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Taxonomic and morphological studies in *Hypecoum* sect. *Hypecoum* (*Papaveraceae*)

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Abstract: *Hypecoum* sect. *Hypecoum* comprises 8 species, one with 2 additional subspecies, in the Mediterranean area and the Middle East. Five of these are recognized for the first time, viz. *Hypecoum procumbens* L. subsp. *fragrantissimum* Å. E. Dahl, *H. procumbens* L. subsp. *atropunctatum* Å. E. Dahl, *H. trullatum* Å. E. Dahl, *H. angustilobum* Å. E. Dahl and *H. torulosum* Å. E. Dahl. *H. dimidiatum* Delile and *H. pseudograndiflorum* Petr., which have generally been included in *H. imberbe* Sm., are reestablished as distinct species. Morphology and variation patterns are described and discussed with special reference to mating systems. Self-incompatibility is dominating but *H. procumbens* subsp. *procumbens* and *H. torulosum* are self-compatible. The broad variation ranges of the former taxon in traits presumably related to mating system (petal, anther and stigma sizes as well as pollen-ovule ratios) indicate varying rates of outcrossing. SEM micrographs are given of petal and stigma surfaces and of pollen grains. Chromosome counts are presented for seven taxa. All are diploid with $2n = 16$.

The purpose of this investigation is to analyse the morphological variation and to make a taxonomic evaluation of the taxa within *Hypecoum* L. sect. *Hypecoum*, and to provide a base for confirmatory genecological studies.

The genus *Hypecoum* belongs to subfam. *Fumarioideae* of the *Papaveraceae* (for a discussion of the taxonomic position and phylogeny, see Lidén 1986). The genus is easily defined by its peculiar flowers; the inner petals are deeply trilobate with a central ("fimbriate") lobe specialized for secondary pollen presentation (see Morphology, Figs. 11 and 12).

Five different sections within the genus *Hypecoum* L. can be discerned on characters of flowers, fruits and foliage. Sect. *Hypecoum* is recognized by the oblong and usually truncate fimbriate lobe of the inner petals, by the fairly broad and erect lomentum and by the ultimate leaflets, which usually are linear-flabellate, but sometimes are lanceolate. All taxa hitherto studied are diploid with $2n = 16$.

The study of herbarium specimens and living spontaneous and cultivated material has been conducted parallelly to artificial crossing experiments. The results of these have affected the taxonomic evaluation, but will be accounted for in detail elsewhere.

Fig. 1. *A Hypecoum imberbe* (Spain, prov. of Almeria, Laujar). *B Hypecoum procumbens* subsp. *fragrantissimum* (Greece, Kikladhes, island of Mikonos). *C Hypecoum procumbens* subsp. *atropunctatum* (Greece, Dodecanese, island of Mitilene). *D Hypecoum torulosum* (Greece, Kikladhes, island of Mikonos)

The morphological differences that are discernible in dried specimens are often subtle, and it is necessary to correlate herbarium studies with studies of living plants in the field as well as in cultivation to make the taxonomic evaluation. To the present study, the results of the artificial crossing experiments have been of great help in localizing the discontinuities in morphological characters.

Previous treatments

LINNAEUS (1753) recognized three *Hypecoum* species, viz. *H. erectum, H. pendulum,* and *H. procumbens,* of which only the latter belongs to sect. *Hypecoum.* The treatments by some of the most important post-Linnean authors are summarized in Appendix 1. Most of these treatments are included in local floras, and Fedde's monograph (1909) alone scopes the entire genus without any geographical boundaries. It is evident from the survey that there has been great disagreement about the rank and circumscription of many of the taxa. During the decades around 1900, the authors tended to generously describe many infraspecific taxa. Some of these represent mere phenotypical modifications, whereas others represent entities which are recognized also in the present study, even if it is under different rank or name. Authors working later in the twentieth century usually have a wider species concept but as before, the treatments often suffer from the difficulty to interpret the variation pattern from herbarium studies alone and from the lack of investigations of extensive material. The number of taxa is thus often underestimated in modern Floras, or else the authors have used characters that are the result of, e.g., the drying of plants, as in Mowat & Chater (1974).

Species concept

The species concept adopted in this text is the evolutionary one, as formulated by Wiley (1978), as far as it goes "An evolutionary species is a single lineage of ancestor-descendant populations which maintain its identity from other such lineages ...". However, I am not willing to accept the continuation "... and which have its own evolutionary tendencies and historical fate", if this formulation implies that a species is an evolutionary unit. Recent research shows that gene flow is generally too restricted to be a prime integrating force within species (Ehrlich & Raven 1969, Levin 1981). The entities that we apprehend as species are thus probably assemblages of more or less independent populations. These have a common ancestry and are kept phenotypically similar mainly by some other force, presumably stabilizing selection. Highly integrated and balanced genomes, in which epistasis and linkage are of great importance will be favoured (Carson 1975, 1982, Templeton 1981, 1982, Carson & Templeton 1984), as well as canalization of the phenotypic expression. The presence of coadapted gene complexes will make the populations reluctant to change as fitness usually will be drastically reduced if the gene blocks are broken by recombination. When changes do occur, however, whether they are of anagenetic or cladogenetic nature, they are bound to be local. The species that we recognize is thus usually a historical unit in the same way as higher taxa, as opposed to the view of Wiley (1981). The population, or a close group of populations, is the probable unit of speciation (cf. Raven 1976, 1980; Jonsell 1984).

It is sometimes said that incompatibility is a doubtful criterion in the recognition of different taxa (e.g., Rosen 1979, Sokal & Crovello 1970, Sokal 1973) for several reasons. It is, e.g., said that non-crossability only indicates what might happen if representatives of these taxa would meet and not necessarily what is actually taking place. Furthermore, the individual plants used in crossing experiments are said to represent, out of necessity, only a small sample of the natural populations. A third objection is that the non-crossability is often an effect of secondary contact between species formerly isolated by prezygotic barriers. In annual plants, however, several cases are known where it is possible to find a correlation between hybridization barriers and morphological discontinuities ("the *Layia* pattern", Grant 1981). This is also the case in *Hypecoum*. Furthermore, it is likely that cross-incompatibility arises as a by-product of differentiation in annual, sexually reproducing, diploid organisms of this kind, and not only as an effect of secondary contact. Thus, it is reasonable to let the results of the artificial crossing experiments affect the taxonomic conclusions. Hybridization between the subgroups within *Hypecoum procumbens* gives fertile progeny in F 1, as opposed to hybrids formed by artificial crossing with other form series. As the *H. procumbens* subgroups also share certain apomorphies, the subspecific rank is considered to be the most appropriate one.

The following taxa are recognized in this study: *Hypecoum procumbens* L. subsp. *procumbens*, *H. procumbens* L. subsp. *fragrantissimum* Å. E. DAHL (subsp. nova), *H. procumbens* L. subsp. *atropunctatum* Å. E. DAHL (subsp. nova), *H. trullatum* Å. E. DAHL (spec. nova), *Hypecoum pseudograndiflorum* PETR., *H. angustilobum* Å. E. DAHL (spec. nova), *H. dimidiatum* DELILE, *H. imberbe* SM., *H. duriaei* POMEL and *H. torulosum* Å. E. DAHL (spec. nova). Descriptions are given in the taxonomy chapter.

Material and methods

Herbarium studies were made on specimens from C, COIM, E, G, GB, GDA, H, HUJ, ISTE, JACA, K, LD, M, MAF, MPU, S, SEV, UPS, W, and WU (abbreviations according to HOLMGREN & al. 1981), and from the private herbaria of Dr K. P. BUTTLER (Berlin) and Dr A. HANSEN (Copenhagen). About 2 000 herbarium specimens were seen.

Measurements of vegetative characters were made on dried herbarium material, whereas those of floral parts were made on remoistened or fixed flowers. Certain characters, such as floral pigments, change or disappear during preparation. Observations on these were recorded from living cultivated material only in the cases when the author did not see the species alive in nature (that is, in *H. dimidiatum* and *H. duriaei*). The terminology used follows STEARN (1983).

The cultivated material was raised from seeds sown in clay pots, in a mixture of sand and standard soil in the proportions 9 : 1. After germination, the seedlings were planted ion clay pots with the same ingredients in the proportion 1 : 2. The pots were placed in a greenhouse. During the first two cultivation seasons plants belonging to the same collection were placed together; plants cultivated during later years were placed in a completely randomized design.

The somatic chromosomes were studied in root-tip mitoses prepared by either of the following two techniques: (1) The plants were kept overnight at +3° C and the root-tips were then fixed in the Svalöf modification of Navashin-Karpechenko. The material was embedded in paraffin wax and sectioned at 10 µm, and the sections were then stained with crystal violet. (2) The root-tips were pretreated with 2 mM 8-hydrooxyquinoline for four hours and then fixed in Carnoy (3 parts absolute alcohol : 1 part glacial acetic acid) for at least one hour. After hydrolysis for 8 minutes in 1-N HCl at 60° C, the tips were stained in orcein on a slide for some minutes and then squashed under a cover slip.

Meiosis was studied in squash preparations. Young buds (1 – 2 mm) were fixed in Carnoy as described above. They were then hydrolyzed in 9 parts acetic orcein : 1 part 1-N HCl at 60° C for about 10 minutes and kept in a 2% solution of acetic orcein overnight. Next morning, the anthers were squashed under a cover slip in a droplet of acetic orcein.

Pollen/ovule ratios were determined from flowers fixed in 70% ethanol during the first day of anthesis, when the pollen mass was still kept enclosed by the fimbriate lobe. The lobe was cut out and the pollen diluted in 2 ml lactophenol (10 g phenol, 10 ml lactic acid, 10 ml distilled water, c. 0.5 g water soluble cotton blue). The total number of pollen grains in 0.5 ml was then counted with the aid of an ocular with a grid in a light microscope, and the result multiplied with 8 to estimate the total number of pollen in a flower. The number of ovules was counted directly under a dissection microscope (12× magnification). Pollen/ovule ratios were calculated by dividing the calculated number of pollen with the number of ovules in an ovary.

The growth of pollen-tubes in pistils was studied in fluorescence microscope after maceration in 8 N NaOH overnight at room temperature and staining in 0.1% cotton blue (0.1 g water soluble cotton blue powder in 100 ml 0.1 N K^3PO^4 solution) for about one hour.

Records of self-sterility were made after enclosure of the inflorescences in pergamyn bags before anthesis.

The distribution maps are based on the herbarium collections used for the study. A complete specimen index is preserved at GB. A list of the collection numbers of the specimens used for the biometrical studies that are accounted for in the text and diagrammes of section 2 and 3 of this paper is given in Appendix 3. Collections from the same or neighbouring localities are indicated by a single symbol. The geographical names follow the Times Atlas (Bartholomew 1956) except when herbarium labels are cited, when the spelling of the collectors are followed.

Voucher specimens are kept at GB, unless otherwise stated.

Morphology

Cotyledons. The shape of the cotyledons is very homogeneous throughout the section. They are always cylindric and acute (Fig. 2 A). In a few cases, tricotyledonous seedlings were observed, most often in plants of hybrid origin.

Habit and lifelength. All species within the section are rosulate annuals. In cultivation, lifespan from germination to death is about five months in spring and early summer, but is often extended if the seeds germinate during autumn. Replanting of self-sterile plants, which generally did not set fruit in the greenhouse unless they were artificially pollinated, could also prolong life-length a couple of months, but not longer. Fertilization led to allocation of the limited nutrition in the soil of the pots and in the green parts of the plant to the fruits, and self-compatible plants, in which all or most fruits developed, thus soon "fructified to death".

Of all the herbarium specimens studied during the investigation, only two were collected during the autumn. Most taxa within the section occur only in areas with severe summer drought, which is likely to put an end to life for most of these plants in nature.

Foliage. The rosette leaves are pinnate with pinnately lobed primary segments (Fig. 3). The very first leaves that develop after the cotyledons are very small with undivided or sparsely lobed primary segments, and elaboration increases to the seventh or eight leaf, after which all the following ones look essentially similar (Fig. 2 B – G). This is called "elaboration heterophylly" by Stebbins (1974) and is said by him to occur in plants adapted to take quick advantage of short periods of moisture in arid or semi-arid situations, which is the case in *Hypecoum*.

Troll (1964) described the ontogeny of the primary segments. The lowest and last developed of these segments always consist of ultimate leaflets that are dilated towards the usually trifid apex. In the primary segments situated nearer the tip, the shape of the ultimate leaflets is found to be useful as a "key" attribute, and

Fig. 2. *A* Cotyledons (general habit). *B – G* The first rosette leaves produced of *Hypecoum procumbens* subsp. *procumbens*. *H* Rosette leaves of a hybrid between a Spanish and a Greek population of *Hypecoum imberbe*, in which some of the primary segments are partly undivided

seems to be correlated to pollen colour. The taxa with yellowish-white pollen, i.e. *H. pseudograndiflorum* and *H. procumbens*, have ultimate leaflets that are lanceolate to obovate, have a undivided, acute, sometimes cuspidate apex and are usually not dentate, but sometimes have one lateral tooth (Figs. 22 – 24.4 and 27.4). In *H.*

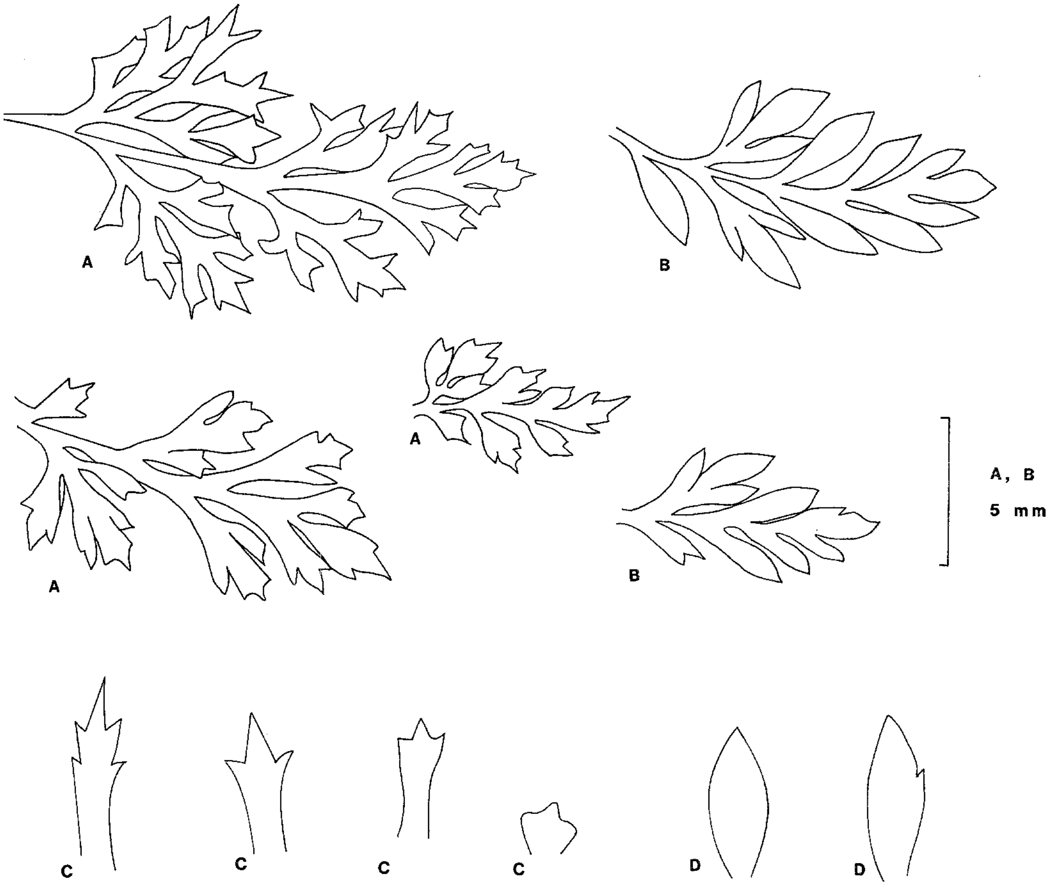

Fig. 3. Primary segments in which most of the ultimate leaflets are (*A*) dilated towards an usually trifid apex and (*B*) lanceolate to obovate with an undivided apex. Ultimate leaflets that are (*C*) dilated towards an usually trifid apex, (*D*) lanceolate to obovate with an undivided apex

dimidiatum, H. torulosum, H. imberbe and *H. duriaei,* the pollen is orange-yellow, and the ultimate leaflets have an apex that is usually trifid (Fig. 3). Generally, the width of the leaflet is then more or less dilated towards the apex, and there are also often one to several lateral teeth (Figs. 30, 31.4, 33.4, and 36.4). *H. imberbe* and *H. torulosum* are almost monomorphic in this respect, while the percentage of leaflets with a trifid apex varies in *H. dimidiatum* and *H. duriaei,* as well as in *H. angustilobum* with unknown pollen colour and in which the leaflets are usually very narrowly linear-lanceolate.

The inflorescences are bracteate. The elaboration of the bracts is very varying. In the most elaborate bracts, the shape of the segments resembles that of the ultimate leaflets in the rosette leaves. The leaflets of the most reduced bracts are always dilated towards the apex.

Rosette leaves with some of the primary segments partly undivided (Fig. 2 H) were found in some plants, namely, in the progeny of spontaneous material of *H. imberbe* from Athens (Greece) and Granada (Spain), in herbarium specimens of *H. dimidiatum* from Aleppo (Syria), and in *H. procumbens* subsp. *atropunctatum* from Istanbul (Turkey).

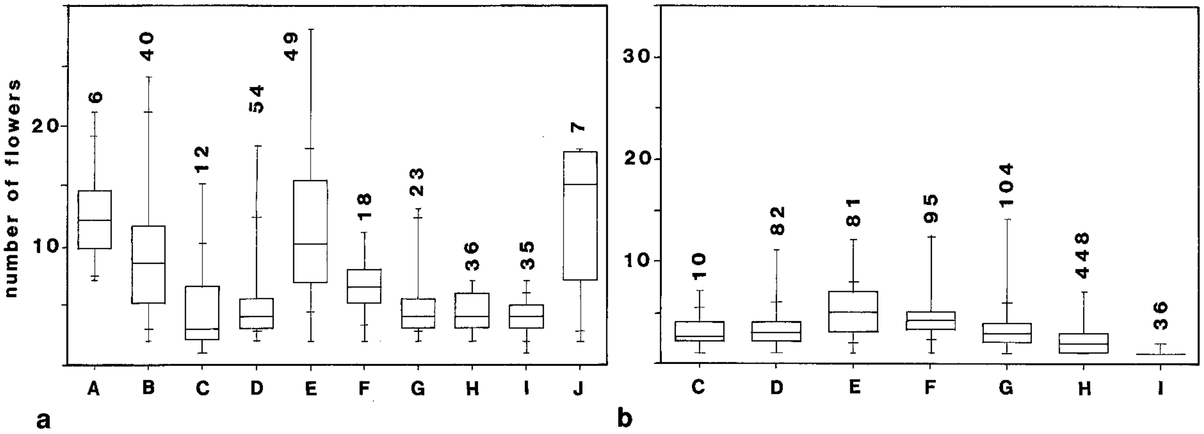

Fig. 4. Maximum number of flowers produced in one inflorescence, *a* from herbarium specimens, *b* in the green-house. (The outer limits of the whiskers show min. and max. values, the other horizontal lines show the 10, 25, 50, 75 and 90th percentiles.) *A Hypecoum angustilobum. B H. dimidiatum. C H. duriaei. D H. imberbe. E H. pseudograndiflorum. F H. procumbens* subsp. *atropunctatum. G H. procumbens* subsp. *fragrantissimum. H H. procumbens* subsp. *procumbens. I H. torulosum. J H. trullatum.* The figures above the boxes indicate the number of specimens counted

The variation in glaucosity has sometimes inspired earlier authors to describe new taxa, i.e. *H. glaucescens* GUSS. and *H. grandiflorum* BENTH. var. caesium HAUSSKN. *H. torulosum* is always glaucous throughout, a fact that may have given rise to the idea that this taxon is the same as *H. glaucescens* GUSS. In other taxa, however, the glaucosity appears to be susceptible to environmental conditions. The tops of the leaves are often glaucous whereas the lower parts, concealed in the rosette, are green.

Neither the leaves nor any other part of the plant carry any indumentum.

Inflorescence. The inflorescence, basically a dichasium in which the last ramifications are often reduced and hence are monochasial, has been described by TROLL (1964). Flowering is acropetal.

There seems to be an upper limit for the maximum number of flowers produced in one inflorescence (Fig. 4). The diagrammes show observations from herbarium specimens and from cultivated plants. In the self-compatible taxa, *H. torulosum* and *H. procumbens* subsp. *procumbens*, the number of flowers in one inflorescence never exceeds seven, whereas it is always higher in the self-incompatible ones, though varying. In cultivated plants, the observed maximum numbers are generally lower than in the herbarium material studied, maybe as a result of the limited nutrition available in the pots. This could also be an effect of the tendency of the collectors to choose the most beautiful and multiflowered plants of the populations.

Reproductive output, measured as the number of flowers produced by one plant, was specially observed in the green-house from 1982 to 1986, in plants isolated from pollinators, and is shown in Fig. 5, where all records from each taxon are accounted for in the same box-and-whiskers' diagramme. It is obvious that the self-incompatible taxa have a much wider range in this respect than have the self-

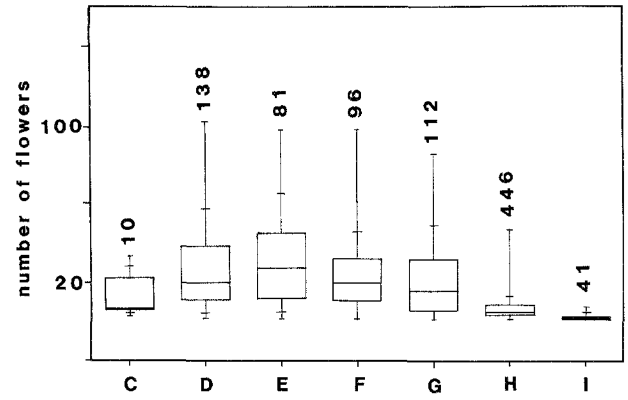

Fig. 5. Maximum number of flowers per plant individual in the green-house. Symbols as in Fig. 4

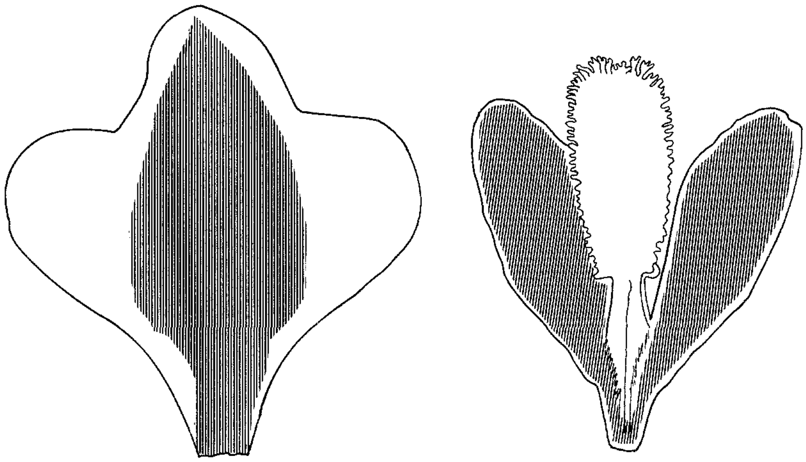

Fig. 6. UV-absorbing (shadowed) and non-absorbing (white) areas of petals of *Hypecoum procumbens*

compatible ones, and that the connection "small flowers – many flowers" does not exist in sect. *Hypecoum*. The lower reproductive output in the self-compatible taxa (Fig. 5 H, I) may be an adaptation to a short vegetation period, involving an effective allocation from the production of unfertilized flowers to the development of fruits for reproductive assurance. All flowers produced by self-incompatible plants of sect. *Hypecoum* seldom develop into fruits in nature. If this is due to limited pollination, a strong reproductive output involving a protracted flowering will be favourable.

Sepals. The two sepals are green with a more or less membraneous margin, which may be entire, erose or dentate. They have the same basic shape in all the taxa treated. The tip is sometimes bi- or trifid in *H. imberbe, H. dimidiatum, H. pseudograndiflorum,* and *H. torulosum.* The variation ranges of width and length vary between taxa but overlap, and it is not possible to discern any discontinuities. The sepals are sometimes shed during anthesis, but usually persists until the flowers wither.

Petal colour and UV-pattern. The colour of the petals is orange-yellow in *H. imberbe,* in some populations of *H. procumbens* subsp. *atropunctatum* and in the

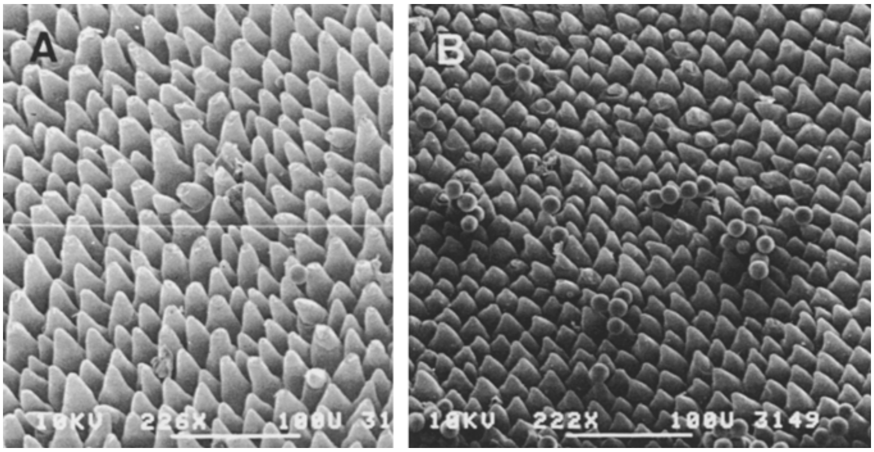

Fig. 7. Scanning electron micrograph of the surface of the outer petal in *Hypecoum imberbe* (Greece, nom Thessalonikis, Diavatha, 22. IV. 1984, DAHL). *A* Cells in the central part of the petal. *B* Cells in the lateral part of the petal

fimbriate lobes of *H. duriaei.* In the other taxa where living plants were available for this study, the petals are lemon-yellow, except for *H. duriaei,* which is unique in the section in having white and purple-tinged outer petals and lateral lobes of the inner petals. The base of the lateral lobes of the inner petals have very dark purple or blackish spots, except in *H. procumbens* subsp. *procumbens* and subsp. *fragrantissimum.* In *H. pseudograndiflorum* the spots are usually few and faint, and can also be completely lacking. In *H. imberbe,* they are usually many and minute, and in *H. procumbens* subsp. *atropunctatum* few and coarse.

The only population of *H. procumbens* subsp. *procumbens* in which a few, faint black spots were observed was found on the island of Kithnos (Greece). At the collection event, this population consisted of seven living plants, in which the percentage of stainable, morphologically well-developed pollen was reduced. It is possible that the occurrence of the spots in these plants is a result of inbreeding.

The lateral lobes of the outer petals have the ability to reflect UV-light, whereas the central part does not (Fig. 6). The resulting pattern could sometimes also be perceived by the human eye in very strong day-light in *H. imberbe.* The central part then appears thicker and is pale whitish-yellow, while the lateral ones are golden yellow and seem translucent. SEM-studies showed that the two kinds of areas differed with respect to the height of the surface cells. These cells were about twice as high in the central part of the petal as those in the lateral part (Fig. 7). BAAGØE (1978) reported a similar dimorphism in *Rudbeckia, Lasthenia* and other asteraceous genera.

Morphology of petals. The ontogeny of the petals was discussed by MURBECK (1912). The variation in size and outline of outer petals is shown in Figs. 8 and 9. In all self-incompatible taxa, the petals are distinctly trilobate, but vary in length of claw, outlines of lateral lobes, relation of length to width, etc. In Aegean populations of the self-compatible *H. procumbens* subsp. *procumbens* are the lateral lobes, which are the last parts to develop during the ontogeny of the petal, often more or less absent. In *H. torulosum,* also self-compatible, the lateral lobes are small and usually involute, and the outer petals appear rhombic.

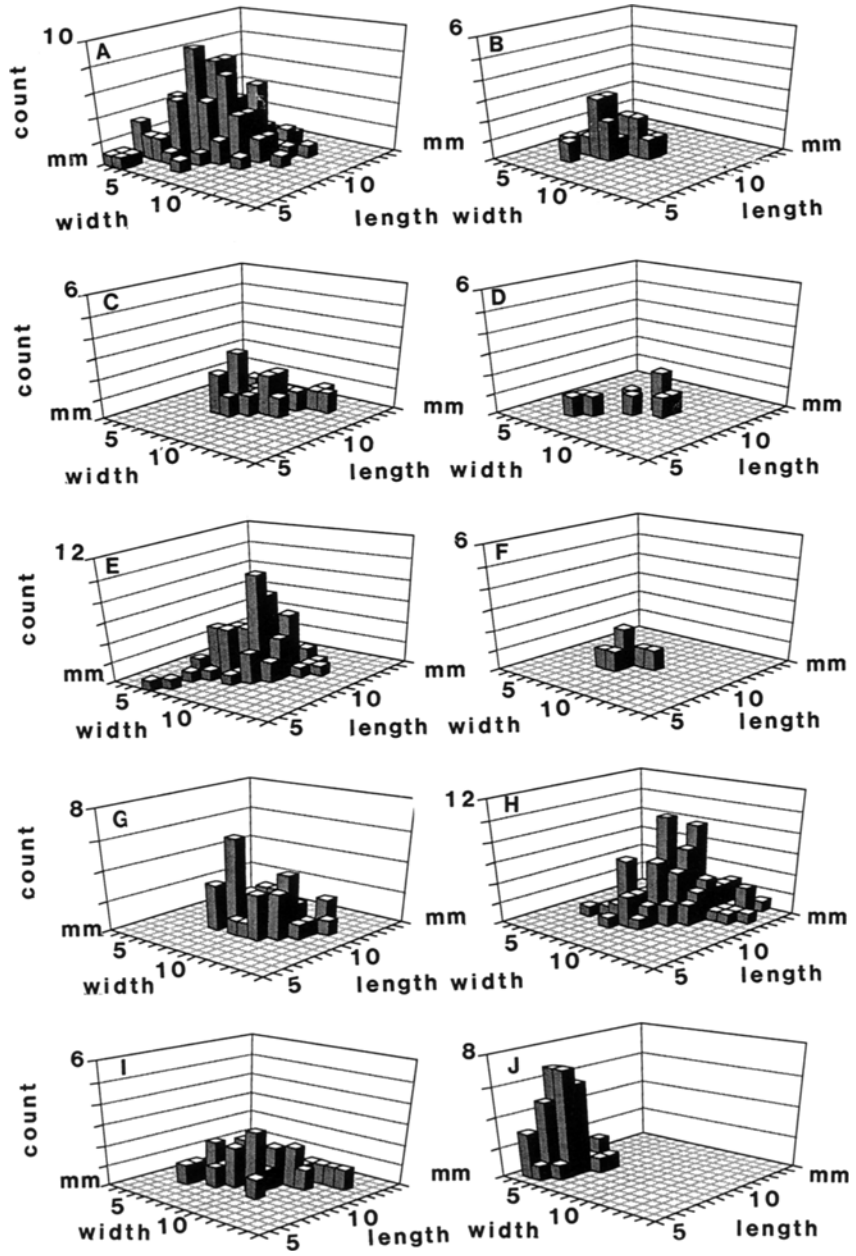

Fig. 8. Three-dimensional histogram of width and length of outer petals. *A H. procumbens* subsp. *procumbens*. *B H. procumbens* subsp. *fragrantissimum*. *C H. procumbens* subsp. *atropunctatum*. *D H. trullatum*. *E. H. pseudograndiflorum*. *F H. angustilobum*. *G H. dimidiatum*. *H. H. imberbe*. *I H. duriaei*. *J H. torulosum*. Note that the count scales are not equal

The claw-length varies within taxa, but is generally comparatively less in *H. pseudograndiflorum* and *H. dimidiatum* and larger in *H. procumbens* and *H. duriaei*.

The lateral lobes are obtuse in outline in *H. imberbe, H. procumbens* subsp. *procumbens* and subsp. *fragrantissimum*. They are more distinctly angled to give the petals a wedge-like shape (i.e. they are cuneiform) in *H. procumbens* subsp.

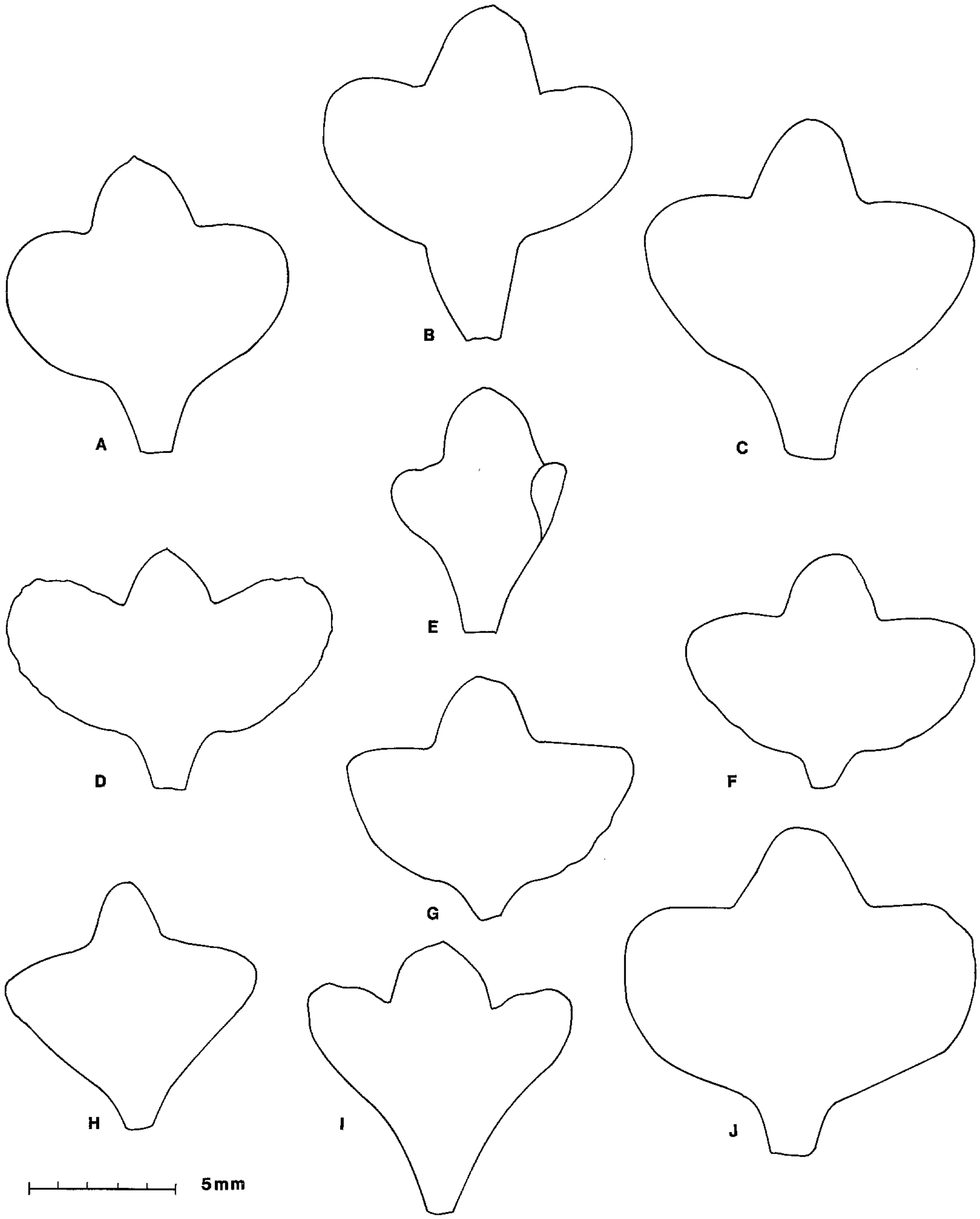

Fig. 9. Variation in outline of outer petals. *A H. procumbens. B H. procumbens* subsp. *fragrantissimum. C H. procumbens* subsp. *atropunctatum. D H. dimidiatum. E. H. torulosum. F H. pseudograndiflorum. G H. duriaei. H H. angustilobum. I H. trullatum*

atropunctatum, H. duriaei, H. angustilobum, and sometimes in *H. dimidiatum.* In the self-compatible *H. torulosum,* the lateral lobes are usually involute. The lateral lobes are often more or less undeveloped in Aegean populations of *H. procumbens* subsp. *procumbens,* also self-compatible (Fig. 22).

The variation ranges of length and width of outer petals are similar in self-sterile taxa, except for *H. procumbens* subsp. *fragrantissimum* in which the ranges

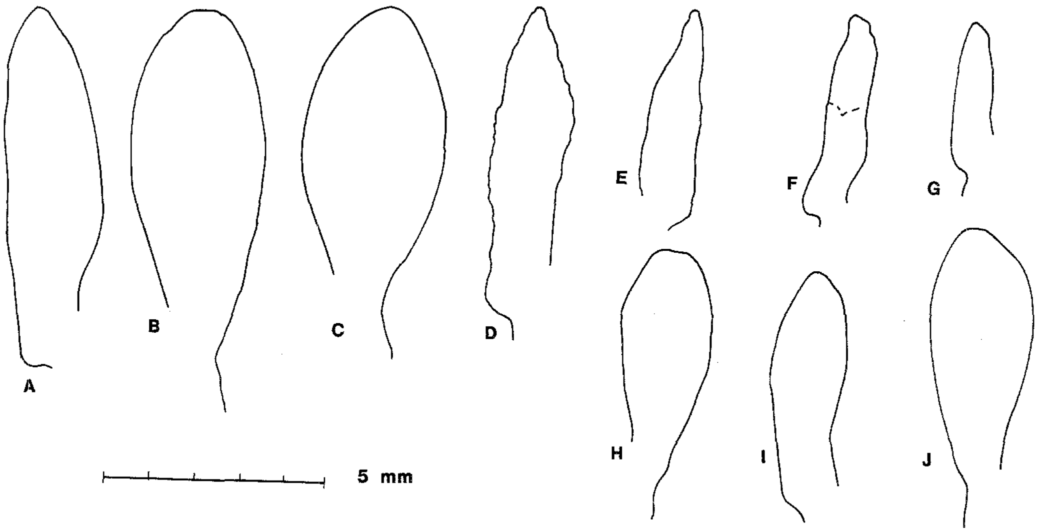

Fig. 10. Variation in outline of lateral lobes of inner petals. *A H. procumbens* subsp. *atropunctatum*. *B H. procumbens* subsp. *fragrantissimum*. *C H. imberbe*. *D H. dimidiatum*. *E H. angustilobum*. *F H. trullatum*. *G H. torulosum*. *H H. pseudograndiflorum*. *I H. duriaei*. *J H. procumbens* subsp. *procumbens*

are more narrow than in the others, probably because of the limited distribution of this taxon. The self-compatible taxa *H. procumbens* subsp. *procumbens* and *H. torulosum* differ much in variation ranges, being much narrower in the latter, although the taxa resemble each other in distribution pattern and area (Figs. 21 and 34). This might reflect a higher variation in outcrossing rate in the former taxon, as size of petals is likely to be correlated with the degree of outcrossing. In *H. duriaei* there is a clinal variation in petal size from south to north (Fig. 35).

The shape of the lateral lobes of the inner petals varies between the taxa (Fig. 10). The lobes are linear and obliquely subacute in *H. dimidiatum* and *H. angustilobum*, ovate and subacute in *H. trullatum*, obovate and obtuse in *H. imberbe, H. pseudograndiflorum, H. procumbens* subsp. *procumbens* and *fragrantissimum*, etc. The relation between the length of the lateral lobes and that of the central, fimbriate one of the inner petals varies in *H. dimidiatum*, in self-sterile subspecies of *H. procumbens*, in *H. imberbe* and in *H. duriaei*, but the lateral lobes are always much longer in *H. trullatum,* and almost always shorter in *H. procumbens* subsp. *procumbens, H. pseudograndiflorum, H. torulosum*, and *H. angustilobum*. In many Aegean populations of *H. procumbens* subsp. *procumbens* the lateral lobes get progressively shorter in relation to the fimbriate lobe as the general size of the flowers is decreased. The same situation is found in populations of *H. duriaei* south of the Haut Atlas.

The central lobe of the inner petals is always fimbriate. The specific epithet of *H. imberbe* ("beardless"), which is intended to describe the opposite condition, is thus misleading. The fimbriae are longest in the self-sterile taxa. Their length varies within *H. procumbens* subsp. *procumbens*, where it seems to be correlated with the length of anthers and petal size. The surface of the fimbriate lobe is colliculate (Fig. 11). The lobe plays an important part in the mechanism of secondary pollen presentation. The development of the flower of *H. procumbens* subsp. *procumbens*

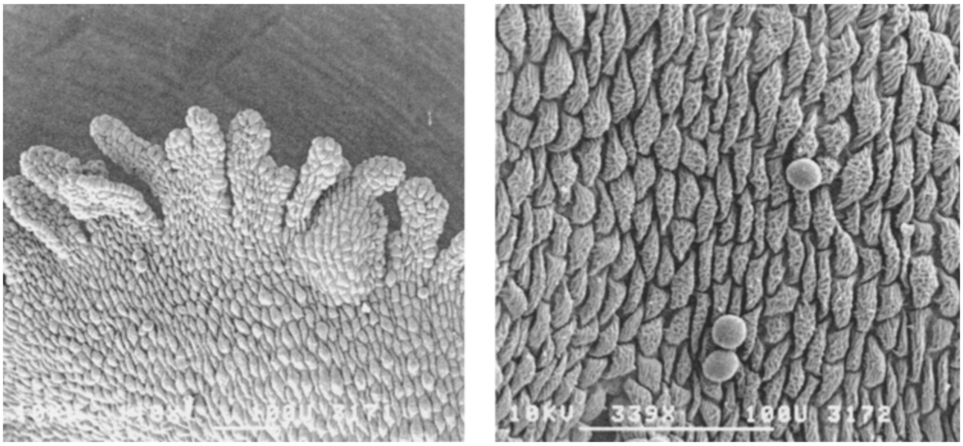

Fig. 11. *H. procumbens*. Scanning electron microscope micrographs of surface of fimbriate lobe. (Spain, prov. of Almeria, Cabo de Gata, DSBG 5020)

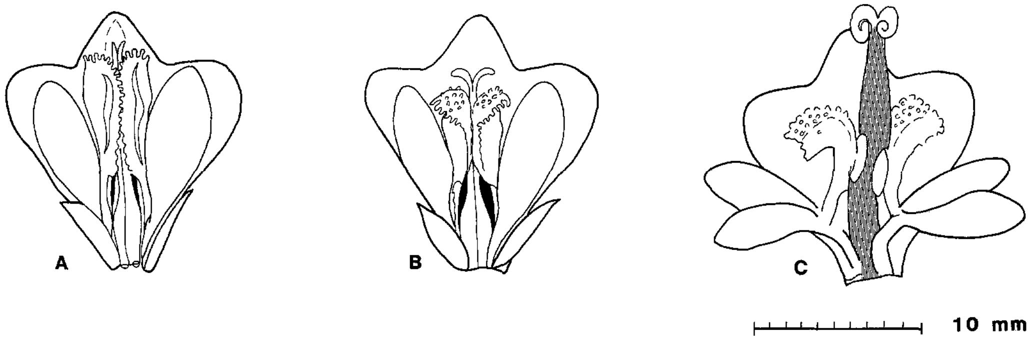

Fig. 12 A – C. Floral development during anthesis in *Hypecoum procumbens*. (Greece, Kikladhes, Kea, Ormos Xila, 24. IV. 1983, DAHL)

during anthesis is shown in Fig. 12. The anthers open already in the flower bud, during which period the ovary and the stamens are embraced by the concave fimbriate lobe, which will receive the pollen mass on its adaxial, colliculate side. In the first day of anthesis, the fimbriate lobes remain in this position, concealing the pollen and the ovary while the stigma lobes are exposed to visiting insects. After about one day, the lobe is deflexed backwards until it finally becomes convex, and thus also the pollen mass is available to the visitors. As stated by DOMINGUEZ-VILCHES & al. (1986), the flowers thus appear functionally protogynous, a mechanism favourable in the self-compatible taxa as cross-pollination may occur before the stigma lobes curl to touch the pollen masses attached to the ovary and the fimbriate lobe.

In my investigation, flowers of *H. procumbens* subsp. *procumbens* from several populations and with different means of petal and anther sizes were isolated from pollinators and fixed on the first day of anthesis. When studied in a fluorescence microscope, pollen tubes were observed in the styles of these flowers. The stigma lobes and the pollen mass were found to be in contact already in flower buds. This

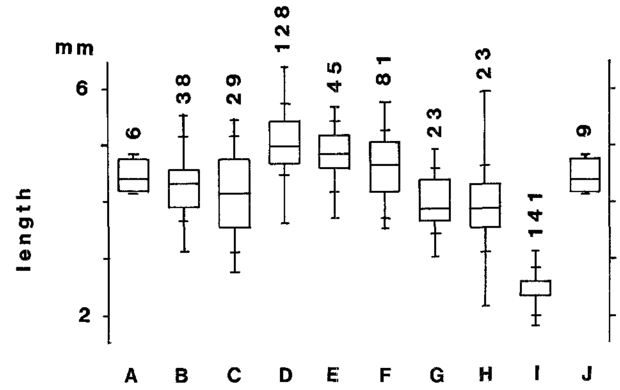

Fig. 13. Variation in length of fimbriate lobe. *A Hypecoum angustilobum. B H. dimidiatum. C H. duriaei. D H. imberbe. E H. pseudograndiflorum. F H. procumbens* subsp. *atropunctatum. G H. procumbens* subsp. *fragrantissimum. H H. procumbens* subsp. *procumbens. I H. torulosum. J H. trullatum.* The figures above the boxes indicate the number of specimens measured

condition does not necessarily exclude high rates of cross-ferilization, however, as pollen-tubes from other plants may grow faster than those of selfed pollen. In one case only the stigma lobes were completely "clean", namely in flowers from a population from Berja in the province of Almeria, Spain. This population was unfortunately represented only by the progeny of one single plant.

The fimbriate lobe (Fig. 13) is always comparatively small in *H. torulosum* and *H. trullatum.* In *H. duriaei* it is possible to find the same clinal trend in size from south to north as in outer petal size. The other taxa treated do not differ much from one another, except *H. dimidiatum* where the fimbriate lobe tends to be wider in relation to length than in the others.

The base of the fimbriate lobe is truncate in all taxa, except in *H. duriaei,* where it is attenuate (Fig. 33.2). This taxon is also easily distinguished on the stalk of the fimbriate lobe, which constitutes more than 20% of the entire distance from the apex of the fimbriate lobe to the base of the petal, and is up to 2 mm long, whereas it does not esceed 1.7 mm in the other taxa. The relation between stalk and the entire length of the lobe is the same in *H. torulosum* as in *H. duriaei,* but the absolute length of the stalk is shorter and the variation range is entirely congruent with those of other taxa. In these, the stalk always constitutes less than 20% of the entire length.

Stamens and pollen. The androeceum consists of four stamens. The median ones are vascularized by two bundles and the transversal ones by one. The tips of the vascular bundles are visible on top of the thecae. The developmental history of the androeceum was discussed by MURBECK (1912) and LIDÉN (1986).

There are two nectaries at the base of the filaments. Nectaries were found to be lacking in some flowers in small-flowered populations of *H. procumbens* subsp. *procumbens* on the island of Kithnos.

The filaments of all four stamens are broadly alate. The median filaments are always broader than the transversal ones and vary in shape between the taxa. The median filaments of *H. dimidiatum, H. imberbe, H. torulosum,* and *H. duriaei,* i.e. all the taxa with orange-yellow pollen and in which most ultimate leaflets are dilated towards a usually trifid apex, are narrowly triangular, as are also those of *H. pseudograndiflorum* (yellowish-white pollen, lanceolate to obovate ultimate leaflets with an undivided apex). The median filaments of *H. angustilobum* are also triangular, and the ultimate leaflets are narrow but of varying shape, but the pollen

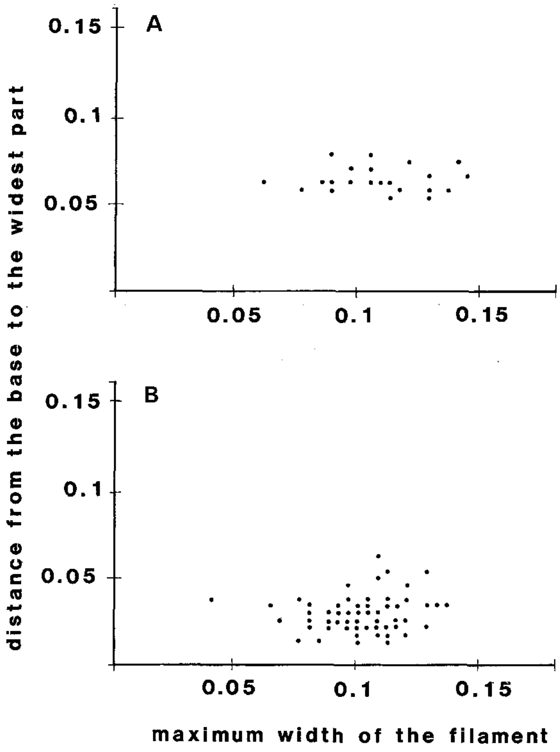

Fig. 14. Maximum width in relation to the distance from the base to the widest part of the filaments of two sympatric taxa. *A H. procumbens* subsp. *atropunctatum*, with narrowly ovate filaments, and *B H. pseudograndiflorum*, with narrowly triangular filaments

colour is unknown. In *H. procumbens*, the median filaments are narrowly ovate. *H. trullatum* differs from all others in having all four filaments abruptly dilated just below the middle. The shape of the median filaments is thus a very useful "key" attribute, especially when dried material is to be identified and other valuable characters are lost. The diagrams in Fig. 14 show the maximum width in relation to the distance from the base to the widest part of the filament (excluding the nectariferous part) in the sympatric *Hypecoum pseudograndiflorum* and *H. procumbens* subsp. *atropunctatum*, i.e. in one species with narrowly triangular and one with narrowly ovate filaments.

The shape of the narrower transversal filaments is similar to that of the median ones. As MURBECK (1912) stated, the bases of the transversal stamens are strongly curved, and thus appear folded. In, e.g., *H. dimidiatum*, with broad filamental alae, these will fall to one side as a result of the curved base, if the stamen is exsected and laid on its adaxial side on a table. The stamen then appears as alate only on one side – hence the misinterpretation of DELILE, repeated by FEDDE (1909), which led to applying the epithet "*dimidiatum*" to this taxon.

The anthers open extrorsely with longitudinal valves, already in the flower bud. The box-and-whiskers'diagrams in Fig. 15 show the variation in anther length within the section *Hypecoum*. Anthers shorter than 1.4 mm are found only in the self-compatible taxa *H. procumbens* subsp. *procumbens* and *H. torulosum*, and in the southernmost populations of *H. duriaei*, in which the degree of self-compatibility is unknown. The variation range of *H. procumbens* subsp. *procumbens* overlaps with that of the self-incompatible taxa within the section, whereas there is almost no overlapping between the latter and *H. torulosum*.

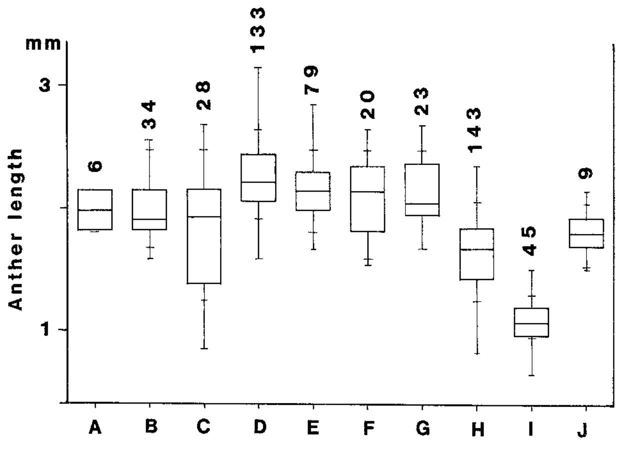

Fig. 15. Variation in anther length. *A Hypecoum angustilobum*. *B H. dimidiatum*. *C H. duriaei*. *D H. imberbe*. *E H. pseudograndiflorum*. *F H. procumbens* subsp. *atropunctatum*. *G H. procumbens* subsp. *fragrantissimum*. *H H.procumbens* subsp. *procumbens*. *I H. torulosum*. *J H. trullatum*. The figures above the boxes indiate the number of specimens measured

The outcrossing rate could be expected to vary between populations and sites within a self-compatible taxon, as a result of different selection regimes. The broad variation ranges in e.g. petal size and anther size of *H. procumbens* (and perhaps also that of *H. duriaei*) might reflect such an intraspecific variation, reported from a number of species (Schemske & Lande 1985). Cruden (1977) advocates the use of pollen/ovule (P/O)-ratios as indicators of mating system. The more efficient the transfer of pollen grains to the stigmas, the lower the P/O-ratio should be. Thus, cleistogamous flowers should have the lowest ratios, and autogamous flowers should have lower ratios than xenogamous flowers. Most investigations where P/O-ratios are applied deal with interspecific differences, but comparisons of conspecific populations were performed by Cruden (1976), Schoen (1978), Lindsey (1982), and Wyatt (1984). Schoen (1978) found good agreement between P/O-ratios and conclusions about mating system based on other characters in *Gilia achilleifolia*, and Wyatt (1984) noted the consistence between P/O-ratio and degree of protandry in *Arenaria uniflora*. Wyatt (1984) also found that P/O-ratios varied little between plants and between years in the same population, and that most of the variation in pollen grain number and P/O-ratios was expressed as differences among populations. As one of the nine populations incorporated in Wyatt's investigation deviated strongly in ovule number, Wyatt concluded that this parameter and pollen number do not always vary in concert, and recommended that they should be considered separately.

Calculations of both pollen number and P/O-ratios in a few populations of *H. procumbens* are shown in Table 1. The results are consistent with the hypotheses based on the morphological pattern and indicate differences in outcrossing rates even between geographically close populations of the self-compatible subsp. *procumbens*. Although only a few plants from each population were investigated, it is apparent that the intrapopulation variation is small. The variation is much greater, however, in the only population of the self-incompatible subsp. *fragrantissimum* included in the study, and it is obvious that a sample of five plants is not enough in this case.

If compared to Cruden's (1976) calculations, the results of the present study would show that the investigated populations of subsp. *procumbens* vary between a mating system classified as "facultative autogamy" and "facultative xenogamy".

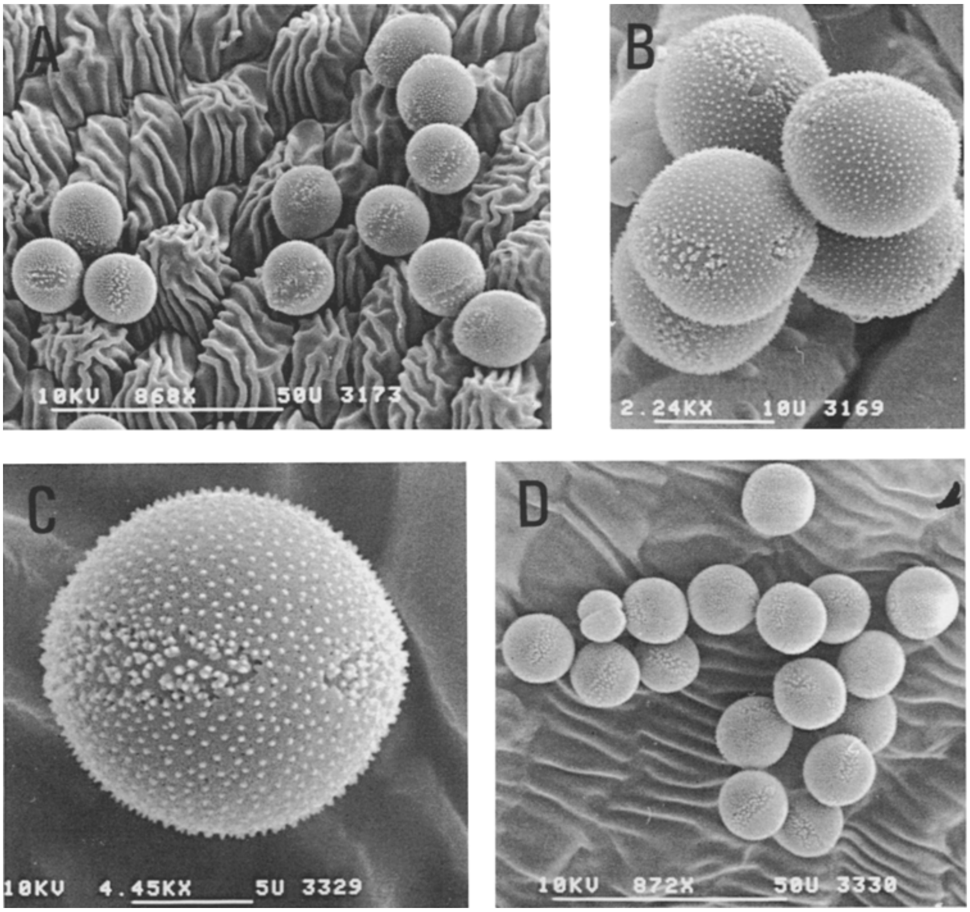

Fig. 16. Scanning electron micrographs of *Hypecoum* pollen. *A Hypecoum procumbens* subsp. *procumbens*, Spain, prov. of Almeria, Cabo de Gata, DSBG 5020. *B* – Greece, Kikladhes, island of Andros, Batsi, 10. IV. 1984, DAHL. *C, D Hypecoum imberbe,* Greece, Nom. Thessalonikis, Diavatha, 22. IV. 1984, DAHL

Table 1. Examples of pollen numbers and pollen-ovule ratios from some populations of *Hypecoum procumbens*. The cultivation numbers are indicated after the localities. *n* Number of investigated plants

Origin	Number of pollen (mean ± SD)	P/O-ratio (mean ± SD)	n
subsp. *procumbens*:			
Greece, Kikladhes: Andros, Batsi (258)	7 844 ± 1 657.7	464.5 ± 184	4
Spain, Almeria: Cabo de Gata (147)	10 806 ± 1 393	558.6 ± 139	5
Greece, Kikladhes: Mikonos, Megali Ammos (205)	9 906 ± 1 517	668.3 ± 133.3	5
Greece, Kikladhes: Kea, Kourissia (231)	21 980 ± 2 611.4	1 286 ± 134.8	4
Greece, Kikladhes: Tinos, S. of Chora (251)	21 450.5 ± 2 161.6	1 293 ± 233.5	4
subsp. *fragrantissimum*:			
Greece, Kikladhes: Mikonos, Ormos Korfos (210)	67 124.8 ± 33 778	4 934.4 ± 3 087	5

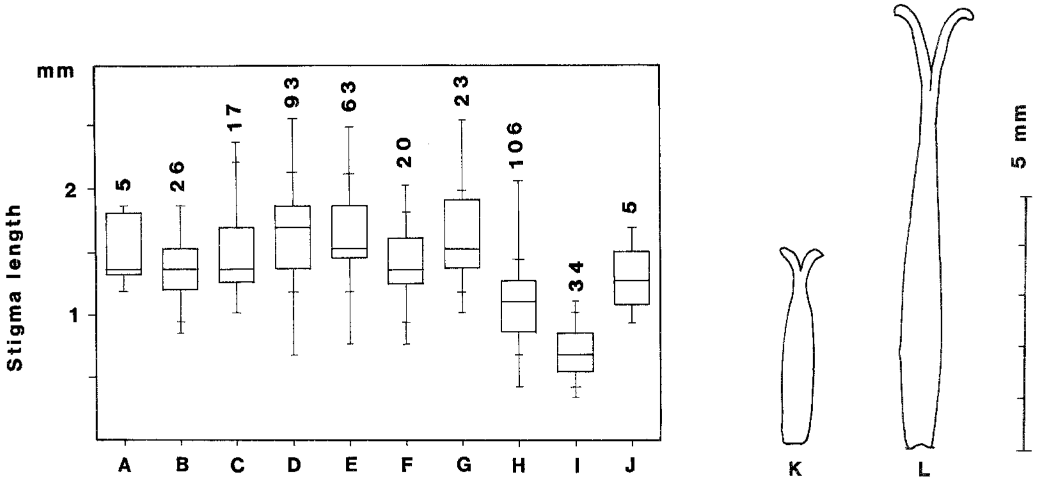

Fig. 17. Variation in stigma length. *A Hypecoum angustilobum. B H. dimidiatum. C H. duriaei. D H. imberbe. E H. pseudograndiflorum. F H. procumbens* subsp. *atropunctatum. G H. procumbens* subsp. *fragrantissimum. H H. procumbens* subsp. *procumbens. I H. torulosum. J H. trullatum.* Ovary, general shape. *K H. torulosum* (Rhodos, Carlström 6380, LD). *L H. imberbe.* (Livadhia prope Larnaca, 20. III. 1880, Sintenis LD). The figures above the boxes indicate the number of specimens measured

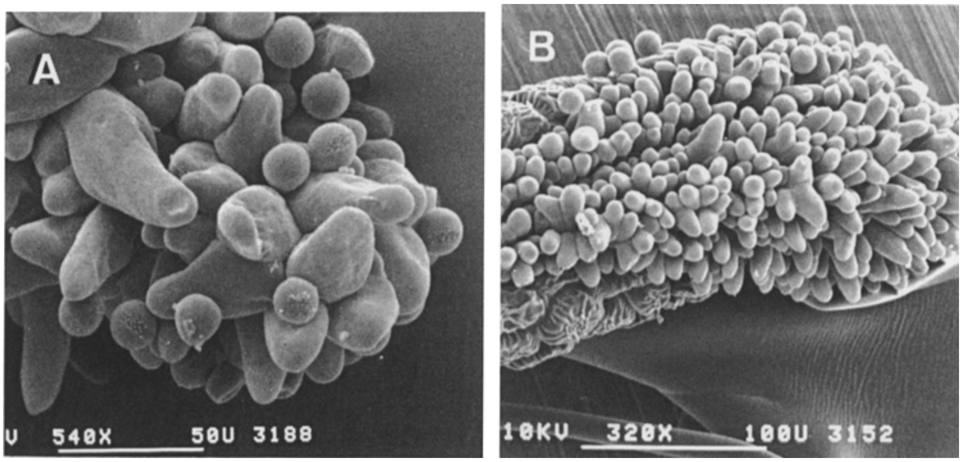

Fig. 18. Scanning electron micrographs of stigma surfaces. *A Hypecoum procumbens* subsp. *procumbens* (Greece, Kikladhes, island of Mikonos, road to Plati Gialos, 29. IV. 1983, Dahl) *B H. imberbe* (Greece, Nom Thessalonikis, Diavatha, 22. IV. 1984, Dahl

It is to be remembered, however, that *Hypecoum* may produce some pollen in excess as the flowers are often visited by beetles, and that the ratios may thus be skewed. Some pollen is likely to be consumed by the visitors.

The pollen of *Hypecoum* was desribed as 2-colpate by Erdtman (1952), which is confirmed by the SEM investigations of the present study (Fig. 16) and by light microscope photographs in a study by Layka (1976). Layka also published SEM photographs, but as Lidén (1986) stated, the pollen in these is collapsed and its shape hence difficult to interpret. Lidén's statement that *Hypecoum* pollen has an

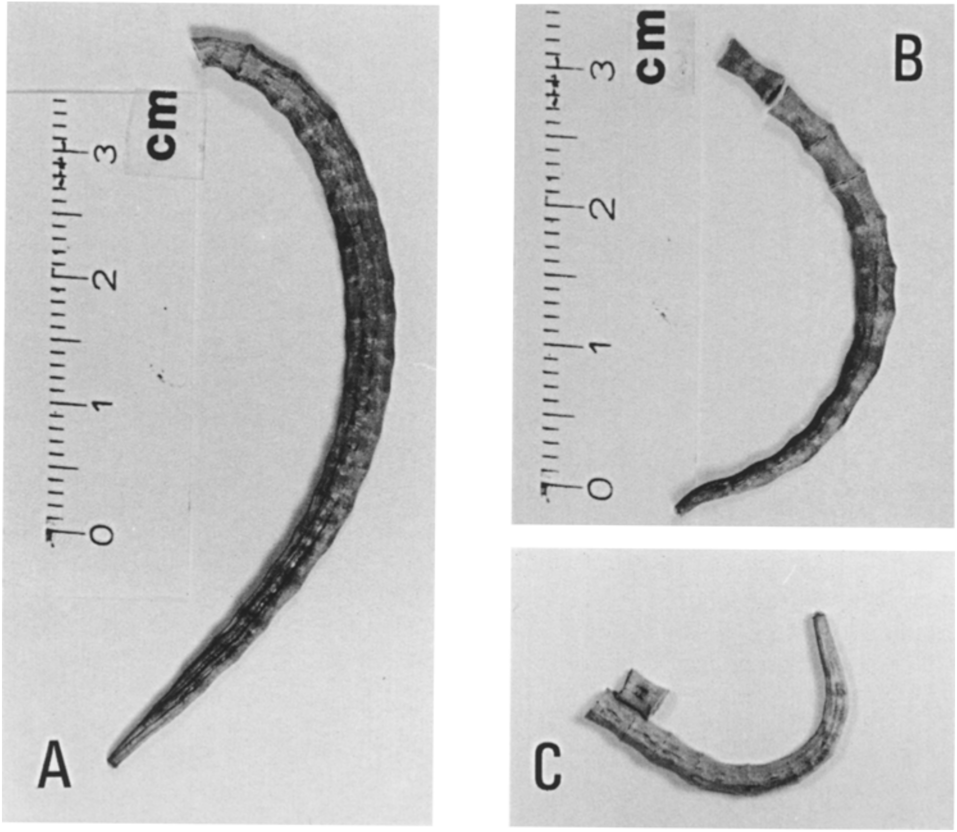

Fig. 19. Fruits of *Hypecoum* spp. *A H. procumbens* subsp. *procumbens*: Bordighera, 30. III. 1898 Bicknell (GB). *B H. imberbe*, 31. V. 1926, Hayek. *C H. pseudograndiflorum*: Niş, V. 1895, Adamovic. The scale of *C* is equal to *B*

synaperture does not apply to sect. *Hypecoum* (in *H. erectum* and *H. leptocarpum* the pollen is syncolpate).

The pollen is generally radially symmetric (Fig. 16 C, D), but in *H. procumbens* subsp. *procumbens* and in subsp. *fragrantissimum* it is in some populations transversely elliptic (Fig. 16 A).

Pollen of two colours occurs in the section, and as was already mentioned there seems to be a correlation between the pollen colour and the shape of the ultimate leaflets. In the taxa where the pollen colour is known, those in which all or most leaflets are dilated towards a generally tridfid apex have orange-yellow pollen, and those with lanceolate – obovate leaflets with undivided apex yellowish-white.

Ovary. The ontogeny of the ovary was discussed by Gonnermann (1980) and Lidén (1986) and will not be further treated here. The general shape is shown in Fig. 17. It is basically the same throughout the group.

The variation in stigma length is shown in Fig. 17. As in the case of anther length, the shortest stigmas are found in the self-compatible taxa, but the variation range is wider in *H. procumbens* subsp. *procumbens* than in *H. torulosum*. In contrast to the situation of anthers, the variation pattern in *H. duriaei* is not similar to that of *H. procumbens* subsp. *procumbens*, but to that of the self-sterile taxa.

The stigma lobes are papillate (Fig. 18). The papillate area is smaller in populations of *H. procumbens* subsp. *procumbens* than in the self-incompatible *H. procumbens* subsp. *fragrantissimum* and *H. imberbe.*

Fruit and seeds. The fruit is a more or less arcuate lomentum, 3 – 5 cm long. The anatomy was described by BRÜCKNER (1982). The fruits differ in appearance among the taxa within sect. *Hypecoum* (Figs. 19 and 20). Most characteristic in this respect are *H. torulosum* and *H. angustilobum*, in which the fruits are markedly torulose with very pronounced septa, as indicated by the specific epithet of the former. The fruits of *H. procumbens* subsp. *procumbens* are often broader than those of other taxa. They are also readily identified on their oblique septa which are only slightly pronounced. *H. pseudograndiflorum* usually has more slender fruits than other taxa.

ZOHARY (1937) claimed that a number of *Hypecoum* spp. found in Palestine are "heteromericarpous", i.e., the outermost joints of the lomentum are abscissed spontaneously soon after maturity, while the others keep together and are dispersed as one unit. Dispersal entities which consist of two or more seeds or one-seeded fruits were termed synaptospermous (MURBECK 1919) and occur throughout the Plant Kingdom, but mainly in arid regions (ZOHARY 1962). The tendency of the joints to fall apart varies within the section, but as the transition from well-developed abscission layers to more or less vestigial ones is gradual, it is hard to delimit the dehiscent and the synaptospermous parts in definite numbers of joints. However, the fruits of *H. procumbens* subsp. *procumbens* seem to be the most reluctant to shattering, and complete loments are often found, even though abscission of the ultimate joints also occurs frequently. The fruits are often arcuate and could easily hook around the feet or in the fur and wool of grazing animals, and thus be dragged away from the mother plant together with the entire infructescence. This is bound to happen now and then, but ZOHARY (1937) stressed that many features that are often interpreted as adaptations to epizoochory instead may be mainly favoured by selection in that they hamper dispersal in keeping the fruits stuck in pits or fissures of the ground surface. In low-growing therophytes with decumbent inflorescences, the "safe sites" of which should most probably be found in the proximity of the mother plants, this function is especially plausible. The infructescences of *H. procumbens* subsp. *procumbens* and subsp. *fragrantissimum* are often found lying on the ground around the mother plants. Often, many plants are found growing closely together, obviously originating from the same fruit. Fruits of *H. torulosum* where almost all the joints are abscissed are often found. The wind may have some importance, as it easily breaks the fruits and scatters the joints on the ground. However, "tufts" of up to eight plants growing closely together as in *H. procumbens* have also been found, indicating synaptospermy. ZOHARY (1937) stated that even if the synaptospermous as well as the dehiscent part of the fruit are reluctant to telochory, the small, single-seeded joints are more so, as they easily fall to the ground and disappear in pits and fissures. PLITMAN (1986) stated that most plants are opportunistic with regard to dispersal, possessing combined strategies that allow telechory as well as atelechory.

A high degree of synaptospermy may be favoured in plants occurring as weeds among cereals, as this increases the likelihood for the fruits to be harvested and dispersed along with the crop (HARPER 1966). In *H. imberbe,* which often occurs

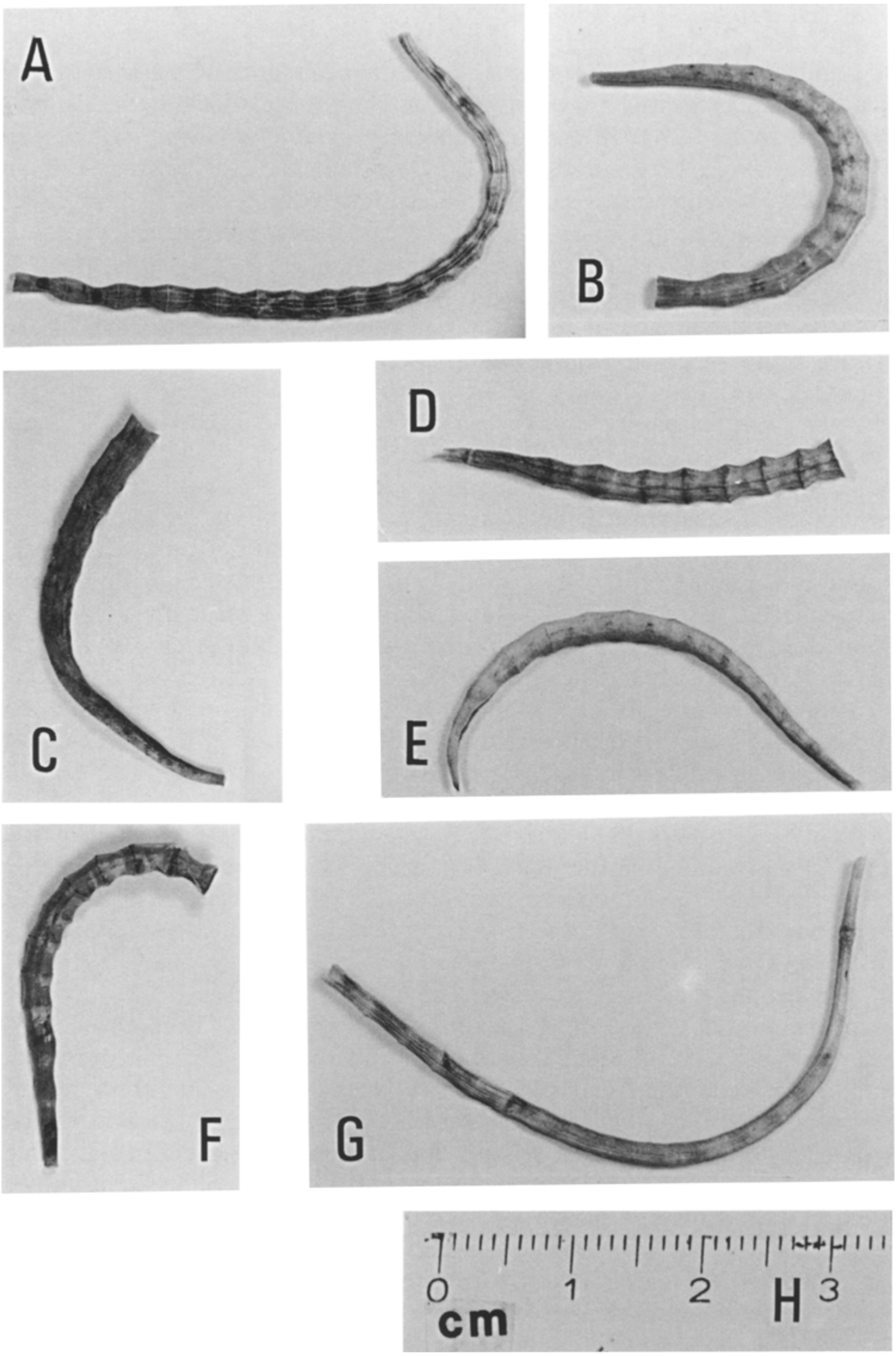

Fig. 20. Fruits of *Hypecoum* spp. *A H. trullatum*: Hatay, Iskenderun – Antakya, W. of Amik Göl, Davis & Hedge 27274 (K). *B H. procumbens* subsp. *atropunctatum*: İzmir, road İzmir – Çesme, crossing İnciralti/Agamemnon, Buttler 12387 (Buttler priv. herb.). *C H. duriaei*, 2 km E. of La Macta, SSW. of Mostaganem, Anderson 678 (LD). *D H. torulosum*: Attica, Phaleron, Heldreich (W). *E H. procumbens* subsp. *fragrantissimum*: Greece, island of Mikonos, Ormos Korfos, 19. IV. 1981, Dahl. (GB) *F H. angustilobum*, Regio Transcaspica, Krasnowodsk, Sintenis (C). *G H. dimididiatum*: Syria, env. de Hamma, Haradijan 4272 (S). *H* Scale

in fields, almost the entire fruit is synaptospermous, as usually only one or two joints are shed at maturity.

The seeds are D-shaped in outline and have a dark brown testa in the entire sect. *Hypecoum*. As in the entire genus, the testa is covered with oxalate crystals (BRÜCKNER 1983). The connection between germination and seed weight was not specially studied, but I have noted that the seeds sometimes could be quite shrivelled but still able to germiante in the greenhouse.

Some kind of dormancy seems to be at hand, as germination of sibling seeds sown on the same occasion could be extended over at least 2–3 years in the greenhouse. Dormancy is well known in desert annuals (references in HARPER 1977) from areas with short and often sporadic periods of moisture. Among annuals in Mediterranean environments, the ability to distribute the germination of a seed-litter over a number of years would be favourable as well as in the desert. The growth conditions vary between years in these semi-arid areas, and, e.g., failure of winter rain during the sensitive germination phase could exterminate the entire population if all seeds available should sprout at one time. During this study, certain populations were found to vary extremely in size between different years in Southern Spain. Many of the annual species in the Mediterranean originate in disturbed environments (e.g., trampled ground, screes, etc., ZOHARY 1973) and may be adapted to take advantage of short but recurrent favourable growth conditions in the same way as desert lants. Dormancy of buried seeds is a common feature of arable weeds (GRIME 1979), many of which stem from the Mediterranean are. The abscissed ultimate segments of the *Hypecoum* fruits could easily fall into small pits in the ground and contribute to the build-up of a seed-bank. The evident simultaneous germination of several seeds originating from the same fruit (see above) that was recorded in nature during this study indicated that sibling seeds do not always differ in germination time, but that the observed dormancy in the green-house might be induced by, e.g., the burying of seeds at the sowing.

Taxonomy

The taxonomically most useful characters within sections are generally floral, but the shapes of the fruits (Figs. 19 and 20) and of the smallest leaf divisions (hereafter called "ultimate leaflets") are also valuable. Living plants are readily identified, but in order to classify dried specimens it is often necessary to remoisten and dissect flowers. Examples of important "key" attributes which could not be studied otherwise are the shape of the lateral lobes of the inner petals (Fig. 10) and the shape of the median filaments (e.g., Figs. 22, 26, and 27). When plants are collected in nature, it is important to make a note of the colour and nuance of petals and pollen, and whether the petals are spotted or not. The variation ranges of the characters that remain in dried plants are often partly overlapping between taxa, and it is necessary to check the determination of each specimen against the full descriptions. Some vegetative characters, such as general size and size of leaves, are subject to much modification.

The synonymy includes all names at the specific, subspecific and varietal levels that are known to have been applied to the taxa described.

All countries where a taxon is present are mentioned under the heading "Distribution". In addition, the relevant geographical units used in TUTIN & al. (1974)

and GREUTER & al. (1984) are mentioned, when a country (as a political entity) comprises more than one such unit.

***Hypecoum* sect. *Hypecoum*.** Erect or procumbent, rosulate plants, 1 – 40 cm. Ultimate leaflets lanceolate – obovate with entire apex or dilated towards a usually trifid apex, seldom linear. Inflorescences with dissected, foliose bracts and 1 – 24(28) flowers. Sepals herbaceous with membranaceous margins, entire, erose or dentate, 2 – 7 × 1 – 3 mm. Petals yellow or white and purple-tinged; the outer ones usually unguiculate, rhombic to shallowly trilobate, apex-lobe usually ± greenish, ± cucullate, ± keeled, 3.7 – 13.6 × 1.9 – 15 mm; the inner ones deeply divided into 3 lobes, the lateral ones linear, ovate or obovate, entire to erose, the inner ones obovate with truncate, seldom attenuate, base, stalked and fimbriate. Filaments broadly alate, the median ones narrowly ovate or narrowly triangular, or abruptly dilated just below middle. Fruit an erect to patent lomentum, often arcuate, often torulose, 1 – 4 mm wide at broadest septa. Seeds D-shaped in outline, dark brown. Only diploid plants recorded ($2n = 16$).

Key to the taxa of *Hypecoum* sect. *Hypecoum*

1 Filaments abruptly dilated just below middle. (SE Anatolia) . 2. *H. trullatum*

– Filaments gradually dilated in lower third 2

2 Median filaments narrowly ovate 9

– Median filaments narrowly triangular 3

3 Stalk of fimbriate lobe of inner petals > 20% of total length (from base of petal to apex of fimbriate lobe) 4

– Stalk of fimbriate lobe of inner petals < 20% of total length 5

4 Outer petals white, tinged with purple, 6.6 – 11.6 × 4.8 – 12.4 mm, lateral lobes flat; base of fimbriate lobe usually attenuate (Algeria) . . . . . 7. *H. duriaei*

– Outer petals yellow, 4.4 – 7.9 × (2.2)2.9 – 6.0 mm, lateral lobes involute; base of fimbriate lobe usually truncate . . . . 8. *H. torulosum*

5 Outer petals 4.4 – 7.9 × (2.2)2.9 – 6.0, length usually > 1.2 times their width, lateral lobes usually involute; fimbriate lobe 1.8 – 3.1 × 1.4 – 2.8 mm; anthers 0.7 – 1.5 mm . . . . 8. *H. torulosum*

– Outer petals 6 – 13.6 × 5.2 – 14(15) mm, length usually < 1.2 times their width (in *H. imberbe* seldom more), lateral lobes flat; fimbriate lobe 3.1 – 6.4 × 1.2 – 3.6 mm; anthers 1.5 – 2.1 mm 6

6 Lateral lobes of inner petals obovate with broad, obtuse apex, width 0.8 – 4.6 mm; lateral lobes of outer petals always roundish 7

– Lateral lobes of inner petals linear with narrow, oblique, subacute apex, width 1 – 2.9 mm; lateral lobes of outer petals roundish or cuneiform 8

7 All or most of the ultimate leaflets of the upper primary leaf segments dilated towards the trifid apex, often with 1 – several lateral teeth. Pollen colour orange-yellow. Fruit 2 – 3.5 mm wide at the broadest septa, septa ± thickened (European part of Mediterranean Area, Cyprus, ? Algeria) . . . . 6. *H. imberbe*

– All or most ultimate leaflets in the three or four uppermost primary segments lanceolate to obovate and acute, not expanding towards the undivided apex, usually with no or seldom one lateral tooth. Pollen colour yellowish white. Fruit 1.5 – 2.5 mm at the broadest septa, septa not thickened. (Asia Minor, N. Balkan peninsula) . . . . 3. *H. pseudograndiflorum*

8 Outer petals 7 – 9 mm wide, width usually equal to or shorter than length; lateral lobes of inner petals 5.3 – 5.8 mm long. A majority of the ultimate leaflets linear to narrowly lanceolate with an undivided apex, often almost filiform, only a few of them dilated towards a trifid apex (Armenia, E. & S. Transcaspian area) . . . . 4. *H. angustilobum*

– Outer petals 6.7 – 13.1(15) mm wide, width usually exceeding length; lateral lobes of inner petals (4.2)5.8 – 8.4(10) mm long. A majority of the ultimate leaflets usually dilated towards the trifid apex (their length is often so short in relation to their width that they appear cuneiform; seldom are all ultimate leaflets lanceolate). (SE. Anatolia, Middle East) . . . . . . 5. *H. dimidiatum*

9(2) Lateral lobes of outer petals ± cuneiform, lateral lobes of inner petals linear to ovate with subacute apex; with black spots . . . . 1 c. *H. procumbens* subsp. *atropunctatum*

– Lateral lobes of outer petals ± roundish, lateral lobes of inner petals obovate with usually obtuse apex; without black spots 10

10 Inflorescences with 1 – 7 flowers, all developing into fruits (self-fertile); scent of fresh flowers faint . . . . 1 a. *H. procumbens* subsp. *procumbens*

– Inflorescences with 1 – 14 flowers, ovaries of withered flowers often undeveloped; strong scent in fresh flowers . . . . 1 b. *H. procumbens* subsp. *fragrantissimum*

Descriptions of the taxa within sect. *Hypecoum*

1. *Hypecoum procumbens* L.

Linnaeus, Sp. Pl. 1: 124 (1753). – Type: "Prope Lunellam Gallia narbonensi spontae", Burser, Hortus siccus 9: 53, IDC no. 1.04 (lectotype, UPS!).

Note: This is a lectotype, designated by Dahl (1986) in Castroviejo & al. The specimen 171.1 at the Linnean Society (LINN) is commonly referred to as the type of *Hypecoum procumbens* L. This is, however, a plant belonging to *Hypecoum imberbe* Sm. Linnaeus cites *Hypecoum* from Dodonaeus (1616), Bauhin (1623), Linnaeus (1738), and Royen (1740). Names cited by Linnaeus from Bauhin's Pinax (1623) are often linked to specimens which Linnaeus saw in Burser's herbarium at UPS which was arranged according to the Pinax. The specimen in vol. 9, fol. 53 corresponds to the traditional comprehension of *Hypecoum procumbens* L. The indicated locus "Gallia narbonensi" may be the source of Linnaeus' reference to the area in Linnaeus (1738, 1753). The Bauhin name is repeated in the Hortus Cliffortianus (Linnaeus 1738), but there is a specimen in the Clifford Herbarium which also must be regarded as a syntype. I have chosen the Burser specimen as a lectotype. (I am indebted to Dr C. E. Jarvis at the British Museum, who supplied me with most of the information presented in this paragraph.).

Syn.: See under the subspecies.

Plant 1 – 40 cm high, green or glaucous. Ultimate leaflets lanceolate – obovate, with undivided, sometimes cuspidate apex, sometimes with 1 lateral tooth. Inflorescences decumbent to erect, with 1 – 14 flowers. Sepals 2 – 7 × 1 – 2.5 mm, apex entire. Petals lemon yellow or yellowish orange. Outer petals 3.7 – 12.1 × 1.9 – 12.1 mm, distinctly unguiculate, rhombic to distinctly trilobate, length usually exceeding to equal to width, lateral lobes flat, roundish or cuneiform.

Inner petals with or without black spots (differs between the subspecies), lateral lobes 2.5 – 9.3 × 0.7 – 3 mm, shorter than, equal to or longer than the fimbriate lobe, which is 2.2 – 6 × 1.1 – 3.1 mm, with truncate base, and has a stalk 0.2 – 1.7 mm long, 10 – 20% of length from the base of the petal to the top of the fimbriate lobe. Filaments of median stamens narrowly *ovate*, anthers 0.8 – 2.6 mm. Pollen yellowish-white. Fruit with not or moderately thickened septa, 1 – 3.5 mm wide at the broadest septa. Mating system varies between the subspecies. 2n = 16.

1 a. *Hypecoum procumbens* L. subsp. *procumbens*

Syn.: *H. glaucescens* GUSSONE, Pl. Rar. 1: 79, t. 15. (1826), p.p. – *H. procumbens* L. var. *glaucescens* (GUSS.) MORIS, Fl. Sard. 1: 85 (1837). – *H. procumbens* L. var. *procumbens* subvar. *glaucescens* (GUSS.) COSS., Comp. Fl. Atl. 2: 73 (1887). – *H. procumbens* L. subsp. *euprocumbens* f. *glaucescens* (GUSS.) MAIRE, Flore de l'Afrique du Nord 11: 323 (1964). – Type: "In arensosis maritimis Calabriae orientalis, Lucaniae, Japygiae et in Corsica".

Note: Most of GUSSONE's herbarium is in NAP, where I have not had the opportunity to study it. I have seen one syntype in C ("Calabria", GUSSONE), which was a specimen of *H. imberbe*. The description and illustration of GUSSONE does, however, better fit *H. procumbens* subsp. *procumbens*.

H. ponticum VELEN, Sitz. Boehm. Ges. Wiss. 2: 37 (1894). – Type: "In arenosis ante Poros prope Burgas" (lectotype, designated by B. KUZMANOV, PRC!)

Plant 5 – 30(– 35) cm high. Inflorescences decumbent to erect, with 1 – 7 flowers. Sepals 2 – 7 × 1 – 2.2 mm. Petals lemon yellow. Outer petals 3.7 – 12.1 × 1.9 – 10(11.4) mm, rhombic to distinctly trilobate, lateral lobes roundish. Inner petals without black spots, lateral lobes 2.5 – 9 × 0.7 – 3 mm, linear-obovate, obtuse, fimbriate lobe 2.2 – 6.0 × 1.1 – 2.9 mm, its stalk 0.2 – 1.7 mm long. Anthers 0.8 – 2.3 mm long. Fruit 2 – 3.5 mm at broadest septa. Self-fertile.

Distribution: Western coast of Black Sea, coastlands of Mediterranean area, rare in the inland. Algeria, Bulgaria, Cyprus, France (Co, Ga), Greece (Ae, Cr, Gr), Italy (It, Sa, Si), Malta, Morocco, Portugal, Spain (Bl, Hs), Tunisia, Turkey (An, Tu).

Habitat: Sandy shores (usually on non-mobile sand), sandy ruderal ground, sometimes in cultivated fields.

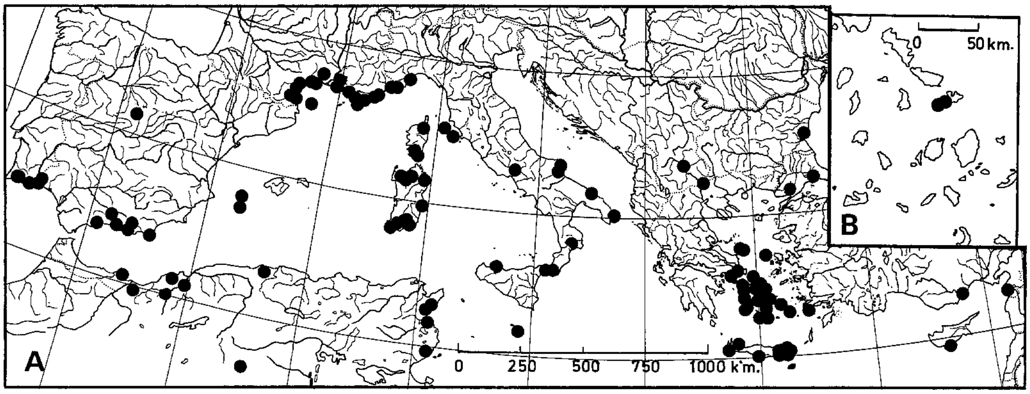

Fig. 21. Known distribution of *H. procumbens* subsp. *procumbens* (*A*) and *H. procumbens* subsp. *fragrantissimum* (*B*)

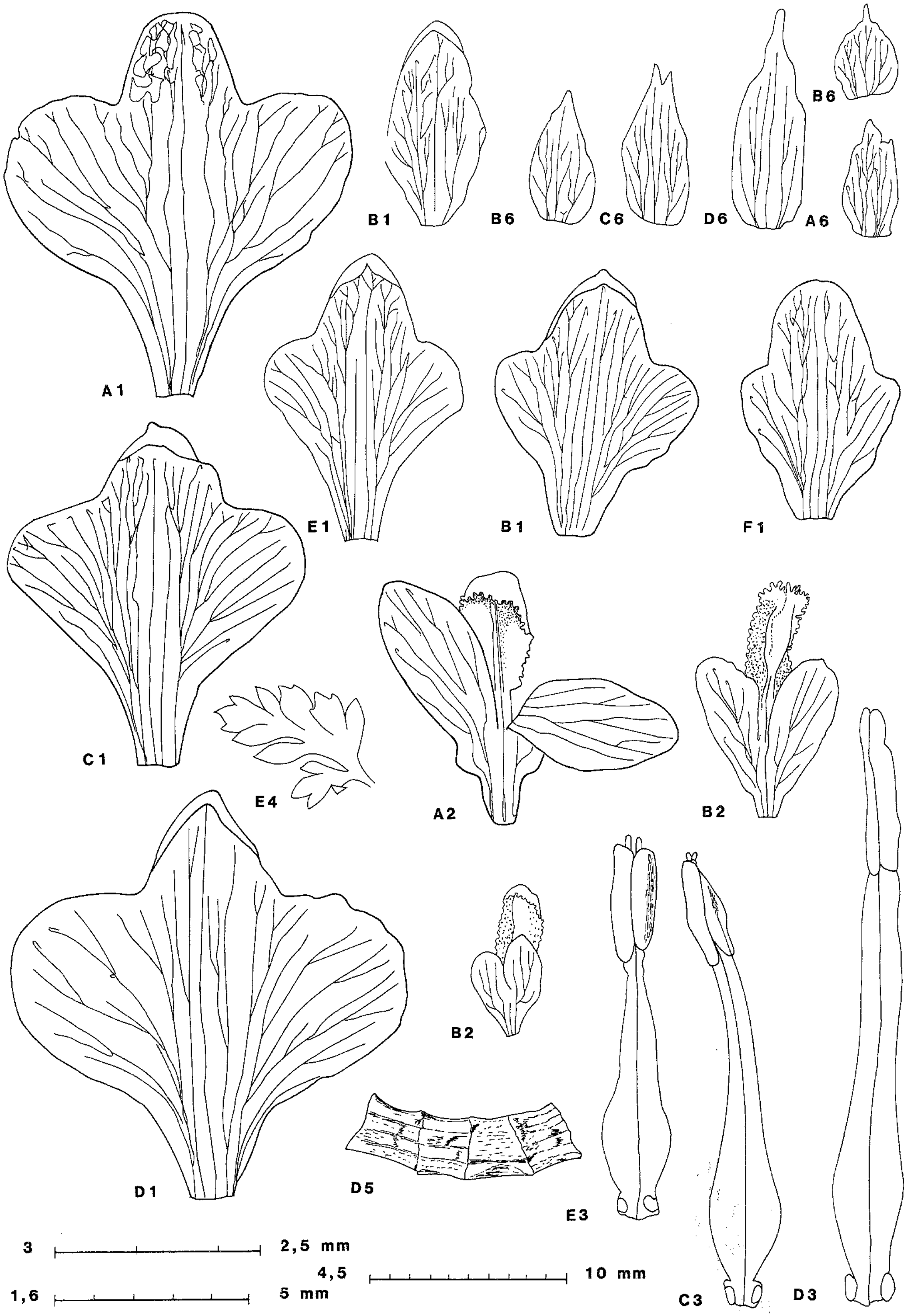

Fig. 22. *Hypecoum procumbens* subsp. *procumbens*, outer petals (1), inner petals (2), median stamens (3), primary leaf segment (4), fruit (5), and sepals (6). *A* Greece, island of Kithnos, c. 1.5 km N. of Loutra, 20. IV. 1983, DAHL (alc. fix.). *B* Greece, island of Kea, Ormos Xila, 24. IV. 1983, DAHL (alc. fix.). *C* Corsica, 27. IV. 1880, REVERCHON (W). *D* Liguria, Bordighera, 23. IV. 1890, BICKNELL (UPS). *E* Spain, Prov. of Almeria, Cabo de Gata, DSBG 5020 (GB). *F* Greece, island of Kithnos, c. 1 km N. of Loutra, 20. IV. 1983, DAHL (alc. fix)

Flowering period: (I –)III – VI(– VII, X). (The records of the earliest flowering are from North Africa and those of the latest from Italy and Greece. Two records, from Marseille and Milos, are from October.)

Hypecoum procumbens subsp. *procumbens* varies much in floral size, especially in the Aegean area, where the outer petals often have a rhombic outline. Accompanying this and the overall reduction in size is a shortening of the lateral lobes of the inner petals in relation to the fimbriate lobe. In the Aegean, a variation of these characters sometimes occurs even within populations (Fig. 22 B 1, B 2), in connection with developmental disturbances and with a lowered number of morphologically well-developed pollen. The number of plants in such populations may be low – sometimes less than ten, seldom more than one hundred, why it may be presumed than the lowered vitality and fertility are due to inbreeding depression. Unfortunately, it has not yet been possible to test the effects of prolonged inbreeding on populations of *Hypecoum procumbens* subsp. *procumbens* experimentally to corroborate this assumption. The size differences in floral characters between populations in the distribution area indicate differences in adaptation to outcrossing and autogamy, respectively.

In the island of Mikonos, small-flowered representatives of subsp. *procumbens* occur in mixed populations with subsp. *fragrantissimum*. A number of strongly disturbed and sterile plants, presumably hybrids, were found. Artificial crossing between the subspecies yielded semi-sterile to almost fully fertile plants (fertility measured as per cent morphologically well-developed and stainable pollen).

Collections from the province of Liguria in northern Italy (Fig. 22 D 1) and one from the other side of the French border (Menton) are characterized by petals which much exceed those of all other populations of subsp. *procumbens* studied in size, as well as those of subsp. *fragrantissimum*.

In a single population from Kithnos in the western Aegean, plants with faint black spots were recorded.

1 b. *Hypecoum procumbens* subsp. *fragrantissimum* Å. E. DAHL, subsp. nova

Herba 5 – 40 cm alta. Inflorescentiae decumbentes vel erectae, 1 – 14-florae. Sepala 2 – 4 × 1.2 – 2.2 mm. Petala citrina; duo externa 6.1 – 9.3 × 4.8 – 9.1 mm, distincte triloba, lobis lateralibus rotundatis; duo interna immaculata, lobis lateralibus 4.4 – 8 × 0.9 – 2.9 mm, obovatis, apice obtuso, lobus fimbriatus 3.1 – 4.9 × 1.5 – 2.9 mm, stipes eius 0.3 – 1.4 mm longus. Antherae 1.6 – 2.6 mm longae. Lomentum 2 – 3.5 mm (in septis latissimis mensum).

Type: Greece, Mikonos, pasture at Ormos Korfos, c. 2 km of Chora, DAHL 158 (holotype, GB!)

Plant 5 – 40 cm high. Inflorescences decumbent to erect, with 1 – 14 flowers. Sepals 2 – 4 × 1.2 – 2.2 mm. Petals lemon yellow. Outer petals 6.1 – 9.3 × 4.8 – 9.1 mm, distinctly trilobate, lateral lobes roundish. Inner petals without black spots, lateral lobes 4.4 – 8 × 0.9 – 2.9 mm, obovate, obtuse, fimbriate lobe 3.1 – 4.9 × 1.5 – 2.9 mm, its stalk 0.3 – 1.4 mm long. Anthers 1.6 – 2.6 mm long. Fruit 2 – 3.5 mm at broadest septa. Self-sterile.

Distribution: Greece: Islands of Mikonos and Rinia (Fig. 21).

Habitat: Shores, pastures and road-sides on non-mobile sand.

Flowering time: III – V (based on few records only).

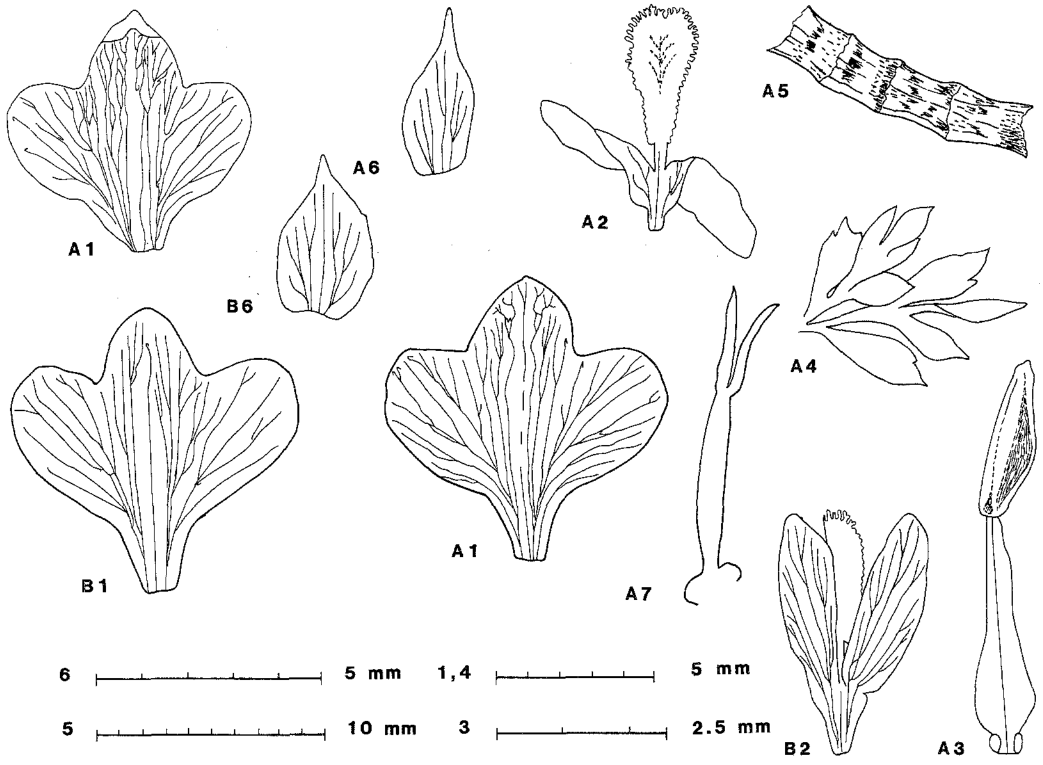

Fig. 23. *Hypecoum procumbens* subsp. *fragrantissimum,* outer petals (1), inner petals (2), median stamen (3), primary leaf segment (4), fruit (5), and sepals (6). *A* Greece, island of Mikonos, Ormos Korfos, 19. IV. 1981, Dahl (GB) *B* Greece, island of Mikonos, Megali Ammos S. of Chora, 19. IV. 1981, Dahl (GB)

Hypecoum procumbens subsp. *fragrantissimum* differs from subsp. *procumbens* in being strongly self-incompatible and in presumably related characters such as reproductive output, means of length of stigma and of anthers, and the number of components of the floral scent. Subsp. *fragrantissimum* is the most intensely scented of all the taxa of the sect. *Hypecoum,* and the one with the widest spectrum of such components – hence the subspecific epithet (the composition of the scents will be described elsewhere).

1 c. *Hypecoum procumbens* subsp. *atropunctatum* Å. E. Dahl, subsp. nova

Herba 1 – 35 cm alta. Inflorescentiae erectae, 1 – 11-florae. Sepala 2 – 5.5 × 1.5 – 2.5 mm. Petala citrina ad aurea; duo externa 7.7 – 11.6 × 6 – 11(12.1) mm, distincte triloba, lobis lateralibus cuneiformibus; duo interna maculata, lobis lateralibus 5.8 – 9.3 × 0.7 – 2.6 mm, linearibus ad ovatis, apice subacuto, lobus fimbriatus 3.5 – 5.8 × 1.6 – 3.1 mm, stipes eius 0.7 – 1.6 mm longus. Antherae 1.5 – 2.6 mm longae. Lomentum 1 – 3 mm latum (in septis latissimis mensum).

Type: Turkey, prov. Izmir, E. of Gümüşsu, saline, sandy shore, 28. IV. 1983, Runemark & Carlström 49135 (holotype, LD!).

Plant 1 – 35 cm high. Inflorescences erect, with 1 – 11 flowers. Sepals 2 – 5.5 × 1.5 – 2.5 mm. Petals lemon yellow to yellowish orange. Outer petals 7.7 – 11.6 × 6 – 11(12.1) mm, distinctly trilobate, lateral lobes cuneiform. Inner pe-

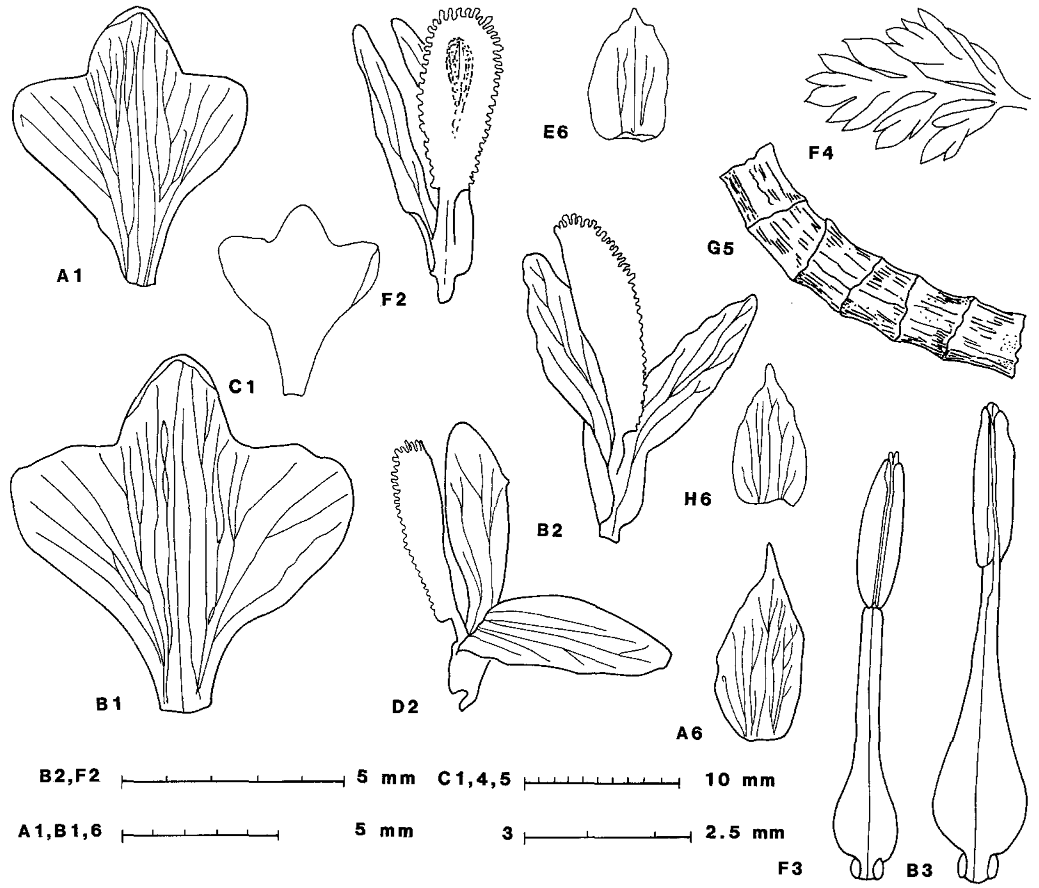

Fig. 24. *Hypecoum procumbens* subsp. *atropunctatum*, outer petals (1), inner petals (2), median stamens (3), primary leaf segment (4), fruit (5), and sepals (6). *A* Muğla, Euromos RUNEMARK & CARLSTRÖM 49381 (LD). *B* İzmir to Çesme, near İçmeler, 27. II. 1967, A. & T. BAYTOP (ISTE). *C* Greece, island of Khios, Monasteri Agios Mina, 3. V. 1982, DAHL, cultivated 1983. *D* Muğla, road Milas – Yatağan, RUNEMARK & CARLSTRÖM 49631: (LD). *E* Brussa, (Bursa) PICHLER V – VI 1874 6W). *F* Thymbra, In valle Scamandri, SINTENIS 241 (S). *G* Smyrna, prope Thomasio, IV. 1906, BORNMÜLLER (W). *H* De Smyrna à Boursache, 3. V. 1899, AUCHER (W)

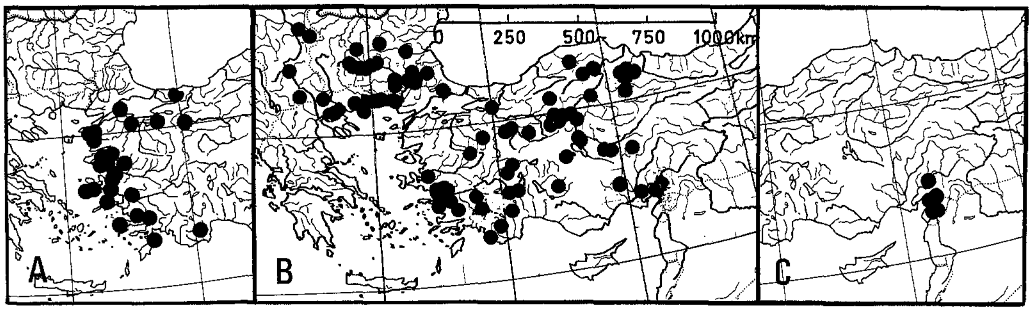

Fig. 25. Known distribution of *H. procumbens* subsp. *atropunctatum* (*A*), *H. pseudograndiflorum* (*B*) and *H. trullatum* (*C*)

tals with black spots, lateral lobes 5.8 – 9.3 × 0.7 – 2.6 mm, linear to ovate, subacute, fimbriate lobe 3.5 – 5.8 × 1.6 – 3.1 mm, its stalk 0.7 – 1.6 mm long. Anthers 1.5 – 2.6 mm long. Fruit 1 – 3 mm wide at broadest septa. Self-sterile.

Distribution: Greece (AE), the Mediterranean area in W. Turkey (An.) (Fig. 25).

Habitat: Occurs in secondary habitats, such as roadsides, groves, planted pine forests and pastures; sometimes on sandy shores.

Flowering period: II – IV.

Cultivated plants of Khios material had brightly lemon-coloured petals, whereas the petals of plants from Kalimnos and Lesvos were more golden yellow. Otherwise this subspecies seems to be morphologically homogeneous, but shows a continuous variation in floral size and length of unguiculus of outer petals.

SCHWARZ (1934) made the combination *H. grandiflorum* subsp. *pseudograndiflorum* (PETROVIĆ) O. SCHWARZ. A couple of specimens from Izmir in B, collected by him and determined as that taxon, belong, however, to *H. procumbens* subsp. *atropunctatum*.

2. *Hypecoum trullatum* Å. E. DAHL, spec. nova

Herba 5 – 25 cm alta, viridis vel glauca. Folia radicalia segmentis ultimis lanceolatis versus apicem trifidum dilatatis, interdum lateraliter unidentatis. Inflorescentiae decumbentes vel erectae, 1 – 18-florae. Sepala 2.5 – 4 × 1.5 – 3 mm. Petala lutea; duo externa 5.8 – 9.6 × 5.9 – 10.6 mm, distincte unguiculata et triloba, longitudine plerumque latitudinem aequante, lobis lateralibus planis, rotundatis et erectis; duo interna maculata, lobis lateralibus 4.9 – 8.6 × 0.9 – 2 mm, ovatis, apice obtuso vel subacuto, lobum fimbriatum valde superantibus, lobus fimbriatus 2.8 – 3.5 × 1.7 – 2.6 mm, basi truncata, stipes eius 0.4 – 1.1 mm longus, 10 – 20% totius longitudinis ad apicem lobi fimbriati a basi petali. Omnia filamenta abrupte dilatata sub medio, antherae 1.5 – 2.1 mm longae. Color pollinis ignotus. Lomentum septis paene non inspissatis, circiter 2.5 mm latum (in septis latissimis mensum).

Type: "Inter oppidum Iskenderum (Alexandretta) et urbem Halep (Aleppo), prope Kyryk Han ad pedem Amani, in phryganis, substrato serpentinico; c. 180 m.", HANDEL-MAZZETTI (holotype, W!).

Plant 5 – 25 cm high, green or glaucous. Ultimate leaflets usually lanceolate-obovate with entire apex, or dilated towards a trifid apex, sometimes with a lateral tooth. Inflorescences decumbent to erect, with 1 – 18 flowers. Sepals 2.5 – 4 × 1.5 – 3 mm, apex entire. Petals yellow. Outer petals 5.8 – 9.6 × 5.9 – 10.6 mm, distinctly unguiculate, distinctly trilobate, length usually equal to width, lateral lobes flat, roundish, pointing upwards. Inner petals with black spots, lateral lobes 4.9 – 8.6 × 0.9 – 2 mm, ovate with obtuse or subacute apex, much exceeding the fimbriate lobe, which is 2.8 – 3.6 × 1.7 – 2.6 mm, with truncate base, and has a stalk 0.4 – 1.1 mm long, 10 – 20% of length from the base of the petal to the top of the fimbriate lobe. Filaments of all stamens abruptly dilated below middle, anthers 1.5 – 2.1 mm. Fruits with only slightly thickened septa, c. 2.5 mm at broadest septa. Pollen colour, mating system and chromosome number unknown.

Distribution: Turkey (An), provinces of Hatay, Seyhan and Maraş (Fig. 25).

Habitat: Cultivated fields, pastures and waste places.

Flowering period: II – III.

I have not seen this species either in nature or in cultivation, but it is easily

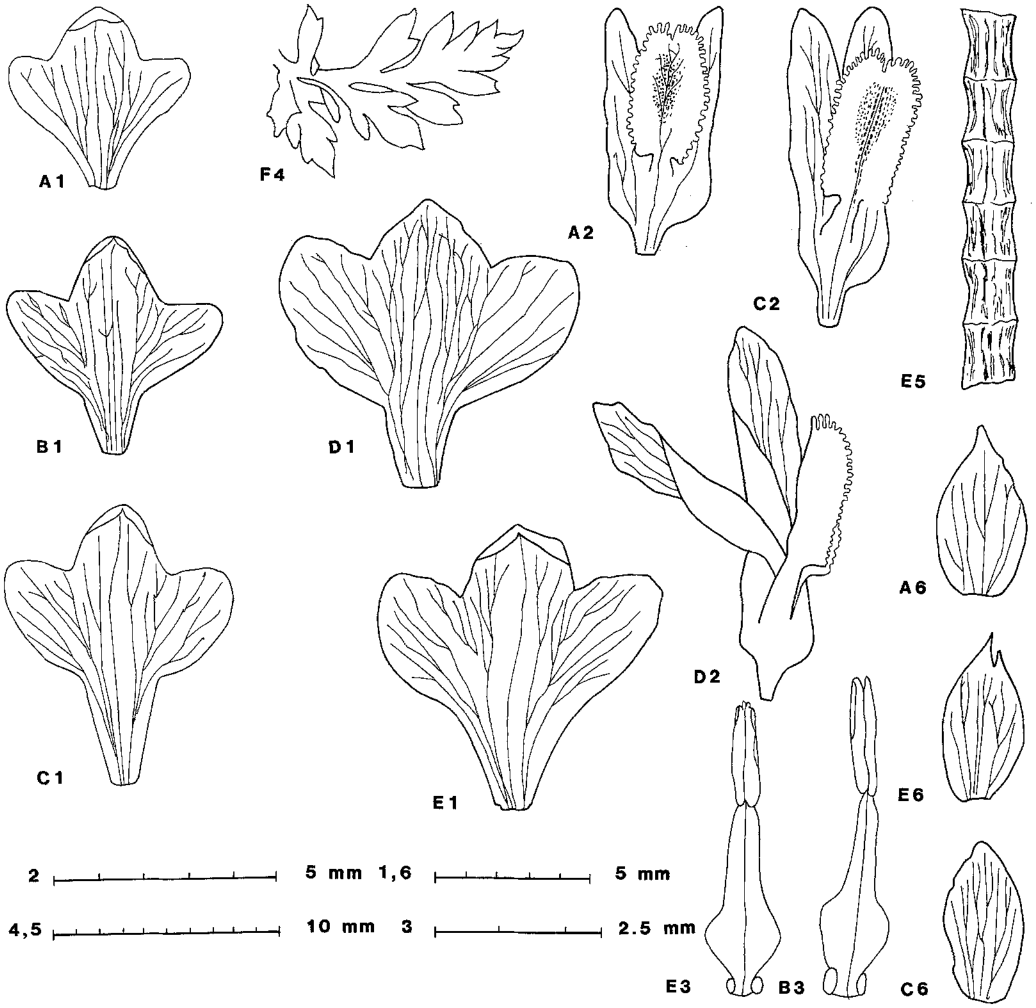

Fig. 26. *Hypecoum trullatum,* outer petals (1), inner petals (2), median stamens (3), primary leaf segment (4), fruits (5), and sepals (6). *A* Prov. Adana, distr. Bahce, Haruniye 500 m.s.m., Davis & Hedge 267860 (E). *B* Seyhan, Zoprak Kali nr. Seyhan, Balls 734 (E). *C* Hatay, İskenderun – Antakya, W. of Amik Göl, Davis & Hedge 734. *D* Inter oppidum İskenderun et urbem Haleb, prope Kyryk Han ad pedem orientalem Amani, Handel-Mazzetti 150 (W). *E* Maras, 7 miles S. of Andirin, Coode & Jones 17. V. 1965 (E). *F* Hatay, Davis & Hedge 27274 (K). *G* Syria septentrionalis, Alexandretta, in pascuis, 25. II. 1888, Sintenis (K, LD, W)

recognized by the "hips" on all four stamens and on the unusually short fimbriate lobe, which is always much exceeded by the lateral ones.

3. ***Hypecoum pseudograndiflorum*** Petr.

Petrović, Addit. Fl. Nyss.: 25 (1885). – *Hypecoum grandiflorum* Benth. var. *pseudograndiflorum* (Petr.) Bornmüller & Fedde, Fedde in Engler, Pflanzenreich 4: 92 (1909). – *Hypecoum grandiflorum* Benth. subsp. *pseudograndiflorum* (Petr.) O. Schwarz, Feddes Repert. 36: 85 (1934). – *Hypecoum imberbe* Sm. subsp. *pseudograndiflorum* (Petr.) E. Mayer & Nikolić, in Greuter & Raus, Willdenovia

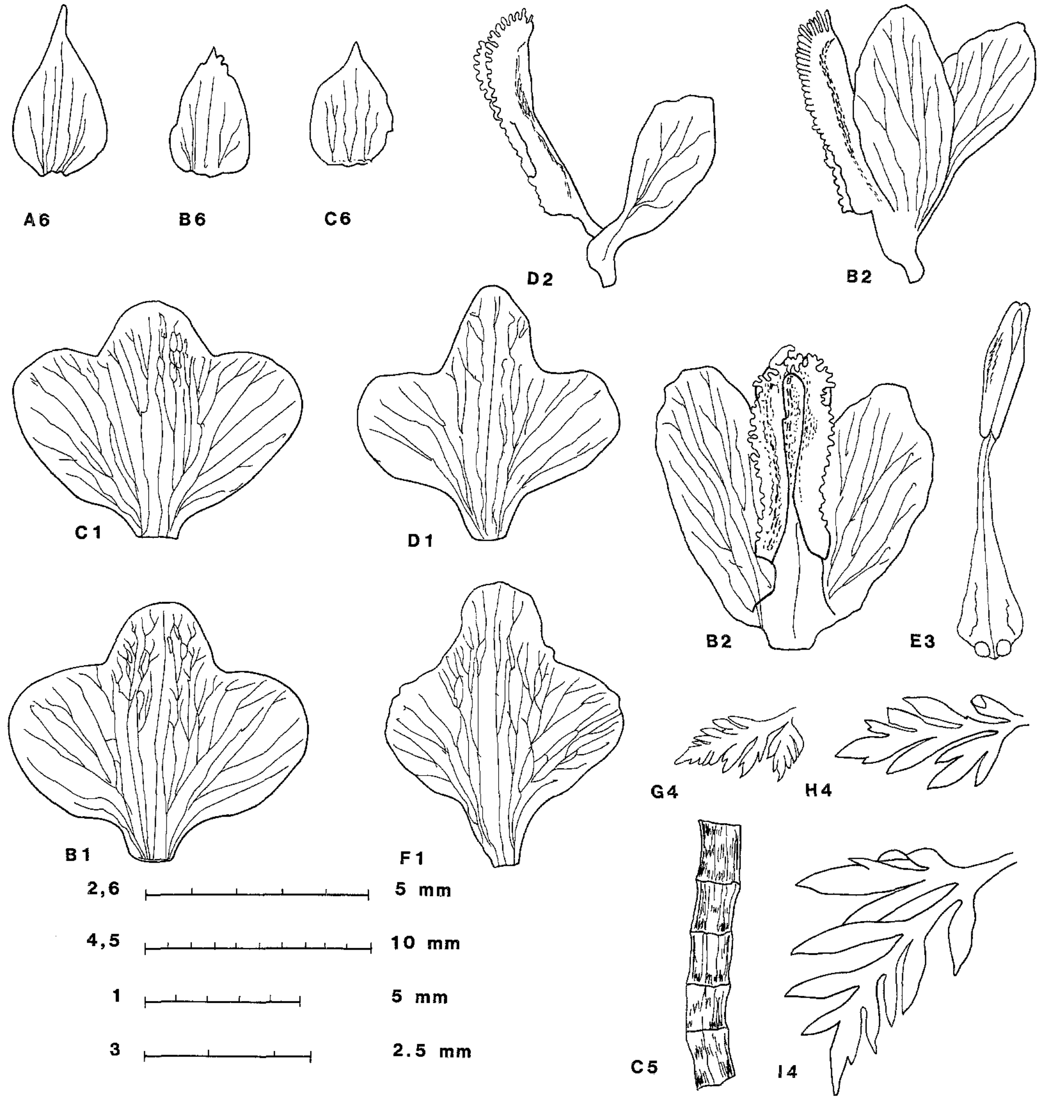

Fig. 27. *Hypecoum pseudograndiflorum*, outer petals (1), inner petals (2), median stamen (3), primary leaf segments (4), fruits (5), and sepals (6). *A* Nom. Kavalas, Keramoti, OXELMAN & TOLLSTEN 130. (GB). *B* Greece, Nom. Evrou, Road Alexandroupolis – Avas, c. 2 km N. Alexandroupolis, 26. IV. 1984, DAHL (alc. fix.). *C* Greece, nom. Eurou, Evros, river bank, OXELMAN & TOLLSTEN 51 (GB). *D* "Ad Karlovo", UROMOFF 1902, (GB). *E* Nom. Thessalonikis: Malio, between Peristerona and Loutra Volvis, 24. IV. 1984, DAHL (alc. fix.). *F* Sakarya, 3 km from Pamu Kova, 17. IV. 1976, BAYTOP (ISTE). *G* Tekirdag, 7 km from Çurlu to Seymen, 22. IV. 1970, BAYTOP (ISTE). *H* Nom. Thessalonikis, Langadikia, OXELMAN & TOLLSTEN 18 (GB). *I* Nom. Kavallas: Litochori, 10 km E. Kavalla, OXELMAN & TOLLSTEN 32 (GB)

13: 286 (1983). – Type: "In arce Nisch, Serbia" IV. 1884, PETROVIĆ (lectotype, here designated, in W!, isotypes in WU Herbarium HELDREICH!, M!).

Plant 5 – 40 cm high, green or glaucous. Most ultimate leaflets lanceolate to obovate with undivided apex. Inflorescences decumbent to erect, with 1 – 18(– 28) flowers. Sepals 2.5 – 5.1 × 0.9 – 2.5 mm, apex sometimes bi- or trifid. Petals lemon yellow. Outer petals 6 – 10.9 × 5.9 – 11(– 22) mm, not or shortly unguiculate, distinctly trilobate, length only slightly exceeding or less than width, lateral lobes flat, roundish. Inner petals with or without black spots, lateral lobes 3.3 – 8 × 0.8 – 2.8 mm, obovate with obtuse apex, not exceeding the fimbriate lobe, which is 3.8 – 5.6 × 1.2 – 3.4 mm, with truncate base, its stalk 0.3 – 1.4 mm long, 5 – 20% of length from base of petal to top of fimbriate lobe. Filaments of median stamens narrowly triangular; anthers 1.6 – 2.8 mm long. Pollen yellowish-white. Fruit 1.5 – 2.5 mm at broadest septa, septa not thickened. Self-sterile. 2n = 16.

Distribution: Mediterranean and Submediterranean area of N. Balkan and Asia Minor. Bulgaria, Greece (Gr), Turkey (An, Tu), Yugoslavia (Fig. 25).

Habitat: Ruderal places, roadsides and railway banks, fields, olive groves, etc. According to herbarium labels, the species occurs in sandy places or stony woodland and steppe in the eastern part of the distribution area.

Flowering period: (II –)IV – V(– VII).

Notes: *H. pseudograndiflorum* often occurs in vast populations when it grows as a weed. The leaflets are usually all lanceolate – obovate with an undivided apex, or a few of them expanding towards a trifid apex. In dwarf plants, they could appear triangular. Cultivated plants, originating from Kavalla (Greece), were rather variable with a higher proportion of leaflets dilated to a trifid apex than is usually seen in spontaneous material. Soem of these had even partly undivided primary segments, a condition also seen in artificial hybrids between populations of *H. imberbe* from different parts of the distribution area. The occurrence of black spots in the lateral lobes of the inner petals is highly variable. When spots do occur, they are often faint and few as compared with those, e.g., of *H. imberbe* and of *H. procumbens* subsp. *atropunctatum.*

FEDDE (1909), MAYER & NIKOLIĆ (1983), and others have not considered this taxon worthy of specific rank. In dried material the flowers of *H. imberbe* and *H. pseudograndiflorum* often appear very similar. The variation ranges of several floral characters are overlapping, but not identical in the two species (e.g., Figs. 8 and 13). Living plants of *H. pseudograndiflorum,* however, are easily distinguished from *H. imberbe,* as the flowers differ both in petal and pollen colour. Herbarium plants can be identified on the shape of the ultimate leaflets. Hybrids from artificial crossings are highly sterile and usually die as chlorotic seedlings. I do not see any reason not to consider the two taxa as separate species.

4. *Hypecoum angustilobum* Å. E. DAHL, spec. nova

Herba 5 – 40 cm alta, viridis vel glauca. Folia radicalia segmentis ultimis anguste linearibus ad anguste obovatis, vel versus apicem interdum trifidum dilatatis. Inflorescentiae erectae, 1 – 21-florae. Petala lutea, duo externa breviter unguiculata, cuneiformia vel triloba, 7.5 – 8.8 × 6.7 – 9 mm, longitudine latitudine breviore vel hanc superante, lobis lateralibus planis, cuneiformibus; duo interna maculata, lobis lateralibus 5.3 – 5.8 × 1.0 – 1.7 mm, lineraribus, saepe erosis, apice oblique subacuto, lobum fimbriatum numquam superantibus, lobus fimbriatus 4.1 – 4.7 × 1.8 – 2.9 mm basi truncata, stipes eius 0.6 – 1.1 mm longus, 10 – 20% totius longitudinis ad apicem lobi fimbriati a basi petali. Filamenta mediana anguste triangularia; antherae 1.7 – 2.1 mm longae. Color pollinis ignotus. Lomentum septis satis inspissatis, 2 – 3.5 mm latum (in septis latissimis mensum).

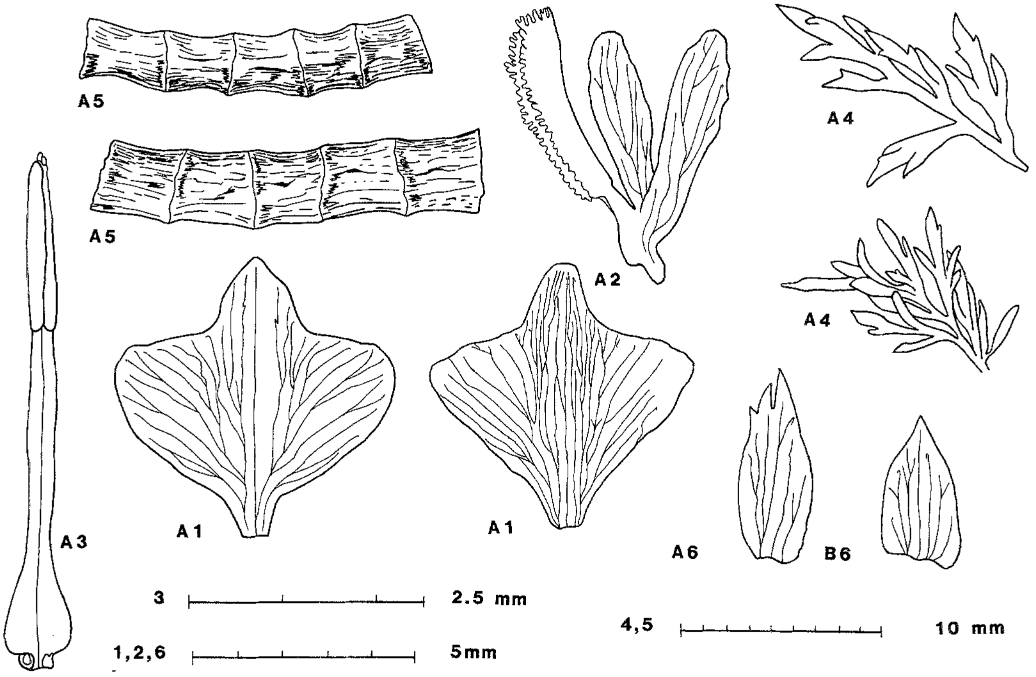

Fig. 28. *Hypecoum angustilobum*, outer petals (1), inner petals (2), median stamen (3), primary leaf segments (4), fruits (5) and sepals (6). *A* Armenia rossica, SZOVITS (M, S, UPS, W). *B* In collibus vinis ad Akantai, V. 1829, SZOVITS (H)

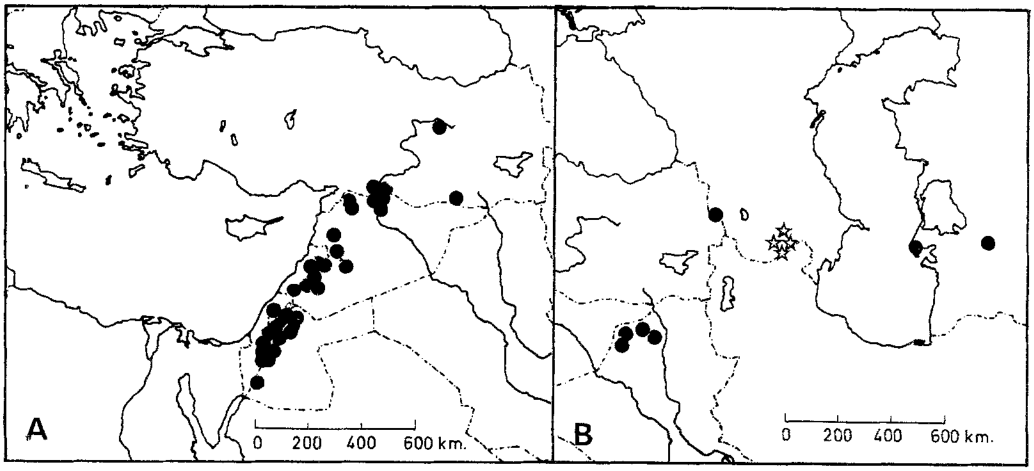

Fig. 29. Known distribution of *H. dimidiatum* (*A*) and *H. angustilobum* (*B*). The stars indicate the distribution of "*H. grandiflorum* BENTH." in the Caucasian area according to GROSSHEIM (1950); these records seem to represent the taxon described as *H. angustilobum* in the present study

Type: "Armenia rossica", SZOVITS (W, holotype!; isotype in UPS!, WU!, C!, S!).

Plant 5 – 40 cm high, green or glaucous. Ultimate leaflets narrowly linear to narrowly obovate with undivided apex, or sometimes dilated towards a trifid apex. Inflorescences erect, with 1 – 21 flowers. Sepals 3 – 5.5 × 1.5 – 2 mm. Petals yellow.

Outer petals 7.5 – 9 × 6.7 – 9 mm, shortly unguiculate, cuneiform to trilobate, length shorter or longer than width, lateral lobes flat, cuneiform. Inner petals with black spots, lateral lobes 5.3 – 5.8 × 1.0 – 1.7 mm, linear, with obliquely subacute apex, often with erose margin, never exceeding the fimbriate lobe, which is 4.1 – 4.7 × 1.8 – 2.9 mm, with truncate base, its stalk 0.6 – 1.1 mm long, usually 10 – 20% of the distance from base of petal to the apex of the fimbriate lobe. Filaments of median stamens narrowly triangular; anthers 1.7 – 2.1 mm long. Pollen colour unknown. Fruit 2 – 3 mm wide at broadest septa, septa quite thickened. Mating system and chromosome number unknown.

Distribution: Soviet Union (Armeniya, Azerbaydzhan, Turkmenya), N. Iraq (Fig. 29).

Habitat: According to POPOV (1937): Artemisia-steppe and stony ground.

Flowering period: ? – V – ?

Notes: This species has a narrow variation range in floral characters and is invaryingly small-flwoered. The dried specimens studied were all many-flowered and erect. The flowers of specimens from the Soviet Union seem to be very pale in dried condition, almost cream-coloured like those of *H. duriaei,* but this is not in accordance with the information of local Floras (e.g., POPOV 1937).

5. *Hypecoum dimidiatum* DELILE

DELILE in LABORDE, Voy. Arab. Petr.: 84 (1884). – Type: "Arabie Petrée", 1828, LABORDE (holotype, G!).

Plant 5 – 40 cm high, green or glaucous. Most of the ultimate leaflets dilated towards the trifid apex (seldom lanceolate), with one to several lateral teeth. Inflorescences decumbent to erect, with 1 – 24 flowers. Sepals (2.5 –)3 – 5.5 × 1.5 – 3 mm, apex sometimes bi- or trifid. Petals lemon yellow. Outer petals 7.1 – 11.4 × 6.7 – 13.1(15) mm, shortly to distinctly trilobate, unguiculate, length usually shorter than width, lateral lobes flat, wedgelike to roundish. Inner petals with black spots, lateral lobes (4.1)5.8 – 8.4(10) × 0.9 – 2.9 mm, linear, with obliquely subacute apex, often with strikingly erose margin, often exceeding the fimbriate lobe, which is 3.1 – 5.5 × 1.7 – 3.4 mm, with truncate base, its stalk 0.5 – 1.4 mm long, usually 10 – 20% of the distance from the base of the petal to the apex of the fimbriate lobe. Filaments of median stamens narrowly triangular; anthers 1.5 – 2.2(– 2.5) mm long. Pollen orange-yellow. Fruit with not or only moderately thickened septa, 1.5 – 4 mm at the broadest septa. Self-sterile. Chromosome number unknown.

Distribution: Mediterranean and steppic areas of Middle East. Israel, Lebanon, Syria, SE. Turkey (An) (Fig. 29).

Habitat: Steppe. Gravelly, often stony soil in orchards, fields, pastures, waste land.

Flowering period: II – IV.

Notes: One collection from Malatya (BAYTOP 9. IV. 1971, ISTE), one from Samaria (BERLINER 10. III. 1977, HUJ) and one from W. Syria (KOTSCHY 1855, "Circa Zebdaine prope Damascum", W), deviate from other specimens studied in the shape of the ultimate leaflets, which are all lanceolate. In all three specimens, however, the flowers are typical of *H. dimidiatum*. In a collection from NW. Syria (KOTSCHY, "Prope Aleppum", UPS), some of the ultimate leaflets are linear and

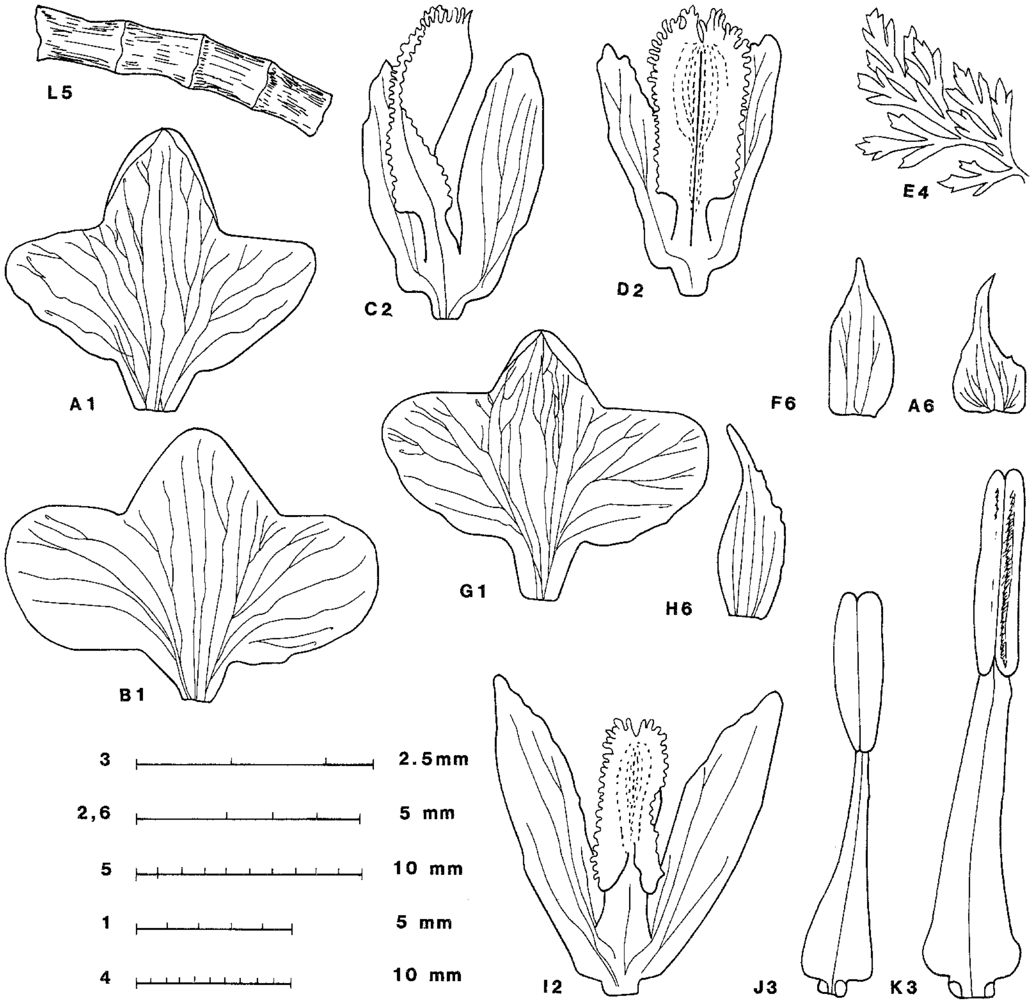

Fig. 30. *Hypecoum dimidatum*, outer petals (1), inner petals (2), median stamen (3), primary leaf segment (4), fruit (5), and sepals (6). *A* Transjordania, Petra, Alonzo (S). *B* In agris v. Aintab, alt. 2000 pd, 15. IV. 1856, Haussknecht (W). *C* Circa Zebdaine prope Damascum, 1855, Kotschy (W). *D* Jerusalem, Atsmon (HUJ). *E* Aleppo, 1841, Kotschy (W). *F* Antilibanon, Ouadi Karn, Wall (S). *G* Syria borealis, Bal Kuz pres de l'Euphrate, Haradijan 1008 (W). *H* Bozani supra Adana, 1917, Christian (W). *I* Jerusalem Botanical Garden, cultivated material. *J* E. Samaria, N. slopes of Sartaba, 10. II. 1977, Berliner (HUJ). *K* Inter segetes sol. calc. Aleppo, 15. III. 1865, Haussknecht (W). *L* Syrien, nr. Jab. Saman, Dinsmore 14460 (S)

extended, reminiscent of those in cultivated material of *H. pseudograndiflorum* from Kavalla and in artificial hybrids of different populations of *H. imberbe* (Fig. 2).

6. ***Hypecoum imberbe*** Sm.

Sibthorpe & Smith, Fl. Gr. Prodr. 1: 107 (1806). – Type: "In insula Cypro", 1787, Sibthorpe (lectotype, designated by Meikle 1956, OXF!).

Syn.: *Hypecoum grandiflorum* Benth. Cat. Pl. Pyr.: 91, (1826). – *Hypecoum procumbens* L. var. *grandiflorum* (Benth.) Cosson, Compl. Fl. Atl. 2: 73

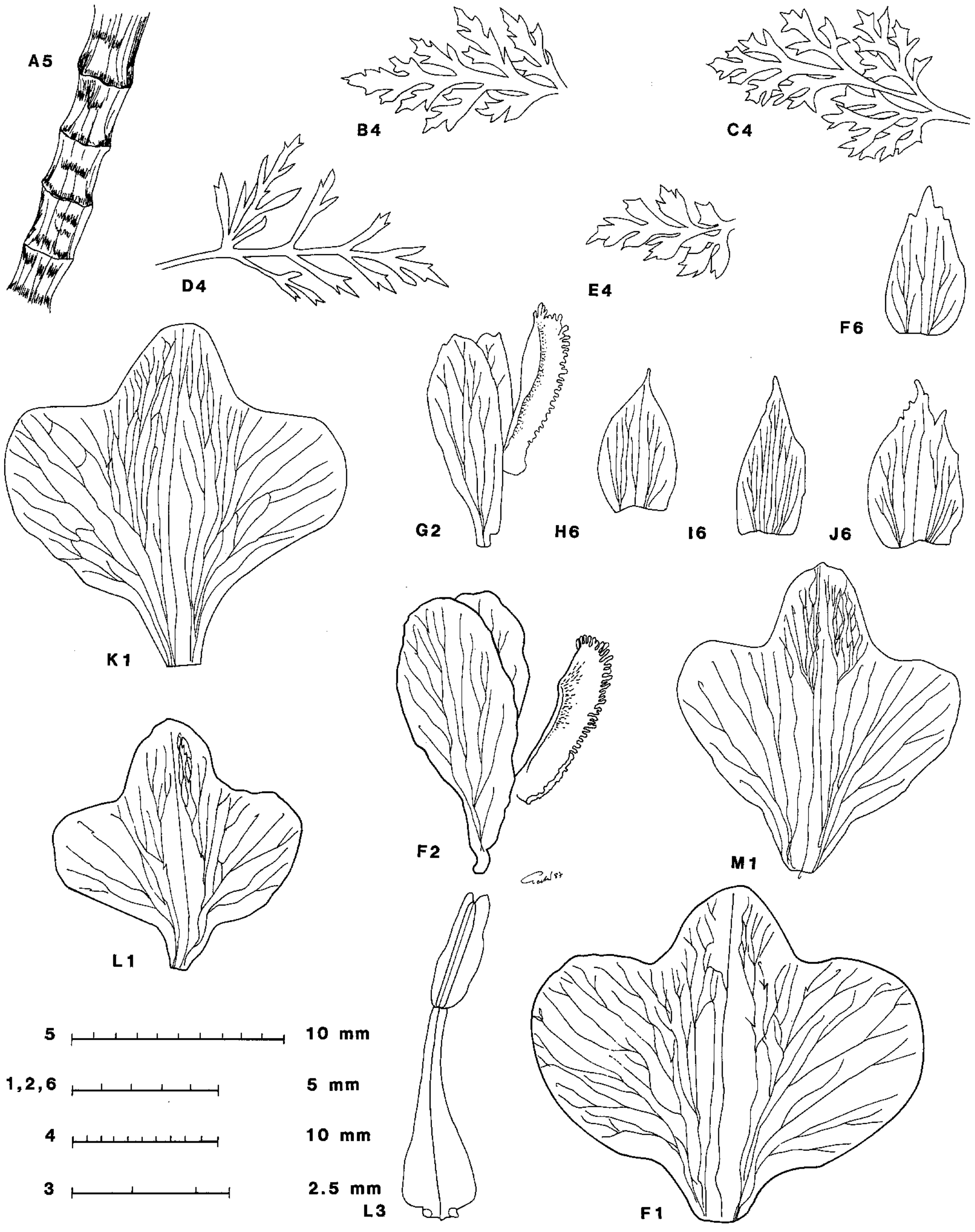

Fig. 31. *Hypecoum imberbe*, outer petals (1), inner petals (2), median stamen (3), primary leaf segments (4), fruit (5), and sepals (6). *A* Espagne, Prov. de Valence, Sierra de la Cueva Santa, VI. 1891 Reverchon (W). *B* Graecia, prope Athenas, inter Eleusis et Skaramanga, 27. V. 1939, Lindberg (H). *C* Le Télagh, 8. IV. 1926, Faure (GB). *D* Cyprus, N. of Famagusta, 20. III. 1973, Hansen (C). *E* Alicante N. of Jijona, Scholz & Hiepko (B). *F* Nom. Viotias, above Arachova, Oxelman & Tollsten 652 (GB). *G* Toscana, Livorno da Marcuni, 1. VI. 1865, Herb. R. Musaei Florentini (FI). *H* Phocis prope Itea, 22. V. 1911, Halácsy (WU, Herb. Halácsy). *I* Prov. de Murcia, Puerto Lumbrenos, III. 1972, Esteñe (GDA). *J* Prov. de Huesca, Campo junto al carrascal al E de la carretera, Sesa, 2. V. 1980, *Montserrat (JACA)*. *K* Argolis, inter segetes prope Tiryns, 17. IV. 1911, Halácsy (WU, Herb. Halácsy). *L* Prope Athenas, Kiphissia, 22. V. 1939, Lindberg (H). *M* Bord de l'agly de Rivesalts, 30. IV. 1882, Gautier (UPS)

(1887) – *Hypecoum procumbens* L. subsp. *grandiflorum* (Benth.) Bonnier & Layens, Tabl. Syn. Pl. Vasc. France: 13 (1894). – Type: "Bas Rousillou, Catalogne" (K). *Hypecoum glaucescens* Guss., Pl. Rar.: 79 (1826), p.p. (see under *H. procumbens* subsp. *procumbens*).

Hypecoum procumbens L. var. *macranthum* Rouy & Fouc. Fl. Fr. 1: 160 (1893). – Type: "Corse à Bonifacio", Kralik, in (LY, Herb. Rouy).

Hypecoum grandiflorum Benth. var. *caesium* Haussknecht, Mittl. Thür. Bot. Ver. 3 – 4: 101 (1893). – Type: In Acropoli Athenarum" (B, lectotype, here designated!, isotype in K!).

Hypecoum aequilobum auct., non Viviani, Fl. Lib. Spec. 7 – 8.

Plant 1 – 40 cm high, green or glaucous. Ultimate leaflets dilated towards the trifid apex, with one to several lateral teeth. Inflorescences erect, with 1 – 18 flowers. Sepals 2.5 – 6 × 1.3 – 3 mm, seldom bifid. Petals orange-yellow. Outer petals 6.7 – 13.6 × 5.2 – 14 mm, distinctly unguiculate, distinctly trilobate, length shorter than, equal to or exceeding width, lateral lobes flat, roundish. Inner petals with black spots, lateral lobes 5.2 – 10.3 × 1.4 – 4.6 mm, obovate with obtuse apex, sometimes exceeding the fimbriate lobe, which is 3.6 – 6.4 × 1.9 – 3.6 mm with truncate base, stalk 0.6 – 1.7 mm long, 10 – 20% of length from the base of the petal to the top of the fimbriate lobe. Filaments of median stamens narrowly triangular; anthers 1.5 – 3.1 mm. Pollen orange-yellow. Fruit usually with thickened septa, 2 – 3.5 mm at the broadest septa. Self-sterile. $2n = 16$.

Distribution: Mediterranean and Submediterranean parts of Algeria (?), Cyprus, France (Co, Ga), Greece (Gr), Italy (It, Si), Portugal, Spain (Bl, Hs), Yugoslavia (Fig. 32).

Habitat: Often on cultivated, fertile soil in olive groves, vineyards, etc. Sometimes on ruderal ground and in pastures.

Flowering period: II – V.

Notes: Like *H. pseudograndiflorum*, this species often occurs in vast populations of several thousand individuals in fields and olive groves. It is not possible to discern any character discontinuities between areas within Europe or to identify the geographic origin of a singular individual. Artificial crosses between Spanish and Greek populations yielded fully fertile and vital hybrids. The Cyprus populations differ

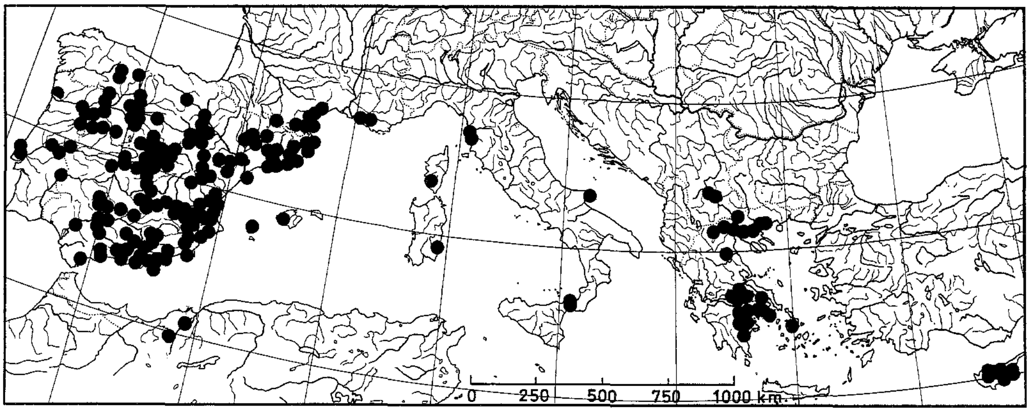

Fig. 32. Known distribution of *Hypecoum imberbe*

from the European in having narrow, almost linear leaflets. Only a few Cypriotic plants were kept in cultivation, and thus only a few artificial crosses with plants from other areas were possible. Hybrids between plants from Athens and from Cyprus were sterile or semi-fertile.

H. imberbe and *H. pseudograndiflorum* occur sympatrically in the environments of Thessaloniki. A few plants with the floral characteristics of *H. imberbe* and leaves like *H. pseudograndiflorum* were recorded in the villages of Exochi and Asvestochoria NE. of the city. In some of these plants, the percentage of stainable pollen was lowered as compared with other *H. imberbe*. It is possible that introgression occurs to some degree, although artificial hybrids usually die as chlorotic seedlings, or have very low fertility when they live as long as to reproductive age.

A couple of herbarium specimens from N. Africa (Algeria, Dep. Oran: Le Télagh, 8. IV. 1926, FAURE, LD, S, GB; Environs de Magenta, 21. IV. 1927, FAURE, B, LD, W) were found to resemble *H. imberbe* in floral characters. The ultimate leaflets deviate, though, in being generally shorter than in European plants, and they are thus more or less cuneiform. The taxonomic position of these plants remains uncertain until more material is available for study.

7. *Hypecoum duriaei* POMEL

POMEL, Nouv. Mat. Fl. Atl.: 246 (1874). – *Hypecoum procumbens* L. subsp. *duriaei* (POMEL) BATT. in BATTANDIER & TRABUT, Flore de l'Algerie 1: 23 (1888). Type: "Oran" (lectotype, here designated, MPU Herb. Pomel!).

Hypecoum albescens BALANSA nom. nud. in sched. Pl. Alger. exs. no. 72 (1851)! – *Hypecoum procumbens* L. var. *albescens* COSSON, Comp. Fl. Atl. 2: 73 (1887). – *Hypecoum procumbens* L. subsp. *duriaei* (POMEL) BATT. var. *albescens* Coss. in MAIRE, Fl. Afr. Nord. 11: 324 (1964).

Hypecoum procumbens L. subsp. *duriaei* (POMEL) BATT. var. *micranthum* MAIRE, Contributions à l'étude de la flore de l'Afrique du Nord 2186, Bull. Soc. Hist. Nat. Afr. Nord 25: 133 (1937). – Type: "Géryville", POMEL (lectotype, here designated, MPU Herb. POMEL!).

Hypecoum albiflorum DUR. nom. nud. in WILLKOMM & LANGE, Prodr. Fl. Hisp. 3: 877 (1880).

Plant 3 – 20 cm high, green or glaucous. A majority of the ultimate leaflets dilated towards the trifid apex, with 0 – 2 lateral teeth. Inflorescences decumbent to erect, with 1 – 8(– 15) flowers. Sepals 2.5 – 5(– 6) × 1 – 2.5 mm. Outer petals white, tinged with purple, 6.6 – 11.6 × 4.8 – 12.4 mm, distinctly, unguiculate, distinctly trilobate, length/width quotient varying, lateral lobes flat, cuneiform. Inner petals with black spots, lateral lobes white, tinged with purple, 3.3 – 9.5 × 0.4 – 2.8 mm, ovate and subacute, not exceeding the fimbriate lobe, which is orange-yellow, 2.8 – 5.3 × 1.4 – 2.6(3.6) mm, obovate, with usually attenuate base, its stalk orange-yellow, 1.6 – 2.6 mm long, > 20% of length from the base of the petal to the tip of the fimbriate lobe. Filaments narrowly triangular; anthers 0.9 – 2.6 mm. Pollen orange-yellow. Fruit with only slightly thickened septa, 2 – 3.5 mm at broadest septa. Self-sterile, at least in the north (see below). $2n = 16$.

Distribution: Algeria (Fig. 34).

Habitat: In mobile sand or in grassy, sandy ground, sometimes in cultivated fields.

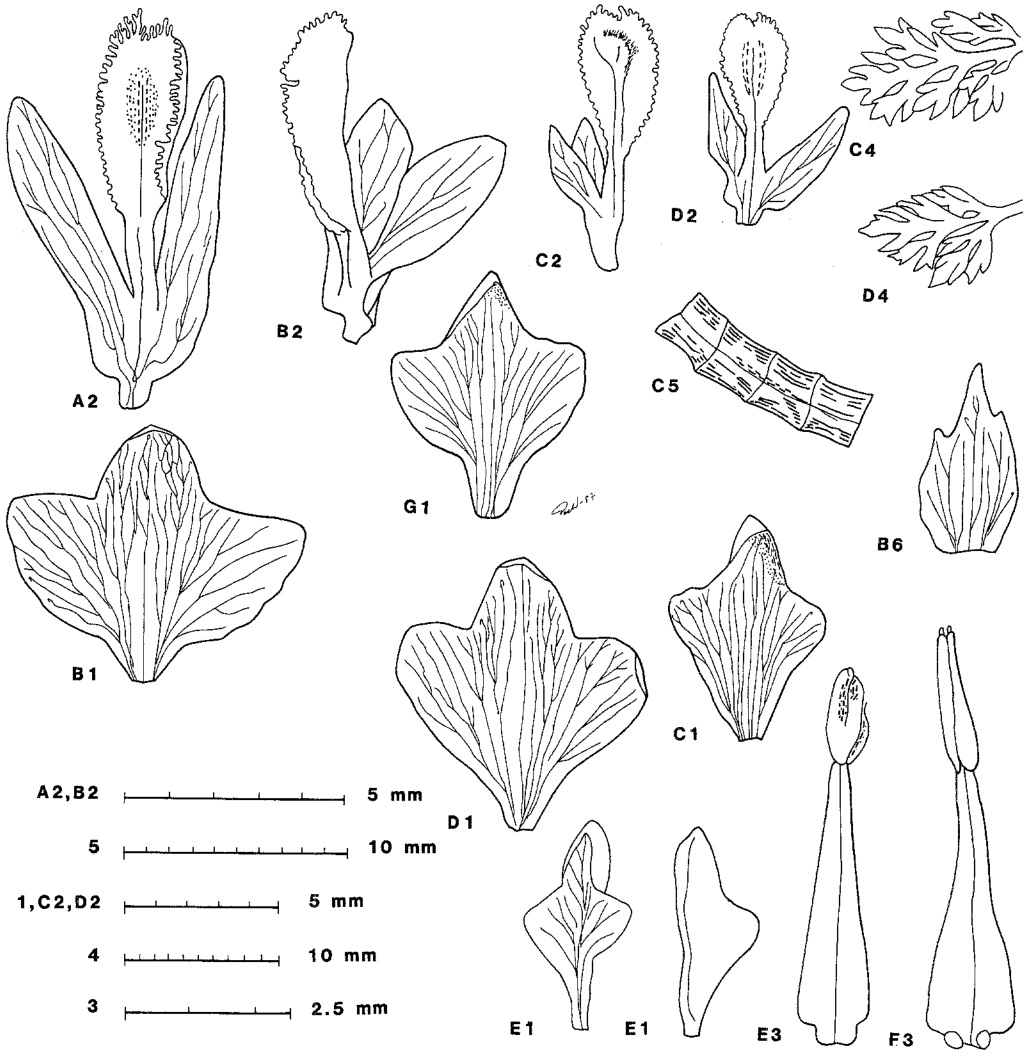

Fig. 33. *Hypecoum duriaei*, outer petals (1), inner petals (2), median stamens (3), primary leaf segments (4), fruit (5) and sepals (6). *A* Le Sig, 22. IV. 1891, DOMERGUE 89. *B* Near mouth of Oued Cheliff, N. of Mostaganem, DAVIS 51751. *C* Sah. Atlas, Djebel Aissa, UGGLA (S). *D* Djebel Aissa, 20. IV. 1936, SAMUELSSON (S). *E* Steppberget Djebel Aissa, N. Ain Sefra, 20. IV. 1936, WALL (S). *F* La Macta, pres de Mostaganem, 20. IV. 1913, FAURE (UPS). *G* Sud Orainais, Ain Sefra, IV. 1934, WEILLER (FI)

Flowering period: (II−)III−V(−VI).

Notes: The situation in *H. duriaei* might be a parallel to that in *H. procumbens*, with one self-sterile and one self-fertile form series, the latter consisting of populations which vary between one another in floral size. Two populations from La Macta in the vicinity of Mostaganem in the Mediterranean zone of Algeria, were kept in cultivation. These were self-sterile. Otherwise only herbarium material was available for this study, and the evidence is thus only circumstantial. A scatter diagram of length and width of outer petals shows clinal variation with increasing size from south to north (Fig. 35). One dot in the diagram represents one specimen, and samples form the three different phytogeographical zones of Algeria, distin-

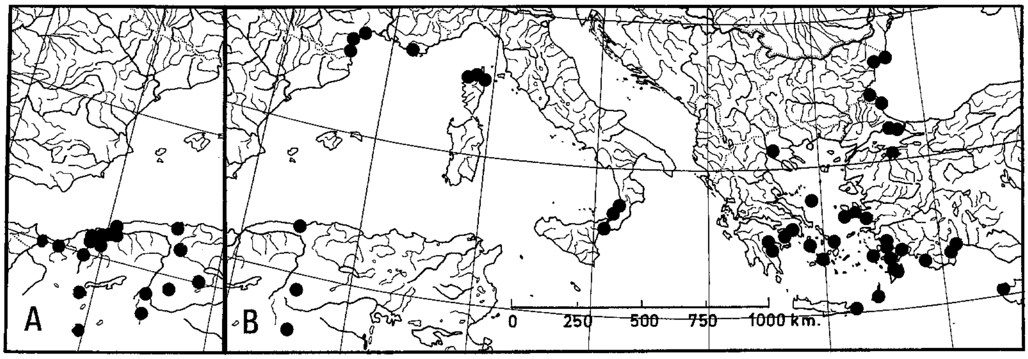

Fig. 34. Known distribution of *Hypecoum duriaei* (*A*) and *H. torulosum* (*B*)

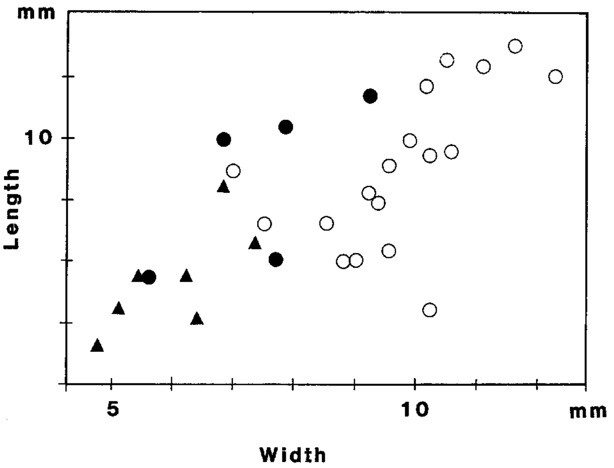

Fig. 35. Clinal variation in length and width of outer petals from south to north in *H. duraiei*. Specimens are indicated with symbols with regard to their origin in the phytogeographical regions of Algeria as described by Cosson (1881). ▲ Saharian region, ● region of Haut-Atlas, ○ Mediterranean region

guished by Cosson (1887), are represented by different symbols. The variation ranges of several characters are comparable to the corresponding ones in *H. procumbens*. In other taxa within sect. *Hypecoum,* only self-fertile populations are known to have as small anthers as the small-flowered *H. duriaei* from the steppic zone of Algeria. Maire (1937) described these as var. *micranthum*. This taxon may be restored as a subspecies in the future, in consequence with the recognition of *H. procumbens* subsp. *fragrantissimum* on the basis of mating system.

8. ***Hypecoum torulosum*** **Å. E. Dahl, spec. nova**

Herba glauca, 5 – 12(16) cm alta. Folia radicalia segmentis ultimis cuneiformibus, apice trifido. Inflorescentiae decumbentes vel erectae, 1 – 7-florae. Sepala 2 – 5 × 1 – 2(– 4) mm, interdum apice bifido vel trifido. Petala citrina; duo externa unguiculata, distincte triloba, 4.4 – 7.9 × (2.2)2.9 – 6.0 mm, longiora quam latiora, lobis lateralibus rotundatis, saepe intus revolutis ita ut videantur rhombea; duo interna maculata, lobis lateralibus 3 – 5.9 × 0.3 – 1.4 mm lobo fimbriato plerumque brevioribus, lobus fimbriatus 1.8 – 3.1 × 1.4 – 2.8 mm basi truncata, stipes eius 0.7 – 1.6 mm longus, 15 – 35% totius longitudinis ad apicem lobi fimbriati a basi petali. Filamenta mediana anguste triangularia; antherae 0.7 – 1.5 mm longae. Pol-

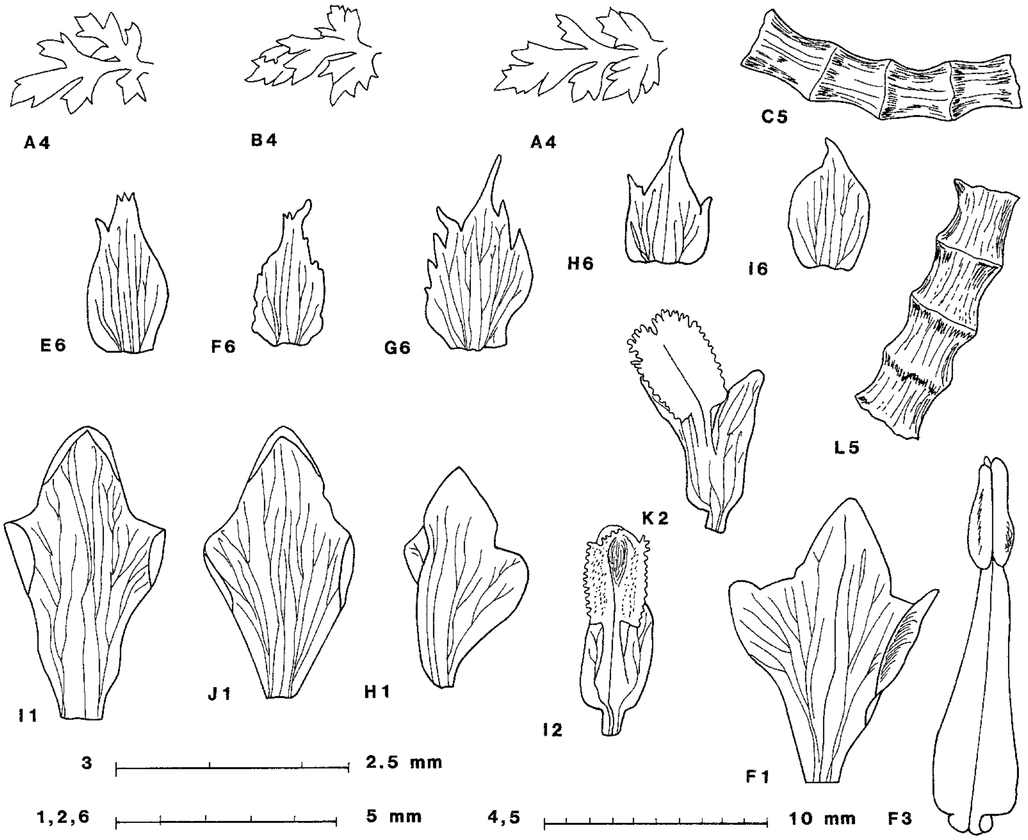

Fig. 36. *Hypecoum torulosum,* outer petals (1), inner petals (2), median stamen (3), primary leaf segments (4), fruits (5), and sepals (6). *A* Attica, 20. IV. 1854, Heldreich (W). *B* Algerie, Ain-Taya, 3. V. 1894, Gay (WU). *C* Antalya, Hennipman & al. (B). *D* Corsica, Saint Florent, Mabille 103. *E S. of Katavia, Rhodos, 30. IV. 1965,* Hansen (C). *F* Sardinia, prov. de Sassaro, Porto Torres, 1843, Terraciano, Fiori & Nannetti (WU). *G* In insula Cythno, 14–15. III. 1901, Tuntas (WU, Herb. Halácsy). *H* Thrakien, Igneada 6. V.–5. VI. 1967, Bauer & Spitzenberger (W). *I* Nauplia, Herb. Zuccarini (M). *J* Rhodos, Charakion, cultivated material Runemark & Wendelbo 41603. *K* Italy, Messina, 1844, Nyman (LD). *L* In arenosis maris Propontidis prope S. Stefano Eu. (Constantinopolis), Wimmer 265 (W)

len aurantiacum. Lomentum septis valde inspissatis, 2–3.5 mm latum (in septis latissimis mensum).

Type: "In arenosis maritimis Phaleri", 12. V. 1891, Heldreich 1108 (W, holotype!; isotypes in B!, K!, LD!, M!, WU Herb. Halácsy!).

Hypecoum glaucescens auct. (Haussknecht 1893, Halácsy 1901, Fedde 1909), non Gussone, Pl. Rar.: 79, t. 15 (1826).

Plant 5–12(–16) cm high, glaucous. Ultimate leaflets cuneifoirm with trifid apex. Inflorescences decumbent to erect with 1–7 flowers. Sepals 2–5 × 1–2(–4) mm, sometimes with a bi- or trifid apex. Petals lemon yellow. Outer petals 4.4–7.9 × (2.2–)2.9–6.0 mm, unguiculate, distinctly trilobate, length always exceeding width, lateral lobes roundish, involute giving the petal a rhombic appearance. Inner petals with black spots, lateral lobes 3–5.9 × 0.3–1.4 mm, linear, subacute, usually not exceeding the fimbriate lobe, which is 1.8 – 3.1 × 1.4 – 2.8 mm, with truncate base, its stalk 0.7 – 1.7 mm long, 15 – 35% of total length from the base of the petal to the tip of the fimbriate lobe. Filaments of median stamens narrowly triangular; anthers 0.7 – 1.5 mm. Pollen orange-yellow. Fruit with strongly thickened septa, 2 – 3.5 mm at broadest septa. Self-fertile. $2n = 16$.

Distribution: Western coast of Black Sea, coastlands of the Mediterranean area. A few inland localities. Algeria, Bulgaria, Cyprus, France (Co, Ga), Italy (It, Si), Greece (AE, Cr, Gr), Romania, Turkey (An, Tu) (Fig. 34).

Habitat: Sand dunes.

Flowering period: III – V.

Notes: The geographical distributions of *H. torulosum* and *H. procumbens* subsp. *procumbens* are similar, and both taxa are self-compatible, but the variation ranges of the floral characters of *H. torulosum* are strikingly narrow as compared to those of the latter taxon. Four cultivated populations of *H. torulosum* from Greece and Turkey were strongly autogamous, and the uniformity of stigma and of anther lengths indicates that there is little variation in outcrossing rates in the entire distribution area of this species, which thus differs in this respect from *H. procumbens* subsp. *procumbens*. The shape of the petals does not vary as much in *H. torulosum* as it does in *H. procumbens* subsp. *procumbens* and in small-flowered *H. duriaei*. Small differences in size are, however, discernible. The flowers of plants from Sicily and Calabria tend to be big, and flowers of plants from the Aegean islands tend to be small as compared with the entire variation range, but the variation is continuous and the ranges overlapping between areas. A herbarium specimen from Ain-Taya in Algeria (WU) differed from others in being unusually big and multiflowered.

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Appendix 1.

A summary of previous treatments of the taxa recognized in the present study.

Author	Year	Mentioned taxa (equivalent taxa recognized in the present study in brackets)	Other taxa present in the area concerned
LINNAEUS	1753	*procumbens* (= ***procumbens*** subsp. ***procumbens***)	***imberbe,*** ***torulosum, duriaei,*** ***pseudograndiflorum*** ***dimidiatum,*** ***procumbens*** subsp. ***fragrantissimum*** and subsp. ***atropunctatum*** ***trullatum,*** ***angustilobum***

Author	Year	Mentioned taxa (equivalent taxa recognized in the present study in brackets)	Other taxa present in the area concerned
Gussone	1826	*procumbens, glaucescens* (includes ***procumbens*** subsp. ***procumbens*** p.p., ***imberbe*** p.p.)	***imberbe,*** ***torulosum***
Bentham	1826	*grandiflorum* (= ***imberbe***)	***procumbens*** ***torulosum***
Clementi	1854	*grandiflorum* (= ***imberbe***) *littorale* auct. (= ***torulosum***)	***procumbens***
Boissier	1867	*procumbens* (includes (= ***procumbens*** subsp. ***procumbens*** ***pseudograndiflorum,*** ***imberbe***) *grandiflorum* (= ***dimidiatum***)	***torulosum*** ***trullatum*** ***angustilobum*** ***procumbens*** subsp. ***atropunctatum*** and subsp. ***fragrantissimum***
Willkomm	1880	*procumbens,* *procumbens* var. *glaucescens* (= ***procumbens*** subsp. ***procumbens***)	
Cossson	1887	*procumbens* var. *procumbens* (includes ***procumbens*** subsp. ***procumbens, dimidiatum, torulosum***) *procumbens* subvar. *glaucescens* (= ***procumbens*** subsp. ***procumbens***) *procumbens* var. *grandiflorum* (= ***imberbe***) *procumbens* var. *albescens* (= ***duriaei***)	
Battandier & Trabut	1888 to 1890	*procumbens* (= ***procumbens*** subsp. ***procumbens***) ***duriaei***	***torulosum*** ***imberbe***
Nyman	1889	*procumbens* (= ***procumbens*** subsp. ***procumbens***) *grandiflorum* (= ***imberbe***)	***torulosum*** ***pseudograndiflorum***
Haussknecht	1893	*grandiflorum* (= ***imberbe***) *grandiflorum* var. *caesium* (= ***imberbe***) *glaucescens* (= ***torulosum***)	***procumbens*** subsp. ***procumbens*** ***pseudograndiflorum***
Halácsy	1901	*procumbens* (= ***procumbens*** subsp. ***procumbens***) *grandiflorum* (= ***imberbe***) *grandiflorum* var. *caesium* (= ***imberbe***) *glaucescens* (= ***torulosum***)	***pseudograndiflorum***

Author	Year	Mentioned taxa (equivalent taxa recognized in the present study in brackets)	Other taxa present in the area concerned
de Rey-Pailhade	1905	*procumbens* var. *genuinum* (= ***procumbens*** subsp. ***procumbens***) *procumbens* var. *macranthum* auct. (= ***procumbens*** subsp. ***procumbens***?, ***pseudograndiflorum***) *procumbens* var. *aequilobum* auct. (= ***imberbe***) *glaucescens* (= ***torulosum***)	
Fedde	1909	*procumbens*, (= ***procumbens*** subsp. ***procumbens***) *grandiflorum* var. *pseudograndiflorum* (= ***procumbens*** subsp. ***procumbens***, ***pseudograndiflorum***) *grandiflorum* (= ***imberbe***, ***procumbens*** subsp. ***atropunctatum***) *procumbens* var. *glaucescens* (= ***torulosum***) *albescens* (= ***duriaei***) ***dimidiatum***	***procumbens*** subsp. ***fragrantissimum*** ***trullatum*** ***angustilobum***
Hayek	1925	*procumbens* (= ***procumbens*** subsp. ***procumbens***) *grandiflorum* var. *pseudoprocumbens* (= ***procumbens*** subsp. ***procumbens***) *ponticum* (= ***procumbens*** subsp. ***procumbens***) *grandiflorum* (= ***imberbe***) *grandiflorum* var. *caesium* (= ***imberbe***) *grandiflorum* var. *pseudograndiflorum* (= ***pseudograndiflorum***)	***torulosum***
Popov	1937	*grandiflorum* (= ***angustilobum***)	
Rechinger	1943	*procumbens* (includes ***procumbens*** subsp. ***procumbens***, subsp. ***fragrantissimum***) *grandiflorum* (= ***imberbe***, ***procumbens*** subsp. ***procumbens***?, subsp. ***atropunctatum***, ***pseudograndiflorum***) *procumbens* f. *glaucescens* (= ***torulosum***)	

Author	Year	Mentioned taxa (equivalent taxa recognized in the present study in brackets)	Other taxa present in the area concerned
QUEZEL & SANTA	1962	*procumbens* subsp. *procumbens* (= ***procumbens*** subsp. ***procumbens***) *procumbens* subsp. *grandiflorum* (= ***imberbe***) *procumbens* subsp. *duriaei* (= ***duriaei***)	
MAIRE	1964	*procumbens* subsp. *euprocumbens* (= ***procumbens*** subsp. ***procumbens***) *procumbens* subsp. *grandiflorum* (= ***imberbe***) *procumbens* f. *glaucescens* (= ***torulosum***) *procumbens* subsp. *duriaei* (= ***duriaei***)	
CULLEN	1965	*procumbens* (includes ***procumbens*** subsp. ***procumbens,*** = ***procumbens*** subsp. ***atropunctatum*** p.p.) *imberbe* (includes ***procumbems*** subsp. ***atropunctatum*** p.p., ***pseudograndiflorum, dimididatum***)	***torulosum*** ***trullatum***
JORDANOV	1970	*procumbens* (includes ***procumbens*** subsp. ***procumbens***) *imberbe* var. *imberbe* (= ***imberbe***) *imberbe* var. *pseudograndiflorum* (= ***pseudograndiflorum***) *ponticum* (probably = ***torulosum***)	
MOWAT & CHATER	1974	*procumbens* (= ***procumbens*** subsp. ***procumbens***) ***imberbe*** *ponticum* (= ***procumbens*** subsp. ***procumbens***)	***pseudograndiflorum*** ***procumbens*** subsp. ***fragrantissimum*** ***torulosum***
MEIKLE	1977	*procumbens* (= ***procumbens*** subsp. ***procumbens***) ***imberbe***	***torulosum***
JAFRI & EL-GADI	1977	*procumbens* (= ***procumbens*** subsp. ***procumbens***) *imberbe* (= ?)	
CULLEN 1980	1980	*imberbe* (= ***dimidiatum***)	

Appendix 2.

Origin of collections determined as to chromosome number. No other records than 2 n = 16 or n = 8 were found. The cultivation number and an indication of whether the haploid or the diploid number was counted are given after the localities. My own collections have the same collection and cultivation number. All collections made by Professor H. Runemark that are cited in this appendix were cultivated and prepared by him, and were made accessible to me by his courtesy. All voucher specimens are at GB unless otherwise stated.

Hypecoum imberbe Sibth. & Sm.: Greece, Kikladhes, Siros, N. of Messania (between Parakopi and Talanda), 15. IV. 1981, Dahl 157 (2 n); Greece, Attica, Athens, Amarussion, 13. IV. 1981, Dahl 150 (2 n); Spain, Granada, Malà, DSBG 5012 Dahl 146 (2 n); Greece, Thessalonikis: Nea Matridis, 24. IV. 1984, Dahl 274 (n); Spain, Almeria, Laujar, DSBG 5055 (149, 2 n); Spain, Granada, Huetor Santillar, 1981, Pascal 168 (2 n); Spain, Granada, Ochichar, 1981, Pascal (167, 2 n); Spain, Zaragoza, Suera, rive droite du Gallégo à 6 km N. du village, env. 350 m., Raynal 15484/7412 (061, 2 n).

Hypecoum procumbens L. subsp. *atropunctatum* Å. E. Dahl: Greece, Khios, Mon. Agios Minà, 3. V. 1982, Dahl 180 (2 n); Greece, Dodecanese, Kalimnos, Metochi, pasture along the road to Vathi, 21. IV. 1982, Dahl 189 (2 n); Greece, Lesvos, Mitilini, outside the Kastro, 4. V. 1982, Dahl 182 (2 n); Greece, Kalimnos, Hansen 81 (080, 2 n).

Hypecoum procumbens L. subsp. *fragrantissimum* Å. E. Dahl: Greece, Kikladhes, Mikonos, pasture at Ormos Korfos, c. 2 km S. of Chora, 19. IV. 1981, Dahl 158 (2 n): Greece, Kikladhes, Mikonos, S. part of Megali Ammos S. of Chora, 28. IV. 1983, Dahl 206 (2 n, n); Greece, Kikladhes, Mikonos. The island of Rinia, the S. part, Runemark, Strid & Gustafsson 39362 (R 5226, 2 n, LD); Greece, Kikladhes, Mikonos. Rinia, the S. part, Runemark & Engstrand no. 36325 (R 5659, 2 n, LD).

Hypecoum procumbens L. subsp. *procumbens*: Greece, Kikladhes, Kea, Ormos Xila 24. IV. 1983, Dahl 234 (n); Greece, Kikladhes, Mikonos, S. of Chora, the road towards Plati Gialos and the airport, 19. IV. 1981, Dahl 160 (2 n); Greece, Kikladhes, Tinos, Pirgos, 28. V. 1968, Hansen (068, 2 n); Greece, Kikladhes, Mikonos, road to Plati Gialos, c. 1 km N. of Plati Gialos, 29. IV. 1983, Dahl 221 (n); Greece, Kikladhes, Mikonos, road to Plati Gialos, c. 1 400 m N. of Vrissi, 29. IV. 1983, Dahl 219 (n); Botanical Gardens of Göteborg 1978 (origin unknown) (015, 2 n); Greece, Crete, Sitia, Vai, 8. IV. 1971, Kaae (204, n); Greece, Kikladhes, Naxos, the sandy shore N. of Mitria, Runemark 3064 (R 869, 2 n, LD). Greece, Kikladhes, Tinos. NW. of Aetofolia, Runemark, Strid & Gustafsson 39952 (R 5227, 2 n, LD). Greece, Kikladhes, Dilos. Rinia, the N. part, Runemark & Engstrand 35997 (R 5658, 2 n, LD).

Hypecoum pseudograndiflorum Petr.: Greece, Kavalas, Kavalla, Odos Tenedou on the road to Kalamitsa, 5. V. 1982, Dahl 183 (2 n, n); Greece, Kavalas, Kavalla, the Kastro, 5. V. 1982, Dahl 184 (2 n); Greece, Xanthis, just W. of Porto Lagos 41°02′ N., 25°06′ E, Oxelman & Tollsten 449; Greece, Evrou, c. 4 km N. of Alexandroupolis on road to Avas, 9. V. 1982, Strand (198, n); Greece, 1 km W. of Neo Karvalli (14 km W. of Kavalla) 11. V. 1982, Strand (200, 2 n); Greece, Thessaloniki, 2 km W. of Stivros (28 km E. of Thessaloniki) 6. V. 1982, Strand (194, n); Greece, Xanthi, Limnis Mitrikoi, NW. part, 8. V. 1982, Strand (197, n).

Hypecoum torulosum Å. E. Dahl: Greece, Kikladhes, Mikonos, Ormos Panormou (Ftelias), 18. IV. 1981, Dahl 162 (2 n); Greece, Dodecanese, Rodhos, Charakion, Runemark & Wendelbo 41603 (009, 2 n).

Appendix 3.

List of specimens used for biometrical studies. The specimens are listed alphabetically according to the name of the collector. The date of the collection day is given when there is no collection number. Herbaria from which each collection has been studied are indicated by the letter codes of Holmgren & al. (1981). The herbaria of Heldreich, Halácsy and Keck in WU are indicated by the codes WU HHe, WU HHy and WU HK, respectively. The figures in brackets refer to the corresponding number of taxon in the text.

Abbas Al-Ani 9443, 9773 (4) K; – 24. IV. 1892, Abd-ur-Rahman-Nadji (6) WU HK; – Adamovic (6) W; V. 1893 (3) LD; V. 1895 (3) W; – Alava (2) E; – 23. II. 1966, Albury (2) K; – 5. IV. 1924, Alonzo (5) S; 13. III. 1934 (5) S; – Andersson, A. 678, 679 (7) LD – 13. IV. 1982, Aparicio, Garcia & Esteñe (6) SEV; – 27. III. 1949, Atsmon (5) HUJ; – 5. & 20. IV. 1873, Autheman (6) LD; – Balansa 72 (7) W; 9. III. 1854 (1 c) C; – Balls 734 a (5) E; 734 (2) E; – Bauer & Spitzenberger 463 (8) W; – 27. III. 1967, 1971, 8. IV. 1971, 12. IV. 1971, 8. V. 1971, 20. IV. 1978, Baytop (1 c); 2. V. 1966, 4. V. 1966, 22. V. 1966, 22. V. 1970, 8. IV. 1971, 9. IV. 1971, 2. VI. 1973, 7. VI. 1974, 16. VI. 1975, 6. IV. 1976, 17. IV. 1976, (3) ISTE; 9. VI. 1971 (5) ISTE; – 16. V. 1953, Berk (1 c) ISTE; 10. II. 1977, Berliner (5) HUJ; – Bickerich (6) W; 11. III. 1897; – Bicknell (1 a) GB, W; V. 1866 (1 a) FI; 23. IV. 1890. (1 a) UPS; 30. III. 1898 (1 a) B, GB, LD, S, UPS, WU; 259 (1 a) GZU, H, M; – 1. V. 1906, Bornmüller (1 c) W; 154 (3) K, LD, W, WU; 3230, 13706 (3) W; 13707 (3) LD; – Borza, Buia & Guttman 1945 (8) C, W; – IV. 1881, Borzi (8) FI, H, LD, S, WU; – 29. III. 1974, Boulos & El Eisawi (5) C; – 1856, Bourgeau (7) W; – IV. 1839 Bové (7) W; – Bozakman & Fitz 877 (3) W; – Burgeff 814, 1122, 1164, 1167, 1173, 1828 (6) M; – 8. IV. 1871, Burnat (1 a) LD; – 9. IV. 1979, Buttler (8) Buttler priv. herb.; 13266 (3) M; 18207 (8) Buttler priv. herb.; – Carlström 3142, 3212, 3855, 3925, 4211, 5634, 6480 (8) LD; – Cesati, Caruel & Savi 498 (6) WU; – Chakrawarti & Rawi 32112 (4) K; – 2. VI. 1971, Charpin (6) G; – III. 1836, Chesney (5) W; – 4. II. 1902, Chevallier (7) GZU, LD, W, WU; – 1917, Christian (5) W; – 22. III. 1888, Clary (7) C; – 17. V. 1965, Coode & Jones (2) E; – V. 1854, Cosson (7) W; – 10. V. 1930, Cyrén (3) GB; – V. 1922, d'Alleizette (7) C 10; – IV. 1873, D.D.S. (6) S; – Dahl 160, 211, 212, 216 – 226, 229 – 232, 234, 251 – 253, 255, 256 (1 a); 158, 206, 209, 210 (1 b); 180 – 182 (1 c); 183, 273, 275 (3); 150, 151, 155, 227, 228, 261 – 264, 267 – 268 (6); 162 (8) GB; – 11. VI. 1968, Danin & Pery (5) HUJ; – Davis 40574 (1 b); 51751 (7) HUJ; – Davis & Hedge 26760 (2) E; 27274 (2) E, K; – de Geer (1 a) UPS; – 3. VI. 18?, Debeaux (Deleun) (6) GB; 14. IV. – 24. V. 1873, Debeaux (6) LD; 5. IV. 1876 (6) WU; 18. IV. 1876 (6) FI; – 10. IV. 1893, Dimitrjevic (6) W; – 1909, Dimonie (6) GB, M, WU; IV. 1909 (6) GB: 24. II. 1913 (5) LD; 10360, 14460 (5) S; – Domerque 22 (7) C, H; – DSBG 4174, 5020 (1 a); 4372, 5012, 5042, 5055 (6) GB; – 1851, Durando (1 a) W; – 25. II. 1897, Dörfler (6) W; 14 (6) LD, W, WU, WU HHe; – 27. IV. 1933, Eig & Zohary (4) HUJ – 15. III. 1972, Esteñe (6) MA; – Fauche 1840 (8) G; – 20. IV. 1913, Faure (7) B, FI, LD, M; 4. VI. 1928 (1 a) W; 8. IV. 1926 (7) GB, LD, S; 9. IV. 1933 (7) FI; 514 (1 a) LD, S, GB; – 27. IV. 1884, Fiori (1 a) GZU; 24. VI. 1899 (1 a) FI; – Fitz & Spitzenberger 2708 (3) W; – II. 1827, Fleischer (1 c) GB, H, K, M, UPS, W, WU; – Foucaud 467 (6) B; – V. 1847, Francaville (6) W; – Frere Sevetien Jules 3455 (6) WU, W, FI, WU HHe; – Friedrichstal (6) W; – Frivaldsky (1 c) W; – Gadron (1 a) UPS; – Garcia, Lugue & Valdes (6) SEV; – Gasparrini (8) W; – 1. V. 1879, Gautier (6) S; V. 1879 (6) UPS; 17. V. 1882 (8) S; – Gay (Magnier) 2386 (7) LD, S, W, WU HHe; 3556 (8) W, WU, WU HHe; – 18. IX. 1918, Georghieff (3) S; – IV. 1883, Gerald (6) LD; – Greuter 3384 (8) G, LD W; – IV. 1851, Grilli, M (6) FI; – V. 1916, Gros (1 a) MA; – V. 1932, Guinea (6) MA; – 24. III. 1883, Guiniares (1 a) COIM; – 20. IV. 1929, Guiol (6) UPS; 1930 (6) UPS; – 3. V. 1970, Gözler (3) ISTE; – 17. IV. 1911, Haláscy (6) WU, WU HHy; 22. V. 1911 (6) WU HHy; – Handel-Mazzetti (2) LD, W; 15. III. 1910 (5) W; – Hansen 006, 589 (6) C; 108 (8) C; – 5. V. 1906, Haradijan (5) W; 43 (5) W; – Hartman (5) S; – 15. VI. 1856, 15. III. 1865, Haussknecht (5) W; 2. IV. 1885, (6) B; – 31. V. 1926, Hayek (6) GB; – IV. 1844, Heldreich (6) H; 1844, IV. 1844 (8) H, FI WU: II. 1846 (3) W; 21 – 22. IV. 1856 (1 b) WU HHe; 5. III. 1901 (1 a) M, WU; 139 (8) WU HHy, HK; 356 (6), UPS, W, WU HHy; – Hennipman 808 (3) B; 28. IV. 1959 (1 c) B; – Herb. Hort. Bot. Pisani (6) FI, S; V.

(6) C; 1848 (6) W; 1861 (6) S; – III, Herb. Zuccharini (8) M; – Herzog 308 (6) M; – IV. 1933, Hirmer (6) M; – Holmboe 370 (6) C, S; – IV. 1861, Huet (1 a) GB, GZU, UPS: 15. III. 1856, Huet du Pavillon (8) G, UPS, W; – 29. III. 1903, Ibanez (6) MAF; – Ilic 890 (3) LD; – V. 1826, Irat (6) C; – 18. III. 1969, Kaae (1 a) C; – 11. V. 1961, Kerck (3) W; – Kompolites (1 a) B; – III. 1881, Korvetten Gefles exp. (1 a) UPS; – Kotschy (5) UPS, W; – 17. III. 1841 (5) H, W; 1. III. 1862 (6) W; 275, 286 (3) W; 1290 (5) W; – L.B.a.F.s.n. (8) W; – Ladero & Molera Mesa VF 7283 (6) GDA; – Lange (1 a) UPS, C, GB; – 17. III. 1973, Laukkonen (6) H; – Lenormand (1 a) UPS; – IV. 1883, Letourneaux (7) C, S, UPS; s.n. (2) UPS; – 10. IV. 1871, Levier (6) WU, GZU, UPS, FI; 14. IV. 1895 (1 a) FI, GZU; 29. III. 1894 (1 a) FI; – II. 1871, Lindahl (1 a) S, UPS; – 23. V. 1939, Lindberg (6) H; 27. V. 1939 (6) H; – I. 1912, Linder (5) UPS; – 27. V. 1980, Luque & al. (6) SEV; – Mabille 103 (1 a, 8) K, W; – Maire & Wilcek 914 (7) B, S; – III. IV. 1898, Mandon (1 a) GB; – Manisadijan (3) S; 1891 (3) M; 29. III. 1891 (3) W; 1893 (3) GB; – 18. IV. 1975, Markova, Ivanova & Cernova (3) W; – Meikle 2102 (8) C, WU; – Merxmüller 8891 (1 a); – Merxmüller & Wiedmann 343/54 (6) M; – 21. V. 1881, Meyra or Neyra? (1 a) LD; – Montserrat JACA 52480 (6) JACA; – III. 1850, Munby (7) C; 53 (7) W; – 15. II. 1903, Muschler (1 c) B; – Müller s.n. (1 a) HW, M; 1827 (1 a) H; IV. 1827 (1 a) H, M, W; – 7. IV. 1977, Möschl & Pittoni (3) GZU; – Naftolsky (5) HUJ; 16. IV. 1929, 20. IV. 1929 (5) HUJ; – 15. IV. 1897, 17. V. 1896, Nemetz (8) GZU, WU; (8) GZU, WU; – Nicotra (6) B; – Noe 263 (1 c) C, W; – 1896, Frühjahr 1897, 22. IV. 1897, Oberhummer (3) M; – 25. III. 1952, Ophir (5) HUJ; – 10/22. IV. 1850, Orphanides (8) B, UPS, W, W, WU HHy; 22. IV. 187? (8) GB, S, LD, K, WU, UPS, C; 18, 26, 32, 51, 130, 375, 376, 449, 450 (3) GB; 451, 453, 456, 652, 660 (6) GB; – 1850, 1868, Pasqual (8) WU; – 22. I. 1900, Patten (6) S; – 24. V. 1891, Pellat (6) GZU, LD, S, UPS; – 10. III. 1950, Pereg (5) HUJ; – 21. V. 1878, Peres-Lara (6) MAF; – IV. 1885, Petrovic (3) LD, S, W, WU HHe; – 2. VI. 1873, Piccone (1 a) S; – V – VI. 1874, V. 1875, Pichler (1 c) UPS; V – VI. 1874 (1 c) W; – V. 1858, Planchon (1 a) C, LD; – 20. III. 1885, Pons (1 a) LD, W, WU, WU HHe; – 20. V. 1885 (1 a) B, M; V., Porta & Rigo (6) GB: 97 (6) B, G, GB, K, LD, M, W, WU; – 1. V. 1865, R. Musaei Florentini (6) FI; – Reboud (7) S; – Rechinger 336 (1 b) LD; 10158 (3) LD, M, S, W; – 27. IV. 1880, Reverchon (1 a) GZU, K, W, WU HHe; 9. IV. 1881 (1 a) W; VI. 1892 (6) G; 625 (6) B, G, LD, S, W; 4464 (1 a) GB, LD, S; – 16. IV. 1823, Ricasoli (1 a) FI; – 22. IV. 1962, Roessler (6) M; – 7. III. 1930, Rogers (2) K; – 29. III. 1980, Romero, Sanchez & Morales (6) GDA; – Runemark 122, 327, 914, 1419, 1551, 2045, 3064, 3414, 3898, 24034, 25137, 37782, 39400, 40584 (1 a); 5077 (6); 28615 (8) LD; – Runemark & Bentzer 24820, 25947, 27406, 28882, 30187 (1 a) LD; – Runemark & Carlström 49381, 49631 (1 c) LD; 49650 (3) LD; – Runemark & Engstrand 35471 (1 b) LD; 36604 (1 a) LD; – Runemark & Persson 24134 (1 a) LD; – Runemark, Strid & Gustafsson 39362 (b); 39952, 40034, 40867, 42473 (1 a) LD; – Runemark & Wendelbo 41603 (8) GB, LD; – 19. VI. 1978, Saint-Lazer (6) G; – 7. IV. 1933, Samuelsson (5) S; 20. IV. 1936 (7); 1742 (5); 6988 (7) S; – 28. V. 1887, de Sardagna (6) WU; – 15. VI. 1868, Savi (6) LD; Savi Billot 912 (5) LD; – 22. VI. 1967, Scholtz & Hiepko (6) B; – Schwarz 367 (1 c) B; – 3. VI. 1907, Sennen (6) FI, G, GZU, H, M, MA, S, UPS, W, WU HHe; – 13. II. 1880, Sintenis (3) LD; 5. IV. 1883 (1 c) LD, S; 17. IV. 1883 (1 c) LD, K; 25. II. 1888 (2) LD; 9. V. 1888 (5) LD; V. 1901 (4) (S); s.n. (2) E; 71 (2) K, LD; 241 (1 c) S; 419 (5) LD; 786 (6) LD; – 4. V. 1865, Skult (L) (1 a) W; – 14. IV. 1925, Smolly (5) HUJ; – Snogerup 32884, 38723 (1 a) LD; – Snogerup & Bentzer 34596 (1 a) LD; – Snogerup & Gustafsson 42418, 42473 (1 a) LD; – Snogerup & von Bothmer 30187, 34469, 34469, 34596, 38590, 38723, 39047, 39111, 39174 (1 a) LD; – Spruner (8) W, M; 1841 (8) W; – 7. V. 1959, Stainton 8464 (3) W; – Strandhede & al. 1235 (1 a) GB; – 30. IV. 1893, Stribrny (3) M; 10. VI. 1893, V. 1894 (3) W; V. 1908 (3) LD; V. 1909 (3) GB, LD; – 5. IV. 1933, Tannerloher & Gattinger (6) WU; – Tengwall 468 (3) S; – Tenore (1 a) B; – 17. III. 1912, Terraciano, Fiori, Nan-

NETTI (8) W; – IV. 1874, THEVENAU (1a) LD; – 27. III. 1882, THOLIN (1a) LD; – VI., THOMAS (6) M; – TINEO (1a) FI; – IV. 1900, TUNTAS (1a) M, WU HHy; 14. – 15. III. 1901 (8) WU HHy; – 1936, UGGLA (7) S; – UROMOFF (3) GB; – IV. 1893, VACCARI (1a) B; – VYHODCEVSKI 441 (8) C, G, S, UPS, W; – 23. IV. 1922, WALL (1a) S; 13. V. 1932, 18. V. 1932, 24. III. 1933, 1. IV. 1933, 15. IV. 1933, 22. IV. 1933, 18. V. 1938 (5) S: 20. IV. 1936 (7) S; – 3. VI. 1898, WARIOU (6) FI; – WEILLER, herb. Gavioli 21811 (7) FI; – WELLSTED (5) G; – WÄNGSJÖ 5083 (6) LD; – 12. V. 1902, ZEDERBAUER (3) W; – 13. V. 1918, ZERNY (6) W; – 12. III. 1950, ZOHARY (5) HUJ; – ZUCCARINI (8) W; – II. 1830, ZUCCHARINI (6) M; – 23. IV. 1981, ÖNUR (3) ISTE; – 22. V. 1978, ÖZHATAY (3) ISTE.

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