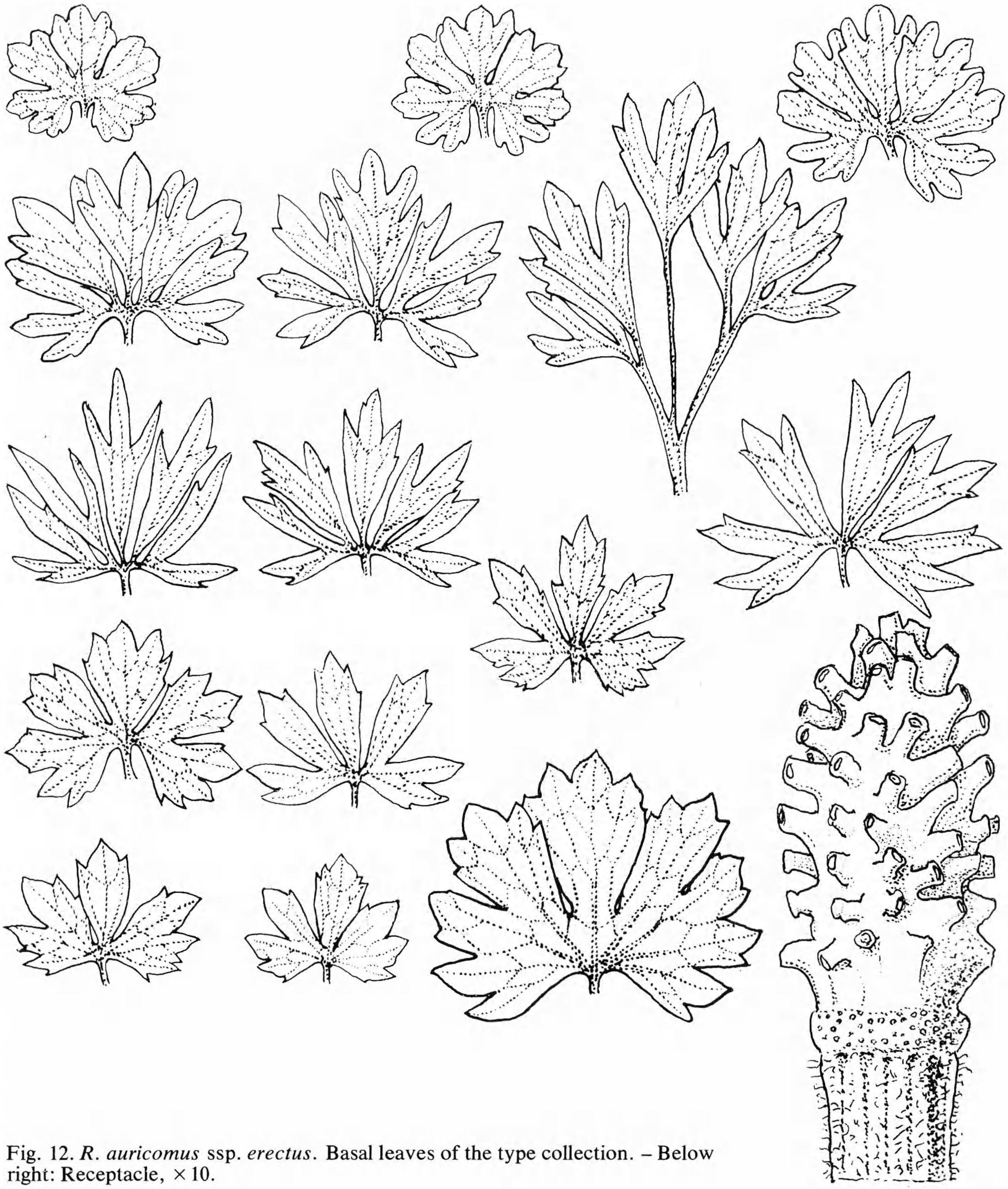


Fig. 12. *R. auricomus* ssp. *erectus*. Basal leaves of the type collection. – Below right: Receptacle, × 10.

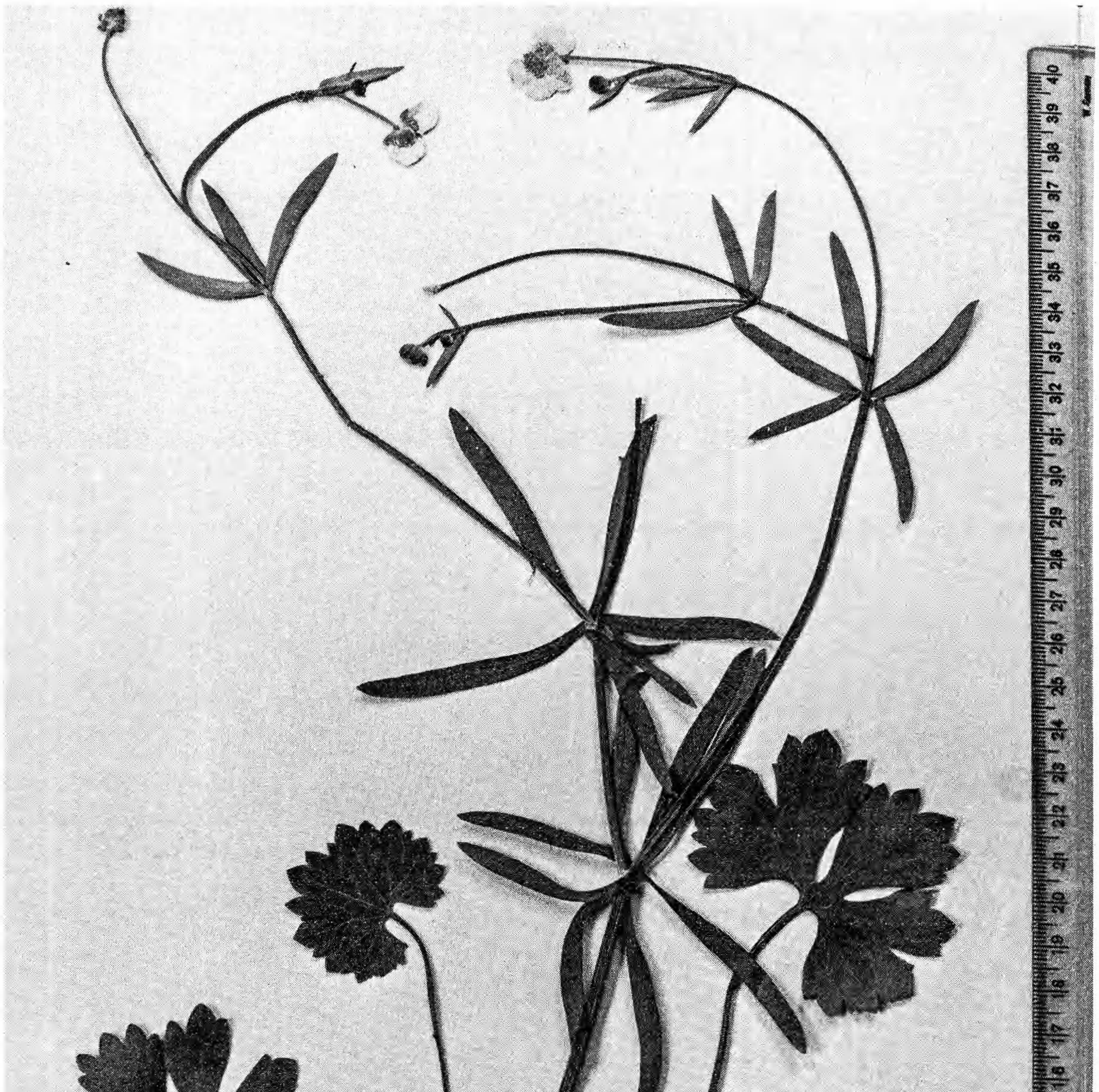


Fig. 14. *R. auricomus* ssp. *expansus*. Holotype.

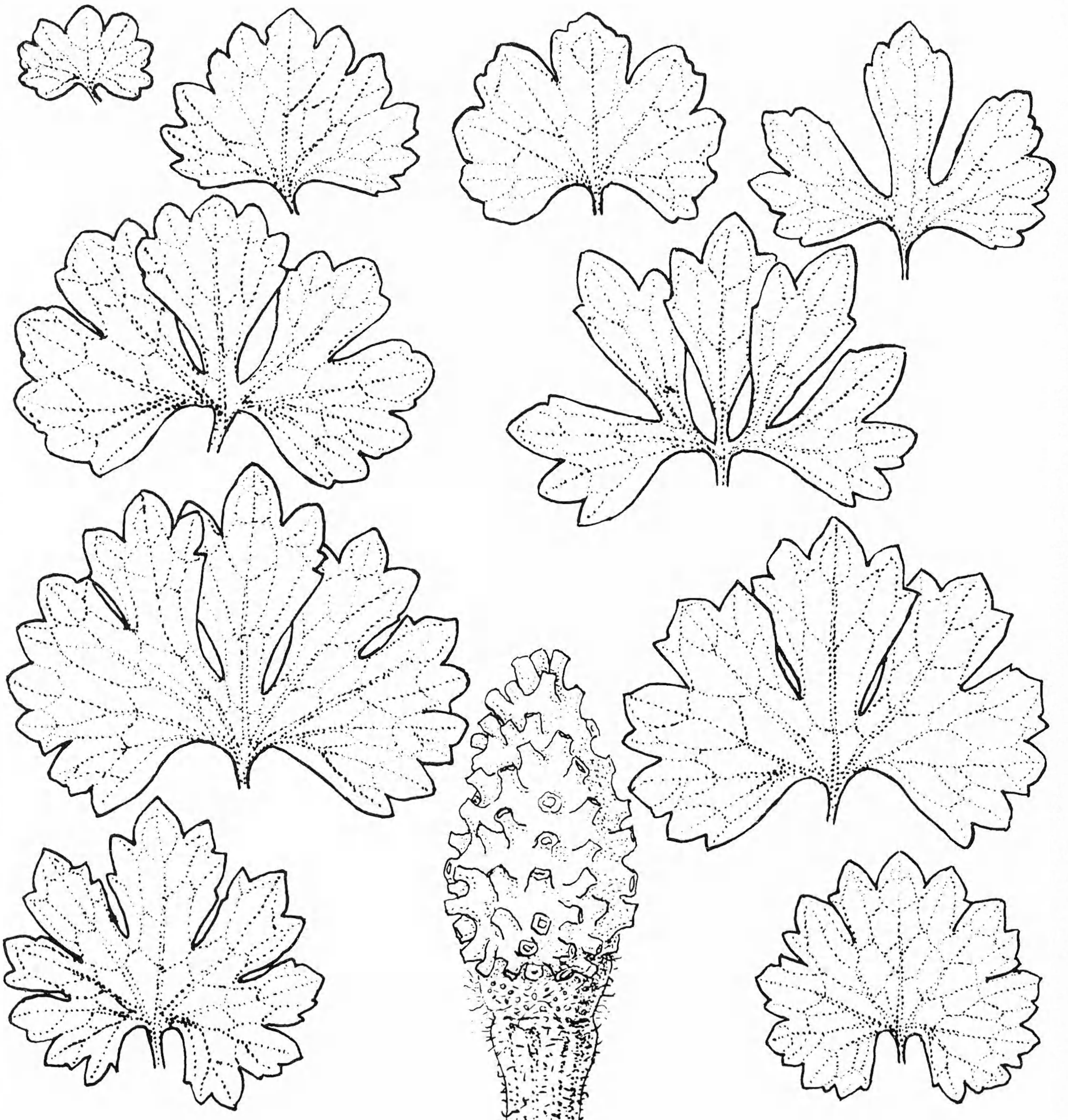


Fig. 15. *R. auricomus* ssp. *expansus*. Basal leaves of the type collection. – Below in the middle: Receptacle, ×10.

vel dentatis. Folia intermedia quinquepartita, segmentis mediis tribus porrectis, cuneatis vel lanceolatis, dentatis vel integerrimis, ceteris transversalibus, lobulatis; segmentis saepe petiolulatis. Folia aestivalia triangulariter dentata, trilobata, lobo medio late cuneato, incisuris inter lobos angustis, lobis lateralibus leviter incisis. *Laciniae foliorum caulinorum* mediocriter longae lataeque, lineari-lanceolatae, obtusulae, integerrimae vel – in folio infimo – dente vel lacinula una alterave praeditae et etiam petiolulatae. *Flores* sat perfecti, petalis nonnullis vel plurimis bene evolutis, ad 20 mm diametro. Sepala viridia, apice languide fulva. Stamina sat pauca, apicem capituli pistillorum fere aequantia. Torus oblongus, c. 5 mm longitudine. Pars apicalis gynoclinii glabra, pars basalis parcissime pilosa. Carpellophora mediocriter longa. Intervallum parcissime pilosum. Androclinium sat dense pilosum.

Sweden: Västmanland. Berg, Skansön at Hallstahammar, river bank 1969 U. Malmgren 20 (holotype).

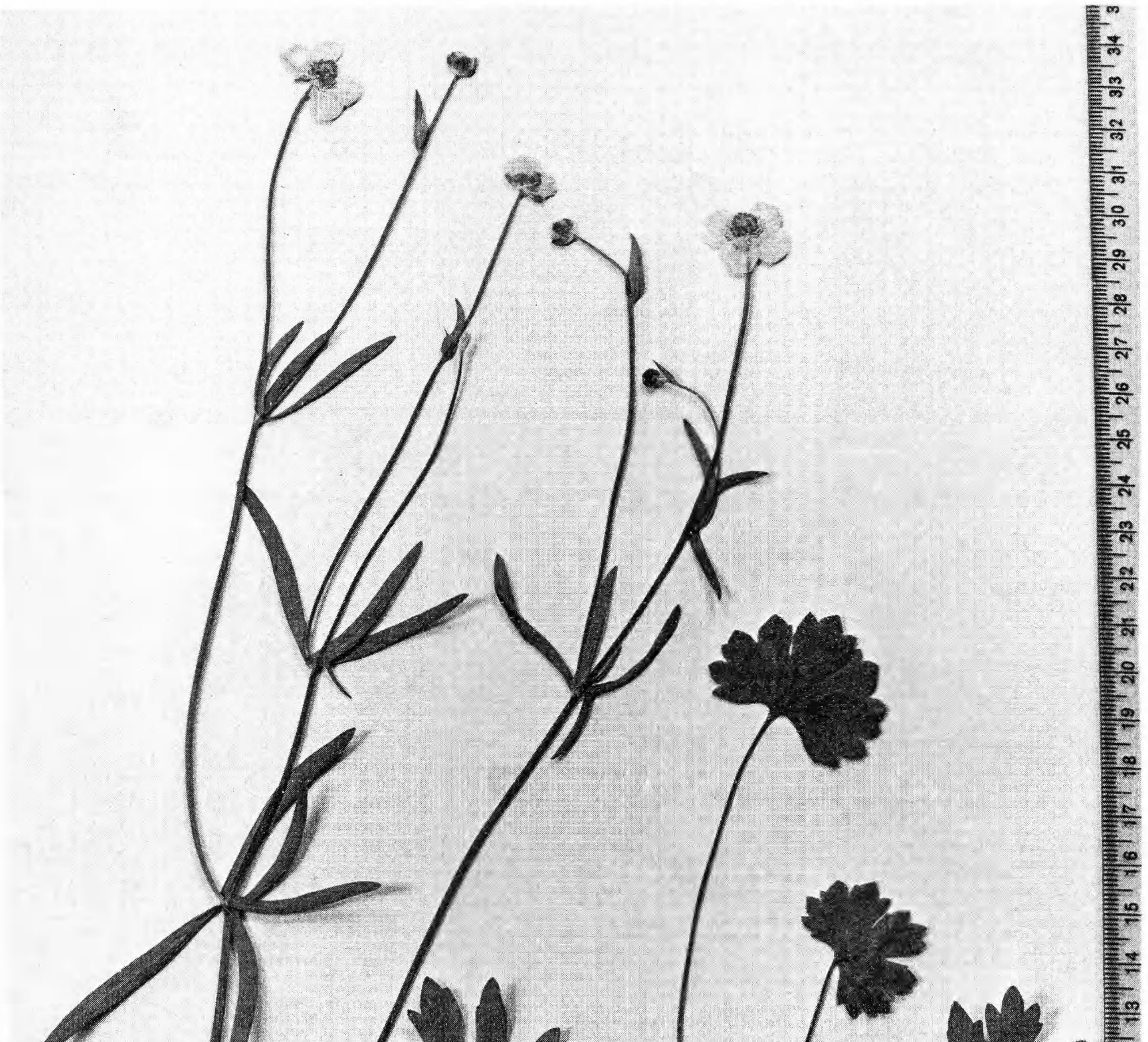


Fig. 16. *R. auricomus* ssp. *hallstaënsis*. Holotype.

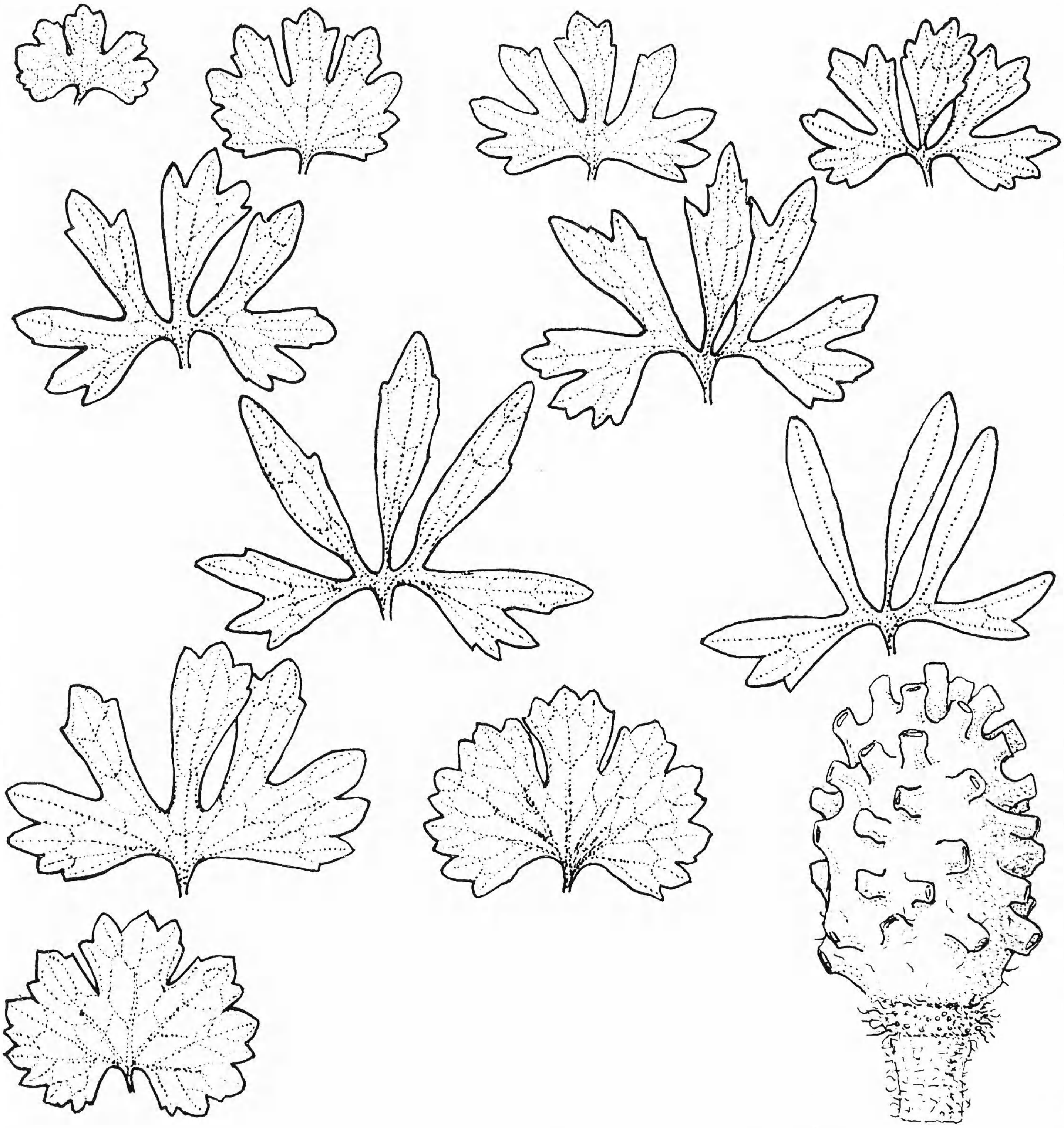


Fig. 17. *R. auricomus* ssp. *hallstaënsis*. Basal leaves of the type collection. – Below right: Receptacle, × 10.

R. auricomus L. ssp. **inconcinnus** Julin ssp. nov.

Holotypus: Suecia, Vestmannia, Svedvi, Hammarängen, in prato juxta flumen Kolbäcksån 11.6.1969 U. Malmgren 23 (UPS).

Planta mediocriter alta, canoviridis. *Caules* erecti, ramos sub angulo acuto emittentes. *Folia rosularia* sinu basali peraperto, saepe inconcinna, exteriora minutissima, cetera mediocria. Folia exteriora apice lobata, lobis integerrimis vel dentibus singularibus praeditis, basi obtuse dentata. Folia sequentia tripartita, segmento medio cuneato ad lanceolato, apice parce dentato, segmentis lateralibus bilobulatis, lobulis anterioribus segmento medio similibus, lobulis posterioribus latioribus, sinibus inter lobulos sat apertis, segmentis saepe petiolulatis. Folia intermedia tripartita vel trilobata, segmento (lobo) medio leviter cuneato, segmentis (lobis) lateralibus latis, mammiformiter dentatis vel paulum incisis. Folia aestivalia fere orbicularia,

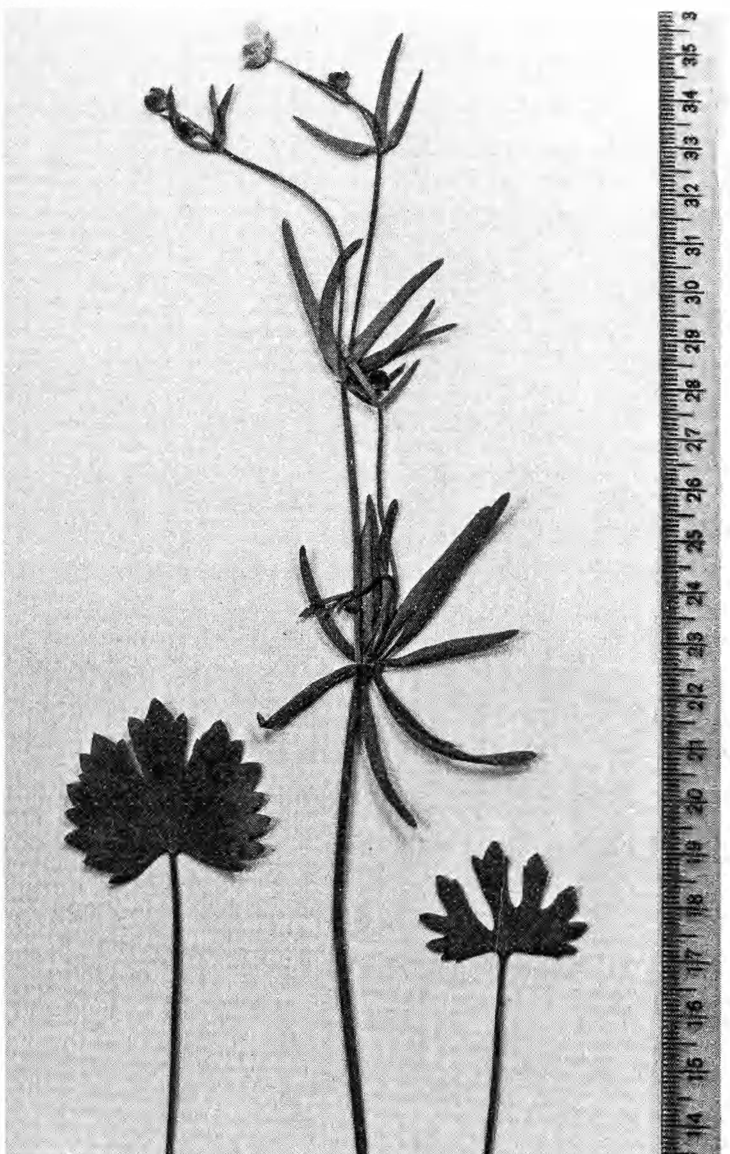


Fig. 18. *R. auricomus* ssp. *inconcinnus*. Holotype.

± acute mammiformiter dentata vel apice leviter incisa. *Laciniae foliorum caulinorum* mediocriter longae lataeque, lineari-lanceolatae, obtusulae, plerumque integerrimae. *Flores* valde imperfecti, petalis plurimis plerumque abortivis. Stamina sat numerosa apicem capituli pistillorum fere aequantia. Torus obovatus ad oblongus, 3 ad 3,5 mm longitudine. Carpellophora mediocriter longa. Gynoclinium et intervallum parcissime pilosa. Androclinium dense pilosum, intervallo dimidio brevius.

Sweden: Västmanland. Fellingsbro, Kåfalla, in deciduous forest surrounding the farm 1977 U. Malmgren 390. – Svedvi, meadow S of Åby 1969 U. Malmgren 11; Hammarängen, riverside meadow at Kolbäcksån 1969 U. Malmgren 23 (holotype).

R. auricomus L. ssp. **inconspectiflorus** Julin ssp. nov.

Holotypus: Suecia, Vestmannia, Romfartuna, juxta templum 29.5.1977 Julin (UPS).

Planta mediocriter alta. *Caules* plerumque curvati, sat graciles, inferne violacei, ramos sub angulo acuto emittentes. *Folia rosularia* exteriora ambitu reniformia, sinu basali peraperto, lobata, lobo medio cuneato, basi lato, apice tridentato, dente apicali lato, fere truncato, lobis lateralibus integerrimis. Folia intermedia foliis exterioribus similia, partita tamen et segmentis anterioribus tribus ± longe mammiformiter dentatis instructa. Folia sequentia acutius dentata. Folia aestivalia ambitu orbicularia, sinu basali angusto, trilobata, lobo medio cuneato, basi lato, apice sensim fere truncato, lobis lateralibus latis, leviter lobulatis, lobis (lobulis) irregulariter crenatis vel triangularidentatis. *Laciniae foliorum caulinorum* mediocres ad breves, lineari-lanceolatae, basin versus latissimae, obtusulae, plerumque integerrimae. *Flores* valde inconspecti, petalis omnibus vel plurimis abortivis. Sepala apice rubro-violacea. Stamina numerosa apicem capituli pistillorum non attingentia. Torus parvus, oblongus. Gynoclinium glabrum, carpellophoris sat brevibus. Intervallum breve, glabrum. Androclinium dense pilosum. (Tori novelli solum visi.)

Sweden: Västmanland. Romfartuna, at the church 1977 E. Julin (holotype).

R. auricomus L. ssp. **longimammus** Julin ssp. nov.

Holotypus: Suecia, Sudermannia, Mellösa, Skiringe, in hortis 3.6.1964 Julin (UPS).

Planta mediocriter alta. *Caules* inferne plerumque curvati, subtus cinereo-violacei, ramos sub angulo sat acuto emittentes; caules laterales inferne saepe pilosi. *Folia rosularia* ambitu reniformia, sinu basali peraperto. Folia exteriora trilobata vel tripartita, lobis (segmentis) crenatis vel crenate lobulatis. Folia intermedia tripartita, segmentis saepe petiolulatis, interdum curvatis, segmento medio cuneate lanceolato vel lanceolato, dentibus longis vel lacinulis obtuse mammiformibus instructis, segmentis lateralibus bilobatis vel bi-

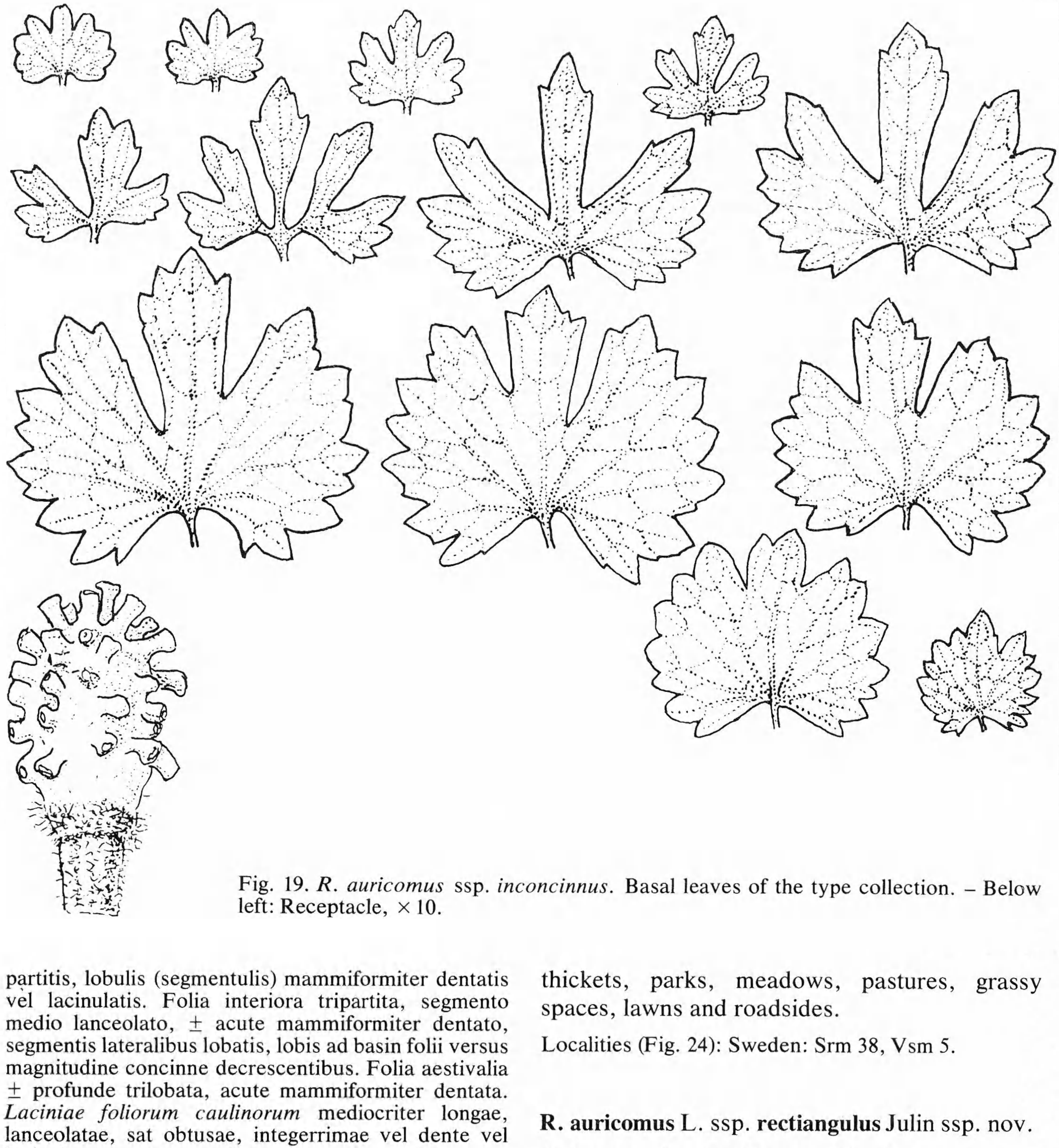


Fig. 19. *R. auricomus* ssp. *inconcinnus*. Basal leaves of the type collection. – Below left: Receptacle, × 10.

partitis, lobulis (segmentulis) mammiformiter dentatis vel lacinulatis. Folia interiora tripartita, segmento medio lanceolato, ± acute mammiformiter dentato, segmentis lateralibus lobatis, lobis ad basin folii versus magnitudine concinne decrescentibus. Folia aestivalia ± profunde trilobata, acute mammiformiter dentata. *Laciniae foliorum caulinorum* mediocriter longae, lanceolatae, sat obtusae, integerrimae vel dente vel lacinula porrecta una alterave praeditae. *Flores* perfecti, petalis plerumque omnibus bene evolutis, c. 17 mm diametro. Sepala apice rubro-violacea. Stamina numerosa capitulum pistillorum rotundum superantia. Torus parvus, rotundate oblongus. Gynoclinium parcissime pilosum vel paene glabrum, carpellophoris mediocribus vel sat longis. Intervallum nullum. Androclinium dense breviter pilosum.

Ecology: Ssp. *longimammus* appears to prefer somewhat drier habitats than the majority of goldilocks subspecies, such as forest meadows, enclosed pastures with scattered oaks, sloe thickets, parks, meadows, pastures, grassy spaces, lawns and roadsides.

Localities (Fig. 24): Sweden: Srm 38, Vsm 5.

R. auricomus L. ssp. **rectiangulus** Julin ssp. nov.

Holotypus: Suecia, Vestrogothia, Tranemo, prope viam ferratam juxta fluvium Jälman 30.5.1965 E. Andersson (UPS).

Planta mediocriter alta. *Caules* erecti vel subtus aliquanto curvati, inferne violacei, ramos sub angulo acuto emittentes. *Folia rosularia* sat parva, sinu basali plerumque c. 90°. Folia exteriora reniformia, crenata, trilobata, lobo medio rotundate cuneato, sinibus inter lobos angustis, parte adversa folii saepe colore violaceo. Folia intermedia ambitu reniformia ad orbicularia, crenata vel obtuse mammiformiter vel triangulariter dentata, multipartita, segmentis cuneatis. Saepe folium sequens multipartitum, segmentis sat anguste lanceo-

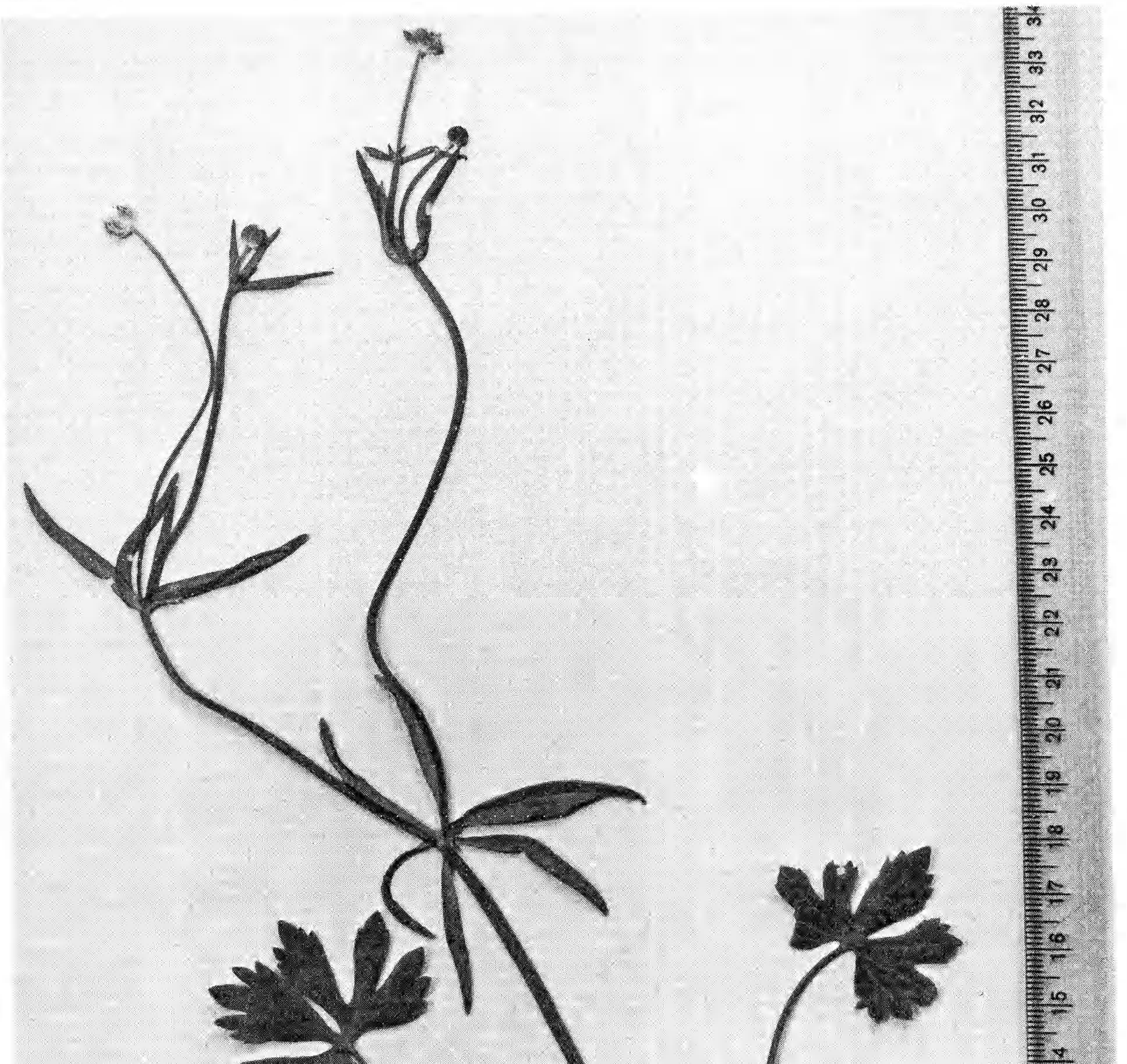


Fig. 20. *R. auricomus* ssp. *inconspectiflorus*. Holotype.

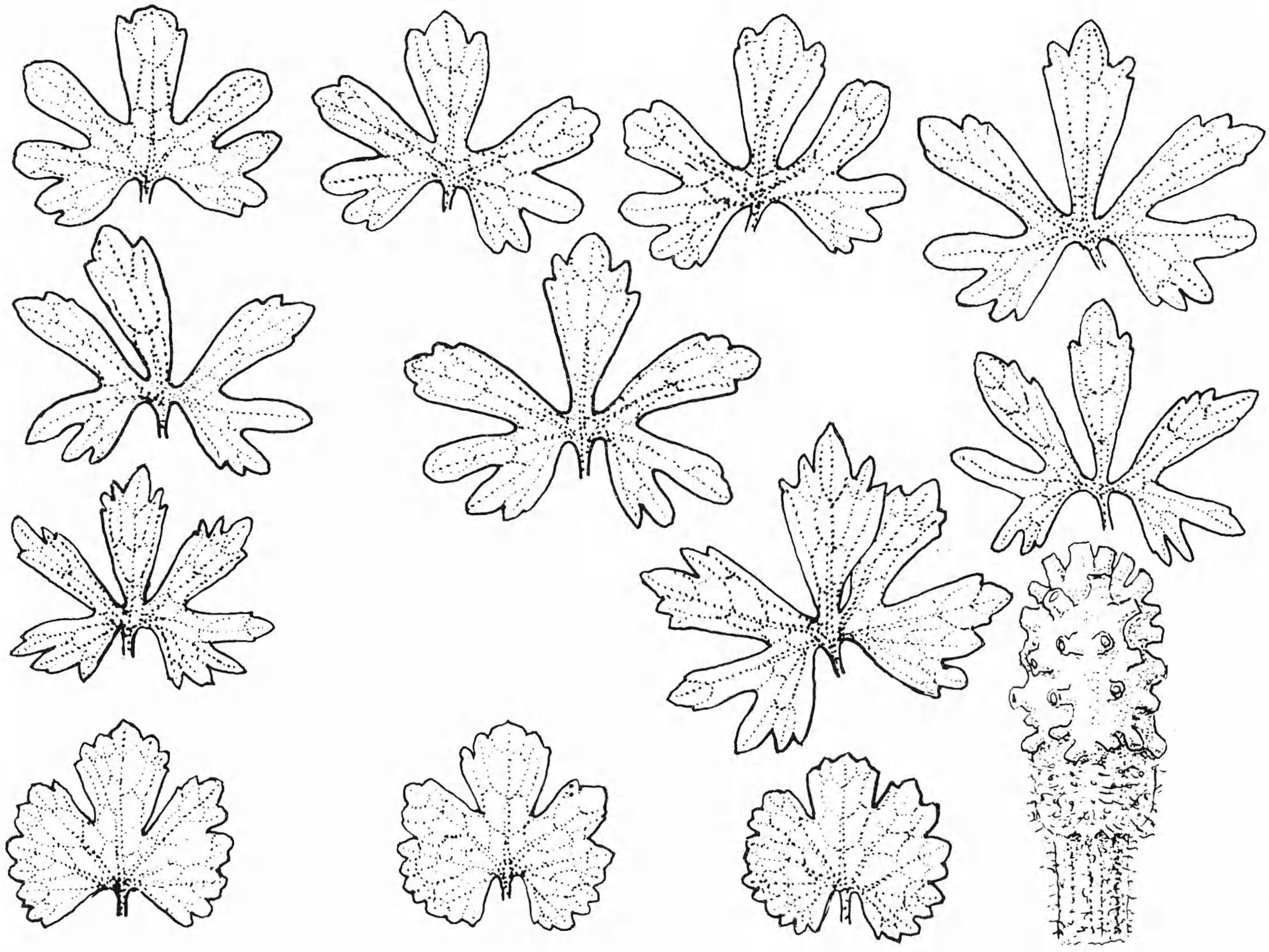


Fig. 21. *R. auricomus* ssp. *inconspectiflorus*. Basal leaves of the type collection. – Below right: Receptacle, ×10.

latis, plurimis integerrimis. Folia interiora ambitu orbicularia, multipartita, segmentis cuneatis, sese partim obtegentibus, ± acute mammiformiter dentatis vel lacinulatis. Folia aestivalia acute mammiformiter dentata, tripartita vel trilobata, segmento (lobo) medio rotundate cuneato, segmentis (lobis) lateralibus incisis vel indivisis. *Laciniae foliorum caulinorum* mediocriter longae, lineari-lanceolatae, plerumque integerrimae. *Flores* imperfecti, petalis nonnullis vel plurimis vel omnibus abortivis. Sepala apice obscure rubro-violacea. Stamina numerosa apicem capituli pistillorum paulum superantia. Torus ± globosus, c. 25 mm longus. Gynoclinium glabrum, carpellophoris mediocriter longis. Intervallum breve, glabrum, vel nullum. Androclinium sursum crassius, dense pilosum.

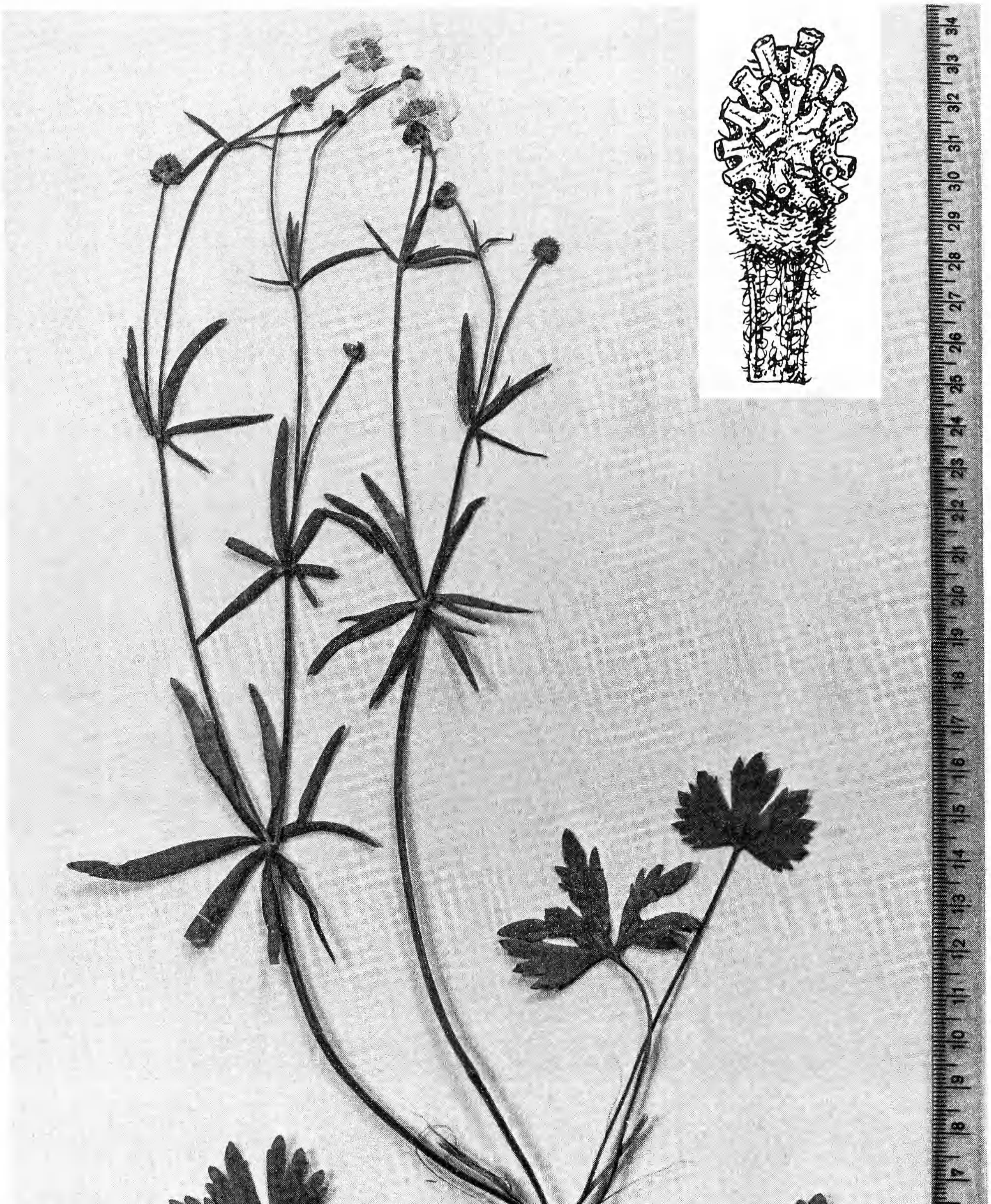
Ecology: This southwestern Swedish subspecies seems to prefer moist habitats, such as river- and lake-shore meadows and other damp meadowland, or *Alnus incana* or *A. glutinosa* carrs, but it also occurs in gardens and parks, on roadsides, and on other more directly man-made habitats.

Localities (Fig. 25): Sweden: Sm 2, Hl 1, Vg 16, Dls 1, Nrk 4, Vrm 13, Vsm 6, Mpd 1.

R. auricomus L. ssp. **robusticaulis** Julin ssp. nov.

Holotypus: Suecia, Sudermannia, Kung Karl, Malmberga, in horto 24.5.1965 T. Sundin (UPS).

Planta sat humilis, robusta. *Caules* erecti vel paulum curvati, inferne violacei, ramos sub angulo sat acuto emittentes; caules laterales teneri, subtus pilosi. *Folia rosularia* ambitu reniformia ad orbicularia, sinu basali vel sat aperto vel angusto vel obtecto. Folia exteriora crenata, multilobata ad multipartita, lobis (segmentis) anterioribus rotundatis, sese partim obtegentibus. Folia intermedia obtuse mammiformiter dentata, multipartita, segmentis perlatis, sese partim obtegentibus, saepe breviter petiolulatis. Folia sequentia foliis intermediis similia sed segmentis angustioribus instructa. Folia interiora acute mammiformiter dentata, tripartita, segmento medio cuneati-lanceolato, segmentis lateralibus profunde lobulatis. Folia aestivalia primo utrimque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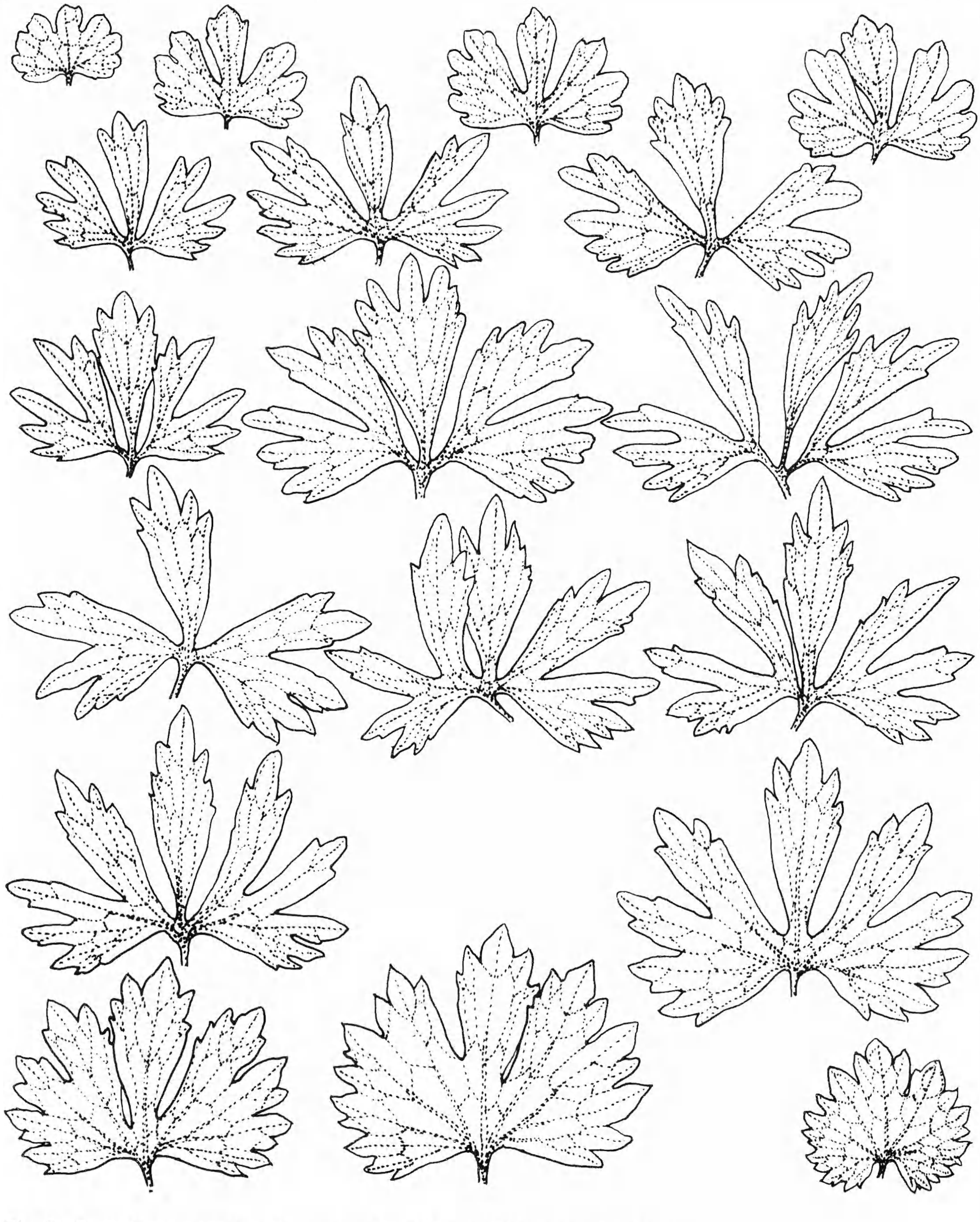

Fig. 23. *R. auricomus* ssp. *longimammus*. Basal leaves of the type collection.

Fig. 22. *R. auricomus* ssp. *longimammus*. Holotype. – Top right: Receptacle, × 10.

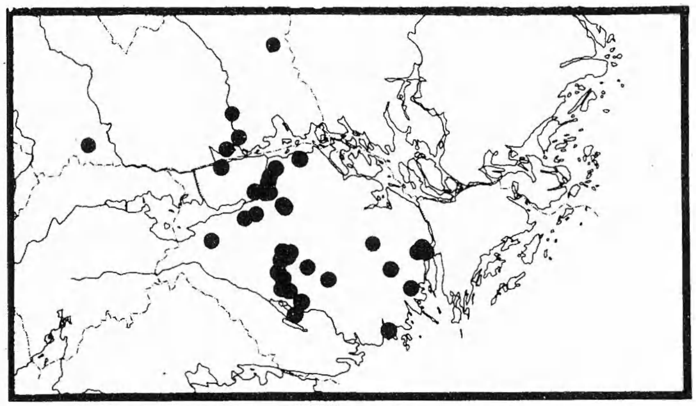

Fig. 24. Known distribution of *R. auricomus* ssp. *longimammus*.

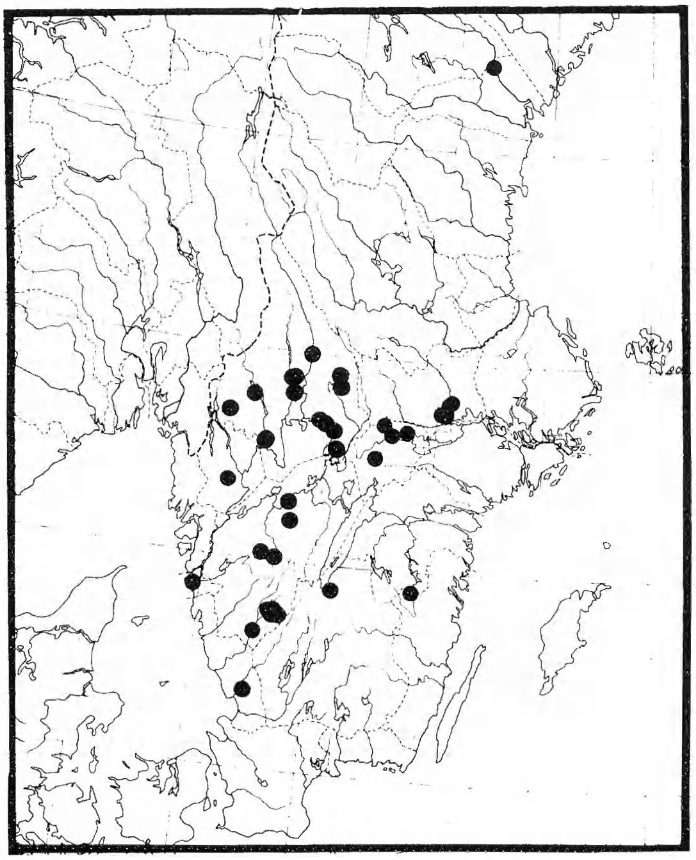

Fig. 25. Known distribution of *R. auricomus* ssp. *rectiangulus*.

pilosa, deinde interdum glabra, acute triangularidentata, ± profunde multilobata ad indivisa. *Laciniae foliorum caulinorum* mediocriter longae, late lineari-lanceolatae, obtusae, integerrimae vel interdum – ut apud ssp. *obtusulum* – juxta post apicem dentibus parvis duobus praeditae; vaginae basales foliorum caulinorum extra rubellae. *Flores* valde imperfecti, petalis omnibus plerumque abortivis. Sepala apice obscure rubro-violacea. Styli longiusculi et sat erecti. Stamina numerosa primo saltem apicem capituli pistillorum valde superantia. Torus rotundatus, pilosus. Carpellophora brevia. Intervallum nullum.

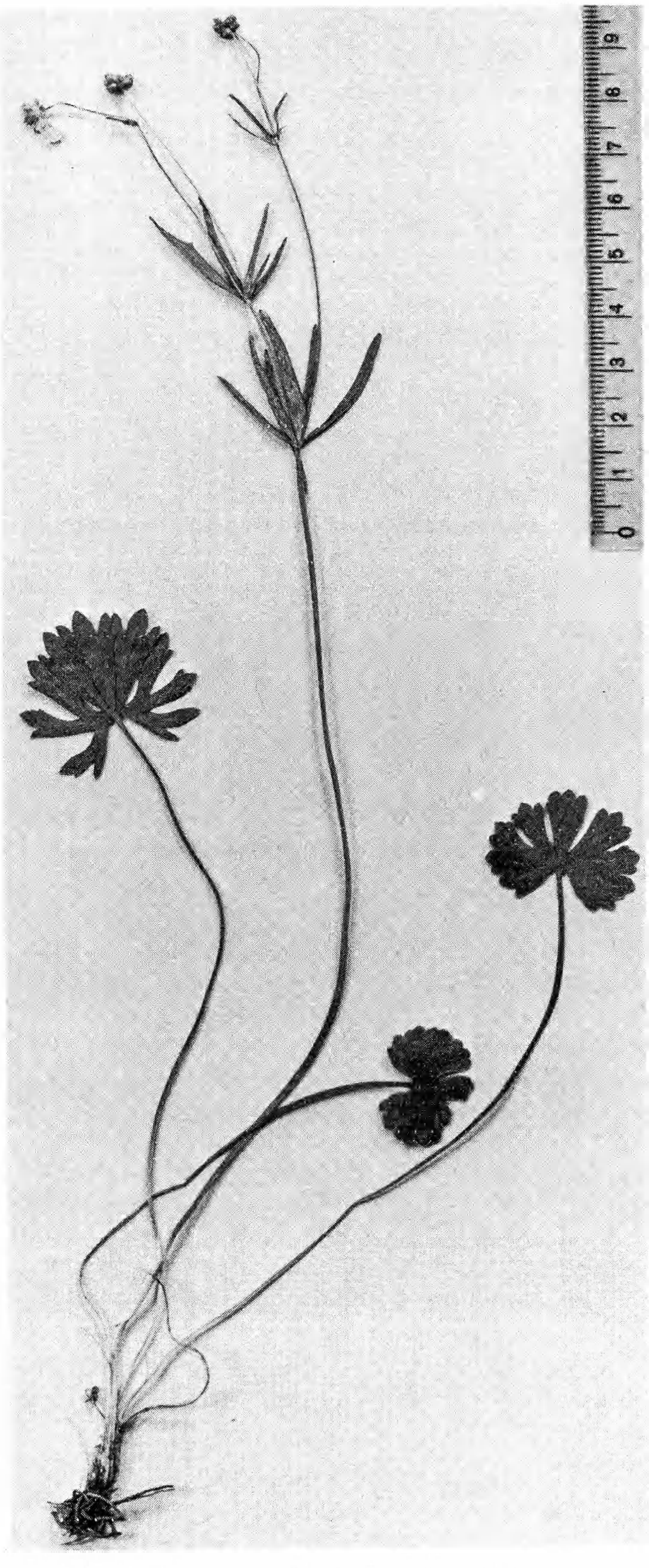

Fig. 26. *R. auricomus* ssp. *rectiangulus*. Holotype.

Sweden: Södermanland. Kung Karl, Gersilla, ditchside 1965 T. Sundin, damp meadow 1966 T. Sundin, river-shore 1970 T. Sundin; Kungsör, grassy slope at Gersillaskolan 1965 T. Sundin; Malmberga, in the garden 1965 T. Sundin (holotype), forest meadow 1965 T. Sundin; Södra Kungsladugården, meadow 1965 T.

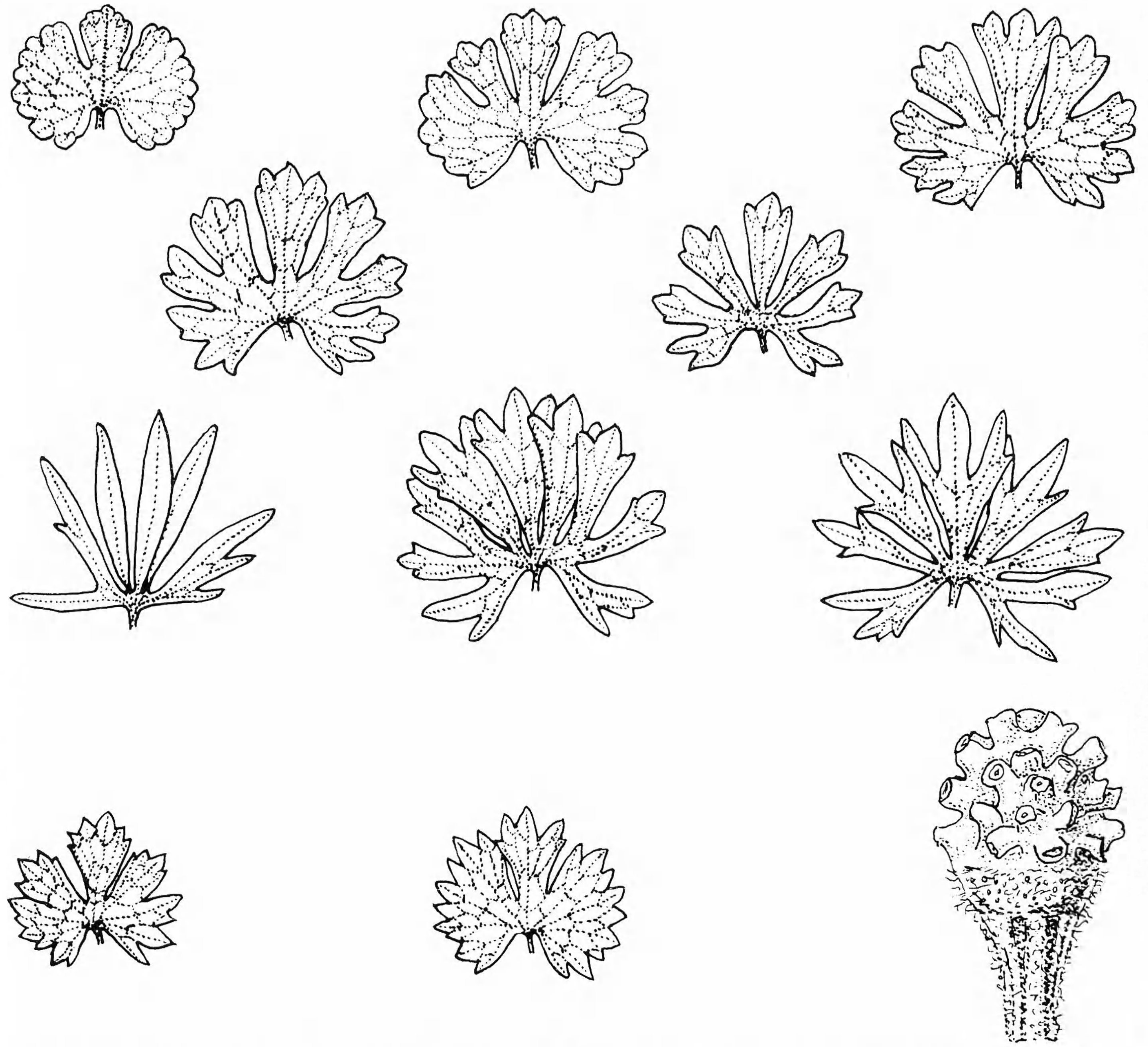

Fig. 27. *R. auricomus* ssp. *rectiangulus*. Basal leaves of the type collection. – Below right: Receptacle, × 10.

Sundin. – Västmanland. Ängsö, lawn in the palace park quite close to the wall of the churchyard 1969 J. A. Nannfeldt 20512b, the car-park at the palace of Ängsö 1969 J. A. Nannfeldt 20509.

R. auricomus L. ssp. sublaetevirens Julin ssp. nov.

Holotypus: Suecia, Sudermannia, Lilla Malma, in frondea silva a NE parte Beckåsen 2 km 14.6.1966 T. Sundin (UPS).

Planta sat alta, laete viridis. *Caules* sat graciles, erecti vel curvati, inferne violacei, ramos sub angulo acuto emittentes. *Folia rosularia* magna, sinu basali ± aperto, exteriora, interiora ac aestivalia ambitu reniformia, intermedia orbicularia. Folia exteriora crenata, leviter lobata vel incisa. Folia sequentia tripartita, segmento medio late cuneato, apice longe crenato, segmentis lateralibus iterim partitis vel lobatis, crenatis. Folia intermedia multisecta, segmentis petiolulatis, ± late lanceolatis, vel dense dentatis, dentibus inaequalibus, subacutis, vel parce dentatis vel integerrimis. Folia interiora multipartita, segmentis lanceolatis, dense inaequaliter serratis. Folia aestivalia acute mammiformiter dentata, tripartita ad trilobata, segmento (lobo) medio cuneato, segmentis (lobis) lateralibus incisis vel indivisis, sinibus inter segmenta (lobos) angustis. *Laciniae foliorum caulinorum* mediocres ad sat longae, lineari-lanceolatae, acutulae, integerrimae vel dentibus vel lacinulis nonnullis praeditae, saepe (in folio infimo longe) petiolulatae. *Flores* parvi, imperfecti, petalis nonnullis vel omnibus abortivis. Sepala apice rubro-violacea. Stamina brevia, interdum sat pauca apicem capituli pistillorum parvuli fere aequantia. Styli tenues. Torus oblongus, viridis. Gynoclinium

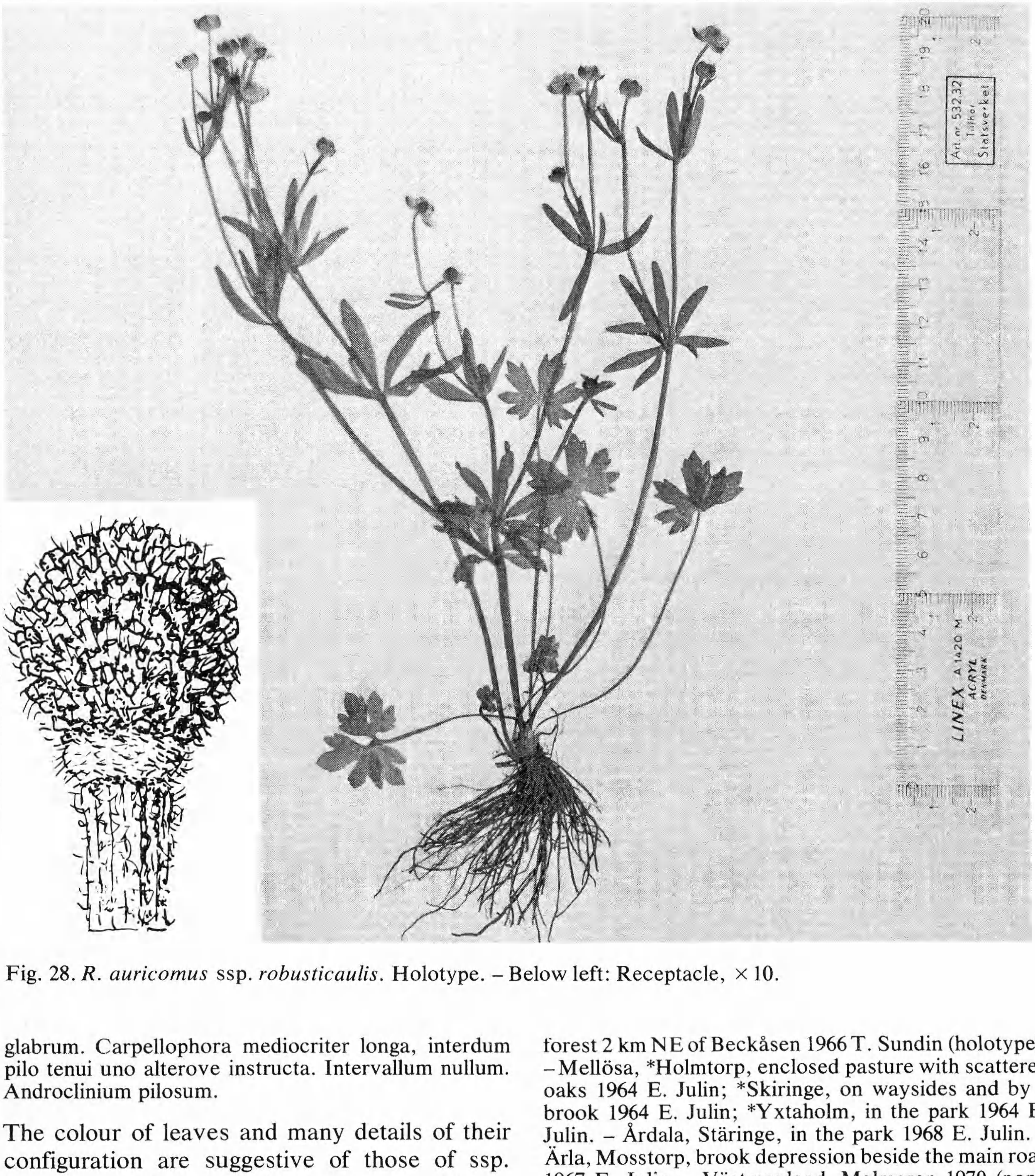

Fig. 28. *R. auricomus* ssp. *robusticaulis*. Holotype. – Below left: Receptacle, × 10.

glabrum. Carpellophora mediocriter longa, interdum pilo tenui uno alterove instructa. Intervallum nullum. Androclinium pilosum.

The colour of leaves and many details of their configuration are suggestive of those of ssp. *laetevirens* Marklund (1961) and ssp. *sublaetevirens* is probably closely related to this subspecies.

In a previous paper (Julin & Nannfeldt 1966 p. 236) four collections of this subspecies were erroneously identified as ssp. *smithii* Julin. They are marked with an asterisk below.

Sweden: Södermanland. *Flen, Mosstorp 1944 E. Asplund. – Hyltinge, brook valley between Henaren and Västersjön 1967 E. Julin. – Lilla Malma, deciduous forest 2 km NE of Beckåsen 1966 T. Sundin (holotype). – Mellösa, *Holmtorp, enclosed pasture with scattered oaks 1964 E. Julin; *Skiringe, on waysides and by a brook 1964 E. Julin; *Yxtaholm, in the park 1964 E. Julin. – Årdala, Stäringe, in the park 1968 E. Julin. – Ärla, Mosstorp, brook depression beside the main road 1967 E. Julin. – Västmanland. Malmgren 1970 (nom. nud.).

R. auricomus L. ssp. **sundinii** Julin ssp. nov.

Holotypus: Suecia, Sudermannia, Nynäshamn, Estö, Änggatan, in prato humido 11.6.1964 T. Sundin (UPS).

Planta alta. *Caules* erecti, ramos sub angulo acuto emittentes. *Folia rosularia* magna, ambitu reniformia ad orbicularia, sinu basali 0° ad 135°. Folia exteriora indivisa, magne crenata. Folia sequentia trilobata, lobo

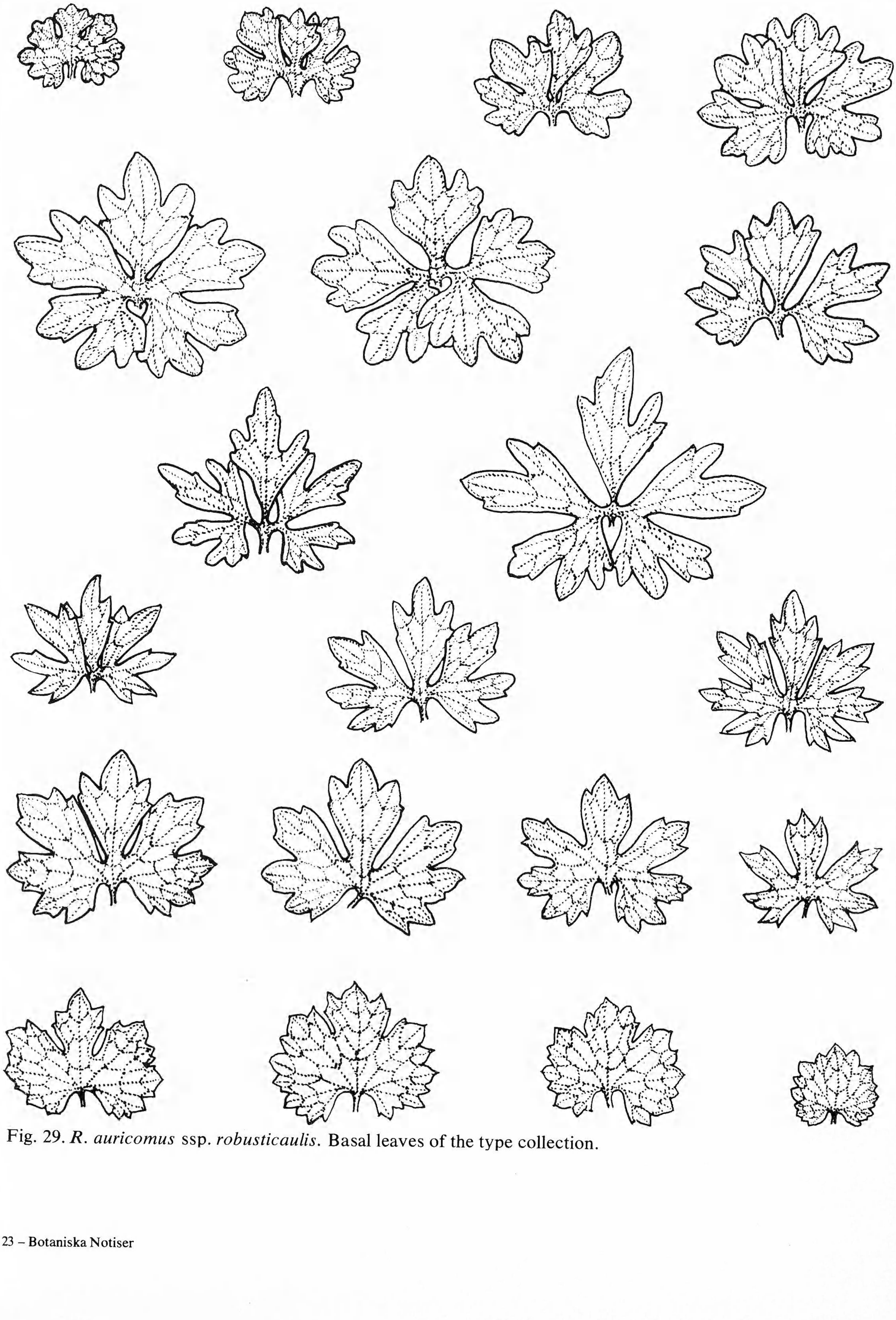

Fig. 29. *R. auricomus* ssp. *robusticaulis*. Basal leaves of the type collection.

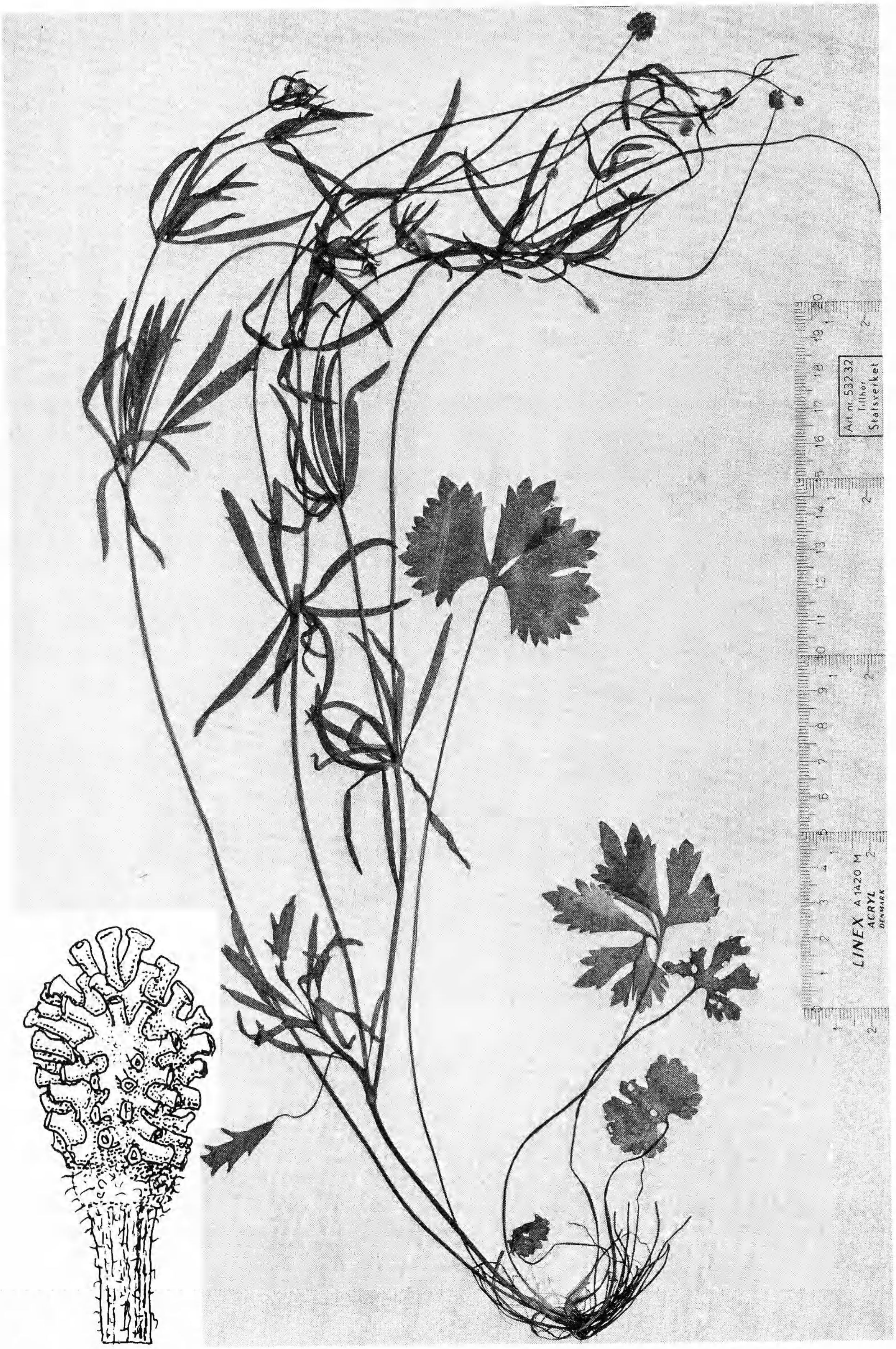

Fig. 30. *R. auricomus* ssp. *sublaetevirens*. Holotype. – Below left: Receptacle, × 10.

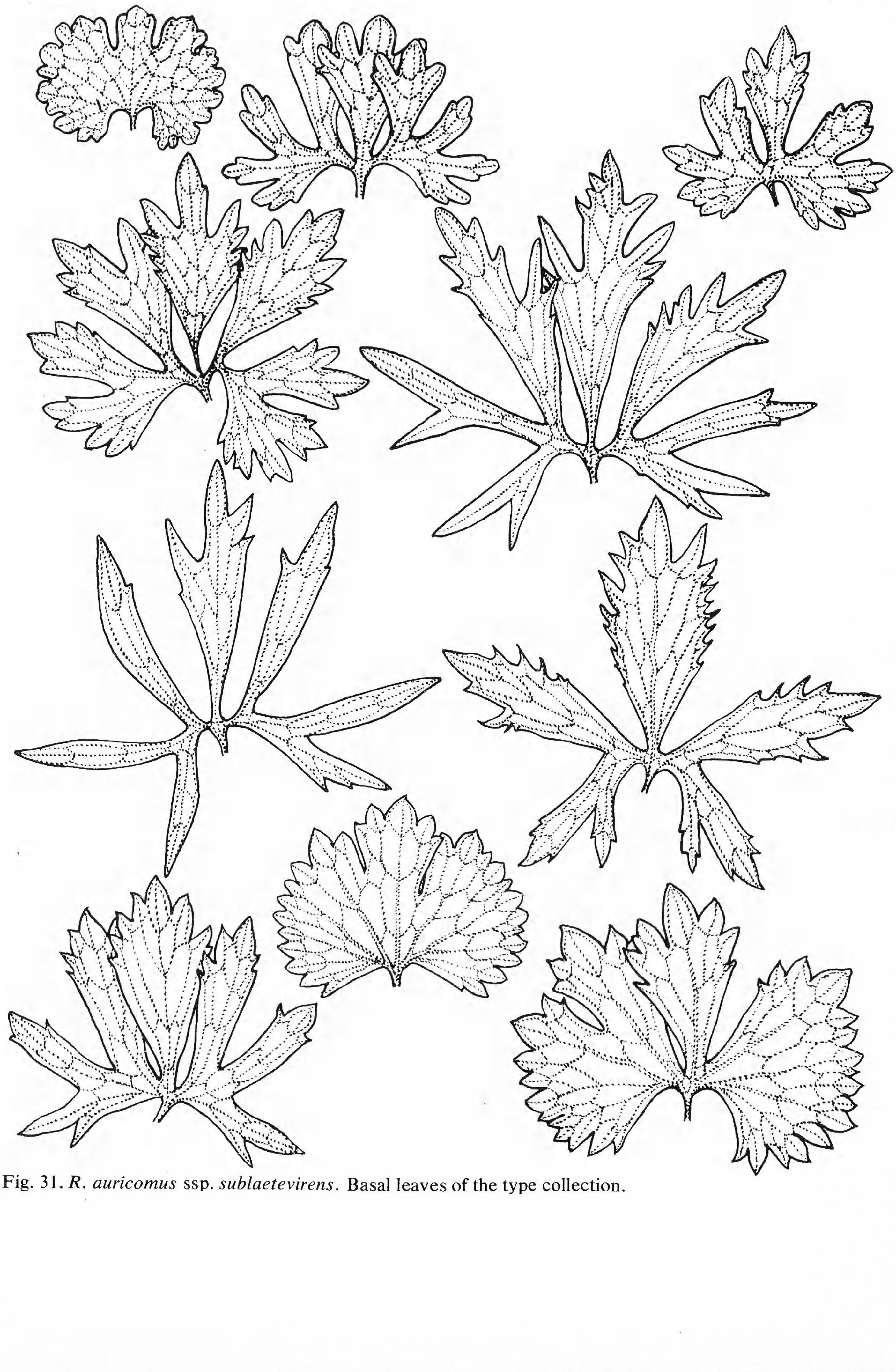

Fig. 31. *R. auricomus* ssp. *sublaetevirens*. Basal leaves of the type collection.

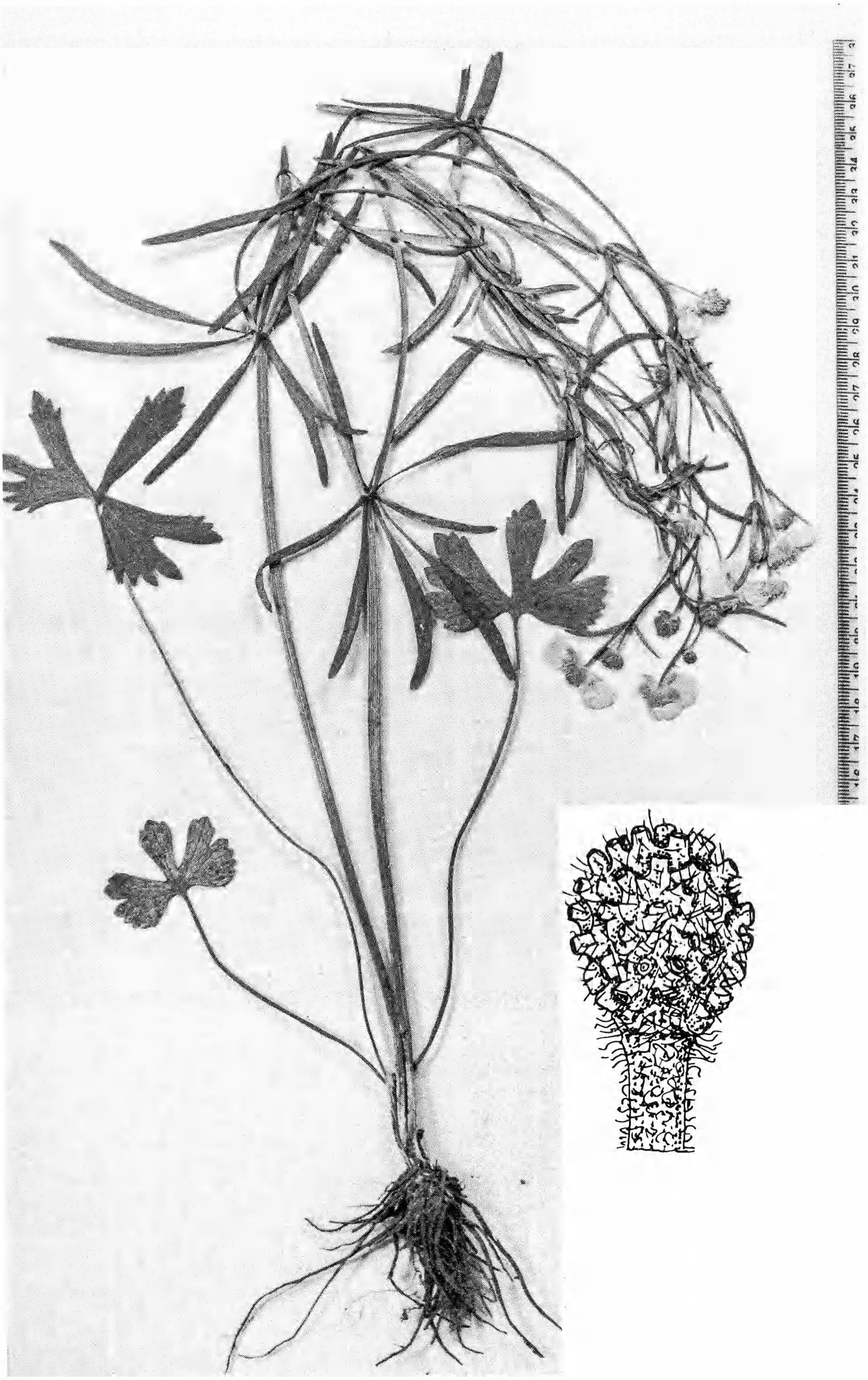

Fig. 32. *R. auricomus* ssp. *sundinii*. Holotype. – Below right: Receptacle, × 10.

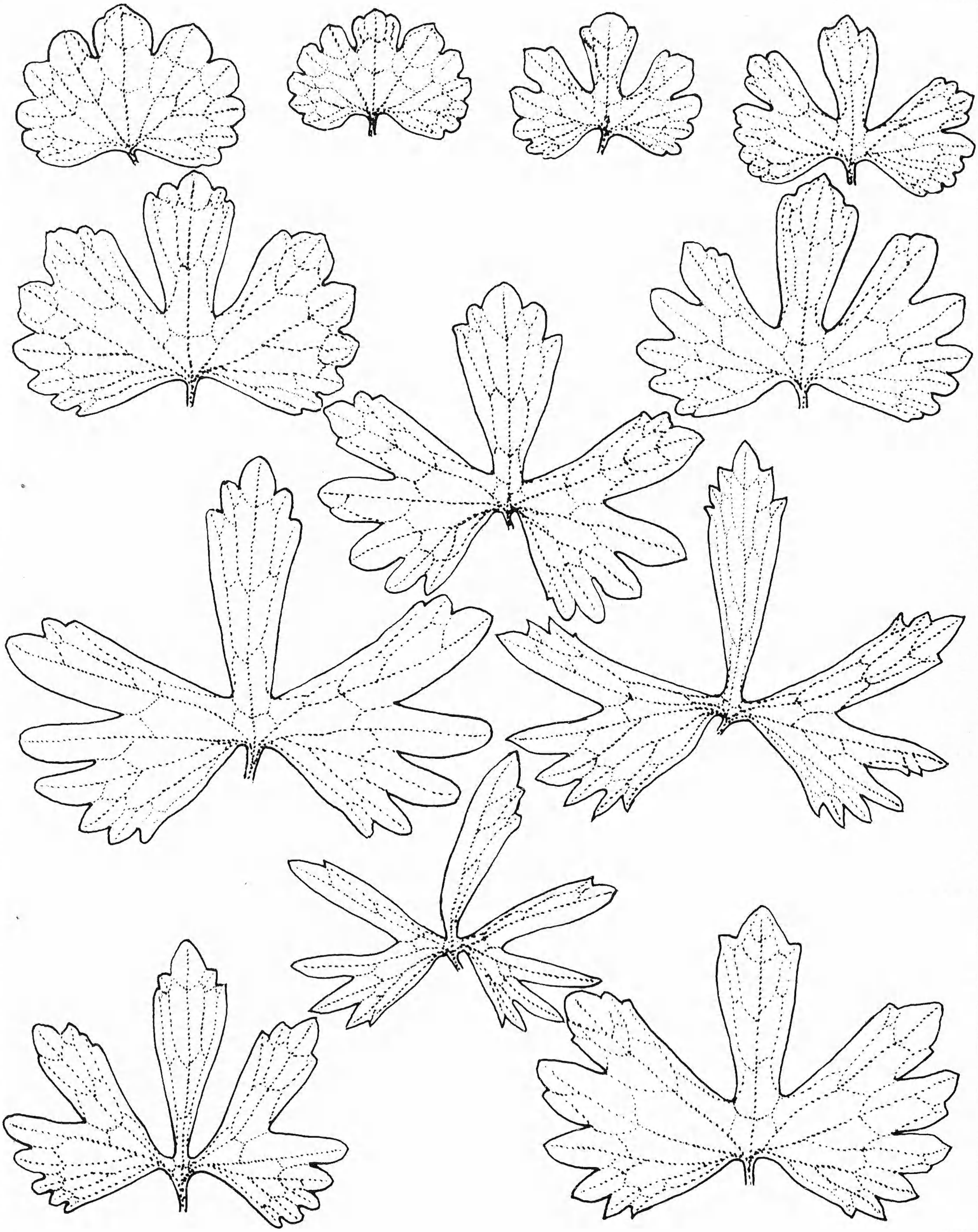

Fig. 33. *R. auricomus* ssp. *sundinii*. Basal leaves of the type collection.

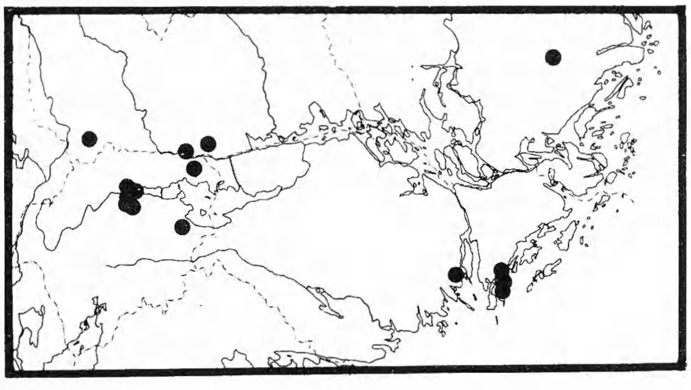

Fig. 34. Known distribution of *R. auricomus* ssp. *sundinii*.

medio longo, cuneato, lobis lateralibus crenatis vel rotundate lobulatis. Folia intermedia tripartita, sinibus inter segmenta latis, segmento medio longo, cuneato vel fere pari latitudine, apice crenato, segmentis lateralibus multilobulatis, lobulis apice rotundatis, integerrimis vel crenatis. Folia interiora foliis intermediis similia, sed segmentis lobulisque acutis vel acute dentatis instructa. Folia aestivalia (desunt in coll. orig.) tripartita ad trilobata ad indivisa, obtuse triangulariter dentata vel incisa. *Laciniae foliorum caulinorum* longae, lineares vel lineari-lanceolatae, obtusae, integerrimae vel interdum dente vel lacinula una alterave praeditae. *Flores* vel imperfecti, petalis abortivis, vel perfecti, petalis omnibus vel plurimis bene evolutis, ad 17 mm diametro. Sepala pallida. Stamina numerosa apicem capituli pistillorum globosi fere aequantia. Torus globosus, dense pilosus. Carpellophora brevia vel mediocria. Intervallum nullum. Androclinium breve.

Ssp. *sundinii* is named in honour of its first, and foremost, collector, Torsten Sundin, B. Sc. (1893 -1972).

Ecology: This subspecies occurs on the borders of ditches, in lake- and seashore meadows and other damp meadowland, on clay fields and similar, more or less damp habitats, but it also occurs in forests of different types, in parks and gardens, and sometimes even in drier habitats such as on grassy slopes and in sloe thickets.

Localities (Fig. 34): Sundin 1968 (nom. nud.) - *New localities:* Sweden: Srm 8, Nrk 14, Upl 1, Vsm 3.

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Calathea elegans and C. spiralis – new Panamanian Marantaceae

Helen Kennedy

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Two new species of *Calathea* (Marantaceae) are described: *C. elegans* from Panama and Colombia and *C. spiralis* from Panama. *Calathea spiralis* differ from other species in *Calathea* subgenus *Calathea* by its spirally arranged bracts.

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Calathea elegans Kennedy, sp. nov. – Fig. 1

Planta 1–1, 85 m alta. Folia longe petiolata petioli parte superiori glabra supra tomentosa, verticalia anguste elliptica basi acuta vel rotundata; lamina supra glabra obscure viridia. Inflorescentiae 1–3, teres; bracteae spiraliter dispositae, dense, tomentosae, acutae vel acuminatae obscure virides vel obscure purpureae, bracteolis membranaceis et linearibus apice indurato-claviculata comitata; staminodia alba; staminodium exterius latissime ovatum, callosum petaloideum.

Rhizomatous herb 1–1.85 m high with 2–3(5) leaves per shoot or shoot system; 1–2 leaves on the main axis, 2–3 leaves on the lateral axis arising in the axil of the lower leaf. These lateral shoots bear both bicarinate prophylls and bladeless sheaths. The internode between the uppermost (subtending) leaf and the next lower leaf commonly is elongated, up to 35–(50) cm, but may be reduced, all the leaves of the main shoot essentially basal. *Rhizome* fibrous, 1–1.5 cm in diameter with internodes 1–1.3 cm long. *Cataphylls* apically papyraceous, slightly fleshy basally, narrowly ovate, apex acute, red-purple, the base occasionally green, densely tomentose, innermost cataphyll 25–51 cm long. *Leaf sheath* very rarely auriculate, dark green tinged purple, margins green tinged purple, scattered tomentose to subscabrid; sheath of uppermost leaf 15–24 cm long, others 27–46(–63) cm long. *Petiole* round in cross-section, dark purple to dark green, upper portion glabrous, subglabrous near sheath, lacking a groove, (5.5–)25–64 cm long. *Pulvinus* swollen, ± round in cross-section, dark reddish brown, glabrous except for a row of hairs above, articulate with petiole, 1.3–3.8 cm long. *Leaf blade* leathery, somewhat stiff, narrowly elliptic, apex acuminate to obtuse with acumen, base obtuse to rounded, occasionally acute in small leaves, 34–82 × 11.5–30 cm; above shiny dark green, almost metallic black-green in some, glabrous, midrib olive-green, minutely puberulent; below opaque dark red-purple or dull grey-green, veins and midrib minutely puberulent. *Stem* dark purple above, reddish brown basally.

Inflorescences 1–3 per aerial shoot or shoot system, spindle-shaped, 5–12 cm high and 1.5–3 cm in diameter; the first terminal, subsequent ones arising either in the axil of the subtending leaf, the axil of the bladeless sheath accompanying the second, axillant, inflorescence, or terminating a leafy lateral axis. Occasionally an inflorescence develops in the axil of the lowermost bract of an inflorescence. *Peduncle* dark purple to green, minutely tomentose, (5–)14–36 (–49) cm long, the base swollen, usually bending and reflexing the inflorescence downward after flowering. *Bracts* (3–)5–14, spirally arranged, subcoriaceous, ovate to obtrullate, apex acute to acuminate, (2.4–)3.2–5.7 cm high and (1.5–) 2.2–2.5 cm wide, each subtending up to 6 flower pairs; outer surface dark purple or dark green, densely velvety tomentose; inner surface green, glabrous below, upper half appressed tomentose. *Bicarinate prophyll* membranaceous, ovate, apex acute, cream to faint greenish, upper 2/3 dark purple, densely velvety tomentose; glabrous within, 2.5–4.6 cm high and 0.7–1 cm wide, carina to carina, 1.2–1.7 cm wide total width. *Secondary bract* membranaceous, ovate-triangular, apex acute, lower half greenish, upper half tinged purple, upper 2/3 densely velvety tomentose 2.5–4.1 × 1.1–1.5 cm. *Bracteoles* usually 3 per flower pair, 2 lateral, membranaceous, faint green, 2.8–3.6 × 0.6–0.9 cm and an indurate claviculate bracteole centrally, (2.4–)2.7–4 cm long.

Sepals narrowly obovate, apex acute, whitish, glabrous throughout or glabrous below, tomentose in upper 1/3, 3.2–3.9 × 0.5–0.65 cm. *Corolla tube* white tinged pinkish above, glabrous, (3.3–) 4.3–4.8 cm long, staminal tube 0.2–0.4 cm long; corolla lobes subequal, elliptic, apex acute to 90°, white basally, upper 2/3 tinged pink, apex bearing short tuft of hairs, 1.5–1.9 × 0.7–0.9 cm. *Outer staminode* broadly elliptic to transverse broadly elliptic, apex shallowly retuse, white, 1.1–1.5 × 0.9–1.1 cm. *Callose staminode* petaloid, very broadly obovate, emarginate, white above, callose portion cream-yellow, (1.2–)1.4–1.7 × 1–1.3 cm. *Cucullate* staminode white, ca 0.6 cm long, provided with a subterminal filiform appendage. *Filament* with lateral petaloid appendage to 2 mm wide, white; anther 2–2.5 mm long. Style and stigma white. *Ovary* cream-colored, smooth, 2–2.5 mm high. *Capsule* obovoid with a raised rim apically, 1.4–1.6 cm high and ca 0.7 cm in diameter. *Seeds* trigonous, 8–9 mm high and 4–4.5 mm in diameter, bearing a white aril to 4.5 mm.

Type. Panama. Prov. Panamá, km 12–14 on the El Llano-Carti road, evergreen wet forest, ca 400 m, 26.3.1975, Kennedy & Dressler 3434 (holotype F, isotypes DUKE, GB, K, MO, US).

Other collections. Colombia. Dept. Chocó, hills behind Bahía Solano (Pto. Mutis), tropical wet forest, 0–250 m, 5.1.1973, Gentry & Forero 7233 (F, MO); Quibdó-Tutunendo road, 15 km from Quibdó, ca 45 m, 7.9. 1976, Forero & Jaramillo 2620 (MO).

Calathea elegans flowers mainly during the dry season, late December through April, in Panama; in Colombia, both September and January flowering dates are known. It occurs within the forest in moderate shade on well-drained slopes but was also observed on the newly disturbed sites along the road.

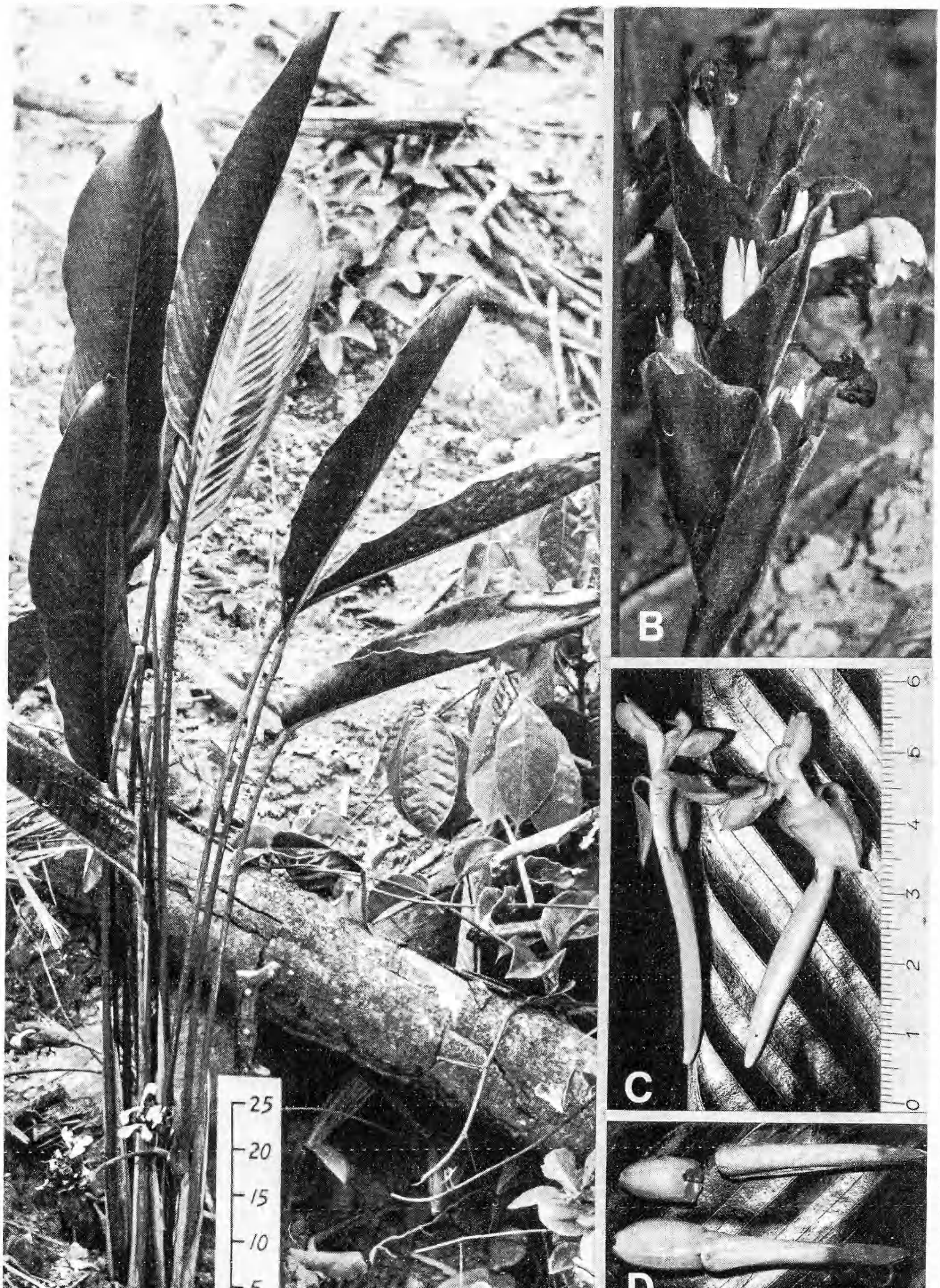
Calathea elegans is distinguished from other species of *Calathea* by vertically positioned, narrowly elliptic leaf blades, glabrous upper leaf surface; reddish brown glabrous pulvinus (except for row of hairs above); glabrous to subglabrous petiole; 1–3 terete inflorescences per aerial shoot or shoot system; erect dark purple or dark green spirally arranged, densely tomentose, acute to acuminate bracts; a single claviculate and 2 membranaceous bracteoles per flower pair; white staminodes; petaloid callose staminode and very broadly ovate outer staminode. *Calathea elegans* is most closely related to *C. robin-fosteri* but differs from it in that the inflorescences are borne terminally or laterally on the leafy shoots rather than on separate leafless shoots directly from the rhizome.

Calathea spiralis Kennedy, sp. nov. – Fig. 2

Planta ad 2,2 m. Folia longe petiolata, petioli parte superiori glabra; ovata, acuminata, basi rotundata. Inflorescentiae 2–4, subcylindricae, rhachidi dense tomentosa; bracteae 11–34 spiraliter dispositae ad 1,8 cm longae, albidae vel albidae parte centrali viridi; paria florum ad 8, bracteolis 2 membranaceis. Capsula ovoidea apice rotundo, flavida; semina cyanea.

Rhizomatous, perennial herb 1.7–2.2 m high, bearing several, usually 4–5 basal leaves and a single cauline leaf. *Cataphylls* coriaceous, narrowly ovate to ovate, green, scabrous. *Leaf sheath* not auriculate (except in unusually small leaves) green, occasionally tinged pinkish brown, glabrous above in subtending leaf, scabrous throughout in others, the basal 1.5 cm sericeous, (6.5–)14–19 cm long in subtending leaf, others 18–60 cm long. *Petiole* green, glabrous in subtending leaves, others scabrous or scabrous near junction with pulvinus but glabrous below, occasionally bearing a groove on the upper side, 3.5–8.5 cm long in subtending leaf, 25–55 cm long in others. *Pulvinus* round in cross-section, yellow-green, glabrous, confluent with petiole, 4–6.8 cm long. *Leaf blade* pliable, somewhat leathery, ovate, apex acuminate, somewhat ec-

Fig. 1. *Calathea elegans*. – A: Habit. – B: Inflorescence. – C: Flowers on upper leaf surface. – D: Capsule with calyx attached. Scale in cm.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centric, base truncate to rounded, subtending leaf 44–60 × 16–25 cm, basal leaves 36–50 × 13–21 cm. Leaf blade with slightly sparkling sheen above, deep green with lighter green along the midrib, glabrous, midrib yellow-green, tomentose; surface below dull green, glabrous to minutely puberulent, midrib below yellow-green, glabrous to minutely puberulent. *Stem* green, scabrous just below the node, the lower portion glabrous. Internode between basal and subtending leaf up to 1.4 m long.

Inflorescences 2–4 per shoot, lax, subcylindric, 9–14 cm high and 3–3.8 cm in diameter, the first terminal, the second produced in the axil of the subtending leaf, subsequent ones in the axil of the bladeless sheath accompanying the second or third inflorescence. The bicarinate prophylls associated with the latter inflorescences green, the margins, carina and apex red-purple. *Peduncle* green, densely tomentose, (1.5–)6–38 cm long. *Bracts* 11–34, spirally arranged, chartaceous, transverse elliptic, apex obtuse or rounded to occasionally subemarginate, upper ones somewhat smaller than lower ones, outer margin and apex erect to recurved, 1.4–1.8 × 2.4–3 cm; each subtending up to 8 flower pairs. Outer surface of bract white, the edge tinged purple, or occasionally green centrally, the sides white, tomentose at base, glabrous above, the apex occasionally subglabrous to sparsely tomentose, inner surface white or light green, glabrous. Rachis green, densely tomentose. *Bicarinate prophyll* membranaceous, broadly triangular-ovate, apex obtuse, white, the base light green, outer surface of carina sparsely puberulent, 1.3–1.65 cm high and 0.55–0.65 cm wide, carina to carina, 1–1.2 cm wide, total width. Secondary bracts membranaceous, broadly triangular-ovate, apex obtuse, white, apex occasionally tinged purple, glabrous, 1.3–1.55 × 1.1–1.4 cm. *Bracteoles* 2 per flower pair, membranaceous, narrowly oblong-elliptic, white, apex tinged purple, glabrous, 1.2–1.45 × 0.3–0.4 cm.

Sepals membranaceous, narrowly oblong-elliptic, apex acute, white, apex tinged yellowish, the margins purple, sparsely minute puberulent apically, glabrous below, 1.5–1.85 × 0.3–0.4 cm. *Corolla tube* pale yellow, pinkish above, minutely puberulent, 1.2–1.7 cm long; corolla lobes subequal, narrowly oblong-elliptic, median lobe acute, lateral lobes obtuse to subobtuse apically, light yellow, densely minute puberulent, 0.7–1.1 × 0.35–0.45 cm. *Outer staminode* broadly elliptic to broadly obovate, apex rounded to retuse, clawed at base, pink-purple, 0.7–0.9 × c. 0.5 cm. *Callose staminode* rectangular, apex bilobed, the lobes petaloid, the rest callose, pink-purple, ca. 0.8 cm long. *Cucullate staminode* pink-purple, dark purple at apex, 0.4–0.5 cm long, provided with a subterminal filiform appendage 2.5 mm long. *Stamen* with lateral petaloid appendage to 1.5 mm wide attached to basal 1/3 of anther; anther 2.5 mm long. Style and stigma pink. *Ovary* smooth, light yellow, glabrous, 2–2.5 mm high. *Capsule* smooth, thin-walled, broadly ovoid, green, glabrous, 0.8–0.9 cm high and 0.65–0.7 cm wide, crowned by a persistent calyx. *Seeds* trigonous, rugose on outer surface, bright blue, 5.5–6.5 mm high and 4.5–5 mm in diameter, bearing a white aril to 4 mm high.

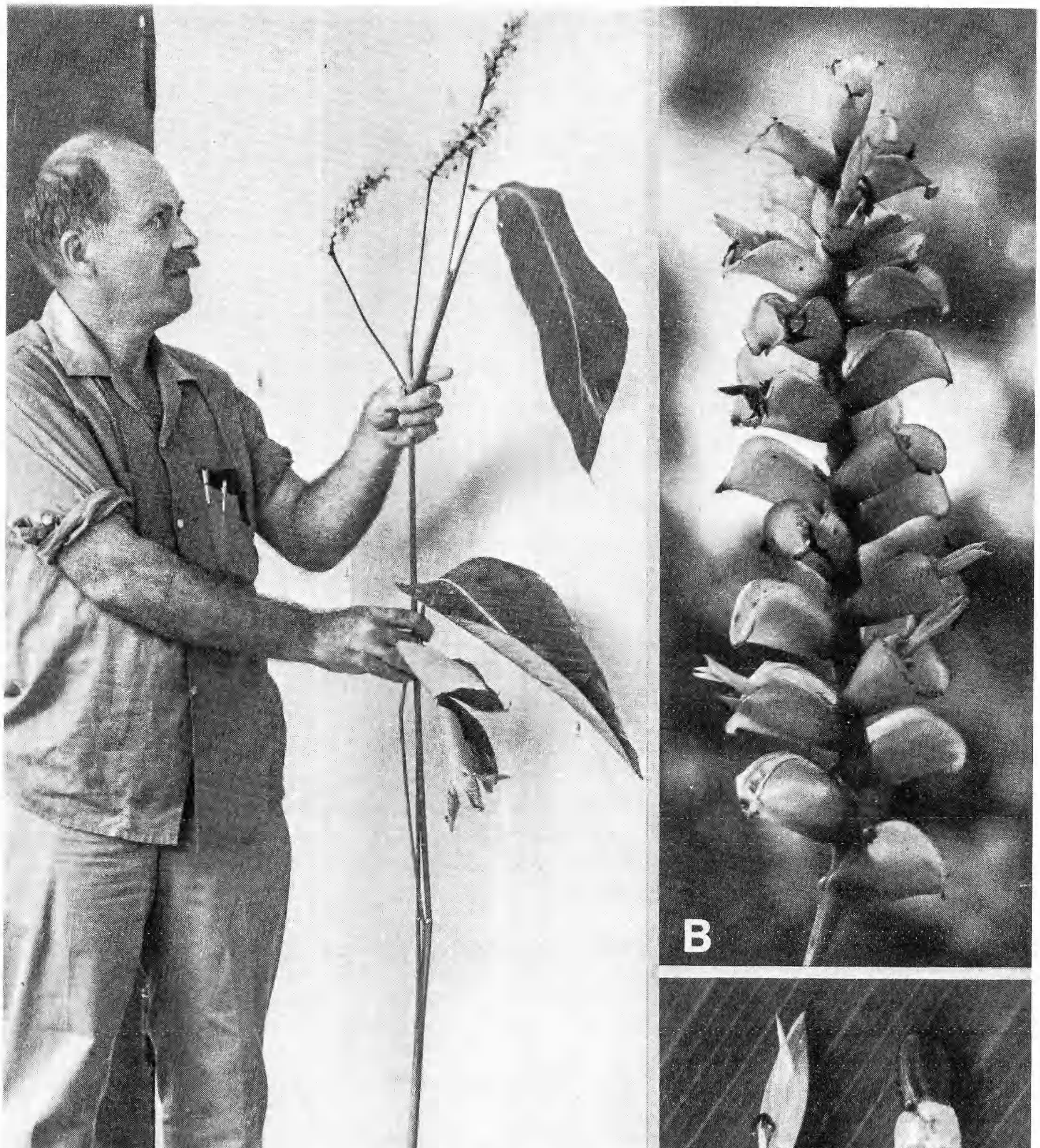
Type. Panama. Prov Chiriquí, Cerro Colorado, N of San Félix, ca 1500 m, 20.9.1977, Dressler 5725 (holotype US, isotypes GH, MO).

Other collections. Panama. Prov. Veraguas, Cerro Tute ca 10 km NW of Santa Fe, on ridgetop in cloud forest above 1000 m, 19.5.1975, Mori 6252 (F, MO) – Prov. Coclé, Cerro Caracoral, elfin forest, ca 1000 m, 19.1.1968, Duke & Dwyer 15125 (NY).

Calathea spiralis appears to flower mainly during the rainy season; the collections are from May through January. This species is known only from cloud forest habitats, from 1000–1500 m.

Calathea spiralis belongs to subgenus *Calathea* Koernicke. In Schumann's (1902 p. 70) key to the subgenera and series within *Calathea*, subgenus *Calathea* (*Eucalathea*) is distinguished by having a laterally compressed inflorescence with numerous, more than five, distichous bracts. This species differs from others in subgenus *Calathea* by its spirally arranged, rather than distichous, bracts. Other characters, such as habit (one cauline and several basal leaves), leaf morphology (the narrow vein spacing), flower morphology (bilobed, predominantly callose, callose staminode) and capsule mor-

Fig. 2. *Calathea spiralis*. – A: Habit. – B: Inflorescence. – C: Seeds and capsule on upper leaf surface. Scale in cm.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phology (thin walled with rounded apex) clearly place it in subgenus *Calathea*. *Calathea spiralis* is most closely related to *C. brenesii* Standley of Costa Rica but differs from it by the spirally rather than distichously arranged bracts, and the obtuse to rounded, subglabrous to sparsely tomentose rather than deeply emarginate densely tomentose bract margin. However, *C. spiralis* and *C. brenesii* have many characters in common and presumably *C. spiralis* represents a relatively recent divergence from the *C. brenesii* line. *Calathea spiralis* differs from other Central American *Calatheas* in its single cauline and several basal leaves; 2–4 inflorescences per aerial shoot; spirally arranged, short (1.4–1.8 cm long), white, occasionally green-tinged, bracts; densely tomentose rachis: membranaceous bracteoles; light yellow capsule and dark blue seeds.

The specific epithet *spiralis* refers to the spirally arranged bracts of this species.

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Pollination ecology of Epipactis palustris (Orchidaceae)

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Observations on the pollination of *Epipactis palustris* (L.) Crantz, mainly from the island of Öland, southern Sweden, are reported. A broad spectrum of insects feeding on the nectar was recorded. Ants, bumble-bees and hover-flies were the most frequent visitors, but generally played a minor role as pollinators. Solitary wasps (Hymenoptera, Eumenidae) were the most important pollen vectors, although only present at low frequencies. Ants were important pollinators in one locality. Entomogamy prevails and the frequency of visits is much lower if the plant is growing in association with entomophilous competitors. Deposition and frequency of pollinairia, morphology and action of the hinged labellum, and the time of flowering all suggest that *E. palustris* is adapted to pollination by solitary wasps, perhaps primarily to males of the genus *Eumenes* Latr. The hinge seems to be an adaptation to the peculiar form of the first abdominal segment of these wasps. The structure of the labellum obliges the wasps to perform an involuntary balance-act which obviously results in efficient contact between head and column. No support was found for Darwin's theory that the distal part of labellum actively throws the insect against the rostellum. Honey-bees seldom acted as pollen vectors and do not fit the flowers morphologically.

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Darwin (1869) stated that *Epipactis palustris* (L.) Crantz was visited by at least four species of insects which were able to remove its pollinaria. The honey-bee *(Apis mellifera* L.) was observed to be a frequent pollinator. Later regular self-pollination was recorded, because when insect visits fail, the pollen falls from the friable pollinia on to the upper edges of the stigma (Kirchner 1922). Wiefelspütz (1970) argued that autogamy is most important and that honey-bees play the major role as external agents in pollination, although some other co-pollinators may occur. However, precise information about insects which visit the flowers has not increased much since Darwin's time (Pijl & Dodson 1966). The primary purpose of the present study was to investigate the visiting insect fauna and the dispersal of pollen by different vectors.

The labellum of *Epipactis palustris* is divided into two halves of which the distal (epichile) is narrowly joined to the basal (hypochile) by a flexible and elastic hinge (Fig. 1 feh). The hypochile is formed like a cup of which the front part has been cut away. Its outer surface is rough with special papillae which are lacking on other parts of the labellum (Ziegenspeck 1936). On the inside it is marked with rosy parallel veins which end in the bottom of the cup in an area of orange-yellow raised spots, between which small amounts of nectar are present. The nectar contains glucose, fructose and sucrose (Percival 1961). The basal part of the epichile is strongly thickened, deeply furrowed in the middle, and has raising sides (Fig. 4 A, 1 fp). The stigmatic surface slopes forwards over the hypochile and the rostellum projects over the middle of its upper edge like a pouch. The pouch contains viscid matter enclosed within a membranaceous wall. When an insect touches the rostellum this wall is ruptured and viscid matter attaches the pollinaria to the insect's body (Darwin 1862). The pollinia lack caudicles and

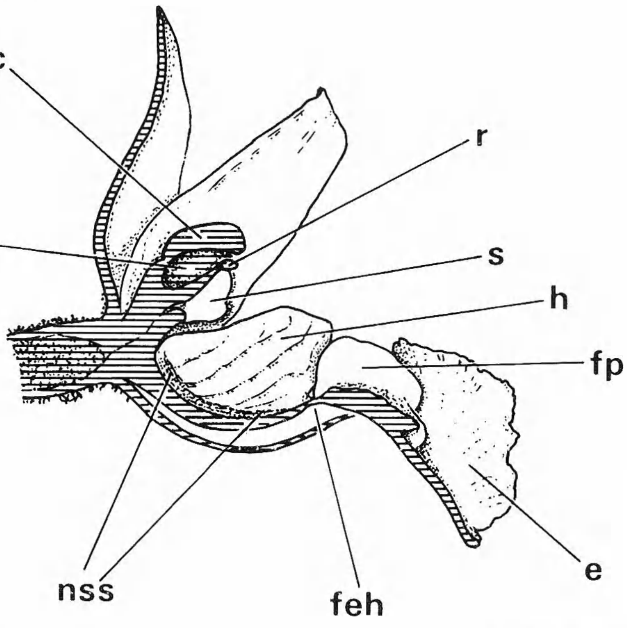


Fig. 1. Longitudinal section of flower of *Epipactis palustris* (4 ×). Abbreviations: ac anther cap, e epichile, feh flexible elastic hinge, fp furrowed plate, h hypochile, nss nectar secreting surface, p pollinia, r rostellum and s stigma.

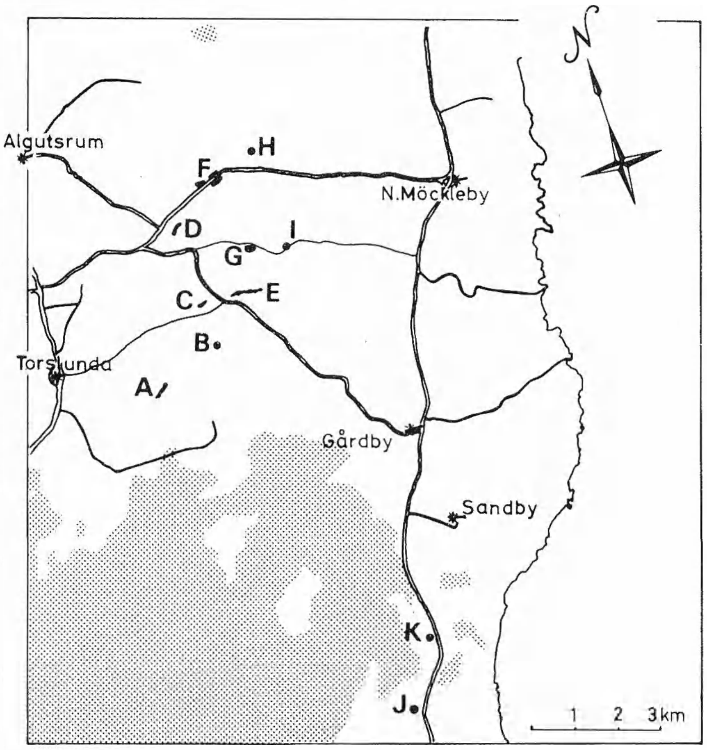


Fig. 2. Observation sites on Central Öland (A–K). Dotted area represents alvar.

are rather friable. The flowers are considered to be scentless (Godfery 1933).

The curious shape of the labellum has naturally invited speculation about its function in the pollination process. Darwin (1862) first believed that depression of the epichile by an insect would favour pollination as an "open gangway is offered" to the visitor for reaching the stigma. However, after his son William had observed pollination by hive-bees in the Isle of Wight he concluded (Darwin 1869) that bees always clung to the epichile whilst sucking the nectar. As the bees left the flowers it seemed that the epichile in regaining its normal position threw them slightly upwards so that their heads brushed against the rostellum. Ziegenspeck (1936) put forward the theory that when the insect backs out of the flower, depression of the epichile cooperates with the possibilities for foothold on the outside of the hypochile to induce a stretching of the body of the insect which brings its head into contact with the rostellum. However, Drawin's "spring-board" theory is still the one generally accepted; see e.g. Summerhayes (1951) and Proctor & Yeo (1973). A modified version has been presented by Wiefelspütz (1970) who concluded that the depressed epichile "reizt... die Bauchhaare der Biene, wodurch diese veranlasst wird, nach oben abzufliegen".

Material and methods

The studies were carried out on Central Öland in 1972–77 and on one occasion in Skåne in 1976. On Öland the study sites are situated to the north and east of the Great Alvar (Fig. 2). They will henceforth be referred to as A–K and the locality in Skåne as L. The populations at A–E, G and H grow in relatively damp meadows surrounded by deciduous wood. Few other plant species growing in this biotope offer nectar during the anthesis period of *E. palustris*. Important in this plant community are: *Gymnadenia conopsea* (L.) R. Br. and *Herminium monorchis* (L.) R. Br. (Orchidaceae), *Prunella vulgaris* L. and *P. grandiflora* (L.) Jacq. (Lamiaceae), *Tetragonolobus maritimus* (L.) Roth. (Fabaceae), *Potentilla erecta* (L.) Räusch. (Rosaceae), *Centaurea jacea* L. and *Inula salicina* L. (Asteraceae). Population F largely occurs along roadside ditches and represents a successful invasion of newly exposed ground with a favourable water supply. Here, other nectar plants are numerous and include most of the common species frequent in drier habitats, e.g. many species of Asteraceae, Apiaceae, Rosaceae and Fabaceae. Stands of *Pastinaca sativa* L. (Apiaceae) are of special importance as they attract considerable numbers of nectar-feeding insects. The slopes at the roadside are rather densely inhabited by several species of ants, especially *Formica fusca* L. and *F. rufibarbis* F. At site I insects visiting the flowers of *Laserpitium latifolium* L. (Apiaceae) were examined for pollinaria of *E. palustris*, from flowering stands at least 100 m away. The localities J and K are not surrounded by trees, but are more open, with scattered bushes. Other nectar plants present mostly the same as those at sites A–E. Population K occurs among low junipers, on the driest and most exposed site of all those studied. Locality L in Skåne is an overgrowing marsh at Stångby.

Flower visitors were collected and their depositions of pollinaria counted. In cases in which the exact numbers of the viscid masses carried were impossible to determine, because of their tendency to fuse with each other, an approximate count was made making a size comparison with those of lumps found on other insects for which proper counts had been possible. On several occasions visitors escaped the net, or were lost when being observed, or became intimidated and escaped during photography. In such cases, if the insect carried an indefinate large mass of pollinaria they were counted as three. Hours spent in observation at the study sites were: A 11, B 2, C 5, D 3.5, E 31, F 19.5, G 13.5, H 1.5, I 1, J 1, K 2, and L 2. The frequency of visitors was low in dull or cloudy weather, i. e. the observations were mainly made on warm and sunny days.

The possible occurrence of floral scent was investigated by collection in pre-column tubes and checked by gas chromatography (cf. Nilsson 1978).

Scent

No emitted compounds could be detected. Since the method has proven to be very sensitive, it seems that emanation of scent from the flowers is very limited. Saturated air over flowers enclosed in glass tubes had no perceptible scent.

Flower visitors

A total of 431 visitors were recorded (Table 1). Hymenoptera and Diptera predominated with 49.7 and 40.8 % respectively. A minor part consisted of Coleoptera (5.8 %), Lepidoptera (2.8 %) and Araneida (0.9 %). Ants (Formicidae), bumble-bees (*Bombus* spp.) and hover-flies (Syrphidae) were the most frequent visitors (Fig. 3, left-hand bars). The most frequent species were *Herina frondescentiae* (Otitidae), *Bombus pascuorum, Formica rufibarbis, F. fusca* and *Syritta pipiens* (Syrphidae). Frequently recorded species were also normally abundant at several of the localities. An exception was *F. rufibarbis,* which was only found at F. Although less numerous, *Hemipenthes morio* (Bombyliidae), *Sphaerophoria scripta* (Syrphidae) and *Bombus pratorum* were observed at several sites. Some insects were found in small numbers at several sites, viz. *Ectemnius continuus* (Sphecidae), *Anoplius nigerrimus* (Pompilidae) and *Eumenes pedunculatus* (Eumenidae). Honey-bees were only seen at two sites and on two occasions. At F 49.5 % of the visitors were ants. The five records of stratiomyids were all made at E in 1976.

The flowers are sometimes visited by hunting spiders. Females of *Misumena vatia* (Thomisidae) were found together with freshly-killed *Bombus lucorum* and *Ancistrocerus parietinus* (Eumenidae) (Fig. 4 F). A smaller thomisid (*Xysticus* sp.) had killed a female of *Scatophaga stercoraria* (Scatophagidae). Also found dead in flowers, obviously the prey of spiders, were one male of *Cerceris quinquefasciata* (Sphecidae) and one female of *Chrysura neglecta* (Chrysididae). Approximately 1.2 % of the visitors were killed by spiders.

Of the visitors, 140 (32.5 %) carried pollinaria. The greatest number was found on Hymenoptera (74.2 %). Diptera, Coleoptera and Araneida had 21.3, 4.0 and 0.5 % respectively. The most frequent nectar feeders were thus comparatively seldom found with attached pollinaria, while some of the less frequent feeders carried heavy loads (Fig. 3). Solitary wasps (Eumenidae) seem to be the most important pollinators. The high score for ants was a result of their frequent visits at F, where these insects carried 43.9 % of all pollinaria. The frequent dispersal of pollen (10.7 %) by digger-wasps (Sphecidae) seems of more general importance. Only 3.1 % of the pollinaria were found on honey-bees.

Behaviour of visitors

Visitors move between individual plants and between the flowers within the same raceme by creeping–climbing or flying. Ants and spiders easily climb the stems and move freely among the flowers due to the hairiness of the plant serving as an excellent foothold (cf. Fig. 4 D). Some types of insects usually climb between flowers but fly between adjacent plants, e. g. beetles, parasitic wasps and *Herina frondescentiae,* sometimes also pompilids and stratiomyids. The majority of other insects fly between flowers. Linear approach from quite a distance, regardless of wind direction, indicates visual guidance only. The small, funny dipteron *H. frondescentiae* can be seen waving its wings in flowers or up and down the stems. Both sexes are present in flowers and courtship often takes place there. Their habits are dangerous, because

Table 1. Visitors to flowers of *Epipactis palustris*. Number with pollinaria within parenthesis. Asterisks indicate observations only.

Visitors	Localities	Number	Number of pollinaria carried
Coleoptera			
Strangalia melanura (L.)	C G	2 ♂♂	
S. maculata Poda*	G	1 ♂ (1)	3
Coccinella septempunctata L.	E	1 ♀ (1)	1
Rhagonycha fulva (Scop.)	C	1 ♂, 2 ♀♀ (2)	2
Cantharis figurata Mnh.	E	1 ♀	
Dasytes plumbea Müll.	A E	2 ♀♀	
Malachius viridis F.	F	1 ♂	
Oedemera femorata Scop.	F	3 ♀♀ (2)	3
O. lurida Marsh.	F	1 ♀	
Isomira murina (L.)	F	1 ♂, 1 ♀	
Meligethes aeneus F.	C E F	8	
Hymenoptera			
Passaloecus singularis Dahlb.	C	1 ♀	
Mimesa rufa (Pz.)	C	3 ♂♂ (3)	4
Cerceris rybyensis (L.)	B I	1 ♂ (1), 1 ♀ (1)	2
C. quinquefasciata (Rossi)	F	2 ♂♂ (1)	3
Crabro cribrarius (L.)	A	2 ♂♂ (2)	5
Ectemnius continuus (F.)	D E G	2 ♂♂ (2), 2 ♀♀ (2)	6
Crossocerus podagricus (v. d. Lind.)	E	1 ♀ (1)	1
Sphecidae*	E	1 (1)	3
Anoplius nigerrimus (Scop.)	A C E	2 ♂♂ (1), 1 ♀ (1)	3
Arachnospila spissa (Schiödte)	E	2 ♀♀ (2)	3
Pompilidae*	E F	3 (2)	4
Dolichovespula norwegica (F.)	E F	4 ☿☿ (4)	14
Euodynerus quadrifasciatus (F.)	A	1 ♂ (1)	5
Ancistrocerus parietinus (L.)	G	1 ♂	
A. oviventris (Wesm.)	F	1 ♀ (1)	3
A. ichneumonideus (Ratz.)	E	1 ♀	
A. trifasciatus (Müll.)	G	1 ♂ (1)	1
Eumenes pedunculatus (Pz.)	A E G	4 ♂♂ (4)	11
Eumenidae*	A E F G	8 (7)	19
Holopyga ovata Dhlb.	E F	2 ♀♀ (1)	3
Chrysura neglecta (Shuck.)	E	1 ♀ (1)	1
Chrysididae*	A	1 (1)	2
Lasius niger (L.)	D F	19 ☿☿ (1)	1
Formica fusca L.	C E F G	23 ☿☿ (13)	13
F. rufibarbis F.	F	24 ☿☿ (11)	11
F. sp.*	G	1 ☿	
Apis mellifera L.	E F	8 ☿☿ (4)	7
Andrena fucata Sm.	A	1 ♀ (1)	4
A. bicolor F.	A	1 ♀ (1)	1
A haemorrhoa (F.)	G	1 ♀ (1)	7
A. spp.*	E F	3 ♀♀ (2)	5
Halictus tumulorum (L.)	A E F	2 ♂♂, 3 ♀♀ (1)	1
Lasioglossum albipes (F.)	E H	1 ♂, 1 ♀	
L. calceatum (Scop.)	F	1 ♂ (1)	2
L. fulvicorne (K.)	E	5 ♂♂ (2)	2
Halictidae*	E	1 ♂ (1)	1
Bombus pascuorum (Scop.)	A B C E F G	1 ♂, 31 ☿☿ (1)	1
B. pratorum (L.)	A B E G	6 ♂♂ (1), 5 ☿☿ (3)	4
B. lucorum (L.)	D E G	3 ♂♂ (2), 5 ☿☿ (1)	
B. hypnorum (L.)	B E	2 ♂♂	
B. lapidarius (L.)	F	1 ☿	
B. spp.*	C F G	3 ☿☿	
Apoidea*	F	2 (1)	1
Pion crassipes (Hlmgr.)	E G	1 ♂ (1), 2 ♀♀ (2)	4
Bathythrix geniculosus Th.	E	1 ♀ (1)	1
Idiolispa analis (Grav.)	F	1 ♀	
Itoplectis viduata (Grav.)	E	1 ♂ (1)	2
Ichneumonidae*	E	1 ♀ (1)	1
Microchelonus erosus (H.-Sch.)	L	1 ♀ (1)	1
Chelonus dauricus Tel.	F	1 ♀	
Tenthredopsis nassata (L.)	E	1 ♀ (1)	1
Tenthredinidae*	F		
Lepidoptera			
Lasiommata maera (L.)	D	1 ♀	
Coenonympha tullia (Müll.)*	E	10	
C. pamphilus (L.)*	C	1	

Visitors	Localities	Number	Number of pollinaria carried
Diptera			
Anomaloptera nigra (L.)	C	1 ♂	
Stratiomys furcata F.	E	3 ♂♂ (3)	8
Stratiomyidae*	E	2 (2)	6
Hemipenthes morio (L.)	A C E F G	15 (16)	7
H. maurus (L.)	E	1 ♀ (1)	1
Empis tesselata F.	C E	1 ♂, 1 ♀	
E. livida L.	C	1 ♂	
E. punctata Meig.	J	1 ♀	
Rhamphomyia caliginosa Coll.	J	1 ♂	
Syritta pipiens (L.)	A C E F J	22 (3)	4
Sphaerophoria scripta (L.)	A C E L	6 ♂♂, 6 ♀♀	
Syrphus vitripennis Meig.	E	1 ♀	
Metasyrphus corollae (F.)	E	1 ♂, 1 ♀	
Melanostoma scalare (F.)	E	1 ♀ (1)	1
Helophilus pendulus (L.)	E F	1 ♂, 2 ♀♀	
H. hybridus Lw.	E	1 ♀	
Syrphidae*	E F	5 (1)	
Herina frondescentiae (L.)	ACDEFJ	81 (13)	13
Sepsis fulgens Meig.	J	1 ♂	
Urophora jaceana (Her.)	A	1 ♀ (1)	1
Trypetidae*	E	1 ♀ (1)	1
Allophora pusilla Meig.	C	1 ♂	
Zophomyia temula Scop.	F	1 ♀	
Exorista rustica Fall.	A	1 ♀	
Cylindromyia auriceps Meig.	F	1 ♂	
Loewia phaeoptera Meig.	A J	2 ♂♂ (1)	2
Lucilia silvarum Meig.	E	1 ♂	
Onesia agilis Meig.	E	1 ♀	
Pollenia rudis (F.)	E F	1 ♂, 2 ♀♀	
Sarcophaga frenata Pand.	F	1 ♂	
Scatophaga stercoraria (L.)	H	1 ♀ (1)	1
Phaonia incana Wied.	J	2 ♂♂ (1)	1
Pegohylemyia brunneilinea (Zett.)	E	1 ♀ (1)	1
Delia angustiventris Zett.	E	1 ♂	
Musca tempestiva Fall.	J	1 ♂	
Araneida			
Misumena vatia (Cl.)	A E G	3 ♀♀ (1)	1
Xysticus Koch sp.	H	1	

their wings often adhere to sticky surfaces in the flowers.

Creeping–climbing visitors like ants enter the labellum from the side and may finally end up under the column (Fig. 5 A). Other visitors sometimes behave rather irrationally when taking nectar (Fig. 4 G). Once a female of *Pion crassipes* (Ichneumonidae) was seen to enter flowers upside down, thereby removing the pollinaria on its underside.

While probing the hypochile bumble-bees grip various parts, sepals or petals or the labellum. Due to their weight the pedicel bends and they often have to work the flowers in an inverted position (Fig. 5 B). Since their mouth-parts are relatively long, body and head are at a distance over the surface of the labellum (Fig. 4 H).

Most bees, wasps and flies alight on the epichile and, depending on their weight, more or less have to compensate for the sinking movement by some kind of behavioural response. Smaller bees and flies, e.g. *Syritta pipiens,* hardly depress the epichile (Fig. 4 E; cf. Kullenberg 1949). The epichile is strongly depressed by social (Vespidae) and solitary wasps, the larger digger-wasps, honey-bees, solitary bees of the genus *Andrena* and by bumble-bees. As Darwin (1869) noted, honey-bees cling to the epichile (Fig. 4 B). The sinking is compensated by stretching the hind legs. When the honey-bee takes nectar from the inner corner of the hypochile its head is forced against the column (Fig. 4 C). When leaving, the bee stretches itself to its full length and flies upwards, outside the

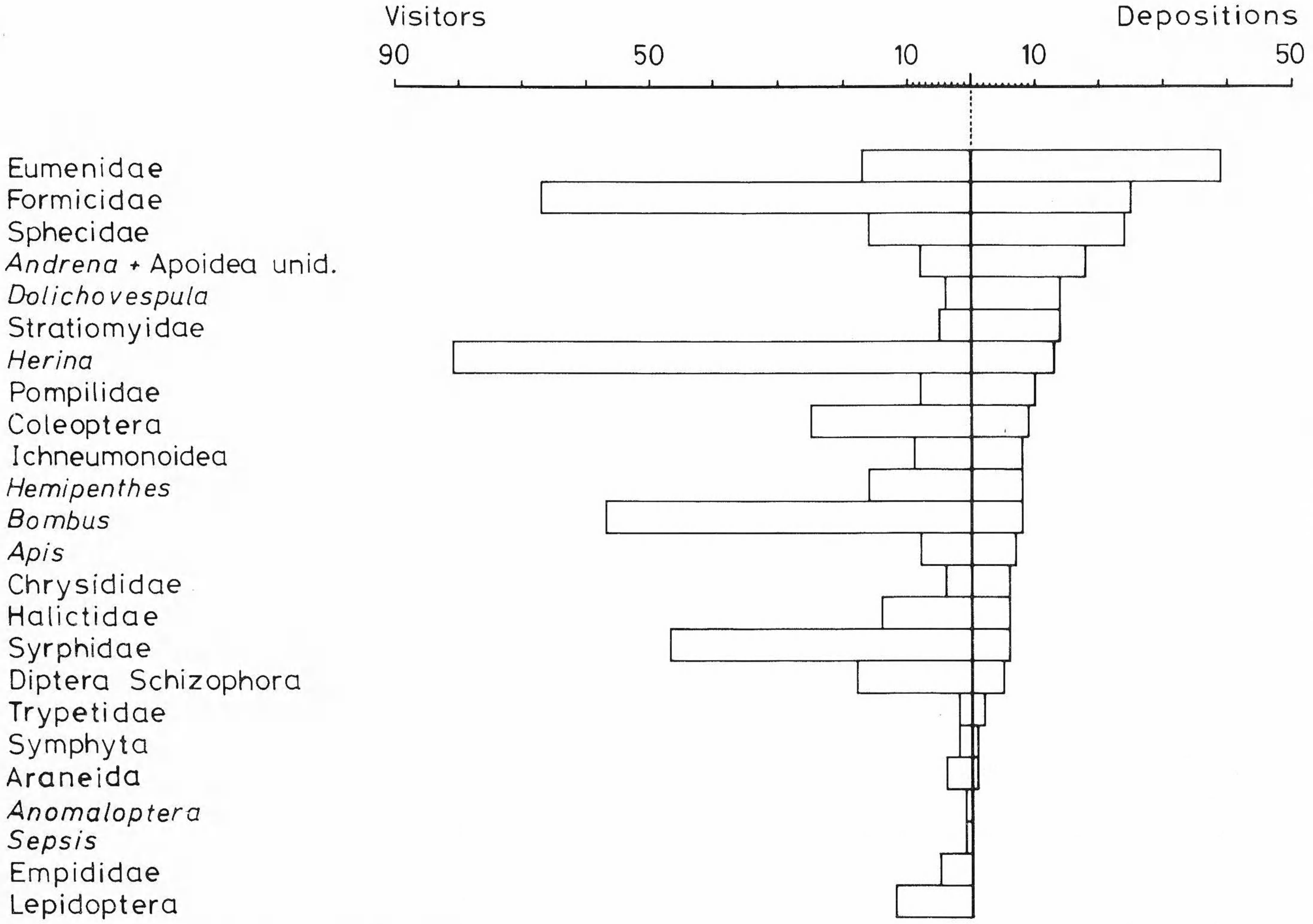


Fig. 3. Number of visitors of different groups to flowers of *Epipactis palustris* and the deposition of pollinaria.

column. No ''spring-board'' effect, produced by the epichile, was observed. Social wasps and the larger digger-wasps have much shorter mouthparts and thus have to move their heads close to the bottom of the hypochile and press it against the base of the column. When they back out of the flower the head is raised and frequently hits the rostellum.

The most striking interaction of insect and epichile occurred during visits by solitary wasps, especially by males of *Eumenes pedunculatus*. Several attempts to take prictures of them on flowers failed, because of their vigilance. Thus their behaviour could not be analysed in detail, except that perceived by the naked eye. The species of *Eumenes* differ from all other visitors in the narrow bell-shape of their first abdominal segment (Fig. 7 E, J). When these wasps alight on the labellum, the epichile moves downwards-backwards. The visitor responds to this by bending its abdomen forwards under the rest of the body and not by trying to ''stand on its hind legs'' as do the honey-bees. At the same time the wasp becomes centered on the labellum. It lowers its head and soon forces it against the stigma in removing the last nectar with its glossa. At that moment a slight returning movement by the epichile can be observed. It seems probable that the wasp effects this by drawing itself into the flower with help of its front claws on the hypochile. However, the exact positions of the claws could not be determined. As the visitor begins to back out of the flower the epichile immediately moves backwards for a second time. In the next moment the wasp leaves the flower with a fresh pollinarium affixed to its face. For a fraction of a second before this happens it seems that the insect partially loses its balance and tips backwards, whereby the head passively brushes against the rostellum from below and withdraws the pollinia from their pocket.

Small or weak insects which receive pollinaria often show behavioural disturbances due to the added weight. In *Herina frondescentiae* the load prevents flight. Such flies were sometimes seen creeping about in the grass around the orchids, obviously unable to carry out pollination. Even stronger insects may suffer from heavy loads of pollinia (Fig. 4 D). Grooming, resulting in removal of pollinia from the body, was not observed but might be expected.

Constancy (i.e. visiting behaviour restricted to *E. palustris)* was regularly seen in wasps and bees. Bumble-bees often abandoned the orchid for *Prunella* spp. which evidently give more adequate stimulus for developing constancy. Altered visits sometimes occurred when *Prunella* spp. grew scattered and the bumble-bees had to pass many orchids during their seeking flight. In places with umbelliferous plants, orchid pollinators were found to have switched their visits, i.e. constancy to *E. palustris* had been broken. Examples are *Dolichovespula norwegica* (Vespidae) taking nectar from *Pastinaca sativa* at F and *Cerceris rybyensis* (Sphecidae) on flowers of *Laserpitium latifolium* at I, both having pollinaria attached to their heads. Constancy was also seen in flies, e.g. *Syritta pipiens* and *Sphaerophoria scripta*.

As expected, pollen disperal was found to be greatly dependent on physical properties, locomotion and life habits of visitors. At F, ants were frequent pollinators in the vicinity of their nests, but their number decreased with distance. Several times the same ant was observed to pollinate all the open flowers in a single raceme one after another and also to make repeated visits to the same flower. Thus the methodical habits of ants certainly lead to a high level of auto- and geitonogamy within their home-range. That dispersal might occur over longer distances, 100 m or more, is indicated by the record of *Cerceris rybyensis* at I.

Functional morphology

The frequency of pollinaria on different types of visitors shows that solitary and social wasps and bees (*Andrena*) are the most well-disposed visitors (Fig. 6). Also digger-wasps and spider-hunting-wasps (Pompilidae) rank high. Honey-bees had less than one pollinarium per individual (Table 1). The four specimens of social wasps, all workers of *Dolichovespula norwegica,* had no fewer than 14 pollinaria.

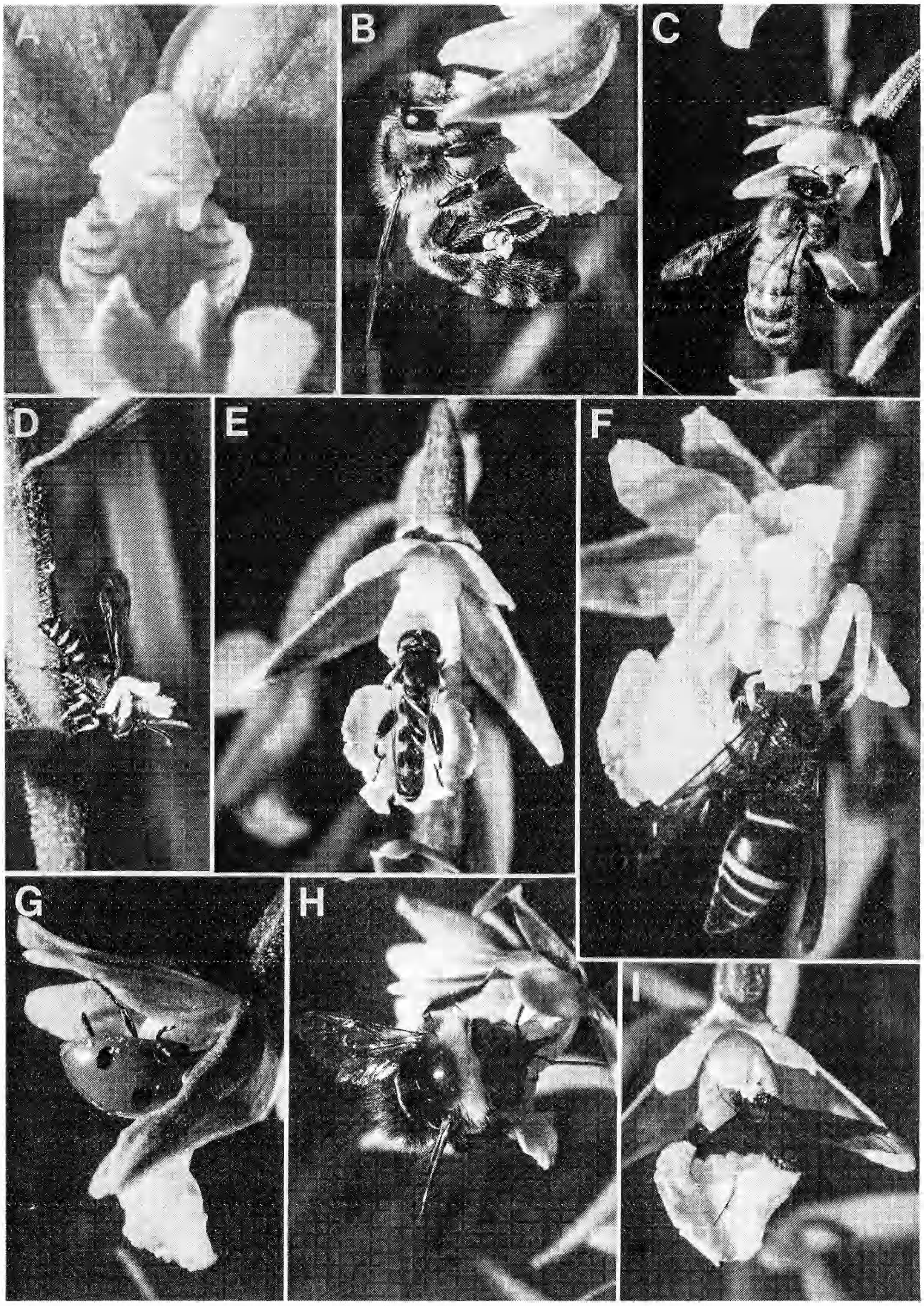
Some of the factors influencing the deposition of pollinaria are evident from Table 2 and Figs. 3–6. Firstly, behaviour must bring some part of the body in touch with the rostellum (see above). Thereafter the visitor must be able to endure viscid matter and be strong enough to withdraw the pollinia. Small insects were sometimes found to have perished, glued to the sticky parts in flowers, e.g. *Sepsis fulgens* (Sepsidae), *Rhamphomyia caliginosa* (Empididae) and *Herina frondescentiae*. Surprisingly, specimens of *Hemipenthes morio* were twice found stuck, being too weak to free themselves (Fig. 4 I).

Pollinaria deposition also depends on the nature of the body surface of the visitor. Long bristles or pubescence are unfavourable for adherence of the viscid mass, e.g. the tachinid flies *Zophomyia temula* and *Exorista rustica* were seen to remove pollinaria, but dropped them immediately as the insects left the flowers. In rare cases, *Pegohylemyia brunneilinea* (Anthomyiidae) for instance, the viscid-mass was recorded adhering to bristles (Fig. 7 M).

Long mouth-parts decrease deposition, because the visitors often reach the nectar without touching the rostellum with their heads (Fig. 4 H). In addition to the butterflies, good examples are the bumble-bees, especially *Bombus pascuorum* which has the longest tongue of those recorded. Of 32 individuals of this species only one had one single pollinarium. With decreasing length of mouth-parts deposition generally occurs further and further up on the head (cf. Fig. 7 F–I). Similarly, increasing size of the insect favour deposition more and more anteriorly on the body (cg. Fig. 7 A–E). The number of pollinaria carried by a visitor depends on the size of that part of the body which hits the rostellum, because deposition on the surfaces of previously received pollinia greatly increases the risk for falling off, a phenomenon noted on many collected specimens.

To sum up, interactions of flower structures and visiting insects produce a varied deposition (Table 2 and Fig. 7 A–O). On insects with the highest frequency of pollinaria, i.e. solitary and social wasps, larger digger-wasps and some solitary bees pollinaria are regularly deposited in the face between the eyes. Others receive attachment further back or irregularly.

Pollination was effected by many types of insects, but efficiency varied widely primarily


A
B
C
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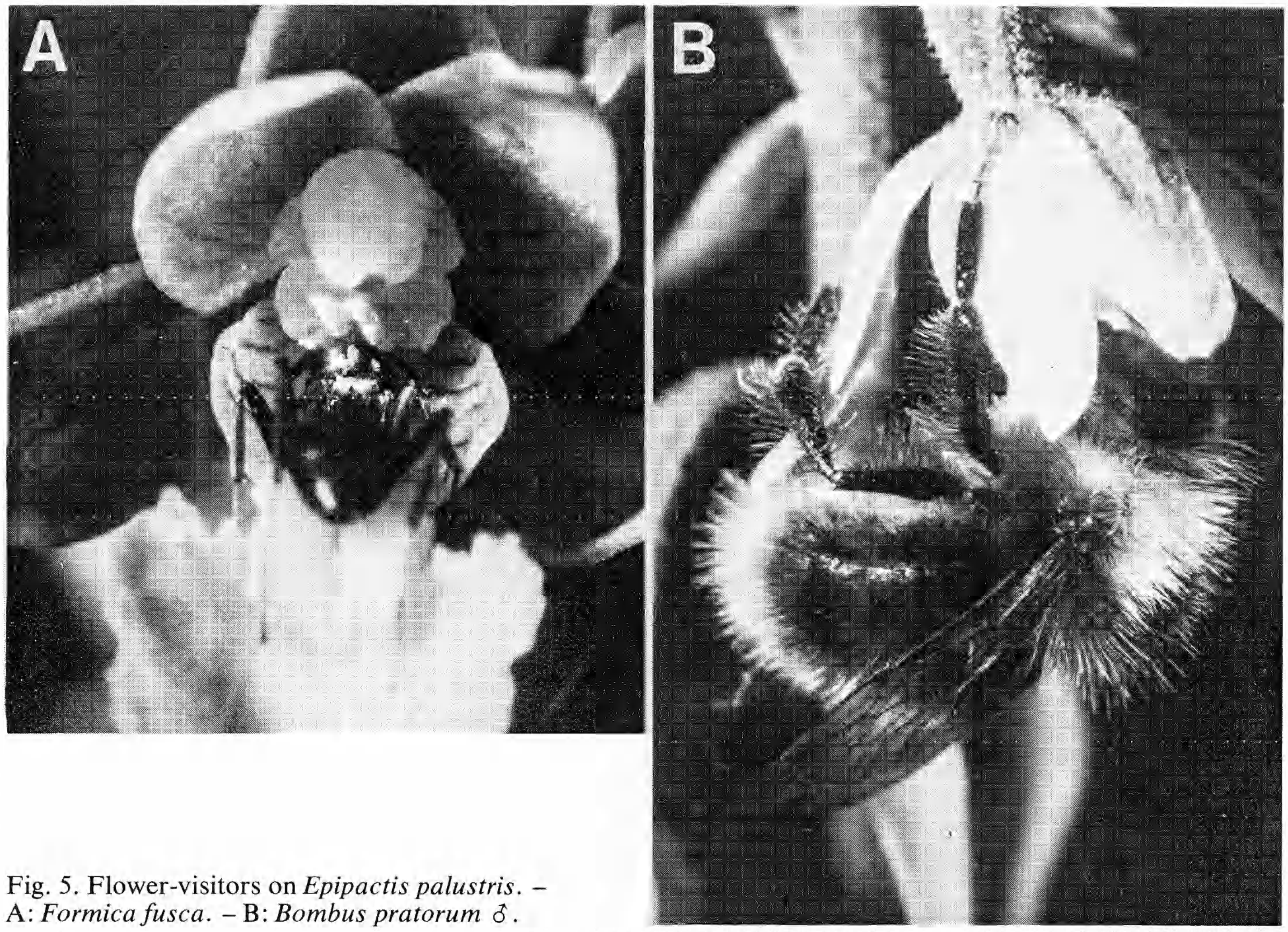

Fig. 5. Flower-visitors on *Epipactis palustris*. – A: *Formica fusca*. – B: *Bombus pratorum* ♂.

due to the relations between flower structures and mouth-parts or the size of the insect. The distance from the posterior margin of the stigma to the inner corner of the hypochile is approximately 1.5 mm and vertically to the bottom 2.5 mm. The stigma itself is about 1.5 mm high. Thus, effective pollination is produced by insects taking nectar at the same time as their clypeus and frons are situated about 1.5–4 mm above the surface of the hypochile, whereby their heads are pressed against the stigma. The length of the labio-maxillar complex in *Cerceris* is 1.5 mm, *Vespula* about 3, *Eumenes* about 4 and in *Apis* 6.1 mm (Kugler 1970). Honey-bees mainly strike the stigma with their long mouth-parts and are therefore ineffective (cf. Fig. 4 C). In *Eumenes pedunculatus* males the maxillae are prolonged (Fig. 7 J) and the distance from the posterior margin of clypeus to the apex of maxillae is 2.4 mm (n 4) and to the apex of glossa 3.1 mm (n 3), i.e. perfect proportions for the face to hit the stigma. When the size permits small insects to crawl up with their head under the column, rather effective pollination may occur from pollinaria attached to the thorax (Fig. 5 A).

The two halves of the labellum indicate morphological adaptations to the body shape of legitimate pollinators. Column contact and support for the visitor is ensured if the length of the hypochile (4–4.5 mm) is a little shorter than head-plus-thorax. In males of *E. pedunculatus* this length is 4.9 (n 4), honey-bees 5.9 (n 4),

Fig. 4. *Epipactis palustris* and flower-visitors. – A: Close view of labellum and column (6.5 ×). – B: *Apis mellifera* clinging to epichile and with pollinaria on clypeus. – C: *A. mellifera* taking nectar from inner part of hypochile. Note forcing of head against column and stretching of hind legs. – D: *Cerceris quinquefasciata* ♂ resting on stem and with heavy load of pollinia on thorax. – E: *Syritta pipiens* taking nectar. – F: *Misumena vatia* ♀ with killed *Ancistrocerus parietinus* ♂ – G: *Coccinella septempunctata* ♀ forcing into flower. Note scattered lumps of pollen on elytra. – H: *Bombus pratorum* ☿ taking nectar. – I: *Hemipenthes morio* ♀ stuck in flower.

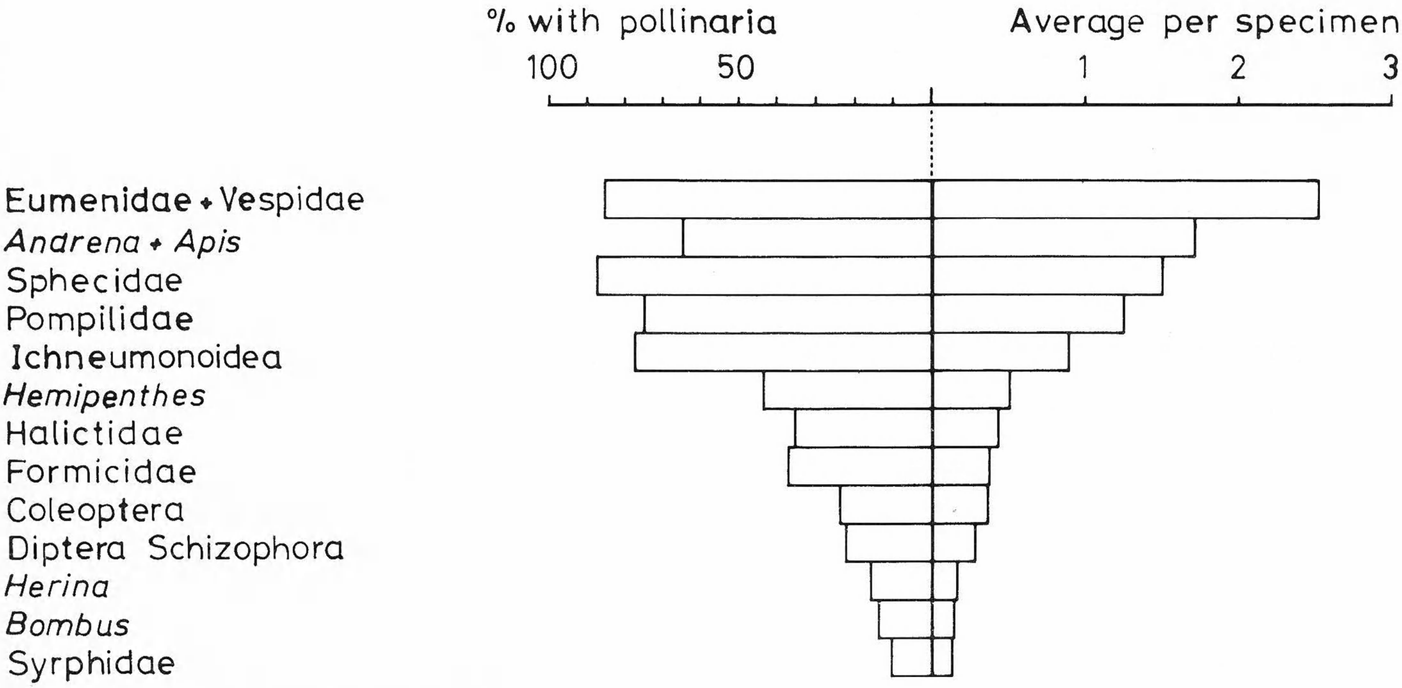

Fig. 6. Frequency of deposition of pollinaria on the most important groups of visitors.

Table 2. Place of deposition of pollinaria on visitors to flowers of *Epipactis palustris*. Underlining marks prevailing mode.

Species	Place of deposition								
	Mouth-parts	Clypeus	Frons	Occiput	Thorax	Antennae	Eyes	Wings	Legs
Coccinella septempunctata L.	.	.	.	.	x	.	.	.	.
Rhagonycha fulva (Scop.)	.	.	.	.	x	.	.	.	.
Oedemera femorata Scop.	.	.	.	.	x	.	.	.	.
Mimesa rufa (Pz.)	.	.	.	.	x	.	.	.	.
Cerceris rybyensis (L.)	.	.	.	x	.	x	.	.	.
C. quinquefasciata (Rossi)	.	.	.	x	x	.	.	.	.
Crabro cribrarius (L.)	.	.	.	x̲	.	x	.	.	.
Ectemnius continuus (F.)	.	.	.	x	x	.	x	.	.
Crossocerus podagricus (v. d. Lind.)	.	.	.	x	.	.	.	.	.
Anoplius nigerrimus (Scop.)	.	.	.	.	x̲	.	.	x	.
Arachnospila spissa (Schiödte)	.	.	.	x	x̲	.	.	.	.
Dolichovespula norwegica (F.)	.	x	x	.	.	.	.	.	.
Euodynerus quadrifasciatus (F.)	.	.	x	.	.	.	.	.	.
Ancistrocerus oviventris (Wesm.)	.	.	x	.	.	.	.	.	.
A. trifasciatus (Müll.)	.	.	.	.	.	.	x	.	.
Eumenes pedunculatus (Pz.)	.	x̲	x̲	.	.	x	.	.	.
Holopyga ovata Dhlb.	.	.	.	x	x	.	.	.	.
Chrysura neglecta (Schuck.)	.	.	.	.	x	.	.	.	.
Lasius niger (L.)	.	.	.	.	x	.	.	.	.
Formica fusca L.	.	.	.	x	x̲	.	.	.	.
F. rufibarbis F.	.	.	.	x	x̲	.	.	.	.
Apis mellifera L.	.	x	.	.	.	.	.	.	.
Andrena fucata Sm.	.	x	x	.	.	.	.	.	.
A. bicolor F.	.	x	x	.	.	.	.	.	.
A. haemorrhoa (F.)	.	x	x	.	.	.	.	.	.
Halictus tumulorum (L.)	.	.	.	x	.	.	.	.	.
Lasioglossum calceatum (Scop.)	.	x	x	.	.	.	.	.	.
L. fulvicorne (K.)	.	.	.	.	.	x	x	.	.
Bombus pascuorum (Scop.)	x	.	.	.	.	.	.	.	.
B. pratorum (L.)	x	.	.	.	.	.	.	.	.
B. lucorum (L.)	x	.	.	.	.	.	.	.	.
Pion crassipes (Hlmgr.)	.	.	.	.	x	.	.	.	.
Bathythrix geniculosus Th.	.	.	.	.	x	.	.	.	.
Itoplectis viduata (Grav.)	.	.	.	.	.	.	.	x	x
Microchelonus erosus (H.-Sch.)	.	.	.	.	.	.	.	x	.
Tenthredopsis nassata (L.)	.	.	.	.	x	.	.	.	.
Stratiomys furcata F.	.	.	x	.	.	.	x	.	.
Hemipenthes morio (L.)	.	.	.	x	x	x̲	x̲	.	.
H. maurus (L.)	.	.	.	.	.	.	x	.	.
Syritta pipiens (L.)	.	.	.	x	.	.	x	.	.
Melanostoma scalare (F.)	.	.	.	.	x	.	.	.	.
Herina frondescentiae (L.)	.	.	.	.	x	.	.	x	.
Urophora jaceana (Her.)	.	.	.	.	x	.	.	.	.
Loewia phaeoptera Meig.	.	.	.	.	x	.	.	.	.
Scatophaga stercoraria (L.)	.	.	.	.	x	.	.	.	.
Phaonia incana Wied.	.	.	.	.	.	.	x	.	.
Pegohylemyia brunneilinea (Zett.)	.	.	.	.	x	.	.	.	.
Misumena vatia (Cl.)	.	.	.	.	.	.	.	.	x

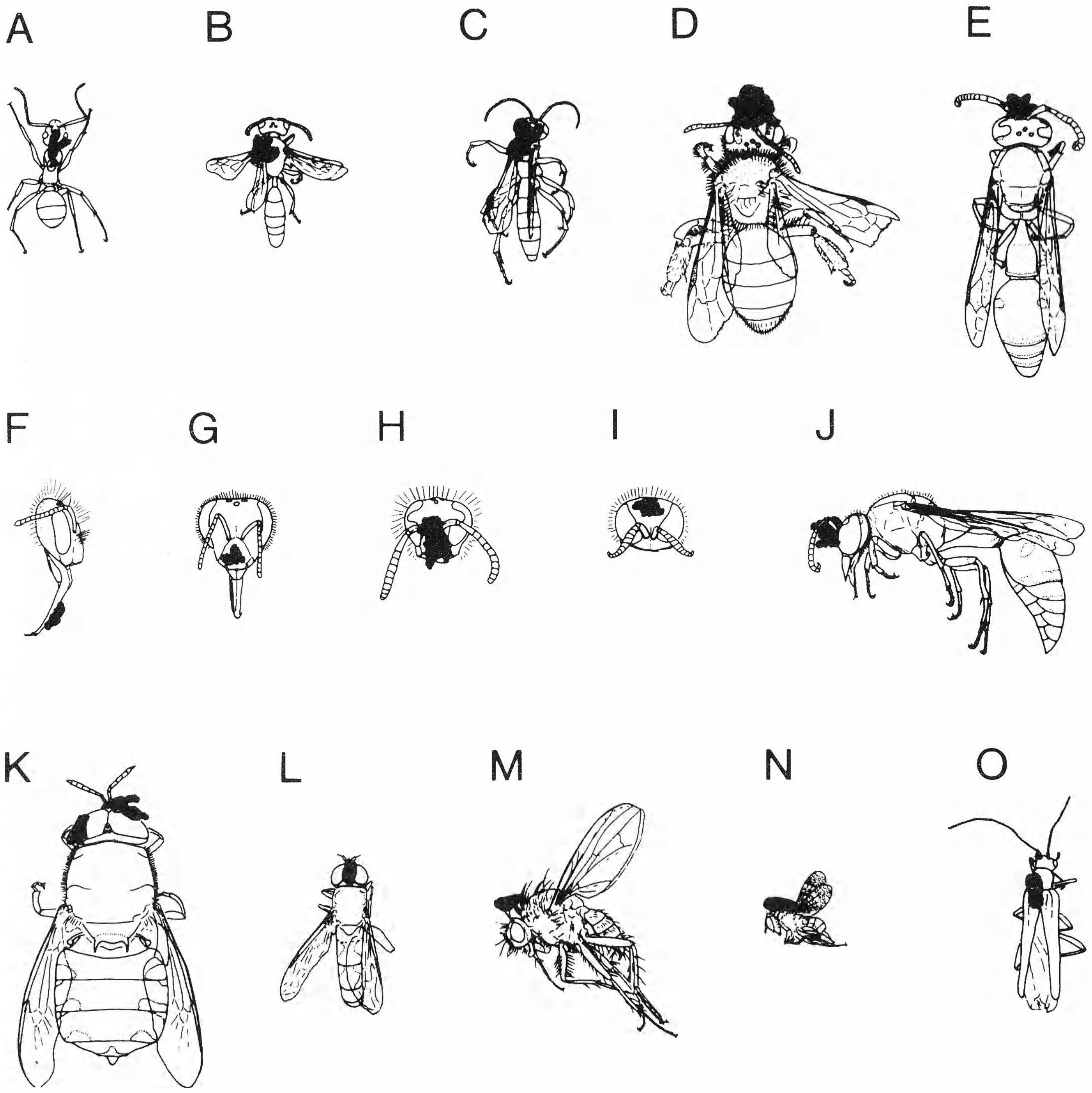

Fig. 7. Depositions of pollinaria on different insects. Drawings of collected specimens (2.8×). Pollinia and viscid-masses are filled black. – A: *Formica rufibarbis,* dorsal view. – B: *Mimesa rufa* ♂, do. – C: *Anoplius nigerrimus* ♂, do. – D: *Andrena haemorrhoa* ♀, do. – E: *Eumenes pedunculatus* ♂, do. – F: *Bombus pratorum* ☿, head, lateral view. – G: *Apis mellifera* ☿, head, front view. – H: *Dolichovespula norwegica* ☿, do. – I: *Crabro cribrarius* ♂, do. – J: *Eumenes pedunculatus* ♂, lateral view. – K: *Stratiomys furcata* ♂, dorsal view. – L: *Syritta pipiens* ♂, do. – M: *Pegohylemyia brunneilinea* ♀, lateral view. – N: *Herina frondescentiae* ♀, do. – O: *Oedemera femorata* ♀, dorsal view.

females of *Andrena haemorrhoa* 5.4 (n 4) and in males of *Crabro cribrarius* (Sphecidae) 6.1 mm (n 2). Thus, head-plus-thorax seems to be too long in the last three species. The inner distance between the raised margins of the furrowed plate of the epichile, measured from photographs, is 1.7 mm. If the morphology of visitors, which are capable of depressing the epichile, is examined, it is evident that the abdomen of only one type of insects fits the size of the plate, viz. the stalked one in solitary wasps. The width of the first abdominal segment of *E. pedunculatus* males is 1.5 mm (n 4), which thus slips perfectly down to become centered on the plate. Other visiting

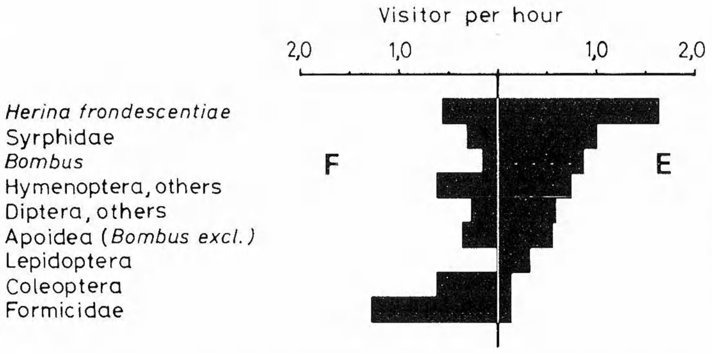

Fig. 8. Frequency of flower visitors (specimens per hour) to *Epipactis palustris* in locality with rich (F) and sparse (E) competing entomophilous flora.

species of Eumenidae have over 2 mm width and honey-bees over 4 mm.

Anthecological status

In the moist meadows A–E, G and H some of the insect species visiting *E. palustris* frequent other plants for nectar. Bumble-bees, e.g. *Bombus pascuorum,* are regularly seen on *Prunella* spp. and *Tetragonolobus maritimus. Hemipenthes* spp. and *Herina frondescentiae* often take nectar from *Potentilla erecta*. The last-mentioned fly is found also on spikes of *Herminium monorchis*. Both the butterfly and the bumble-bee species visit *Centaurea jacea* and *Inula salicina*. However, members of Eumenidae, Vespidae, Sphecidae, Pompilidae, Chrysididae, and Ichneumonidae were not recorded on any other plant than *E. palustris*. In locality F, these insects occurred in great numbers on the flowers of *Pastinaca sativa,* and other Apiaceae which offered plenty of superficial nectar. A comparison of the frequency of visits made to the populations of *E. palustris* at E and F shows that, besides the large abundance of ants at F, all groups of insects except Coleoptera were more often recorded as visitors at E than at F (Fig. 8). The lower rate at F was probably due to competition from more nectar-yielding plants.

In 1973–77 maximum flowering on Öland took place between July 8 and 20. The earliest record for flowering was June 24 (1975) and the latest August 4 (1974). Anthesis does not match the population dynamics in all insect species. Solitary bees like *Andrena haemorrhoa* and *A. fucata* reach their peak in May–June and are almost finished by the middle of the summer. The new generations of *Halictus* and *Lasioglossum* emerge in July, but are at maximum later. Social wasps (Vespidae) reach their highest numbers in August or September when the males appear. Species of Eumenidae, Sphecidae, Pompilidae, Bombyliidae and Syrphidae have more or less strong populations i July.

Table 3. Fruit set of *Epipactis palustris*.

Locality	Year	Specimens	Flowers	Fruit set (%)
F	1976	20	202	64.0
F	1977	61	509	60.1
G	1977	55	409	69.7
B	1977	28	177	60.5

Removal of pollinaria and fruit set

In 1976, 60 % of the pollinaria had been removed from 100 flowers at C (one flower randomly selected from each plant). On the same occasion lumps of pollen had been deposited on the surfaces of 52 % of the stigmas, i.e. they were pollinated by insects. In 1977, 67 and 64 % of the pollinaria were removed from 104 and 41 flowers of 14 and 7 specimens at the localities K and J respectively. Unpollinated flowers, from which the pollinaria had been removed by insects, withered and fell off without developing fruits (also Ziegenspeck 1936). Countings made in autumn give rates between 60 and 70 % fruit set (Table 3). The higher the position of a flower on the raceme, the lower the fruit set (Fig. 9). Ziegenspeck (1936) also noted this phenomenon and suggested that some physiological factor was responsible.

Discussion

The diversity of visitors to *Epipactis palustris* has much in commom with that broad spectrum often found for umbelliferous flowers, both insects with long and specialized mouth-parts and insects with more primitive ones are frequent. The reason is probably the combination of showy flowers and superficial nectar. That "the nectar is unattractive to bumble-bees" (Godfery 1933) or "bumble-bees ... do not seem to be attracted by the flowers" (Summerhayes 1951) is not supported. Bumble-bees also visit *Epipactis helleborine* Crantz (Gerstaecker 1869, Webster 1886) and *E. atrorubens* Schult (Godfery 1933). That honey-bees play a minor role as pollinators conflicts with previous opinions (Godfery 1933, Summerhayes 1951, Werth 1952, Wielfelspütz 1970, Proctor & Yeo 1973). Honey-bees have alson been recorded on *Epipactis muelleri* Godf. (Teschner 1972), *E. atrorubens* (Wiefelspütz 1970) and *E. consimilis* Don (Ivri & Dafni 1977). There is reason to believe that honey-bee management in areas with *Epipactis* will, locally, lead to frequent pollination by these keen foragers.

The importance of solitary wasps as pollinators of *Epipactis* has not been demonstrated previously apart from a record of *Eumenes* on *E. muelleri* (Teschner 1972). *Eumenes pedunculatus* at least sometimes also pollinates *E. helleborine* (Nilsson unpubl.) which is mainly pollinated by social wasps (Darwin 1869, Wielfelspütz 1970, Judd 1972). That digger-wasps might regularly visit *E. palustris* was indicated by Darwin's record (1869) of *Entomognathus (Crabro) brevis* (v. d. Lind.).

Visiting by hover-flies has been observed previously (Heimans & Thijsse 1907, Kullenberg 1949). That hover-flies may act as pollinators within the genus is also known, viz. for *E. gigantea* Dougl. ex Hook. (MacSwain 1966) and *E. consimilis* (Ivri & Dafni 1977). Records of other flies as pollen vectors of *E. palustris* were already made by Darwin (1869), who found *Coelopa frigida* (F.) and *Sarcophaga carnaria* (L.). The tendency of the sticky column to trap small or weak visitors seems to be a general phenomenon within *Epipactis* (Wheldon & Travis 1913, Lingelsheim 1929, Ivri & Dafni 1977).

Observations do not confirm the "springboard" theory invented by Darwin (1869) and furtheron accepted by many others. The interpretation made by Ziegenspeck (1936) is in many ways supported. However, the action of the epichile varies with weight and behaviour of different visitors. With *Eumenes* the hinge probably makes deposition more successful by eliminating the hazardous movements by the wasp when cross-pollination already is achieved and the insect begins to withdraw its head. For a short moment the simple, passive mechanism seems to allow the flower to "take over" what actually happens.

Species of *Epipactis* which are regularly pollinated by social wasps have a rigid and fixed labellum. Obviously, the hinge mechanism is not of positive selective value in that relationship. The most plausible explanation is that social wasps have a "normal" abdomen and not the long and slender, bell-shaped first abdominal segment which is characteristic for solitary wasps.

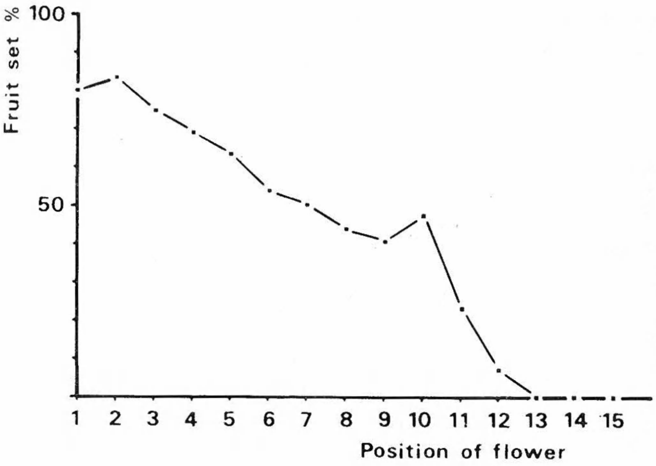

Fig. 9. Fruit set at different levels in racemes of *Epipactis palustris* (n 164). The positions of flowers are numbered from below.

Although no floral scent was detected, the possibility remains that some special compounds, odourless, of high molecular weight or in small amounts, are present and may influence the insect behaviour. In *Epipactis consimilis* it has been suggested that olfactory stimulation releases visiting behaviour by aphidophagous hover-flies, some of which oviposit on the epichile (Ivri & Dafni 1977).

The pollination system seems to be sensitive to competition. Perhaps *E. palustris* has become adapted to moist biotopes due to its weak competitive ability. However, its relatively low production of nectar, which certainly affects the frequency of insect visits, might well be of a secondary nature, i.e. few competitors in moist habitat have favoured selection of less expenditure in the form of nectar. Species of *Epipactis* which secrete large amounts of nectar in the hypochile (e.g. *E. helleborine*) occur on drier ground where there is harder competition for insect visits.

Darwin (1862) found a great majority of the pollinaria cleanly removed from inflorescences, which suggested that insects most frequently act as pollinators. The same is indicated by the present observations. However, according to Wiefelspütz (1970) self-pollination prevails in most cases. Perhaps the facultative process results in a variable extent of allogamy at different times and in different localities, as propounded by Proctor & Yeo (1973).

The fragile nature of the pollinia suggests that predominantly pollinaria deposited on insects during the same day or the same feeding or foraging trip, take part in pollination. Most likely a great loss of pollen occurs by the provisioning or burrowing habits of the females of solitary and social wasps, digger-wasps, solitary bees etc. Orchids which have reached a certain level of anthecological specialization to these groups of Hymenoptera should be subjected to a more or less strong selection towards a closer relationship with the males which do not dig, hunt or nest. In various ways *E. palustris* is perhaps adapted to the swarming of males of *Eumenes*. Hitherto, only males have been observed on the flowers.

To sum up, many facts support that *E. palustris* is closely associated with solitary wasps, viz. flowering time, deposition and frequency of pollinaria, morphology and action of the hinged labellum. It seems that the legitimate pollen vectors are present at low population densities, a situation probably widespread for species within the Orchidaceae. *E. palustris* is in no way a "generalist" as regards its pollinating agents even if it may appear so owing to the simple and unprotected mechanism for deposition of pollinaria in combination with superficially offered nectar.

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The genus Leysera (Compositae)

Kåre Bremer

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

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

History and nomenclature

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

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

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

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

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

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

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

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

Delimitation and systematic position

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

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

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

Morphological aspects

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

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

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

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

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

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

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

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

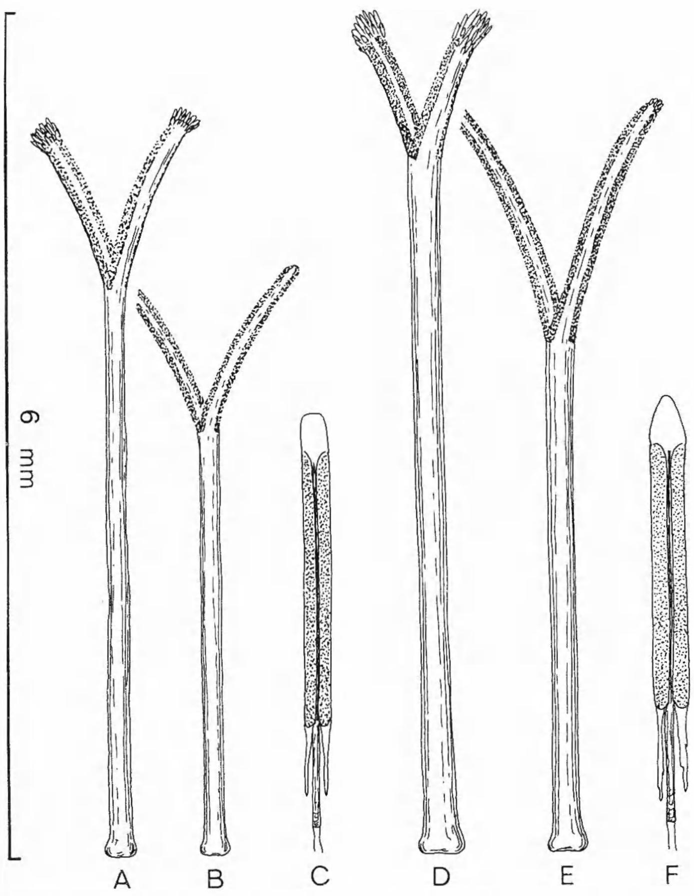

Fig. 1. – Styles and stamens of *Leysera*. – A, D: Disc-floret styles. – B, E: Ray-floret styles. – C, F: Stamens. – A–C: *L. gnaphalodes*, Bremer 167 (S). – D–F: *L. longipes*, Esterhuysen 29941 (BOL).

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

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

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

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

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

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

Chemistry

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

Phytogeography and phylogeny

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

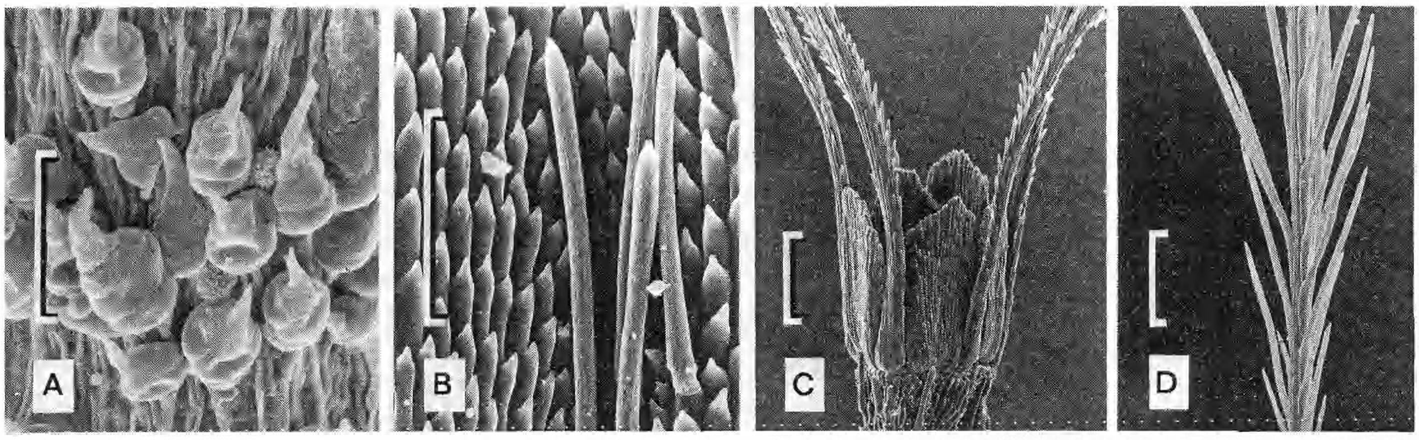

Fig. 2. Electroscan photomicrographs of floret tube hairs and achenes of *Leysera*. The length of the scales is 0.1 mm. – A: Floret tube hairs (and two pollen grains) of *L. gnaphalodes*. Similar hairs occur in *L. tenella* and *L. leyseroides*. – B: Achene surface with imbricated cells and hairs of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

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

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

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

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

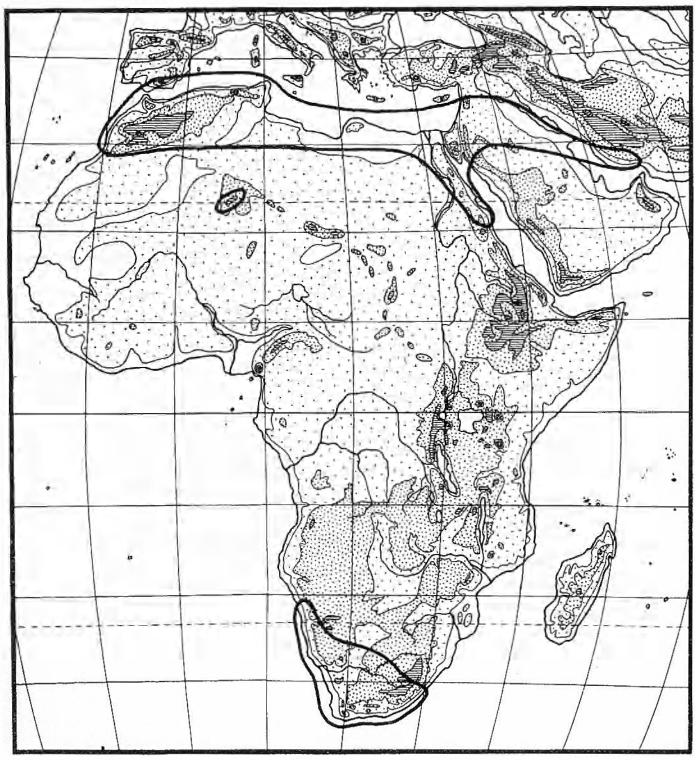

Fig. 3. The approximate total range of *Leysera*.

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

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

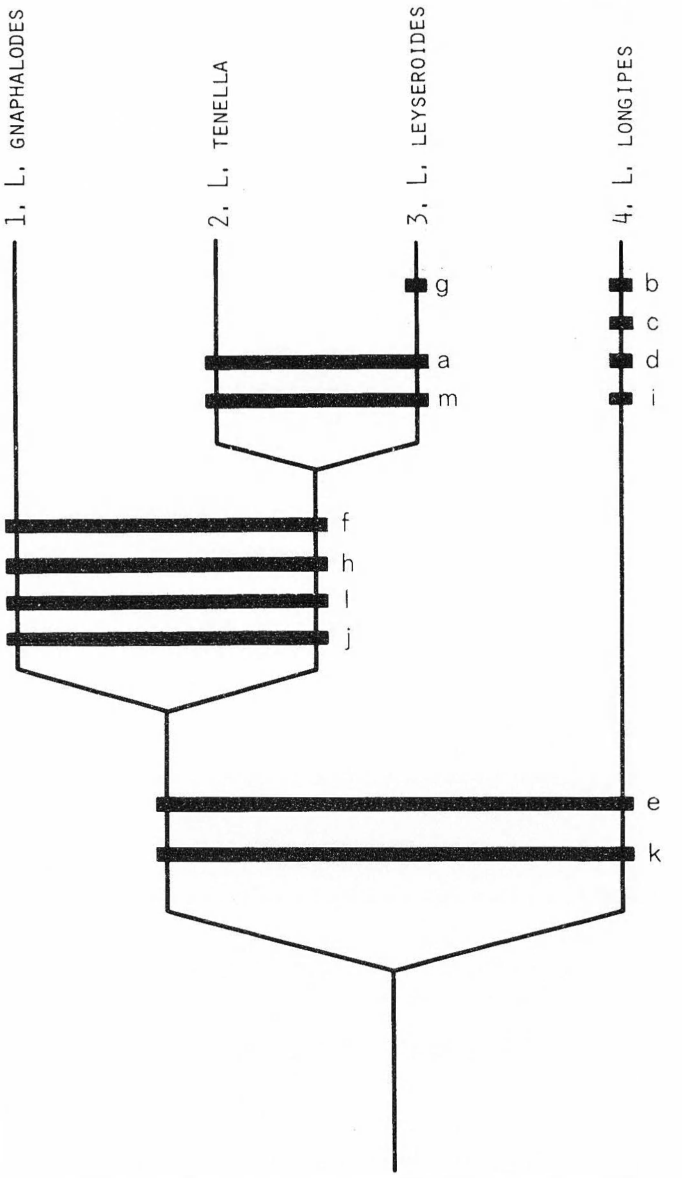

Fig. 4. Cladogram of the *Leysera* species. Bars indicate synapomorphies and letters correspond to the derived conditions in Table 1.

TAXONOMY

Leysera L.

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

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

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

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

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

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

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

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

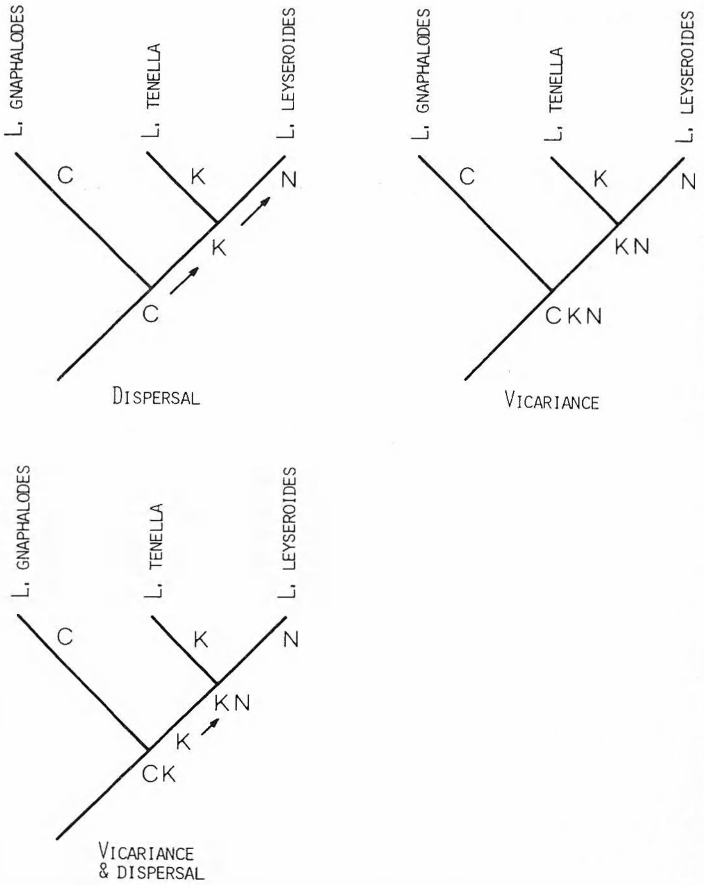

Fig. 5. Dispersal and vicariance models for *Leysera gnaphalodes, L. tenella,* and *L. leyseroides.* Letters indicate geographic regions, C = roughly the Cape region, K = roughly the Karoo region, and N = roughly N Africa. Arrows indicate dispersal.

Key to the species

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

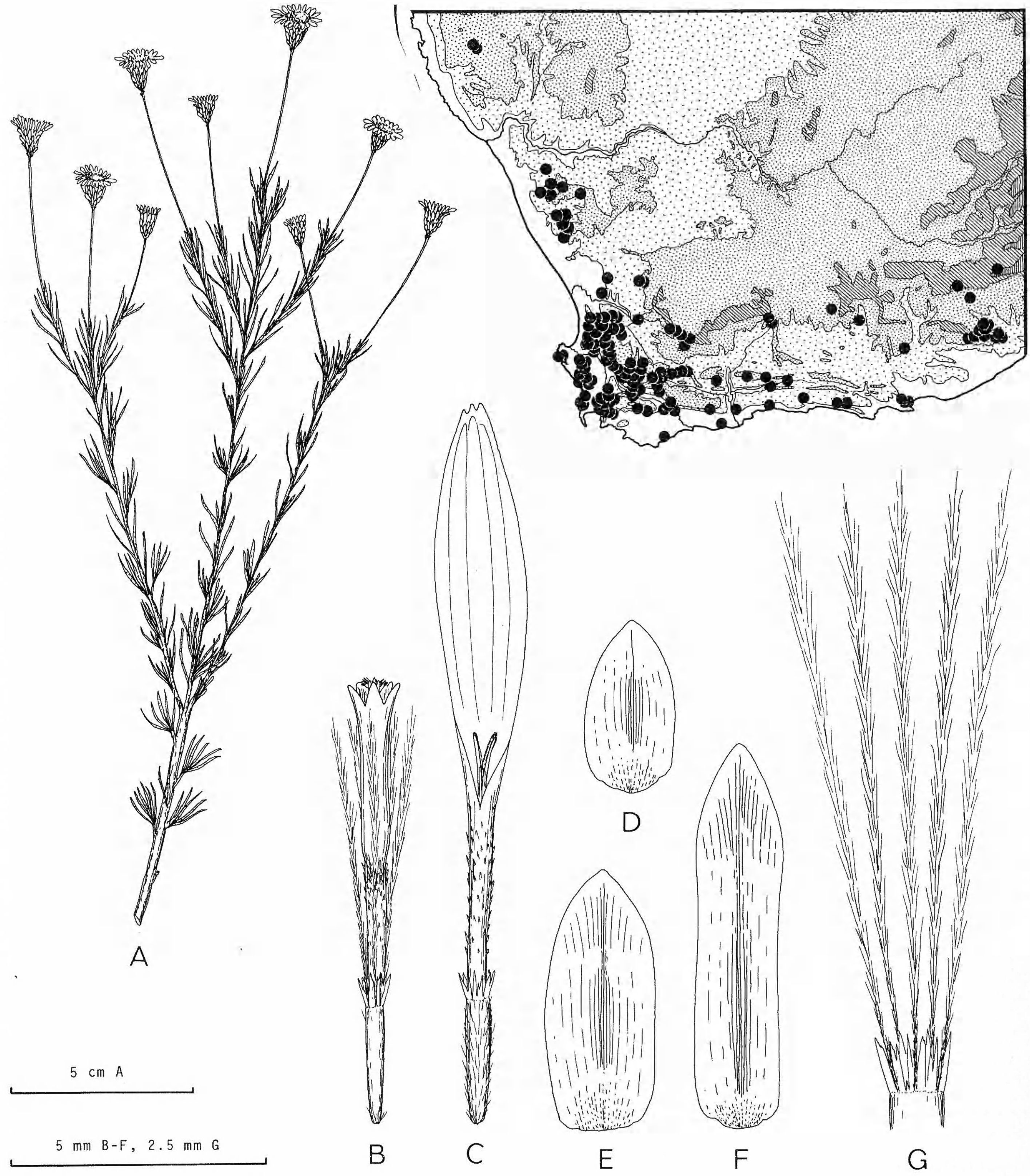

Fig. 6. Distribution and plant parts of *Leysera gnaphalodes*. – A: Portion of plant. – B: Disc-floret. – C: Ray-floret. – D–F: Outer–inner involucral bracts. – G: Pappus of disc-floret achene. – A–G: Goldblatt 3281 (S).

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

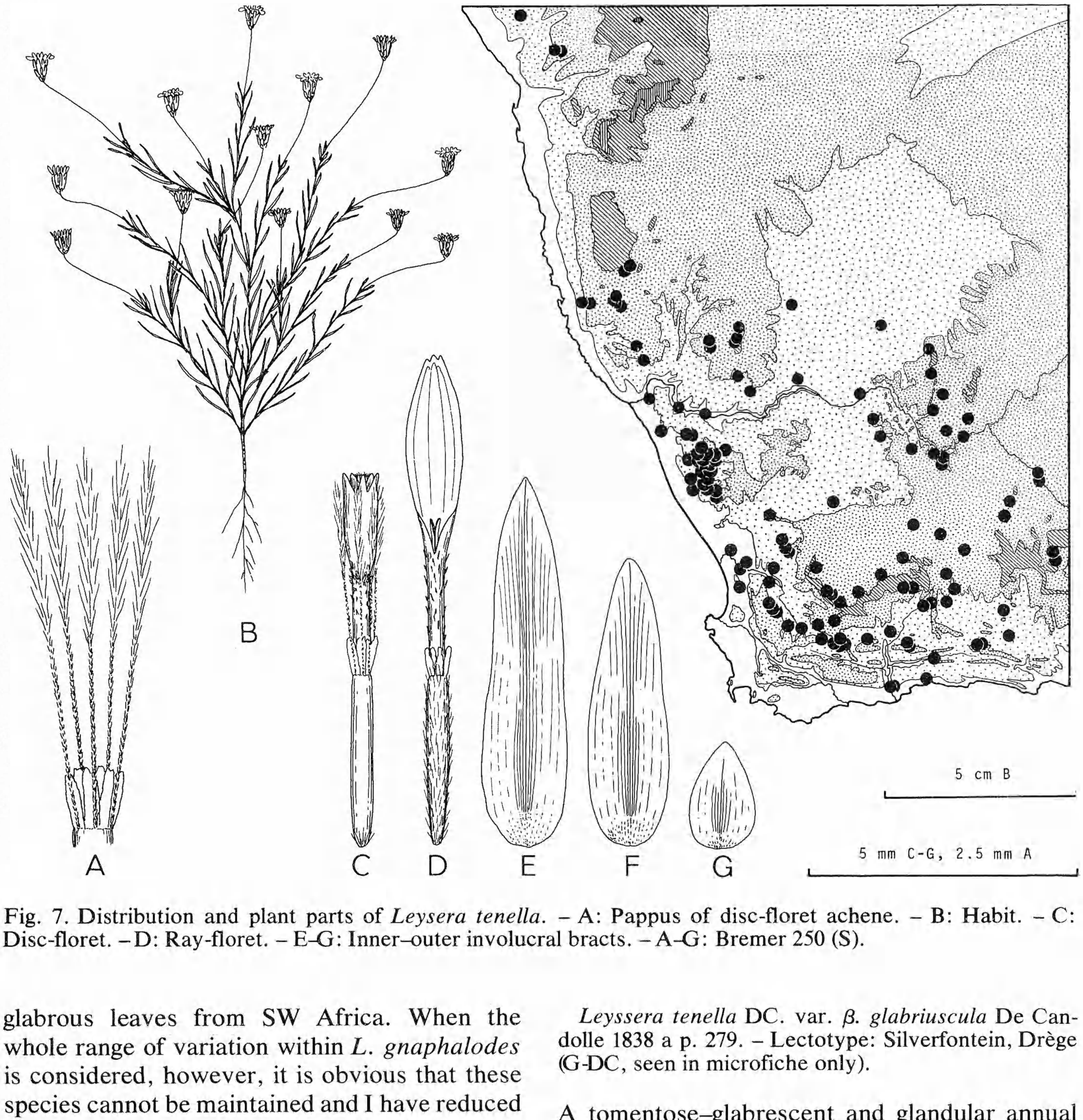

Fig. 7. Distribution and plant parts of *Leysera tenella*. – A: Pappus of disc-floret achene. – B: Habit. – C: Disc-floret. – D: Ray-floret. – E–G: Inner–outer involucral bracts. – A–G: Bremer 250 (S).

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

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

2. **Leysera tenella** DC.

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

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

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

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

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

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

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

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

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

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

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

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

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

Flowering period March–June.

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

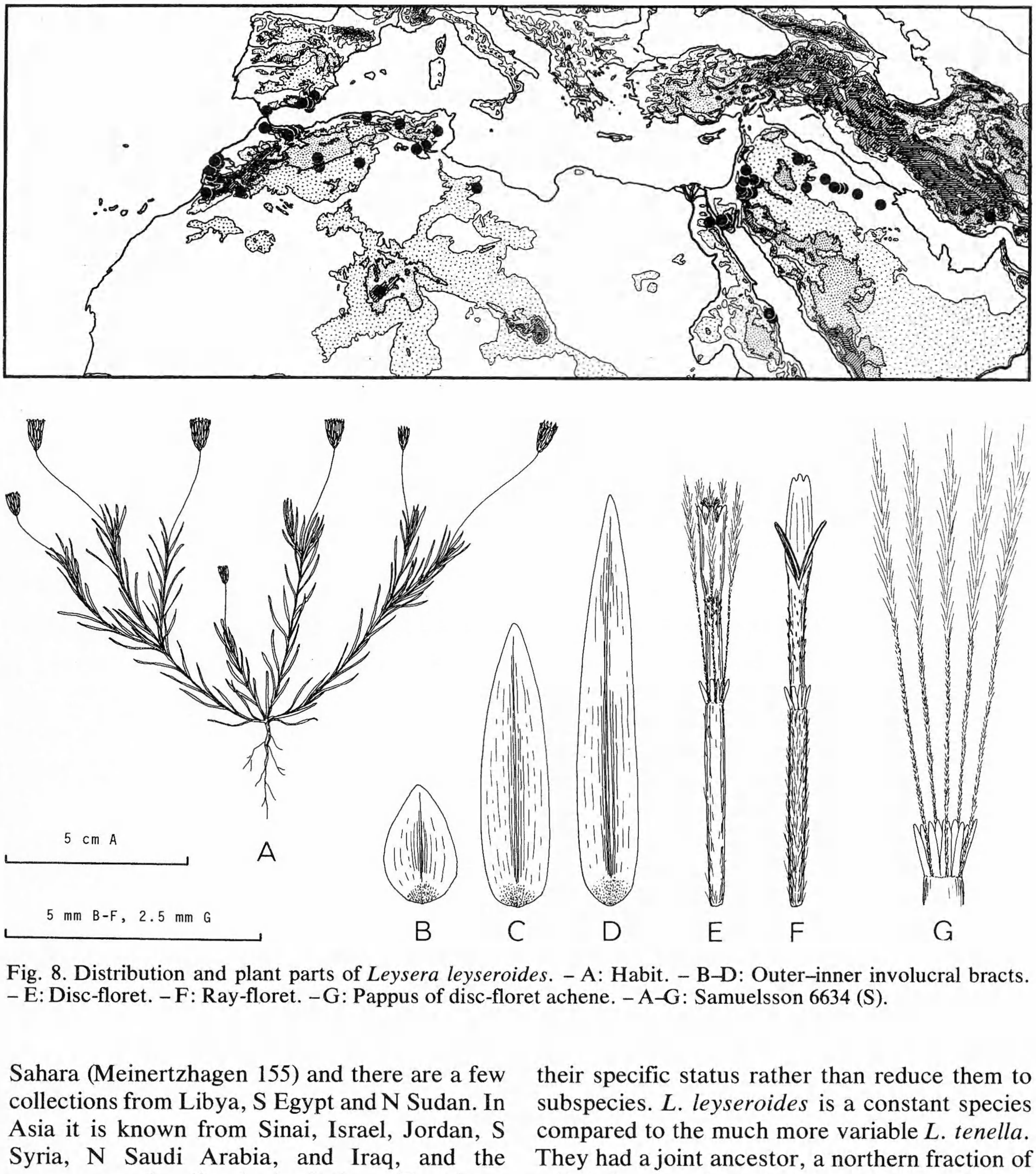

Fig. 8. Distribution and plant parts of *Leysera leyseroides*. – A: Habit. – B–D: Outer–inner involucral bracts. – E: Disc-floret. – F: Ray-floret. – G: Pappus of disc-floret achene. – A–G: Samuelsson 6634 (S).

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

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

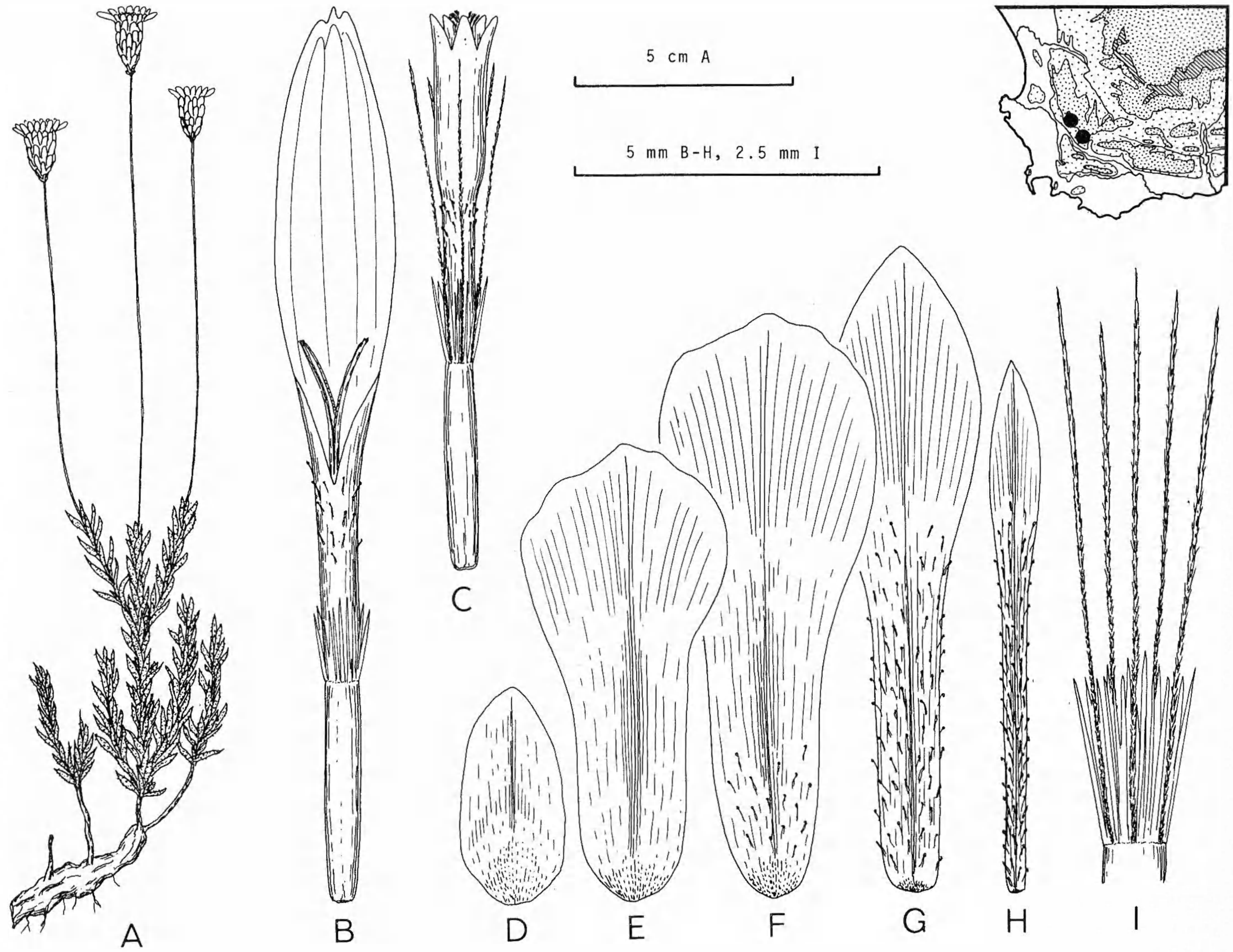

Fig. 9. Distribution and plant parts of *Leysera longipes*. – A: Habit. – B: Ray-floret. – C: Disc-floret. – D–H: Outer–inner–innermost involucral bracts. – I: Pappus of disc-floret achene. – A–I: Esterhuysen 30022 (BOL).

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

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

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

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

Flowering specimens collected in December and January.

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

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

Taxa to be excluded

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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Holubogentia, a new name in Gentianaceae

Áskell Löve and Doris Löve

Löve, Á. & Löve, D. 1978 09 30: Holubogentia, a new name in Gentianaceae. *Bot. Notiser 131:* 385. Stockholm. ISSN 0006-8195.

Since the generic name *Holubia* Löve & Löve, established in 1975 for a new genus of the Gentianaceae, has been found to have an earlier homonym in the Pedaliaceae, it is replaced by the new name *Holubogentia* Löve & Löve, to which the two south European alpine species *H. pyrenaica* (L.) Löve & Löve and *H. boryi* (Boiss.) Löve & Löve are transferred.

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In a paper on the Spanish gentians (Löve & Löve 1975) we described a new genus with the name *Holubia,* in honour of Josef Holub of Praha. In a previous paper, submitted in 1972 (Löve & Löve 1976), we identified it with the genus *Ericala* S. F. Gray, a name that must be rejected (Holub 1973).

However, even the name *Holubia* is preoccupied: it has been used for a S African genus of Pedaliaceae described by Oliver in 1884 in honour of Emil Holub. Therefore *Holubia* Löve & Löve is a later homonym that needs to be replaced.

Holubogentia Löve & Löve

Based on *Holubia* Löve & Löve, Anales Inst. Bot. A. J. Cavanilles 33: 226 (1975). – Type species: *Holubogentia pyrenaica* (L.) Löve & Löve.

Apart from the two S European species here transferred to *Holubogentia,* it is likely that the C Asiatic species *Gentiana grandiflora* Laxm. and its Himalayan relatives also belong here.

Holubogentia pyrenaica (L.) Löve & Löve comb. nov.

Basionym: *Gentiana pyrenaica* L., Mantissa p. 55 (1767).

Holubogentia boryi (Boiss.) Löve & Löve comb. nov.

Basionym: *Gentiana boryi* Boissier, Bibl. Univ. Genève, sér. 2, 13: 410 (1838).

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Request for seeds and flower buds

A. Amin

The genus *Launaea* has a wide range of distribution in temperate, subtropical and tropical areas mainly in C and SW Asia and Africa, NW Australia (one species), New Zealand (one species), S Europe (a few species) as well as C and S America.

To evaluate phylogenetic trends as many characters as possible should be correlated, the chromosome number and morphological characters being of great importance. The chromosome number is known for only a few species (mainly Egyptian material). The involucral bracts as well as the achenes are of diagnostic value. They are used to separate *Launaea* from other related genera as well as to separate the different sections. Involucral scales of many species of *Launaea* have scarious margins. In some species they are distinctly imbricate the whorls increasing in size from the lowest (outer) whorl to the uppermost (inner) whorl. In others there is an inner whorl of long scales and an outer whorl of short basal scales. The number of scales comprising the inner whorl is constant and can be used to separate species. Achenes are heteromorphous, two and sometimes three types occurring though usually one type only germinates.

Seeds and flower buds are needed from the entire range of distribution in particular from Asia, Somaliland, Kenya, Tanzania, Rhodesia, Uganda, Algeria, Morocco, Libya, Tunisia, Arabia, Iran, S Spain, the Canary Islands and the Balearic Islands. Flower buds are fixed in a solution of 3:1 ethyl alcohol:glacial acetic acid. Please send collections to

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Botanical literature

Kubitzki, K. (ed.) 1977: *Flowering plants. Evolution and classification of higher categories*. Symposium, Hamburg, September 8–12, 1976. VIII +416 pp., 118 figs. Springer Verlag, Wien, New York. Price (soft cover) 198 DM.

The Hamburg symposium on the evolution and classification of flowering plants held in 1976 was a meeting place for many of the most devoted taxonomists and phylogeneticists of the present day. Together they contributed a great amount of invaluable information for the solution of many taxonomic problems. Now that the proceedings have finally appeared in print it is interesting to note that many of the contributions are greatly revised versions of the original papers. The editor, K. Kubitzki, is to be congratulated on the result, which has no doubt cost him much time and labour.

The proceedings include the scripts of no fewer than 23 of the papers given. They are divisible into three main categories: General principles and methods, Evolutionary aspects and taxonomic evidence, and Evolution and classification of major taxa. Some contemplative considerations, often with a critical, or even warning, undertone of current systematic trends and methods are presented by the editor, K. Kubitzki, and the two co-organizers of the symposium, V. H. Heywood and H. Merxmüller. Some worrying signs, such as widely-differing circumscriptions of some orders and families (e.g. Liliaceae and Saxifragaceae) are pointed out, as also are the risks involved in taking visual diagrams and models too literally.

Many articles illustrate the varius approaches involved, using different branches of morphology, anatomy, embryology, chemistry etc. in grouping taxa of different magnitude. Among chemotaxonomic characters, for example, R. Hegnauer shows the usefulness of the cyanogenic compounds, provided that they are sub-divided into proper biogenetic groups. Other characters, such as occurrence of isoquinoline alkaloids, are discussed by a team of chemotaxonomists from São Paulo led by O. R. Gottlieb, a specialist in the isoquinoline alkaloids. Anatomical characters of wood and their application to the taxonomy of the families in Magnoliales and Laurales are elucidated by H. Gottsberger, seed characters by J. E. Krach for Saxifragalean taxa, and embryological characters by W. R. Philipson, who shows the significance of the number and morphology of the integuments and of the characters of the nucellus. K. R. Sporne comments upon his previously-presented correlation study, which shows that character correlation is by no means random, but indicates, on the one hand, the main evolutionary trends from which phylogenetic conclusions can be drawn, on the other hand the correlations which may arise in consequence of the multiple adaptation of characters in syndromes, as a response to some particular environmental pressure. H.-D. Behnke describes some microstructural characters, in particular accumulation of protein and/or starch by sieve-element plastids and their taxonomic importance. The sieve tube elements with triangular protein crystalloids prove to be one of the best characters for distinguishing monocotyledons from dicotyledons. Likewise, it is now appreciated that the typical sieve element in Caryophyllales are of great importance in the circumscription of this order. Valuable conclusions may probably be drawn from the character of the sieve element plastids also in Magnoliiflorae, but the scattered occurrence of protein in the sieve tubes of other dicotyledonous families and its significance still remains a riddle. A new and interesting character, the dilated cisternae found in some groups which contain glucosinolates, is a further field for exploration.

A. D. J. Meeuse emphasizes the importance of reinvestigation and reinterpretation of the morphological features of the flower. Conclusions based upon many data can, in his opinion, only be satisfactorily evaluated when various concepts have been clarified and the nature of the first angiosperms correctly understood. It is noteworthy that he considers it likely that the progenitors of the angiosperms were anemophilous.

Hypotheses about the major evolutionary trends found among the angiosperms are presented and discussed by F. Ehrendorfer and A. Cronquist. According to the former, the extant Hamamelidiflorae, with simply-constructed flowers, form a transition between the ancient "Magnoliidae" and the more recent "Rosidae" and "Dilleniidae". This hypothesis is illustrated by floral diagrams. A. Cronquist similarly sketches an evolutionary chemotaxonomic sequence in which plants producing benzylisoquinoline alkaloids were succeeded by others which produced tannins, which in turn were succeeded by groups producing iridoids, and finally by groups producing polyacetylenes and sesquiterpene lactones. Some members of the metabolic groups from each period have survived, while others gradually lost the power of synthesizing the earlier metabolites as these became inessential. The sweeping scope of the theories is fascinating. However, it is more likely, for example, that the group possessing multistaminate androecia like those characterized by different metabolites have developed along parallel lines.

An article by G. Gottsberger is of interest in this connection showing that pollination by beetles, which is found in the Magnoliaceae and other primitive taxa with a centripetally developing, spiral androecium, also occurs in flowers with undoubtedly secondarily multistaminate androecia with centrifugal development.

Very interesting contributions and exemplifications on the major groups of dicotyledons are given by several authors. G. Wagenitz provides a convincing survey of the sympetalous groups. P. K. Endress deals with the Hamamelidales and Fagales, which are shown to have several features in common. C. C. Berg discusses the Urticales, and B. L. Burtt the Gesneriaceae and other groups.

The two presentations of monocotyledonous taxonomy by H. Huber and H. T. Clifford are both rich in information and leads to unconventional conclusions. Huber has considered a number of previously little-used characters. He shows that several "monocotyledonous" features also occur in what we call dicotyledonous orders, viz. Magnoliales (especially in the Annonaceae and Aristolochiaceae), the Piperales and the Nymphaeales. The two latter orders may even, with some right, be included in the monocotyledons. The reader may be surprised to find such superorders as the Tacciflorae, Haemodoriflorae and Pontederiiflorae placed on the same taxonomic level as the Liliiflorae and Commeliniflorae. The reader may doubt whether this is justified, since the Taccaceae are similar to taxa in the Dioscoreaceae, e.g. *Trichopus,* in the Liliiflorae, and the Haemodoriflorae and Pontederiiflorae are similar in numerous features both to one another and to the Bromeliiflorae. In Clifford's numerical treatment of the monocotyledons as many as 51 characters have been considered, for all families for which data were available. Affinity diagrams are provided to show the degree of similarity between these families. The groups and clusters obtained are somewhat surprising and cannot be ascribed entirely to phylogenetical relationships, but may partly be due to convergent evolution, largely in relation to pollination mechanisms (insects, wind or water).

The articles in the present volume cover practically all aspects of angiosperm evolution and taxonomic relationships and also cast fresh light on several ordinal complexes. It is obvious that taxonomy is at a stage of rapid progress. The divergencies between a system such as that presented by R. F. Thorne in one of the articles and the diagram presented by the present reviewer, reflect some of the present differences in opinion in the evaluation of, for example, phytochemical characters. Such systems are likely to be revised in the course of the next few years as a result of the steady flow of new information.

I keenly recommend the present symposium volume to all taxonomists seriously working on the higher plants, and also to students who are seeking a diversified approach to the various methods pertaining to systematics. At the same time I cannot resist expressing my disappointment at the price asked; 198 DM. seems unnecessarily high for a book which will undoubtedly be purchased by innumerable institutes, by a large number of taxonomists and by many various categories of students.

Rolf Dahlgren

Nilsson, S., Praglowski, J. & Nilsson, L. 1977: *Atlas of airborne pollen grains and spores in northern Europe*. 159 pp. Natur och Kultur, Stockholm. ISBN 91-00198-9. Price SKr 210:–.

The two palynologists, Siwert Nilsson and Joseph Praglowski, with the photographer Lennart Nilsson, have together compiled a pollen/spore atlas which covers a limited number of North European vascular plants.

The plant selection has been made with regard to the needs within aeropalynology, which is a growing scientific field. The book includes *pollen/spore types* of the most common anemophilous and entomophilous plants which are caught in pollen traps or incorporated in lake sediments and mire peats. The morphology of each pollen type is illustrated by one or two pages of photographs taken by light microscopy and both scanning and transmission electron microscopy. This makes the atlas extremely valuable for all scientists who have to deal with pollen morphology – in allergology as well as in botanical taxonomy and Quaternary geology.

The book also contains short text descriptions, a glossary of pollen-morphological terms, distribution maps of the plants described, and an index of plant names in different languages. This facilitates usage, making it valuable for amateur as well as professional scientists.

The only disadvantage of this book is the price, although obviously such an atlas must have been very expensive to produce. It can be strongly recommended for institute libraries and for scientists involved in any studies involving pollen morphology. The book will also be a great help to those who teach palynology, because of its skilful pedagogical presentation of the material.

Björn E. Berglund