A revision of the genus *Anacyclus* L. (Compositae: Anthemideae)

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Synopsis

The Mediterranean genus *Anacyclus* is revised. In all, nine species and three putative hybrids, grouped into two sections, are recognized. The generic status and history of taxonomic treatments of *Anacyclus* are discussed in relation to other genera of the Anthemideae. Phylogenetic relationships and the distribution of species are analysed according to the principles of Hennigian phylogenetic systematics. A key to all species, subspecies, varieties and hybrids is given, each taxon is fully described, complete synonymies are included and the relevant taxonomic characters are discussed in detail. Distribution maps for all taxa and illustrations to the species are given, excluding only *A. latealatus*, a rare endemic from Turkey. One new species and two new subspecies combinations are made, and the existence of three, previously unrecognized, hybrids is elucidated. The account ends with a list of excluded taxa and a taxonomic index.

Introduction

The genus *Anacyclus* belongs to the family Compositae tribe Anthemideae, which is restricted to the Mediterranean region and is particularly well represented in the Maghreb countries. The circumscription of the genus has been slightly reduced from that recognized by Jahandiez & Maire (1934), to eliminate those species which belong to the *Anthemis* assemblage.

The principal taxonomic problems in the genus are due mainly to the fact that not only are several of the species extremely variable and closely related annual weeds with sympatric distributions, but the generic relationships are also not at all well known. This is one of two papers dealing with the systematics and biology of *Anacyclus* (see also Humphries, in press, *a*). The nomenclature and descriptive taxonomy are in need of critical revision, and so this has been attempted in the present paper. In addition to the formal taxonomic treatment there are discussions of morphology, phytogeography and phylogeny, and to present the right context for discussion of generic delimitation an historical account is also given.

Materials and methods

The revision is based partly on my own field studies, collections and cultivated material, which are deposited at the British Museum (Natural History) (BM), and largely on herbarium material. I was able to study five of the nine species in the field, four of which have been cultivated in the greenhouses of Chelsea Physic Garden and used in experimental crossing studies (Humphries, in press, *a*). I have studied material from the following herbaria (*Index Herbariorum* abbreviations as in Holmgren & Keuken (1974): AV, B, BM, BR, C, E, FI, G, JE, K, L, LD, LE, M, MA, MPU, P, RNG, S, W, WU, Z, ZT.

The descriptions are based on both dried and living material, where available, and the variation ranges cited attempt to cover the total variation exhibited by a particular species. Abnormal values have been placed in parentheses either before or after the main range of variation. Flowering periods, chromosome numbers, ecological data, locality lists and distribution maps have been compiled almost entirely from specimens, and data from the literature has been included only when substantiated by authentic material. One new species is recognized, two hybrids are described, and several new combinations are made.

Cross-sections of cypselas were made from my own collections, softened in water, embedded in paraffin and ceresin wax, cut by microtome and stained in safranin combined with light green or Clorazal Black E.

The material examined is not normally listed after each species examined. A complete list of all herbarium specimens seen has been placed in the library of the British Museum (Natural History). Unlocalized material of any origin is omitted, except in the case of types and authentic historical material. Formal citations are given for names and authentic records which extend knowledge of ranges or taxonomy of the taxon in question.

Descriptive terminology

The descriptions and terms used in this work follow those outlined in Featherley (1954) and Stearn (1966). The terminology for outlines and plane shapes adopted is that of the Systematics

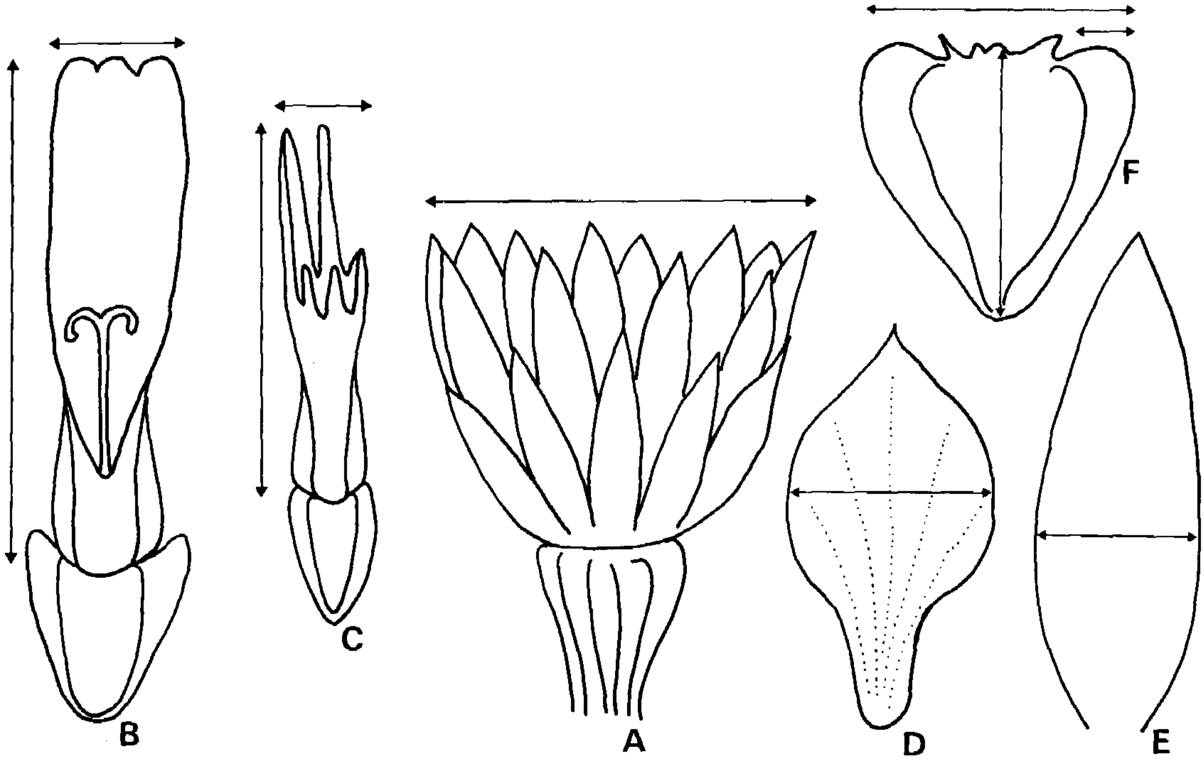

Fig. 1 Capitulum, floret & cypsela measurements: A – involucre, B – ligule, C – disc floret, D – receptacular scale, E – involucral bract, F – cypsela.

Association Committee for Descriptive Biological Terminology (1962). The capitula are usually single and terminal at the end of the peduncle. Sometimes the peduncles are structurally reduced so that the capitula are aggregated into central sessile clusters (a synflorescence) or, on rare occasions, into a single head (a syncephalum). The locations of floret and cypsela measurements are given in Fig. 1. Descriptions of variation in corolla morphology generally follow the scheme used by Jeffrey (1977).

Taxonomic concepts

The taxonomic concepts used in this revision are based on morphology, to some extent from the results of hybridization studies (Humphries, in press, *a*, *b*), distribution data and observations on ecology.

In generic revisions, as Bremer (1976) quite rightly points out, the concept of the genus, and of other categories for that matter, is seldom adequately discussed. Most flowering-plant taxonomists still follow the methods of the Aristotelian essentialist philosophical tradition as practised by Linnaeus and his generations of followers or, by contrast, by the nominalist ideals of Adanson and his contemporary protagonists, the pheneticists, as exemplified by the considerable following botanists have given to the empirical methods of Sokal & Sneath (1963) and Sneath & Sokal (1973). Consequently, in nearly all revisions, particularly in the distinctive families such as the Compositae or Umbelliferae, genera are defined on one or a few *a priori* characters (monothetic groupings) or many uncritically evaluated characters, from which totally artificial, polythetic groupings 'emerge'. This approach is of course unacceptable in phylogenetic studies, since it in no way reflects evolutionary relationships. Generic names, or those of any higher rank, can only really be applied, in phylogenetic classifications, to monophyletic groups. To produce satisfactory monophyletic groups which can be called genera (or tribes, families, etc.) the concept of 'resemblance' must be resolved, so that those features which have undergone transformation (evolution) may be recognized. Then, using only those characters which define monophyletic groups, it is possible to identify 'sister groups', i.e. those groups of species which have demonstrable shared common ancestry (see p. 102 for discussion). In taxonomic terms, taxa of the same age, whether these be large or small groups, should have the same taxonomic rank. To complete such an ideal for the flowering plants is an awesome task, since the greatest percentage of generic names apply to either paraphyletic or polyphyletic groups (see p. 102 for discussion).

Anacyclus, in fact, was originally conceived as a paraphyletic group, but was later to contain polyphyletic elements (see p. 137 for excluded species). The circumscription of *Anacyclus* in this revision has been established according to the principles of Hennig (1965, 1966), details of which are given in the phylogenetic section (p. 102). Consequently, *Anacyclus* is defined on characters unique to those species included within the genus, as assessed by comparison with the sister group *Leucocyclus* and many other species of closely related but less easily definable genera of the northern Hemisphere Anthemideae.

It is believed that this cladistic approach to phylogenetic systematics provides the most suitable biological reference system for handling species relationships. The methods of Hennig (1965, 1966), as practised by many zoologists such as Brundin (1972) and Cracraft (1974), currently provide the most reliable cladistic techniques compatible with the concept of neo-Darwinism and with Darwin's theory of evolution by natural selection (Darwin, 1859). Consequently, it provides a natural classification in the sense that it reveals groups derived by common descent, rather than creates them artificially as is the case with essentialist or nominalist classifications based on general resemblance.

The *species* is a population concept based on a combination of marked discontinuities and, to some extent, crossing behaviour. All species of *Anacyclus* are easily defined and in several cases exhibit vicarious distribution patterns as a result of allopatric speciation. In the widespread annuals, however, vicariant patterns have been obscured as a result of migration into disturbed habitats. The *subspecies* concept has been used mainly in the sense of Du Rietz (1930) to define quantitatively distinctive populations with allopatric patterns of distribution. The term *variety* has been used to define ecological variants or locally deviating populations of a species.

Historical outline

This survey is a chronological account of contributions to the knowledge of *Anacyclus*, giving details of various changing generic and specific taxonomic concepts in the principal works from 1700 up to the present day. The taxonomic history of *Anacyclus* clearly mirrors the changing attitudes and fashions in the subject as marked by the contributions of the significant authors of the systematic tradition. To mark these changes the historical survey of *Anacyclus* is considered in four main phases: (1) from its recognizable inception as a taxonomic entity in 1700 until the publication of Linnaeus's *Species Plantarum* in 1753; (2) the contributions from the time of Linnaeus until the major contributions of perhaps the two greatest synantherologists in the post-Linnean era, Cassini and Lessing in the 1830s; (3) the expansive developments of De Candolle in the same period up to the age of the great compilations of Bentham & Hooker and Engler & Prantl in the latter half of the nineteenth century; (4) the contributions from the post-Darwinian era until the present day.

(1) The first adequate description of an *Anacyclus* species is to be found in Joseph Pitton Tournefort's *Institutiones Rei Herbariae* (1700), where 'Cotula flore luteo nudo' refers to *Chrysanthemum valentinum* in C. de L'Ecluse's *Rariorum Plantarum Historia*: 332 (1610). Tournefort did not invent the name *Anacyclus* but made the Valencian daisy the principal element of his genus *Cotula*. *Cotula* was based on a narrow, but extremely clear concept in the sense that the principal diagnostic features were well indicated. The description of the genus on page 495 in volume 1 of *Institutiones Rei Herbariae* is clearly illustrated in fig. 282 of volume 3 of the same work (Tournefort, 1700). On the evidence of this illustration and, particularly, the note on yellow ligules, the winged compressed obconical cypselas of the rays and the diminutive fruits of the central disc florets, there seems to be little doubt that the generic description and the first two phrase names of the four included species equate with the species currently called *Anacyclus radiatus* Lois. Despite such clarity, subsequent authors, as pointed out by Cassini (1825), completely ignored Tournefort's original concept of *Cotula* by not using the yellow-liguled Valencian

daisy as the principal component of the genus. Vaillant (1719), for example, changed the concept of *Cotula* entirely by applying the generic name almost exclusively to the widespread South African species, now known as *Cotula turbinata* L.: 'Cotula flore albo. Cotula africa, calyce eleganti caesio'. He included other related taxa, such as the weedy *C. coronopifolia* L., in yet another genus, *Ananthocyclus* (1719 : 289); but he correctly considered that the Valencian daisy 'Cotula flore luteo radiato' was not congeneric with *Cotula* and created a new genus *Santolinoides* to accommodate the misplaced species (1719 : 312). Like so many of the eighteenth-century genera, *Santolinoides* was an heterogeneous assemblage consisting of four distinct species, which are currently assigned to diverse genera, including *Anthemis*, *Cotula* and *Anacyclus*.

Linnaeus, in his *Hortus Cliffortianus* (1737) and *Species Plantarum* (1753), augmented Vaillant's modifications by uniting his two genera *Cotula* and *Ananthocyclus* into a wider concept of *Cotula*; in creating a new genus *Anacyclus*, he produced something akin to Vaillant's *Santolinoides* and Tournefort's original *Cotula*.

Linnaeus's definitions of *Anacyclus* were the same in both the first and fifth editions of *Genera Plantarum* (1737, 1754) and seemed to rely on Tournefort's corolla and cypsela characters as diagnostic features:

'. . . Cor. *Composita* radiata: *Corollulae Hermaphroditae* numerosae, in disco. *Femininae* quinque ad decem, in ambitu, disco vix altiores. *Propria Hermaphroditi* infundibuliformes: *limbo* quinquefido, patulo. *Feminea* ligulato: *tubo* compresso: *limbo* ovato, integro . . .Sem *Hermaphroditis* solitaria, oblonga, . . . ala latissima utrinque membranacea, apice emarginata. . . .' This description served admirably to distinguish *Anacyclus* from other members of the 'Syngenesia polygamia superflua' such as *Anthemis:* ' . . . Cor. *Composita* radiata: *corollulae Hermaphroditae* tubulosae, numerosae, in disco convexo. *Femininae* ligulatae, in radio. *Propria Hermaphroditi* infundibuliformis; *limbo* quinquedentato, erecto. *Feminae* ligulata, lanceolata, interdum tridentata . . . Sem. *Hermaphroditis* solitaria, oblonga, nuda. *Feminis* simillima hermaphroditis . . .'. Despite these precise differences Linnaeus apparently used some other character(s) in his *Species Plantarum* (1753) to diagnose the species, since a number appear to be misplaced. Thus, it is rather surprising that of the three species included in *Anacyclus*, two, *A. creticus* L. and *A. orientalis*, in fact belong to *Anthemis* on the basis of the generic descriptions given in *Genera Plantarum*; currently they are recognized as *Anthemis rigida* Sibth. & Sm. and *Anthemis orientalis* (L.) Degen respectively (Fernandes, 1976). On the same grounds two of the species placed in *Anthemis* would have been better placed in *Anacyclus*. Thus, on the basis of cypsela shape, *Anthemis pyrethrum* L. and *A. valentina* L. have a similar fruit morphology to the only other member of *Anacyclus*, *A. valentinus* L. Linnaeus understates the similarity between the two Valencian taxa when, after the description of *Anthemis valentina*, there is a note 'Affinis admodum Anacyclo valentino', the latter taxon differing only by its fewer, shorter ligules (see p. 131). Even a casual observation of the specimens available to Linnaeus shows that the only character which separated *Anacyclus* and *Anthemis* was the presence or apparent absence of ligules. This is a good example, in fact, of how the generic criteria defined in *Genera Plantarum* ed. 5 are not necessarily the same as those used in *Species Plantarum*, even though the generic epithets are the same.

(2) At the turn of the nineteenth century the major surveys of the Anthemidae which appeared in the works of Willdenow (1803) and Persoon (1807) maintained the useful generic criteria outlined by Linnaeus in his *Genera Plantarum* but still followed the designations as given in *Species Plantarum*.

Willdenow, in his *Species Plantarum* (1803 : 2171), stressed the diagnostic features at the beginning of his account: '*Recept.* paleaceum. *Pappus* emarginatus. *Sem.* lateribus membranaceus', but had devised an illogical arrangement where four species with compressed lateral winged cypselas were included in *Anthemis*. In addition to *Anthemis pyrethrum* and *A. valentina* two newly described species, *A. clavatus* and *A. tomentosa*, were included, but these are now considered to be conspecific. *Anacyclus alexandrinus* (=*Tanacetum monanthos* L.), the Egyptian and Libyan desert annual, was also described as new, and two eastern Mediterranean annuals, *A. orientalis* and *A. creticus*, were maintained in his concept of *Anacyclus*.

It was not until Brotero (*Fl. Lusit.* 1 : 239 (1804)), in a footnote to his analytical key to genera, alluded to the fact that certain taxa were artifically separated into *Anthemis* and *Anacyclus* that the idea of re-examining the generic limits within this group emerged. He questioned the division based on the presence or absence of ray florets: 'Genus bifrons; nam accedente radio *Anthemis* est, sicut *Anthemis*, radio deficiente, *Anacyclus;* unde *Anacyclus-Valentinus*, *Anthemis-Valentina*, *Anacyclus aureus*, *Anthemis-aurea*'; but in the actual species descriptions he did a rather illogical thing: *Anacyclus* was considered to be a monotypic genus based on *A. aureus*, and the remaining taxa were placed in *Anthemis*. The use of the name *Anacyclus aureus* L. (*Mantissa* **2** : 287) appears to be based on a misidentification on Brotero's part, as De Candolle pointed out (*Flore Française* **5** : 480 (1815)), since he meant this species to be conspecific with *Anacyclus valentinus* L. Indeed, today it is known as *Chamomilla aurea* (Loefl.) Gay ex Cosson & Kralik.

Persoon (*Syn. Pl.* : 464 (1807)), adhering to the concise style typical of his diagnostic conspectus, distinguished between *Anthemis* and *Anacyclus* very precisely, in that the former genus has tetragonous or cylindrical cypselas without 'borders', whereas the fruits of the true species of *Anacyclus* are invested by a lateral membrane. This division is based on only some of the characters which define *Anacyclus* and so, although it reassociated some of the misplaced *Anacyclus* species, it had the curious effect of excluding the perennial species *Anthemis pyrethrum* and retaining the two Mediterranean species *Anacyclus creticus* and *A. orientalis*. De Candolle (1815) followed Persoon in his use of the winged fruit as the primary diagnostic feature for the genus, but is more consistent in its application. Consequently, *Anacyclus* was taken to comprise the five species *A. valentinus*, *A. radiatus*, *A. purpurascens*, *A. tomentosus* and *A. clavatus*. De Candolle remarked that 'Ces cinq plantes ne forment peut-être qu'une seule espèce. Comme je n'ose cependant l'affirmer absolument, je vaisindiquer ici un peu de mots les caractères, peut-être artificiels, par lesquels on les distingue'. He noted also that *A. purpurascens* differed from *A. radiatus* only in the red stripe of the ligule and that *A. valentinus* was a short-liguled form of the same. Indeed, *A. radiatus* and *A. purpurascens* are synonymous, as also are *A. clavatus* and *A. tomentosus*. As is demonstrated below (p. 131), European plants named *A. valentinus* L. are considered to be possible hybrids between *A. homogamos* and *A. radiatus*.

(3) The activities of the previous period and the start of the new period were punctuated by the contributions of Cassini (1825). When Cassini critically reviewed the existing literature of the Anthemideae, he offered two suggestions to improve the definition of *Anacyclus*: 'Le vrai genre *Anacyclus* tel que nous le concevons, diffère du vrai genre *Anthemis* par deux caractères principaux; 1° les ovaires obcomprimés et munis d'une large bordure sur les deux arêtes laterales; 2° les corolles du disque portant une longue corne calleuse, tres remarquable, sur leur divisions intérieures'. The main consequences when using these characters were to (i) transfer the Maghreb perennial *Anacyclus pyrethrum* from *Anthemis* (as foreshadowed by Link three years earlier (*Enum. Hort. Berol.* **2** : 344 (1822)), (ii) redescribe the genus, (iii) designate *Anthemis valentina* L. as the type of the genus, (iv) suggest a division of the genus into two sections: 'dont la première seroit caracterisée par les ovaires de la couronne aigrettes et articules avec la corolle, la seconde par les ovaires de la couronne inaigrettes et continus avec la corolle', (v) re-assign the misplaced *Anacyclus cretica* to a new genus, called *Lyonettia* Cass., as *L. pusilla* Cass. It is not clear whether Cassini considered *Anacyclus valentinus* L. and *Anthemis valentina* L. to be conspecific, but Loiseleur Deslongchamps (*Fl. Gallica* : 582 (1807)) clarified the issue when he transferred the latter species to *Anacyclus* and correctly gave it a new name, *Anacyclus radiatus* Lois.

Two major contributions providing synthetic classifications for genera of the Compositae, and the Anthemideae in particular, are found in the works of Lessing and De Candolle. This particular period was characterized by an attempt to give greater consistency to taxonomic groups and thus is marked by a wealth of new names and unusual delimitations. Lessing (1831, 1832) presented one of the more extreme views, for example, when he considered the members of the Anthemideae to belong to a much larger tribe, the Senecionideae. Species of *Anacyclus* were dispersed into two subtribes, VI Chrysanthemeae and VII Artemisieae. He divided the Chrysanthemeae still further into two groups, the Chrysanthemineae and the Anthemideae, on the basis of the absence or presence of scales (see Humphries, 1976*a*). Within group I Anthemideae, with receptacular scales, species of *Anacyclus* were dispersed into two genera. The perennial species, following Linnaeus' classification, was maintained as *Anthemis pyrethrum*, alongside *A. cota* L. and *A. tinctoria* L.; *Anacyclus* was taken to comprise two species only, *A. officinarum* Hayne and *A. radiatus* Lois.

The latter taxon was considered to be conspecific with *A. clavatus* Pers. Other known taxa were included in the subtribe VII Artemiseae group 1 Santolineae through the common possession of the following characters 'Capitulis multifloris; corollis staminigeris tubum plano-obcompressum et bialatum stylumque 2 – fidum gerentibus aut teretibus, si achaenium aut cor. ♀ tubulosa piano obcompressa et bialata est; rhachide bracteolata'. Necker's genus *Hiorthia* was maintained and taken to comprise *H. valentinum* (= *Anacyclus valentinus* L.), *H. aureus* (= *Anacyclus aureus* L.), *H. orientalis* (= *A. orientalis*) and *H. alexandrinus* (= *A. alexandrinus* Willd.). The most puzzling innovation was the description of a new monotypic genus *Cyrtolepis* (*Linnaea* **6** : 166 (1831); *Syn. Comp.*: 258–259 (1832)) for *C. monanthos* (L.) Less., based on *Santolina terrestris* Forsk. (= *Tanacetum monanthos* L.), a taxon clearly conspecific with *Anacyclus* (*Hiorthia*) *alexandrinus*.

De Candolle (*Prodr.* **6** : 14–18 (1838)) was considerably influenced by the work of Persoon, Cassini and Lessing when he reclassified the Anthemideae. His main contribution was to use any features which formed natural groups. The homogamous, discoid members having affinities with *Anthemis* were placed in Cassini's genus *Lyonettia* particularly to accommodate the anomalous, dwarf, eastern Mediterranean annual *Anacyclus cretica* L., then considered to be two separate species *L. pusilla* Cass. and *L. rigida* DC. Following Cassini's original suggestion, *Anacyclus* itself was divided into three sections, the first two based on the disc corolla-lobe callosities. Section 1. *Pyrethraria* DC. accommodated the perennial *Anacyclus pyrethrum* and section 2. *Diorthodon* DC. included most of the annual species: *A. pulcher* Besser ex DC. (= *A. officinarum* Hayne), *A. tomentosus* (L.) DC. and *A. clavatus* (Desf.) Pers., *A. pedunculatus* (Desf.) Pers., *A radiatus* Loisel. and *A. valentinus* L. The third section, *Hiorthia* (Necker) DC., was simply a new rank for Necker's genus to accommodate the poorly understood *A. orientalis* L. (*H. orientalis* (L.) Necker), now considered to be a discoid member of the *Anthemis montana* complex (Fernandes, 1975*a*). De Candolle removed Lessing's anomaly by uniting *Tanacetum monanthos* L. and *Anthemis alexandrina* Willd. and called it *Cyrtolepis alexandrina* (Willd.) DC.

(4) The period after De Candolle was mainly an exploration phase in which the acquisition of new material, particularly through French, English, Italian and Swedish expeditions to the Maghreb countries and the eastern Mediterranean, resulted in a wealth of notes, minor records and several descriptions of new species. At least eleven new species and many infraspecific taxa were described, particularly by Ball, Maire, Litardière, Murbeck, Boissier and Reuter, the most recent new species being *A. latealatus* Huber-Morath.

By the turn of the twentieth century *Anacyclus* had become an unnatural group, in an evolutionary sense best described as a polyphyletic genus, containing elements of the genus *Anthemis* (section *Hiorthia*, *Arthrolepis* Boiss.) and the *Achillea* assemblage (*Cyrtolepis*, *Leucocyclus* Boiss.), as in the treatment of Bentham (Bentham & Hooker, *Gen. Pl.* **2** (**1**) : 419 (1873)) and Hoffman (in Engler & Prantl, *Pflanzenfam.* (**4**) **5** : 272 (1894)). As a result of these typo-morphological classifications it has usually been reckoned that the closest affinities of *Anacyclus* are with *Anthemis*, itself a polyphyletic taxon. It is now reasonable to hypothesize that the affinities of *Anacyclus cretica* L. and *A. orientalis* L. are with *Anthemis* (Grierson & Yavin, 1975). Most people would agree that *Achillea* is a very distinct genus clearly separable from the *Anacyclus* group, but Litardière & Maire (1924) blurred the distinction when they named a new and unusual alpine species from the Atlas mountains as *Anacyclus atlanticus*. More recently, Humphries (1977) clarified the status of this species, and Grierson (1975*b*) succinctly compared and contrasted *Anacyclus* with its sister genus *Leucocyclus*. This paper now presents a complete revision of *Anacyclus* and gives an analysis of its phylogenetic relationships.

Delimitation and systematic position

The two genera *Anacyclus* and *Leucocyclus* are distinguished from related genera by their large anterior-dorsally compressed fruits with lateral wings and continuously thickened pericarp walls (Figs. 4, 5). There is little doubt that the type of fruit compression present in a number of different groups of the Compositae–Anthemideae has evolved several times (i.e. in various S. African genera and the southern hemisphere Cotuleae), but since there is no evidence that *Anacyclus* is unnatural in its present circumscription, this observation must, for the time being, be considered a uniquely derived condition and serve to unite the two genera. The monotypic *Leucocyclus formosus* is a herbaceous endemic perennial from Turkey which resembles *Anacyclus* in most respects except that the leaves are almost vermiform, with the small segments suboppositely connected to the rhachis and divided into spinulose-dentate lobes. These genera have approximately vicarious distributions: *Anacyclus* occupies the southern, western and south-eastern Mediterranean areas, particularly in the mountains and the dry, disturbed lowlands, while *Leucocyclus* grows in the lowland montane areas in south central Turkey (Grierson, 1975*b*).

The tribe Anthemideae is usually divided into two subtribes; Anthemidinae Dumort. and Chrysantheminae Less. The Anthemidinae normally have chaff-like, scarious receptacular scales invariably subtending the ovary and, to some degree, the floret as well. The Chrysantheminae by contrast lack scales. Since this division is clearly artificial (Humphries, 1976*a*), it is inappropriate to become involved here in a detailed discussion of the subtribal classification of the Anthemideae, as all taxa allied to *Anacyclus* have receptacular scales and do not have any close allies without scales. It is therefore more appropriate to discuss the genera with which *Anacyclus* has been allied from one time to another and consider its relationships on more recent evidence.

As described in the historical section, species of *Anacyclus* have tended to be confused with taxa of the *Anthemis* assemblage rather than with any other group. Recently, Grierson (1975*a*) has suggested that *Anacyclus valentinus* L. (incl. *A. homogamos*), *A. pyrethrum* and *A. monanthos* are similar to the species of *Anthemis* section *Cota* in having a subterminal corolla. Also, the persistent tubular part of the ray floret corolla on the ripe cypselas of *Anthemis arenicola* Boiss. and *A. davisii* Yavin, a rare feature in *Anthemis*, are also found in the radiate taxa of *Anacyclus*. These trivial convergences or parallelisms are of little consequence in the formulation of phylogenetic hypotheses. Detailed studies of the fruits in genera of the Anthemideae also reveal a number of parallel morphological trends which tend to obscure the genealogical relationships in the group. As pointed out by Humphries (1977), such features include the slightly compressed cypselas of *Anthemis* section *Cota*, which differ during their development in having 7–22 ribs in the pericarp wall (Wagenitz, 1968; Kynčlova, 1970; Reitbrecht, 1974) and 5 vascular bundles (Humphries & Innes, unpublished), rather than 7–22 bundles as was wrongly assumed by the above authors.

Examination of fruit and corolla characters on a wider scale demonstrate that no case exists for making *Anthemis*, itself a polyphyletic assemblage, the sister group of *Anacyclus*. An alternative hypothesis originates from the phytochemical work of Greger (1977, 1978), where he suggests that *Anacyclus* has a cyanogenic glycoside and flavonoid phytochemical profile more closely related to *Achillea* and its allies than to species of *Anthemis*. Genera of the *Achillea* group regularly have tiny cypselas with distinct lateral ribs rather than wings, as well as unusually thin pericarp walls. It is tempting to offer a hypothesis that a group comprising *Anacyclus*, *Leucocyclus*, *Heliocauta* Humphries, *Sclerorhachis* Rech. fil. and *Achillea* L. may be recognized, as these genera all have a reduced vascular system with two lateral vascular bundles in the pericarp wall (Fig. 6), but studies on this aspect are in a preliminary state.

It is fairly clear that difficulties in forming evolutionary hypotheses of relationship at the generic level and above will persist until such a time as monophyletic groups are identified. The only recent attempts at forming natural generic groupings can be found in the work of Reitbrecht (1974; see also Heywood & Humphries, 1977), who considers that the Anthemideae consists of seven provisional groups. His 'Matricaria-gruppe' is taken to comprise *Anthemis*, *Anacyclus*, *Chamaemelum* Miller, *Cladanthus* Cass., *Matricaria* L., *Tripleurospermum* Schultz Bip., *Otospermum* Willk. and *Daveaua* Willk. ex Mariz. There seems to be no improvement in the above classification over the former groupings of Bentham (1873) and Hoffman (1894) since it is a paraphyletic assemblage without any definite character states which adequately link the genera. Such genera as *Achillea* are excluded, as they are considered to have affinities with the wind-pollinated structurally reduced members of the *Artemisia* group, as also are the southern hemisphere *Sphaeroclinium* and its allies, which Mitsuoka & Ehrendorfer (1972) have managed to hybridize with northern hemisphere members of *Matricaria*. Nevertheless, it seems probable that once all the component members can be identified, a combination of the main elements of Reitbrecht's '*Matricaria*-gruppe' with the '*Achillea*-gruppe' will form a natural monophyletic group in the Anthemideae.

Morphology

This section provides a comparative review of the principal morphological features in *Anacyclus*, which are described formally in the taxonomic descriptions. An attempt will be made to emphasize the evolutionary trends so that an understanding of primitive and advanced character states will provide a detailed basis for the phylogenetic reconstruction (p. 105).

Habit

Most species of *Anacyclus* are annuals, a condition found in several of the north temperate genera of the Anthemideae (Heywood & Humphries, 1977). Phylogenetic analysis suggests that this is a derived condition as an adaptation for survival in dry, disturbed habitats. Several species, e.g., *A. nigellifolius*, *A. latealatus*, *A. maroccanus* and *A. linearilobus*, have restricted distributions, but the remainder have relatively wide-ranging distributions in weedy habitats. In natural sandy areas of the desert, the most extreme developments of prostrate annuals with reduced stems and leaves are seen in *A. monanthos* and to some extent in *A. homogamos*. In dry roadside or waddy habitats the vigorous, tough and leafy stems of *A. radiatus* and *A. clavatus* are among the largest growth forms to be encountered in the genus. *A. nigellifolius*, from dry rocky places in the eastern Mediterranean, represents another reduced annual habit with short erect stems (few or no branches emerging from the middle or above the centre of the main stem) and deeply dissected, small leaves.

Many species of the Anthemideae are woody or herbaceous perennials. *A. pyrethrum*, the only perennial species in *Anacyclus*, is a highly specialized montane and subalpine herbaceous perennial from open grassland and rocky places in the mountains of Morocco, Algeria and Spain. It is short-lived, with a dwarfed submerged stem fused with a long taproot to form a basal woody caudex, from which leaves and then flower-bearing peduncles emerge annually. Cross-sections of the caudex from the field suggest that most plants live for two or three or sometimes up to five years, although cultivated specimens can survive for a considerably longer period.

The leaves and peduncles emerge as a prostrate rosette from the centre of the caudex during the spring and persist until the end of the summer. The submerged caudex seems to be an adaptation to the dense snow cover and severe winters of the Atlas mountains.

Leaves

In most species the leaves are arranged alternately on the stem. However, in one or two species, e.g. *Anacyclus pyrethrum*, the leaves are so tightly whorled in a basal rosette that this arrangement is obscured (Fig. 12). Some evidence of leaf rosettes can also be seen in annuals, e.g. *A. radiatus* subsp. *radiatus* (Fig. 17) where the basal internodes are very short. *A. pyrethrum* (Figs 2 A, 12) appears to have heteromorphic leaves, because there are only massive tripinnatisect basal rosette leaves and pedunculate bracts present. A general gradation in leaf size and dissection is absent because of the reduced habit in this species.

The leaves of *Anacyclus* are invariably pinnatisect, whereby the primary divisions cut right through to the axis. The leaves range in dissection from 1- to 3-pinnatisect, depending on their position on the plant, e.g. main axis or peduncles, and, to a lesser degree, the differences between species, e.g. the small, 1- to 2-pinnatisect leaves of *A. nigellifolius* (Figs 2 J, 26). The leaves are usually differentiated into lamina and petiole, although the latter is often absent or reduced. The most distinctive petioles are the persistent cuneate types found on the rosette leaves of *A. pyrethrum* (Figs 2 A, 14) and *A. monanthos* subsp. *monanthos* (Fig. 2 B). The lamina is usually more or less flat, but is distinctly terete in the leaves of *A. pyrethrum* (Figs 2 A, 12). There is a considerable variation in leaf size, the largest leaves being found in the robust annuals *A. radiatus* subsp. *radiatus*, *A.* × *valentinus* (Fig. 2 G) and *A. linearilobus* (Fig. 2 I) and the smallest in the

Fig. 2 Leaf silhouettes: A – *A. pyrethrum*, B – *A. monanthos* subsp. *monanthos*, C – *A. maroccanus*, D – *A. radiatus* subsp. *radiatus*, E – *radiatus* subsp. *coronatus*, F – *A. clavatus*, G – *A.* × *valentinus*, H – *A. homogamos*, I – *A. linearilobus*, J – *A. nigellifolius*.

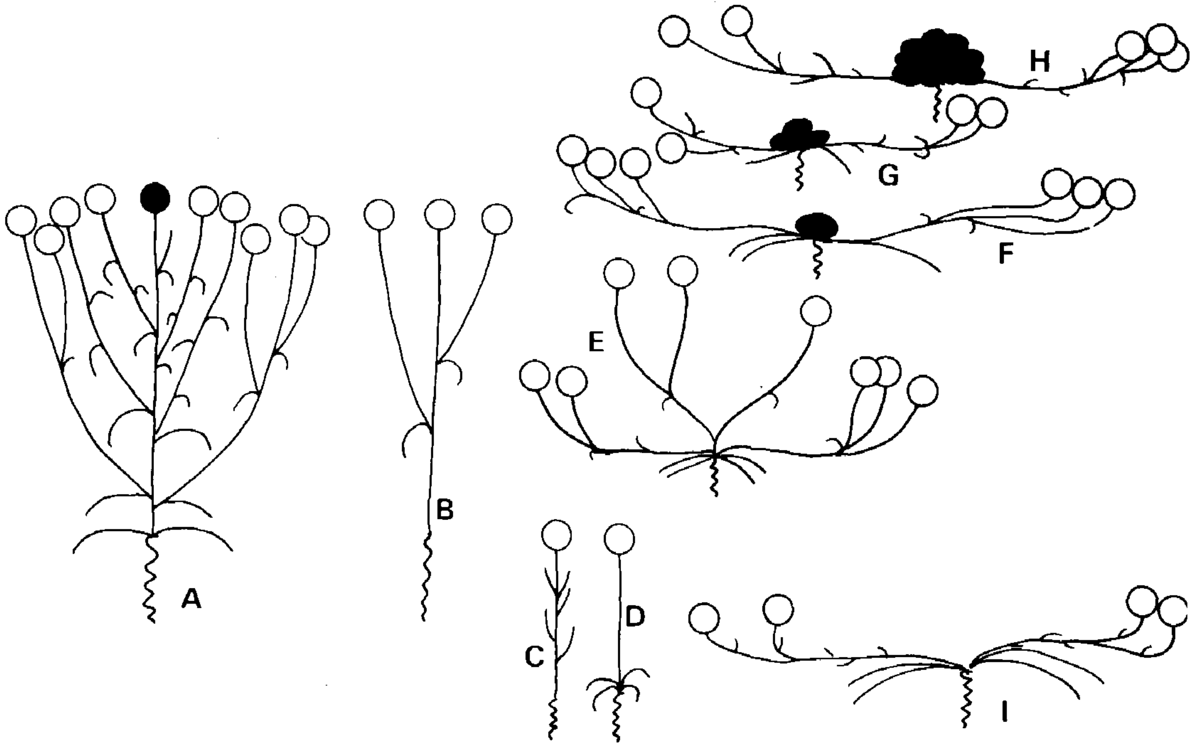

Fig. 3 Inflorescence types (see text for explanation).

eastern Mediterranean annual *A. nigellifolius* (Fig. 2 J). Measurements are given in the descriptions.

Most leaves have a distinctly herbaceous texture, but those of *A. linearilobus* are quite fleshy. *A. linearilobus* (Figs 2 J, 24) has the greatest degree of dissection in the sense that it has a small leaf area relative to the dimensions of the leaves, the wide rhachis internodes and the long, slender lobes.

Some species, e.g. *A. clavatus* (syn. *A. tomentosus*) and *A. pyrethrum* var. *depressus*, have a dense indumentum, whilst others, e.g. *A. nigellifolius* and *A. linearilobus*, are glabrous. This character is extremely variable and has little taxonomic significance. The hairs are invariably simple.

Inflorescence

A conspicuous feature in *Anacyclus* is the variation in arrangement of the capitula. These are borne singly at the end of a single peduncle (as in *A. nigellifolius*) or, more commonly, a branched peduncle (as in *A. radiatus* and *A. clavatus*), or they may be tightly grouped into a central cymose cluster with lateral peduncles emerging from the axil of the leaf or bract (as in *A. monanthos*). Examination of the different inflorescence types reveals that they represent several modifications in a distinct evolutionary trend, which is outlined in Fig. 3.

The most frequent condition is shown in Fig. 3 A; this simply consists of a fairly dense cyme with terminal capitula usually branching from the middle of a main stem. After the flowering of the first capitulum, growth is maintained by lateral alternate branches which develop beneath the capitulum and themselves eventually terminate in new capitula. The shaded capitulum in Fig. 3 A symbolizes a mature, ripe head from an early stage of the flowering period, and the unshaded heads the successive developments. This condition occurs in several species of *Anacyclus*, and it is not uncommon in some of the more robust species (e.g. *A. linearilobus*) to see a main branch lying prostrate with many successive flowering shoots emerging from its axis.

Generally, the flowering period of the most widespread weed species, *A. clavatus* and *A. radiatus*, spans several months, allowing several generations of capitula to develop on one plant. However, by contrast, the time during which conditions are suitable for flowering may often be considerably shortened, hence curtailing the time-span for producing successive generations of capitula. In these situations there can be a considerable reduction in the number of developing branches, and the condition in Fig. 3 B is reached. In extreme situations further branch reduction and loss of leaves on the peduncles can occur to produce eventually habit types indicated in Figs 3 C, 3 D, 26. These are commonplace in the east Mediterranean endemic *A. nigellifolius* and on rare occasions in *A. clavatus* (*A. capillifolius* Maire).

A seemingly independent trend is in contraction of the stem and the peduncles. Many plants of *A. radiatus* and *A. clavatus* appear to have what looks like a protracted basal rosette, with branches of the stem and peduncles emerging nearer the base of the plant. The leaf internodes are extremely short, and the leaves emerge alternately. This condition is illustrated in Fig. 7 E. Often stem reduction is so complete that branching occurs directly from the taproot and there is an almost total loss of the larger leaves making up the rosette (e.g. in *A. monanthos* subsp. *cyrtolepidioides*). In *A. monanthos* subsp. *monanthos* stem loss is combined with peduncle reduction to produce a central acauline, sessile capitulum of the type indicated in Figs 3 F, 14. Lateral peduncles, when present, emerge from the axils of the rosette leaves or branch directly from the vestigial stem below the capitulum. A related trend is the fasciation and tumescence of peduncles as they become further reduced so that a synflorescence with 2–6 capitula is formed (Fig. 3 G). The most derived condition is produced when several or all of the capitula of the synflorescence fuse to form a syncephalum. Here, the lateral peduncles can either emerge from rosette leaf axils directly below the syncephalum or on extreme occasions even appear to emerge from the axils of involucral bracts (Fig. 3 H). In well developed specimens of *A. monanthos* subsp. *monanthos* secondary syncephala and synflorescences have been observed.

In *A. pyrethrum* (Figs 3 I, 12), the only perennial species of the genus, a rather different situation from the synflorescence and syncephalum of *A. monanthos* has developed; the stem is greatly reduced and fused directly with a long woody taproot to form a submerged basal caudex. In early spring large leaves emerge from the centre of the caudex to form a regular dense rosette. Eventually these are succeeded by a whorl of peduncles, emerging from the axils of the innermost leaves. The peduncles are commonly single-headed or only once or twice branched, providing a distinct, although somewhat contracted, flowering period. During the winter the inflorescence and leaves die right down to the ground, to be succeeded in the following season by new flowers. The development in *A. pyrethrum* differs from that in *A. monanthos* for various reasons. It shows no indication of fasciation or tumescence in the peduncles, does not have a synflorescence or syncephalum and has only one generation of flowers, never having a secondary branching point or any means of vegetative spread. The stem reduction in *A. pyrethrum* may well be an adaptation to the alpine environment in which it grows. *A. pyrethrum* is an obligate outbreeder, with a sporophytic, self-incompatible breeding system (Humphries, in press, *a*), and its flowers all exhibit the common Anthemidean, radiate gynomonoecious condition. In *A. monanthos*, stem, peduncle and capitulum modifications may be an adaptation to the hot, dry desert environment in which it is found. It is self-compatible, and its relatively inconspicuous flowers are discoid-hermaphrodite, which indicates that selfing must frequently occur. As we have seen, the evolution of the *A. pyrethrum* and *A. monanthos* inflorescences appears superficially to be very similar. However, the reduced inflorescence in each species appears to be the derivative culmination of an independent parallel trend, since they are unique conditions for the genus as a whole and indeed for the sister group of the genus. This means that the evolution of the *A. pyrethrum* rosette-type inflorescence must have passed through a number of morphological changes, if it did indeed originate from a branched cyme with long peduncles, involving the loss of a determinate capitulum, stem reduction and fusion with a woody taproot. It is interesting in this context that the extinct 'Magdeburg' officinal plant, *A. officinarum* (p. 114), which may simply be an annual derivative of *A. pyrethrum*, produced a long central stem with alternate leaves.

The prospect of secondary condensation cycles occurring in *Anacyclus*, culminating in a rosette, synflorescence or solitary capitulum, leaves the ancestral condition in some doubt, since similar morphological trends can occur in related genera. *Achillea*, for example, normally has a tight corymbose cyme but can have species with solitary capitula, as can *Leucocyclus*. More remotely, *Anthemis* and its allies do commonly have loose cymes but exhibit a number of stem-reduction trends.

Receptacle

The receptacle is flat or very shortly conical and is, in all species, paleate, i.e. furnished with involucral bracts subtending each disc-floret. In all species these are particularly well developed, in fact perhaps the most distinctive in the Anthemideae. They show considerable variation in the genus, the toughest and most persistent being found in *Anacyclus pyrethrum* and *A. monanthos* subsp. *monanthos* (Figs 12, 14) and the most herbaceous in *A. latealatus* and *A. nigellifolius* (Fig. 26). They also show considerable variation in shape and dimensions. In *A. pyrethrum* they are distinctly obcuneate and almost as broad as wide with a tough mucronate acuminate apex, distinctly caniculate and overtopping the ripe cypsela at maturity. In *A. nigellifolius* the opposite extreme occurs, in that the receptacular scales are obovate-acuminate, somewhat flimsy and scarious and only loosely investing the cypsela at maturity.

Correlated with the variation in form is the strength of attachment to the receptacle. In all taxa the receptacular scales and cypselas are loosely attached to the receptacle. In *A. clavatus*, *A. homogamos*, and *A. radiatus* the scales are readily deciduous and will fall off the receptacle at the same time as the involucral bracts and cypselas, after the withering of the capitulum. In *A. pyrethrum* and *A. monanthos* subsp. *monanthos* they are persistent on the receptacle, and since they overtop the cypselas, the whole capitulum is dispersed as a single diaspore. Both these taxa occur in habitats with great climatic extremes, and, as a result, both have a prostrate growth habit. It seems that the mature capitula of the perennial *A. pyrethrum* are deposited a short distance away from the parental plant after it dies down for the winter, and those of the annual *A. monanthos* are left near the site of the parent plant after it disappears altogether.

Involucre

The involucre in *Anacyclus* consists of a hemispherical cup comprised of pluriseriate, brown or brownish-green bracts. Although the actual dimensions of the involucre can vary enormously, the shape can invariably be described as campanulate. The innermost bracts are usually obovate-spathulate, e.g.in *A. clavatus* (Fig.19), with a small to spreading erose apex, e.g. in *A. radiatus* (Fig. 17). Sometimes the limb is virtually absent and the innermost bracts are oblong or triangular, as in *A. pyrethrum* (Fig. 12) or *A. maroccanus* (Fig. 16). The different conditions of the involucre are fairly uniform in particular species and species groups, e.g. *A. radiatus*.

In the annuals the bracts are usually a more or less uniform light-brown colour, moderately scarious and distinctly hairy. However, the opposite extreme conditions can be seen in *A. maroccanus* and *A. pyrethrum*, which have distinctly herbaceous, green involucral bracts with narrow, dark brown margins and are usually subglabrous.

Florets

The floral characters of *Anacyclus* are particularly variable, especially in the presence and absence of ray florets, the size of ray florets, ray-floret colour, lobe size of the disc florets, the degree of compression of the corolla tube and the shape and size of corolla-tube appendages.

Most species are gynomonoecious with a single row of ligulate female florets and a central mass of perfect, hermaphrodite disc florets. *A. monanthos* and *A. homogamos*, by contrast, are monoecious with all the florets hermaphrodite. Robust, apparently discoid plants of northern Morocco and the western European Mediterranean region sometimes have a small number of extremely short female ligules, often hidden below the involucral bracts (Fig. 19). These have been considered by Maire (1932) to be a polymorphic intermediate form between the ligulate and eligulate conditions. One hypothesis to explain such variation would be that these plants represent an intermediate stage in the evolution of the monoecious discoid head. However, data from experimental, morphological and geographical studies would suggest that the heterogamous plants of *A.* × *valentinus* are more likely to be hybrids between the yellow-liguled *A. radiatus* and the discoid *A. homogamos* (sec p. 128; Humphries, in press, *a*).

Within the Anthemideae the commonest ligule colour is white or creamy white. The same is true for *Anacyclus*, where white ligules are found in *A. clavatus*, *A. latealatus*, *A. linearilobus* and *A. nigellifolius*. White ligules are also found in *A. pyrethrum*, *A. radiatus* subsp. *coronatus* and *A. maroccanus*, but the lamina of the ray florets is characterized by having a deep purple stripe on the underside. This feature is always present in *A. pyrethrum* and *A. maroccanus* but is frequently absent from plants of *A. radiatus* subsp. *coronatus*. The only distinctly radiate species to have yellow ligules is *A. radiatus* subsp. *radiatus* and this, like its sister taxon, is known from several sporadic collections to have purple-striped variants frequently referred to var. *purpurascens* DC. The red-purple stripe is a feature common to a number of widely different Compositae, having been reported from *Relhania* in the Inuleae (Bremer, 1976), the Arctotideae, the Cichorioideae (e.g. *Crepis*) and the Anthemideae. There seems to be little or no information about its function; since it is only visible from above during the bud stage of flowering, Bremer (1976) has suggested that it might be a signal block for pollinators in the pre-maturation phase of anthesis.

The disc-florets are invariably yellow, infundibuliform and divided into a lower tube and an upper 5-lobed bell, which contains the anther tube. In all species, the distinction between the bell and the tube is very clear. The corolla lobes are normally regular cucullate triangular appendages, with a papillate surface on the inner face in most taxa; but in some species, e.g. the annuals *A. radiatus*, *A. clavatus*, *A. homogamos* and *A.* × *valentinus*, two of the five lobes can be distinctly longer than the other three. This feature is usually heteromorphic within a capitulum with the most zygomorphic, radiant radiate corollas towards the centre of the head and the most actinomorphic florets towards the periphery. The radiant form seems to be derived by excessive proliferation at the dorsal points of the two hooded lobes and is particularly conspicuous in *A. clavatus* (Fig. 19).

The corolla tubes of both ray and disc florets are compressed in the anterior-dorsal plane. The net result is that the centre part of the tube is somewhat oval in transverse section and is invested on either margin with a wing of varying dimensions, ranging in width from about 0·5 mm in *A. maroccanus* to 3 mm in *A. nigellifolius*. In most taxa the wings have more or less parallel sides and the base of the corolla tube articulates regularly with the ovary. In *A. linearilobus* (Fig. 24) the wings are somewhat rounded and the dorsal margin extends below the top of the ovary. This phenomenon is even more pronounced in *A. nigellifolius* (Fig. 26) and in *Leucocyclus formosus*, where the corolla tube forms an invaginated base shrouding the flattened cypsela on both the anterior and dorsal sides.

The styles and stamens of both the ray and the disc florets are monotonously constant throughout the genus. The anthers have very short tails consisting of slightly elongated, triangular cuneate apices. The style branches do vary somewhat in length but are invariably truncate-penicillate at the apex. Measurements are given with the descriptions.

Cypselas

Despite the pleas of Wagenitz (1976) and Roth (1977) to use the term achene (of Richard, 1808 and de Candolle, 1813) to describe the fruit derived from inferior ovaries, the term cypsela of Mirbel (1815) is used in preference to describe the bicarpellate coenocarpous inferior ovary of the Compositae (after Fahn, 1967), since it is clearly not homologous with other monospermous fruits to which the former term was originally applied by Necker (1790).

In *Anacyclus* the cypselas are essentially homomorphic although there is some tendency towards heteromorphy, simply because there is a gradual reduction in overall structure from the most elaborate fruits of the ray florets to the smaller cypselas of the central disc florets (Fig. 4). The cypselas in *Anacyclus*, as in so many other genera of the Anthemideae (Heywood & Humphries, 1977), provide the unambiguous diagnostic features of the genus. They are flattened in an anterior-dorsal plane with distinct lateral appendages. Anatomical features which appear to be confined to this genus and *Leucocyclus* include a pericarp consisting of a layer of sclerenchyma some 1–3 cells thick, sclerenchymatous ribs, and two laterally orientated vascular bundles (Fig. 5).

There is considerable variation in the general elaboration of wing shape and in the thickness, size and dimensions of the cypselas and, to a lesser extent, the pappus. Since it seems clear that

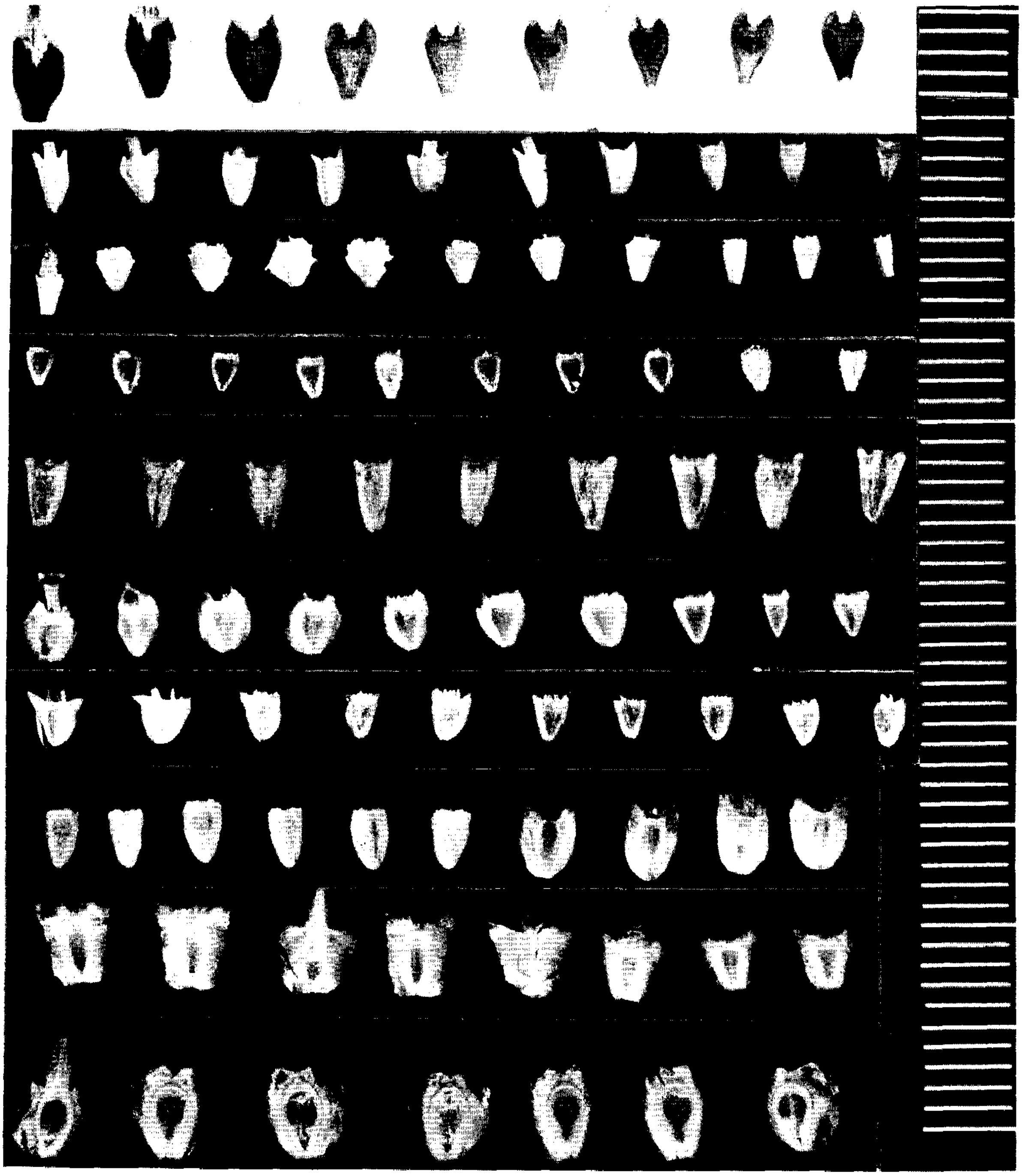

Fig. 4 Variation in cypsela morphology. An example of a transformation series where overall expansion in the wings and increase in pappus size, together with a reduction in the general form of the body, show increasing apomorphy (see Table 1). Species (from top to bottom): *A. pyrethrum* var. *pyrethrum*. *A. pyrethrum* var. *depressus*, *A. monanthos* subsp. *monanthos*, *A. maroccanus*, *A. radiatus* subsp. *radiatus*, *A. radiatus* subsp. *coronatus*, *A. clavatus*, *A. linearilobus*, *A. homogamos*, *A. nigellifolius*.

the compression of the fruit is a derived feature, then it follows that the elaboration of the wing is a consequence of the reduction of the main fruit body, since the overall dimensions of the fruit vary little within the genus. The transformation series is presented in Fig. 4, with the least elaborate fruits in *A. pyrethrum* and those with the broadest wings in *A. latealatus* and *A. nigellifolius*.

Changes accompanying the expansion of the wing include the erosion of the wing margins (as exemplified by the tough spines of *A. monanthos* and the delicate fimbriate margins of *A. maroccanus*), a general correlation between area and thickness of the wing (the broader the wings the more scarious they are), and an increase in pappus size associated again with increase in lamina area. One important species-specific characteristic is the vertically orientated auricles in *A. pyrethrum*, as distinct from the generally outwardly pointing auricles of the annual species.

A feature mentioned by Grierson (1975*a*) is the persistence of ray corolla lobes on the cypsela at maturity. Abscission of the ray corolla at the point below the ligule is frequently encountered in most of the radiate species but is particularly apparent in *A. nigellifolius*, where it appears that the corolla tube is fused with the cypsela through maturity and dispersal.

The pappus is either absent (e.g. in *A. pyrethrum*) or varies from an extremely narrow, marginal corona to a thin, lacerate scarious appendage contiguous with the wing auricles.

In transverse or longitudinal section the individual parts of the cypsela, viz. the ovary wall, the testa, the pericarp and the hypanthial tissue, are impossible to identify fully from anatomical observations. However, it is easily possible to separate the testa from the fruit wall and consider the pericarp as two layers – epicarp and mesocarp. In *Anacyclus*, most variation occurs as modifications to the mesocarp, especially in the thickness and angle of the cells in the wings and the thickness of the anterior and dorsal layers.

The pericarp and integument are often tightly attached to one another but do not coalesce. In the preparations used for Fig. 5, they are clearly seen to be separated from the fruit wall. The integument in all taxa consists of two layers, an outer epidermis with lateral or U-type thickenings and an inner layer of flattened, densely cytoplasmic cells.

The ovary is supplied with two vascular bundles lying marginally in the basal part of the rib (Fig. 6 B). They both divide at the base to provide two embryo traces and again at the apex, just below the pappus, to form two semicircular rings of corolla and stigmatic traces. The semicircular rings are asymmetrical. One of them divides three times to give one stigmatic trace and three corolla traces, whilst the other divides only twice to give two corolla traces and one stigmatic trace. Within the corolla tube the five corolla traces again divide near the base to give five outer traces.

Variation in the pericarp anatomy reflects to a great extent the differences in external morphology, the most important specific differences being the degree of sclerification of the mesocarp, the thickness of the mesocarp in the region of the anterior and dorsal faces, and the relative length of the wings and embryo. In all taxa the mesocarp parenchyma develops wall-thickening during maturation. The sclerenchyma is mostly due to scleroid development. The degree of thickening varies in different parts of the cypsela, particularly in the ribs, the faces and the apical region of the fruit wall. The most obvious and most densely thickened regions in all taxa are the basal regions of the lateral ribs in the portion surrounding or overtopping the vascular bundles. In the majority of the annual species the anterior and dorsal faces of the mesocarp are extremely thin, often only one cell thick. Nevertheless, the cells are heavily thickened to the same degree as the lateral bundles. By contrast, the cells of the pericarp in *A. pyrethrum* are only slightly thickened at maturity but are some 3–4 cells thick in the region of the faces. The epicarp epidermis is invested along the margins and at regular intervals on the surfaces with myxogenic cells (Fig. 6).

The general expansion of wing area and reduction in the main body of the fruit is associated with the development of smaller cotyledons and a thinner mesocarp.

Chromosome numbers

Somatic chromosome numbers have been investigated in five species. All of them have 2n = 18 (see Humphries, in press, *a* and Humphries *et al.*, 1978, for review). The four annuals which have been examined, *Anacyclus radiatus* subsp. *radiatus*, *A. radiatus* subsp. *coronatus*, *A.* × *valentinus* and *A. clavatus*, all differ from the perennial *A. pyrethrum* in having three, instead of two, pairs of

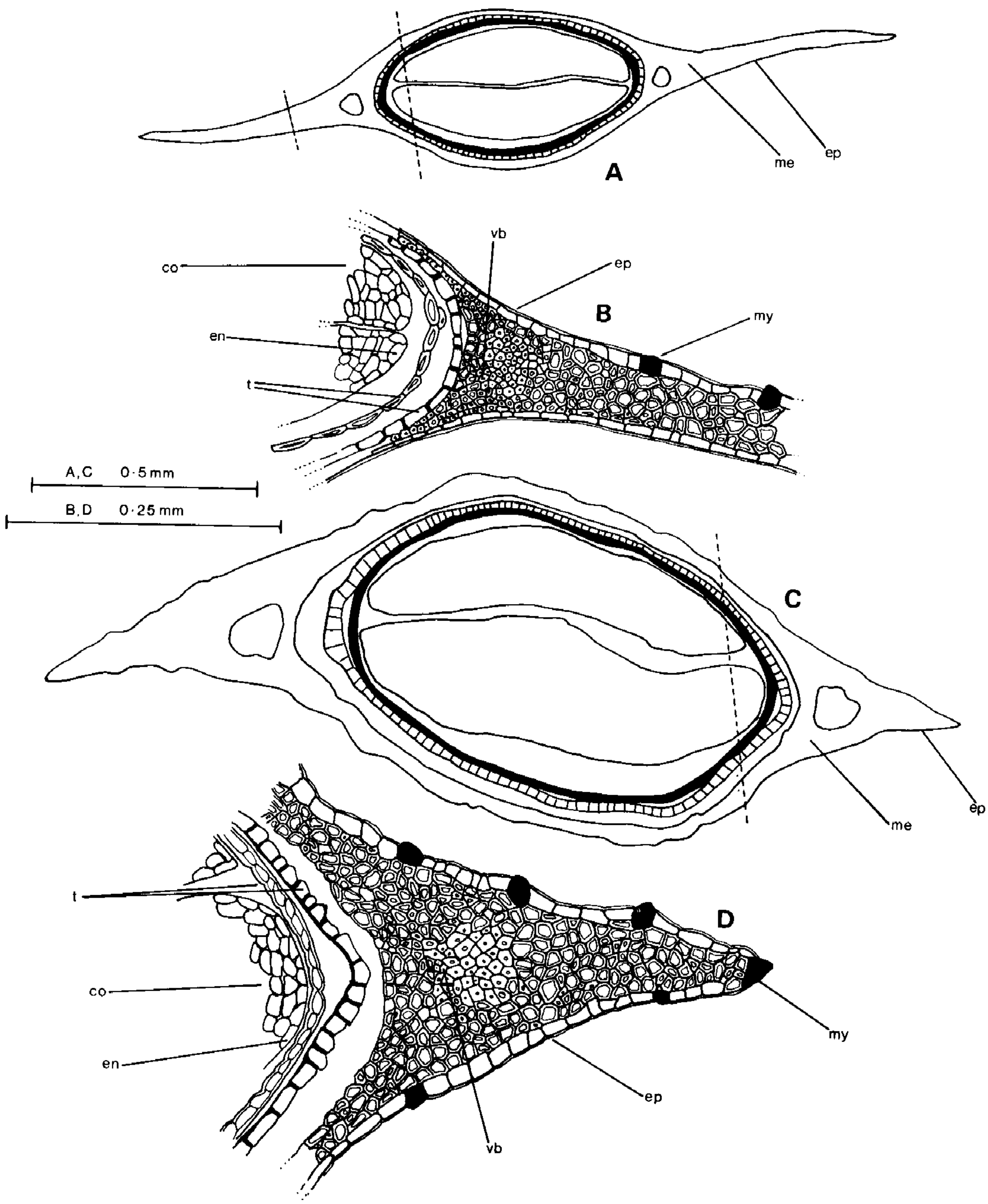

Fig. 5 Median transverse section of mature cypselas: A, B – *A. radiatus* subsp. *coronatus*; C, D – *A. pyrethrum* var. *pyrethrum*. co = cotyledons, en = endosperm, ep = epicarp, me = mesocarp, my = myxogenic cells, t = testa, vb = vascular bundles.

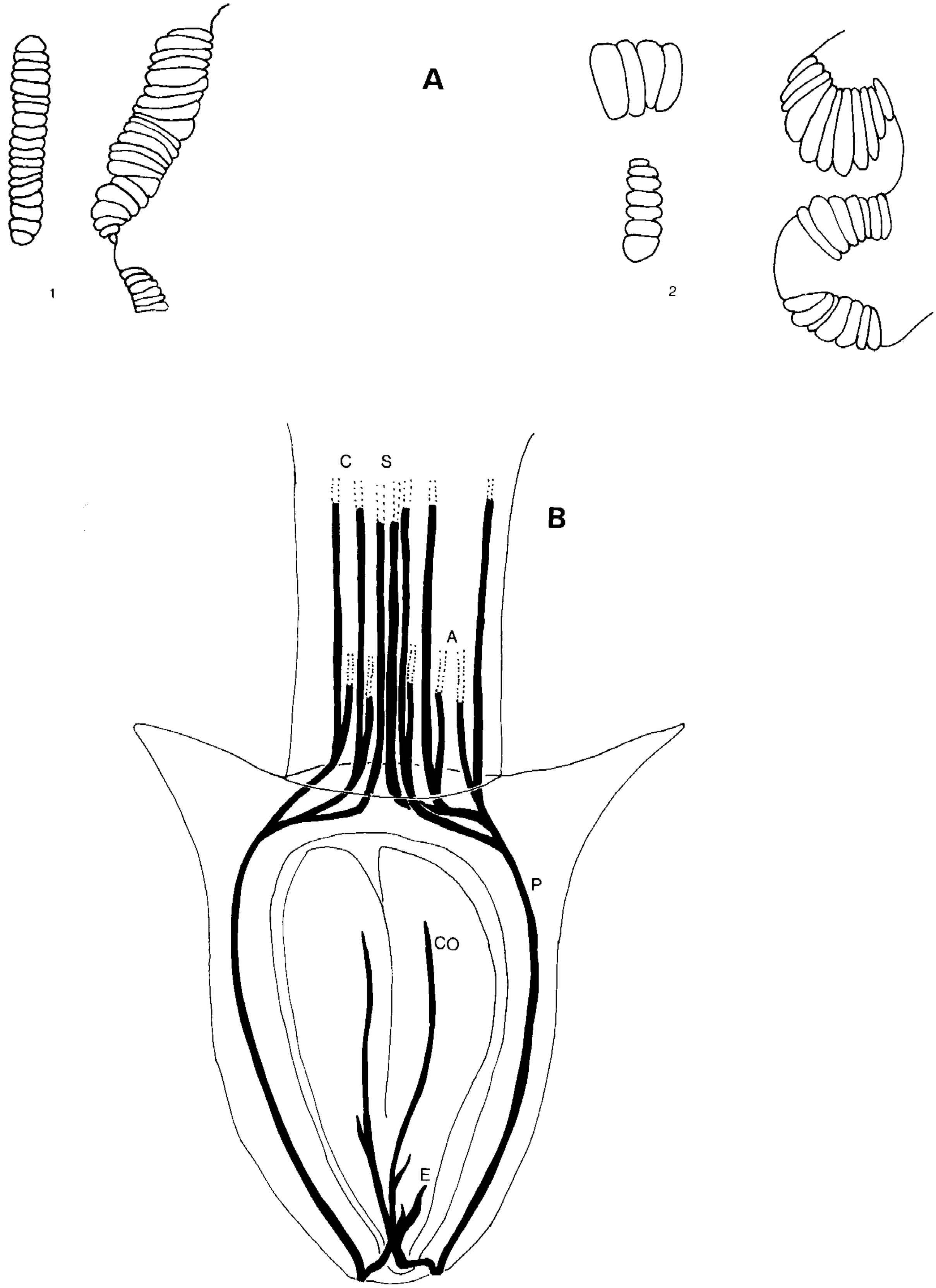

Fig. 6 A – Myxogenic cells: 1 – *A. radiatus* subsp. *radiatus*; 2 – *A. monanthos* subsp. *monanthos*. B – Vascular system in the cypsela and corolla: A – anther trace, C – corolla trace, CO – cotyledon trace, E – embryo trace, P – pericarp trace.

satellited chromosomes. This increase has been correlated with increases in the degree of chromosome banding (Schweizer & Ehrendorfer, 1977) and the self-compatible breeding system (Uitz, 1970; Humphries, in press, *a*).

Phytogeography

The approximate total range of *Anacyclus* is illustrated in Fig. 1i and the distribution of all the species on the maps in Figs 13, 15, 18, 20, 22, 23, 25 and 27 respectively. The main concentration of species is in the Maghreb region of north Africa, particularly in Morocco. It is not the concentration of species that is the main point, however, but rather how the present species relate to one another in terms of their distribution. It can be seen that several taxa, e.g. *A. radiatus* subsp. *radiatus*, *A. clavatus*, *A. homogamos* and *A.* × *valentinus*, are pernicious weeds with an apparently sympatric distribution in parts of their range, particularly in Morocco, Spain and France. However, for the most part, is it obvious that some species e.g. *A. linearilobus*, *A. latealatus* and *A. nigellifolius*, have a discrete, sometimes small vicarious pattern of distribution. It is not possible for this pattern to correspond with a general concept of a centre of origin with subsequent dispersal; but instead it indicates an allopatric process of gradual migration of *ancestors* with repeated isolation and vicariance which has eventually led to the present-day pattern of distribution. The importance of this concept, originally proposed by Croizat *et al.* (1974) and elaborated by Platnick & Nelson (1978) and Rosen (1978), has already been elegantly described by Bremer (1976, 1978) with reference to South African plant distributions; and it seems that a hypothesis that sister monophyletic groups will have vicariant distribution patterns is a general concept applicable to divergent evolutionary situations.

Some examples of vicariance are more obvious than others. *A. radiatus* subsp. *radiatus* and *A. radiatus* subsp. *coronatus* provide us with a good example of two evolving, vicarious sister taxa (Fig. 18). Their ancestor probably had a continuous distribution from north Morocco right down to the Ifni gap on the south-west Atlantic coast. Subsp. *coronatus*, the white-liguled form, has a south-west-Moroccan distribution and is particularly prominent in the Sous valley and the Atlantic seaboard from Ifni to Mogador. At the north end of its distribution there is a quite marked transition to the yellow-liguled form – the more widespread north Moroccan and western European/Mediterranean subsp. *radiatus*. It is interesting that the localized intermediates in the Mogador region have been given a range of different names reflecting their transitional nature (*A. medians* Murbeck, *A. submedians* Maire, *A. radiatus* var. *ochroleucus* Ball and *A. radiatus* var. *typicus* subvar. *concolor* Maire). Their ancestor may well have had a continuous distribution throughout their distribution range. Another example, this time of two vicarious species, is provided by *A. latealatus* and *A. nigellifolius*. They are both annuals growing on the rocky hillsides in the eastern Mediterranean (Fig. 27). *A. latealatus* is known only from the southern Turkish steppe near Tefenni, whereas *A. nigellifolius* has a more widespread distribution in southern Anatolia, Persia and the Lebanon. Such a pattern might be interpreted as quantum speciation (Grant, 1971), where a small peripheral population has budded off from the ancestral species. A similar interpretation might be applied to *A. linearilobus*, a narrow endemic from northern Algeria (Fig. 25) which is the sister species to the more widespread weeds *A. homogamos* and *A. clavatus*.

A third and distinct vicariance pattern at a higher group rank within the genus is that of the perennial varieties of *A. pyrethrum* (sect. *Pyrethraria*) and all the annuals, which together form a monophyletic group (sect. *Anacyclus*). *A. pyrethrum* is an upland species and a characteristic component of the natural treeless, subalpine meadows and rocky habitats of the Atlas mountain ranges of central and north Morocco and in Algeria (Fig. 13). By contrast, all the annuals occupy disturbed, open, lowland habitats except those few species, e.g. *A. homogamos*, which have invaded mountain habitats as roadside weeds. There is therefore a significant distribution pattern resulting from the different ecological requirements of the sister groups.

The answer to the question of the origin of the genus *Anacyclus* will not be found by a search for its centre of distribution. Instead it is much more worthwhile to ask the question: what was the distribution of the ancestor of the present *Anacyclus* species? By way of an answer it is likely that it was a widespread species, perhaps not so widespread as to encompass the present distribution of *Anacyclus* owing to the very weedy nature of *A. radiatus* subsp. *radiatus*, *A.* × *valentinus* and *A. clavatus*, but certainly occurring in the southern Mediterranean region from southern Turkey to the Atlantic coast of Morocco.

Phylogeny

As Bremer (1976) and Bremer & Wanntorp (1978, and in press) point out, the theory of phylogenetic systematics, as described by Hennig (1965, 1966), has had virtually no effect upon the classification of plants. In fact, most publications in botany do not use any cladistics for classification (Humphries, in press, *b*) although in my opinion there is a considerable need for them rather than for the methods of the strictly phenetic and the eclectic or evolutionary biology schools.

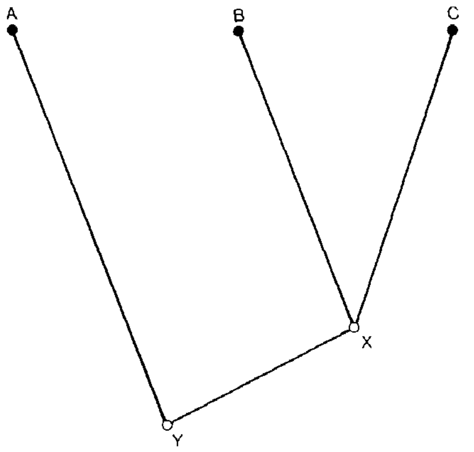

Fig. 7 The concept of phylogenetic relationship. Species B and C share a more-recent common ancestor (species X) which is not shared by species A (redrawn from Hennig, 1965).

Consequently, the construction of 'phylogenetic trees' based on ill-defined principles and the elaboration of nominalistic methods has created considerable disillusionment and disregard of sound phylogenetic discussion. This phenomenon is curious, since a glance at recent volumes of zoological, particularly entomological, literature will reveal that the principles of phylogenetic systematics are considered to be amongst the most erudite of those which advance the understanding of evolutionary relationships. I think it is necessary to re-emphasize that in the 120 years since the publication of Darwin's *Origin of Species* (1859) there has never been a serious refutation of the theory of evolution. Thus, since the advent of this theory, one of the tasks of biology has been to investigate the phylogenetic relationships between species (Hennig, 1965).

The definition of the concept 'phylogenetic relationship' is based on the fact that reproduction is sexual in most organisms, and that it usually takes place within the framework of confined reproductive communities which are isolated from one another. Speciation occurs because parts of existing reproductive communities become externally, or genetically, isolated from one another for extended periods of time. Thus, in divergent evolution, all species which exist at a given time, e.g. the present, have originated by the splitting of older reproductive communities. Thus, the concept of phylogenetic relationship can be demonstrated in a diagram, a cladogram (Fig. 7). Species B is considered to be more closely related to species C than to another species A when B has at least one ancestral species (X) in common with species C which is not ancestral to species A (see Hennig, 1965) (Fig. 7). It becomes the task of systematics, then, to determine monophyletic groups with shared common ancestry.

It is widely believed in angiosperm systematics that, since so few fossil remains are available, phylogenetic reconstruction of monophyletic groups is not reliable and possesses no method of its own. From this it follows that we can interpret the results of morphological systematics only according to the principle that the degree of morphological relationship can be equated with the degree of phylogenetic relationship. This, of course is not so, since any concept of overall resemblance does not have the ability to distinguish between mosaic evolution, convergence and parallelism. The fundamental difference between the methods of the pheneticist and the phylogenetic systematist is that the latter breaks up the simple concept of resemblance (Hennig, 1965).

The concept of resemblance can be divided into various categories of (i) resemblance due to convergence, (ii) resemblance due to common possession of primitive (plesiomorphous) character states, and (iii) resemblance due to common possession of derived (apomorphous) character states.

Convergence occurs because similar organs have evolved adaptations to similar functions from morphological foundations in different organs, so that the character resemblances are merely analogous. Classifications based on resemblances due to convergence then produce polyphyletic rather than monophyletic groups (Fig. 8 C).

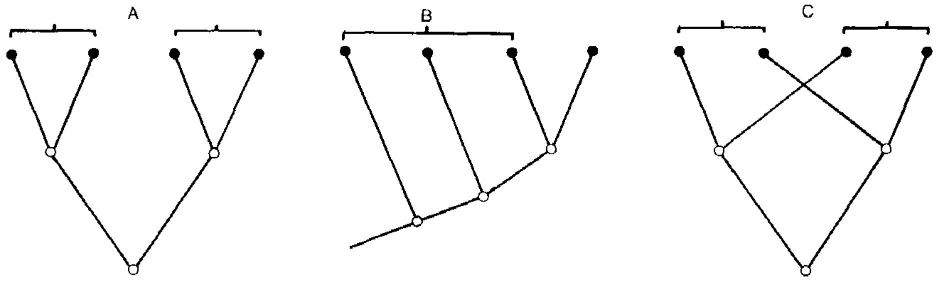

Fig. 8 Group formation and resemblance. Monophyletic groups (A) are recognized by resemblance due to synapomorphy (shared derived character states); paraphyletic groups (B) occur as a result of symplesiomorphy (shared primitive character states); and polyphyly (C) results from resemblance due to independently derived character states (redrawn from Hennig, 1965).

Even when problems of convergence can be easily removed, as of course in many cases it can, overall similarity is still not a satisfactory criterion on which to base a phylogenetic classification because it will not produce monophyletic groups. This is due to the fact that characters can remain unchanged through a number of speciation processes. Therefore the common possession of primitive (plesiomorph) characters which have remained unchanged cannot be evidence of the close relationship of their possessors. A classification based on agreement of resemblance due to shared primitive characters thus produces paraphyletic groups (Fig. 8 B). In botanical systematics there has clearly been an obsession with the possession of primitive characters in common, the obvious consequence being that a large majority of angiosperm classifications are paraphylies. It is possible to cite a whole range of examples of obvious paraphylies at various taxonomic levels, e.g. the Ranales, the Bombacaceae, the Heliantheae, *Felicia*, *Aster*, *Leucanthemum* and *Chrysanthemum* sensu lato. The supposition that two or more species are more closely related to one another, and that together they form a monophyletic group, can only be confirmed by demonstrating their common possession of derived characters (or synapomorphies). When such characters have been demonstrated, then the supposition has been confirmed that they have been inherited from an ancestral species common to only the species showing these characters.

Once this premise has been accepted, i.e. that monophyletic groups can be recognized only when morphological resemblance is due to synapomorphy, then the practical aspect can be described. Using Hennig's (1965) *Argumentation plan* (Fig. 9), every group formation of any rank must be demonstrated by synapomorphous characters. All species or groups of species have a sister group in the modern flora irrespective of divergence through time. Sister groups will then form monophyletic groups of higher rank. It follows, since evolution occurs through the change of one or more characters, that any one particular character must always occur in a more primitive (relatively plesiomorphous) condition in one group than its sister group. The same is true for the other group with regard to other characters. Therefore, it follows that there is a mosaic distribution, or heterobathmy, of character states in any group and there can be *no solely primitive or solely*

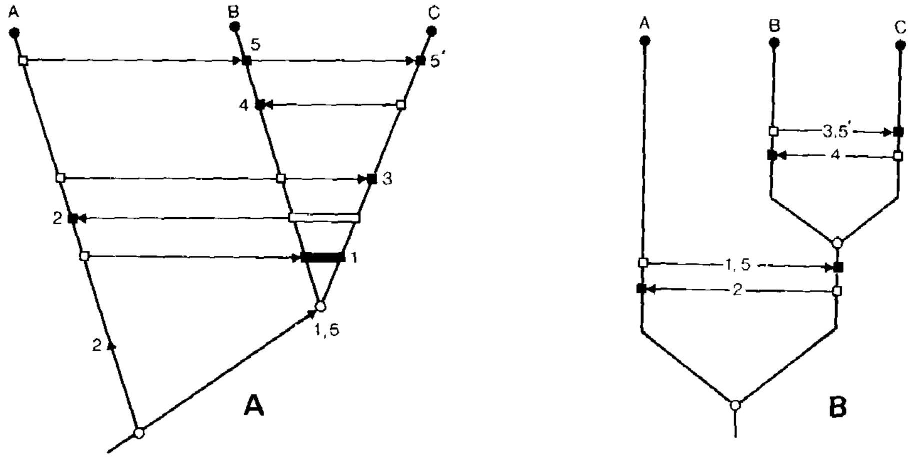

Fig. 9 Argumentation plan for phylogenetic hypotheses (☐ plesiomorph, ■ apomorph) Sister-groups are established on the distribution of relatively apomorphous and relatively plesiomorphous characters. Characters 2, 3 and 4 demonstrate autapomorphous changes for the establishment of species A, B and C; character 1 demonstrates the synapomorphous feature which establishes that B and C share a more recent common ancestry than either do with A. Character 5 demonstrates a three-state transformation series of increasing apomorphy from A to C. A gives the traditional cladogram as used by Hennig, B gives a simplified 'Candelabra' version as used in this work (redrawn from Hennig, 1965).

derivative group. The aim of this method then is to produce the best, internally consistent hypothesis as to the primitive or derivative condition of each character state. The character-state conditions in *Anacyclus* are listed in Table 1, and the distribution of these characters in the species are given in the data matrix in Table 2.

Table 1 Plesiotypic and apotypic character states employed in Fig. 10

	Character state	
Character	Plesiotypic (—)	Apotypic (+)
Habit		
1 Duration	perennial/biennial	annual
2 Stolons	absent	present
3 Secondary thickening	present	absent
4 Main axis internodes	present	absent
Root system		
5 Basal caudex	absent	present
6 Rhizomes	present	absent
7 Fibrous roots	absent	present
Stems/inflorescence		
8 Stems	cauline	acauline or internodes ± absent
9 Inflorescence	branched	solitary
10 Syncephalous heads	absent	present
11 Central capitulum	present	absent
12 Central capitulum	aerial	basal
13 Stems	erect with solitary or corymbose inflorescences	reduced to a rosette of creeping corymbose laterals
14 Corymb laterals	from pedunculate bracts	from involucral bracts
15 Peduncles	terete	clavate
16 Peduncles	unthickened along their length	thickened along their length

Table 1 (*cont.*)

	Character state	
Character	Plesiotypic (−)	Apotypic (+)
Leaves		
17 Leaf rosette	absent	present
18 Leaves	homomorphic	heteromorphic
19 Leaves	herbaceous	fleshy
20 Sinus between 2nd-order lobes	narrow, less than 2 cm	wide, more than 2 cm
21 Basal leaf divisions	many	few
22 Basal leaf divisions	tripinnatisect	bipinnatisect
23 Leaves	vermiform	bi- or tripinnatisect
24 Terminal leaf-lobes	linear-lanceolate	oblanceolate
Capitulum		
25 Capitulum	radiate	discoid
26 Ligule colour	white above/red below	yellow above/red below, ′yellow, ″white
27 Ligules	exerted above involucral bracts	inserted below the involucral bracts
28 Disc corollas	actinomorphic	zygomorphic
29 Disc corollas	articulate	anteriorly vaginate
30 Disc corollas	articulate	posteriorly vaginate
31 Disc corolla articulation	terminal	anterior
32 Disc corolla wings	wingless	winged
33 Wings	narrow, usually parallel	large, oval
34 Receptacular scales	membranous	tough
35 Receptacular scales	unthickened	dorso/anteriorly thickened
36 Receptacular scales	oblanceolate	lanceolate
37 Scales	erect at apex	overlapping at apex
38 Involucral bracts	herbaceous	papery
39 Involucral bracts	obtuse	acuminate or long-pointed
40 Involucral bract margins	fuscate	light brown/hyaline, colourless
41 Inner involucral bracts	herbaceous	expanded, membranous and hyaline at the apex
42 Cypselas	terete	anterior-dorsally compressed
43 Cypsela wings	absent	narrow/thick ′narrow/thin ″ broad/thinner
44 Cypsela wings	margins smooth	margin crispate
45 Cypsela wings	margins smooth	margin spiny
46 Cypsela auricles	absent	thick/pointed ′ thin/pointed ″ thin/rounded
47 Cypsela development	terete or rhomboid during development	flat throughout development
48 Pappus	absent	marginal, ′ marginal coroniform ″ coroniform

By using Hennig's (1965, 1966) methods, it has been possible to reconstruct a phylogenetic cladogram (Fig. 10) which provides the most parsimonious evolutionary model to account for morphological variation within this group and a basis for the interpretation of cytogenetic and biochemical data (Ehrendorfer *et al.*, 1977; Humphries in press *a*). The sister group of *Anacyclus* and *Leucocyclus* is indicated by inclusion in the diagram of other genera within the Anthemideae assemblage – a group taken to comprise *Achillea* and its allies.

Table 2 Data matrix employed in the phylogenetic reconstruction of Fig. 10

Taxon	Character (+ = apotypic; − = plesiotypic)																							
	45	35	16	14	12	10	44	41	25	27	24	20	19	33	29	21	30	9	39	15	38	36	22	46
Anacyclus pyrethrum	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	(±)	−	−	−	−	−	−
A. monanthos	+	+	+	+	+	+	−	−	+	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−
A. maroccanus	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−
A. radiatus	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	+	±	−	−	−	+′
A. clavatus	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+′	+	−	−	−	+″
A. homogamos	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	+′	−	−	−	−	+″
A. linearilobus	−	−	−	−	−	−	−	−	−	−	+	+	+	−	±	−	−	−	+″	+	−	−	−	+″
A. latealatus	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+	+	+″
A. nigellifolius	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+	+	−	+	−	−	+	+	+	+″
Leucocyclus formosus	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	+	+	−	+	−	+	−	−
Anacyclus officinarum	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	+
A. × *valentinus*	−	−	−	−	−	−	−	−	−	(+)	−	−	−	−	−	−	−	−	+′	−	−	−	−	+″
A. × *inconstans*	−	−	−	−	−	−	−	−	±	(±)	−	−	−	−	−	−	−	−	+′	−	−	−	−	+″
	40	26	48	43	32	31	28	37	34	18	17	13	11	8	5	4	2	7	3	1	23	6	42	47
Anacyclus pyrethrum	−	−	−	+	−	+	−	+	+	+	+	+	+	+	+	+	(+)	−	−	−	+	+	+	+
A. monanthos	+	−	−	+	−	−	−	−	+	−	−	−	−	+	−	−	−	+	+	+	+	+	+	+
A. maroccanus	−	−	+	−	+	+	+	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+	+	+
A. radiatus	+	+′,″	+″	+′	+	+′	+	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+	+	+
A. clavatus	±	+″	+′	+″	+	+′	+	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+	+	+
A. homogamos	+	−	+′	+″	+	+′	+	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+	+	+
A. linearilobus	+	+″	+′	+″	+	+′	+	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+	+	+
A. latealatus	+	+″	+′	+″	+	+′	+	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+	+	+
A. nigellifolius	+	+″	+″	+″	+	+′	+	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+	+	+
Leucocyclus formosus	+	−	−	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+
Anacyclus officinarum	−	−	−	+	−	+	−	+	+	+	+	−	−	−	−	−	−	+	+	+	+	+	+	+
A. × *valentinus*	+	−	+′	+″	+	+′	+	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+	+	+
A. × *inconstans*	±	+″	+′	+″	+	+′	+	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+	+	+

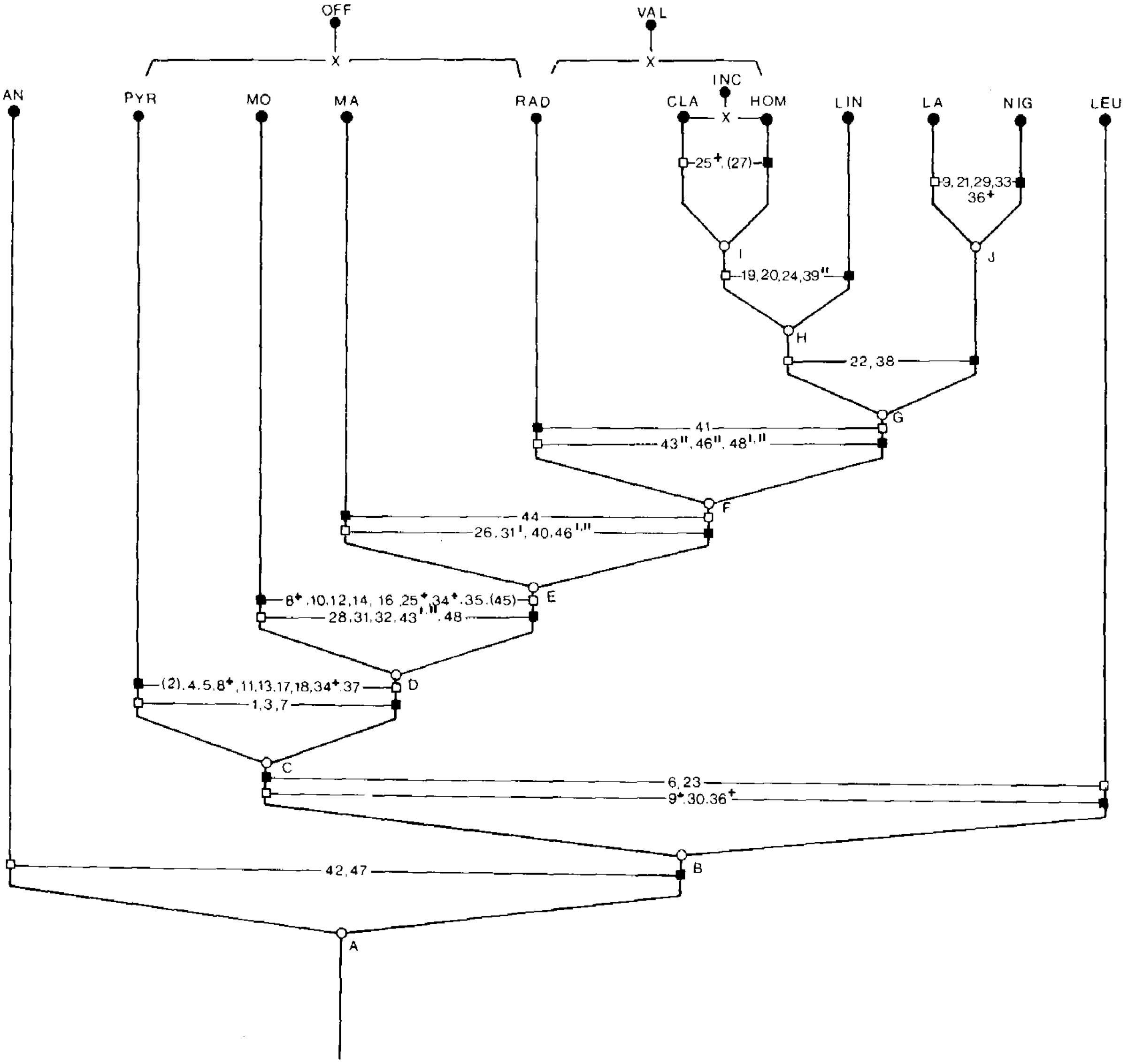

Fig. 10 Cladogram showing phylogenetic relationships in the *Anacyclus* group, based on morphological characters in Tables 1 & 2 and reconstructed according to the principles of Hennig: AN – Anthemideae (*Achillea* and its allies), PYR – *A. pyrethrum*, MO – *A. monanthos*, OFF – *A. officinarum*, MA – *A. marrocanus*, RAD – *A.radiatus*, VAL – *A.* × *valentinus*, CLA – *A. clavatus*, INC – *A.* × *inconstans*, HOM – *A. homogamos*, LIN – *A. linearilobus*, LA – *A. latealatus*, NIG – *A. nigellifolius*, LEU – *Leucocyclus formosus.*

Hennig's method makes it necessary to interpret character states either as primitive or derived conditions. This has been carried out by the principle of sister-group or related-group comparison so that commentary on some of these plesiotypic or apotypic features will help to explain the rationale behind the reconstruction of species relationships within *Anacyclus.*

In general, the systematic distribution of the majority of character states considered to be derived is consistent with the status accorded them here. Thus, for example, the apomorphic conditions found in characters 5, 10, 13, 14, 29, 30, 42, 43, 46 and 47 (Table 1) represent structural modifications which appear to be absent from all groups except those which they help to define. Therefore, *Anacyclus* and *Leucocyclus* form a monophyletic assemblage by the unique possession of the character states 42 and 47 (Tables 1 & 2).

Little more will be said about *Leucocyclus*, except to say that it is the sister-group of *Anacyclus* in the sense that it forms the second dichotomy in the cladogram (Fig. 10 B). Should this be the correct interpretation, then it follows that character states shared by *Leucocyclus* and the two Turkish *Anacyclus* species *A. nigellifolius* and *A. latealatus* (character 36) must be interpreted as independently derived to give the most parsimonious explanation of the data.

The most distinctive taxon within *Anacyclus*, and the one that is cladistically closest to the stem species C, is undoubtedly the polymorphic north African perennial *A. pyrethrum*. Nevertheless, the hypothesis that it is a very specialized derivative species within the genus, and indeed in the northern hemisphere Anthemideae as a whole, is confirmed by its possession of the autapomorphies 4, 5, 11, 13, 17, 18 and 37 (Table 2, Fig. 10 C). These include such character states as a submerged basal caudex, heteromorphic leaves, leaf rosettes and creeping inflorescences, all logically correlated adaptations to the montane habitats in which it occurs. Data on the 'Magdeburg' officinal plant *A. officinarum* are also included, since it seems to possess synapomorphies of both the perennial and annual species, superficially appearing to be an annual derivative *A. pyrethrum* but possibly being an annual hybrid between this and the commonly cultivated annual *A. radiatus* (Fig. 10).

The naturally occurring annual species clearly form a monophyletic group derived from a common ancestor with the perennials, as defined by the synapomorphies 1, 3 and 7. Within this group, *A. monanthos*, a desert plant of eastern Algeria, Tunisia, Libya and Egypt, diverges at the first dichotomy (Fig. 10 D) by possession of the autapomorphic character states 10, 12, 14 and 35. This interpretation makes it necessary to consider that the acauline habit and tough involucral scales (as in *A. pyrethrum*) and the loss of ligules (as in *A. homogamos*) are independently derived (character 25). Since *A. monanthos* seems to bear superficial resemblance to *A. homogamos* and since these species appear to show vicariant distributions (Figs 15, 23) it is tempting to consider that they share recent common ancestry. However, on the basis of such characters as its hard, obovate overtopping receptacular scales and thick, rather unspecialized cypselas which can always be readily distinguished from those of *A. homogamos*, a detailed re-interpretation of character-state trends in *A. monanthos* would have to be considered. *A. maroccanus*, the next closest annual to the stem species (Fig. 10 E), is, by comparison with the rest of the annuals, a rather unspecialized Moroccan endemic retaining a number of plesiomorphous character states, e.g. the red-pigmented undersides to the ligules and the narrow, triangular receptacular bracts of *A. pyrethrum*.

The remaining annual species form two distinct, but closely allied, groups of specialized weeds hereby designated as the '*radiatus*' and '*clavatus*' groups (Fig. 10 F, G, H). *A. radiatus* comprises two distinctive subspecies: *A. radiatus* subsp. *coronatus* has white ligules which are occasionally purple below and cypselas with an expanded lateral wing (Fig. 4); *A. radiatus* subsp. *radiatus*, by comparison, has yellow ligules which are occasionally purple below (var. *purpurascens*) but cypselas with a less widely expanded wing (Fig. 4).

A. clavatus and its allies form the most advanced group in the genus in terms of increasing apomorphy in characters 43, 46 and 48 (Tables 1, 2, Fig. 10 F). *A. clavatus* is cladistically closest to the structurally reduced weed *A. homogamos*, and examination of many different herbarium collections show that the latter species is distinguished mostly by its smaller habit, the absence of ligules, and slightly broader and more auriculate cypsela wings. It is frequently confused with *apparently* rayless forms of *A.* × *valentinus*, which are on the whole much more robust in capitulum size and general habit. Because of the short, yellow ligules in this taxon, *A.* × *valentinus* is considered to be a hybrid between *A. homogamos* and *A. radiatus* (p. 128).

A. linearilobus is a rare endemic, narrowly confined to the sand dunes of northern Algeria (Fig. 25). It can be distinguished from *A. clavatus* by the unique features of the leaf and receptacular bracts (characters 19, 20, 24 and 39).

Finally, *A. nigellifolius* and *A. latealatus*, the eastern Mediterranean vicariant species pair (Fig. 27), form the sister-group of *A. clavatus* and its immediate allies. Both species are structurally simplified annuals showing considerable decrease in leaf area and inflorescence structure, with the most apomorphous conditions apparent in the corolla and cypsela (characters 21, 22, 29, 33 and 36).

Systematic descriptions
Anacyclus L.

ANACYCLUS L., *Gen. Pl.* : 256 (1737); *Sp. Pl.* **2** : 892 (1753); *Gen. Pl.*, cd. **5** : 381 (1754). Type species: *Anacyclus valentinus* L. (= *A.* × *valentinus* L.).

Cotula Tournf., *Inst. Rei Herb.* **1** : 495 (1700), non L. Type species: *Cotula flore luteo radiato* (= *A. radiatus* Lois.).

Santolinoides Vaill., *Hist. Acad. Roy. Sci. Paris* : 312 (1719). Type species: 'Santolinoides annua, erecta, chamaemeli folio' (= *A. radiatus* Loisel.).

Cyrtolepis Less. in *Linnaea* **6** : 166 (1831): *Syn. Gen. Comp.* : 258 (1832). Type species: *Cyrtolepis monanthos* (L.) Less. (*Tanacetum monanthos* L. = *Anacyclus monanthos* (L.) Thell.).

Hiorthia Neck., *Elem.* **1** : 97 (1790); Less, *Syn. Gen. Comp.* : 258 (1832) *pro parte quoad Anacyclus valentinus* L.

Annuals and herbaceous perennials. *Stems* erect, creeping or subterranean, leafy above. *Leaves* alternate, crowded into rosettes to evenly distributed along the stem, glabrous to pubescent, bi- to tripinnatisect, flat to terete with narrow elongate segments. *Capitula* solitary, heterogamous, radiate, rarely discoid, gynomonoecious or homogamous-discoid, usually solitary at the ends of the peduncle branches or sometimes fused into a syncephalum or a syncephalous inflorescence. *Involucre* hemispherical or turbinate-hemispherical to cylindrical-campanulate; involucral bracts 3-seriate, the inner ones membranous, scarious-lacerate at the apex. Receptacle flat to shortly conical, palaeceous; the scales tough, leathery mucronate, carinate, surrounding the florets near the base, to somewhat scarious, obtuse and ± flat. *Ray florets* white, cream or yellow, sometimes with a deep red stripe below, female fertile, anterior-dorsally flattened, the tube persistent on the cypselas at maturity. *Disc florets* yellow, tubular-campanulate, 5-lobed at the apex, sometimes with 2 lobes longer and more erect than the other 3, articulating regularly with the ovary or broadened at the base and capping the ovary on the anterior side. *Cypselas* homomorphic, anterior-dorsally compressed, oblanceolate to obovate, laterally surrounded by a narrow to a very broad scarious wing. *Pappus* a unilateral corona, ± continuous with the lateral wing, otherwise absent.

Nomenclatural note: Linnaeus, in his *Species Plantarum* **2**: 892 (1753), describes three species of *Anacyclus: A. creticus*, *A. orientalis* and *A. valentinus*. The first two species now both belong to *Anthemis* L., leaving the third, *Anacyclus valentinus*, as the type of the genus. The protologue of *A. valentinus* reads as follows:

> 'ANACYCLUS foliis decompositis linearibus: laciniis divisis teretiusculis acutis, floribus flosculosis. *Hort. cliff.* 417. *Roy. lugdb.* 171. Chrysanthemum valentinum. *Clus. hist.* 1. *p.* 332. Buphthalmo tenuifolio simile. *Bauh. hist.* 3. *p.* 125. *Habitat ad* Reg. Valentini *agros & vias. Confer* Anthemidem valentinam',

suggesting that the type can be based on any one of the five elements. Since the description in *Hortus Cllffortianus* : 417 (1737) is virtually unchanged from that in *Species Plantarum*:

> 'Anacyclus foliis decompositis linearibus, laciniis divisis teretiusculis acutis. Cotula flore luteo nudo. *Tournef. inst.* 495. *Boerh. lugdh.* I, p. 107. Buphthalmo tenuifolio simile, Chrysanthemum valentinum clusii. *Bauh. hist.* 3. *p.* 125. Chrysanthemum valentinum. *Clus. hist.* 1. *p.* 332. *Crescit ad margines arvorum & viarum in* Regno Valentino',

the type can be based on a specimen from this herbarium. There are three specimens in the Hortus Cliffortianus collection at the British Museum, and all of them are of the same taxon. One of them is annotated with the following note: 'Chrysanthemum valentinum clusii Hort. 332. Cotula flore luteo nudo' and agrees with both the published phrase names. The specimen is considered to be a hybrid (see p. 128) between *A. homogamos* and *A. radiatus* on account of its few depauperate female ligulate florets in the outer series of the capitulum. Nevertheless, it is a species-equivalent in nomenclatural terms and can therefore be recognized as *A.* × *valentinus* L., eliminating the need for the recognition of *A. valentinus* (L.) Cass. (based on *Anthemis valentina* L.) as the type for the genus (see p. 88).

Distribution: see Fig. 11.

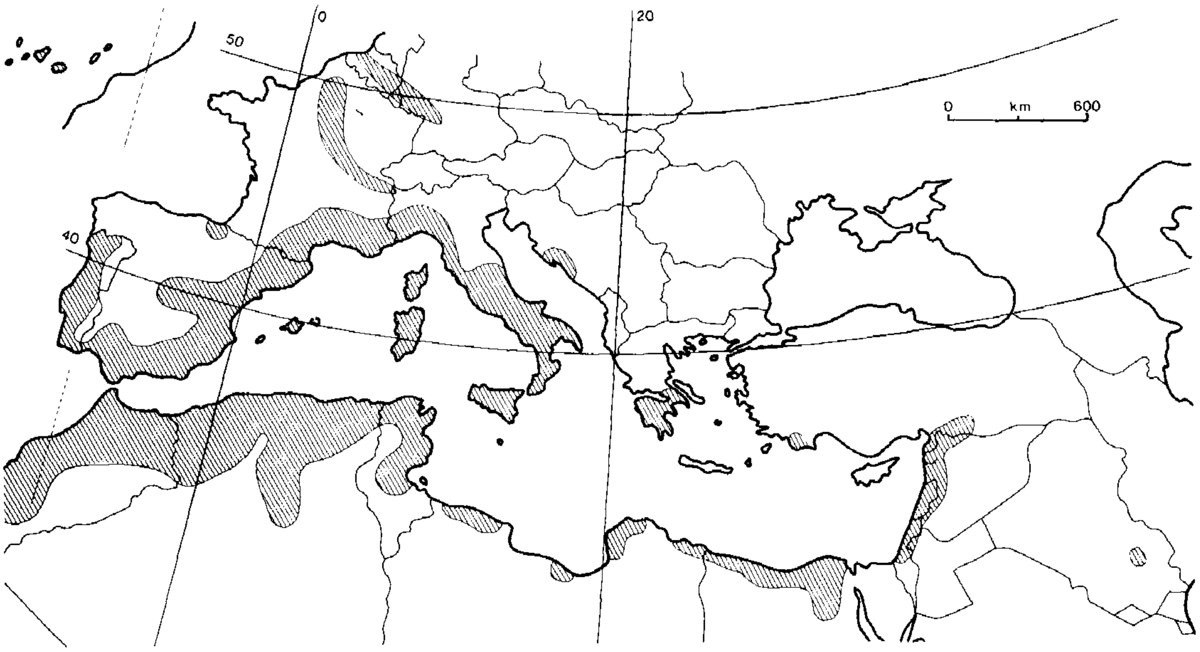

Fig. 11 Approximate total range of *Anacyclus*.

Artificial key to species, subspecies, varieties and hybrids

1. Capitula homomorphic, discoid
  2. Cypselas with erose margins
    3. Central basal capitulum present; peduncles tumescent — 2a. monanthos subsp. **monanthos** (p. 118)
    3. Central basal capitulum absent; peduncles unthickened — 2b. **monanthos** subsp. **crytolepidioides** (p. 118)
  2. Cypselas with entire margins — 6. **homogamos** (p. 127)
1. Capitula heteromorphic, outer florets ligulate, although sometimes shortly so, so that the capitula appear discoid
  4. Ligules ± inserted and hidden in the receptacular bracts
    5. Short ligules white — ×**inconstans** (p. 130)
    5. Short ligules yellow — ×**valentinus** (p. 131)
  4. Ligules clearly visible and exerted from the receptacular bracts
    6. Ligules with a red stripe below
      7. Perennials with a distinct woody caudex
        8. Capitula 13–22 mm in diameter; old leaf-bases persistent — 1a. **pyrethrum** var. **pyrethrum** (p. 114)
        8. Capitula 7–12 mm in diameter; old leaf-bases ephemeral — 1b. **pyrethrum** var. **depressus** (p. 114)
      7. Erect or decumbent annuals with simple roots
        9. Cypsela wings distinctly crenate — 3. **maroccanus** (p. 119)
        9. Cypsela wings ± entire
          10. Ligules yellow — 4a. **radiatus** subsp. **radiatus** (p. 123)
          10. Ligules white — 4b. **radiatus** subsp. **coronatus** (p. 124)
    6. Ligules without a red stripe below
      11. Lower leaves tripinnatisect
        12. Involucral bracts broadly expanded and scarious at the apex; receptacular scales obtuse
          13. Ligules yellow — 4a. **radiatus** subsp. **radiatus** (p. 123)
          13. Ligules white — 4b. **radiatus** subsp. **coronatus** (p. 124)
        12. Involucral bracts not expanded and only narrowly scarious at the apex; receptacular scales with spines — 5. **clavatus** (p. 124)

11. Lower leaves 1–2-pinnatisect
14. Disc corolla-tubes articulating normally with the ovary; cypselas with a lacerate corona; rhachis of upper leaves broad
15. Cypsela wing 2·5–2·75 mm wide; Turkey 8. **latealatus** (p. 134)
15. Cypsela wing 0·3–0·6 mm wide; Algeria 7. **linearilobus** (p. 131)
14. Disc corolla-tubes expanded into an orbicular flattened disc at the base of the dorsal margin, overlapping the ovary; cypselas ecoronate; rhachis of upper leaves narrow 9. **nigellifolius** (p. 135)

Sect. 1. PYRETHRARIA DC.

Anacyclus sect. *Pyrethraria* DC., *Prodr.* **6** : 15 (1838).
Anacyclus sect. *Leucocyclus* Batt. & Trabut, *Fl. Algér.* **3** : 453 (1890).

Herbaceous perennials; stem reduced to a basal, woody subterranean caudex; leaves heteromorphic, tripinnatisect to bipinnatisect; radical leaves occurring in basal rosettes. Peduncles many, prostrate, in annual rosettes. Ray florets white, with a red stripe below.

1. Anacyclus pyrethrum (L.) Link

Enum. Hort. Berol. Alt. **2** : 344 (1822); Cass., *Dict. Sci. Nat.* **34** : 102 (1825).
Anthemis pyrethrum L., *Sp. Pl.* : 895 (1753). Orig. coll.: Herb. Linnaeus 1016. 18. 'Pyrethrum 12' (LINN, lectotypus).
Anacyclus pseudopyrethrum Ascherson in *Bonplandia* **6:** 123 (1858) Orig. coll.: *Hohenacker*, Arznei-u. Handlespflanzen 119 (holotypus destructus).

Illustrations: Figs 2, 12. Edwards, 1799 : tab. 462; Schlectendal & Guimpal, 1833 : tab. 187; Meigen, 1842 : tab. 131e; Reichenbach, 1854 : tab. 999, fig. I, 1–3; Berg, 1861 : tab. 51, fig. 390; Artus, 1862–74 : tab. 144; Argenta, 1864 : tab. 175; Ball, 1878 : tab. 24; Bentley & Trimen, 1880 : tab. 151; Hager, 1887 : tab. 775; Pabst, 1888–90 : tab. 112; Quezel & Santa, 1963 : tab. 97, fig. 2849.

Common names: Agargarha, Agonthas, Akurkurka, Aoud el Athas, Bertram, Guenthous, Igneus, Manzanilla, Pellitory, πυρέθρυ, Piretro, Pyréthre, Pyrethri, Roman Pellitory, Spanish Chamomile, Spanish Pellitory, Tagendest, Tigenthast.

Perennial; stems fused with roots to form a submerged, woody caudex. *Leaves* heteromorphic, slightly pubescent; rosette leaves obovate in outline, petiolate, tripinnatisect, 3·0–14·0 × 0·5–3·0 cm with tiny, acute, linear ultimate segments; primary lobes in 4–9 opposite or subopposite pairs; rhachis slightly caniculate, cuneate at the base, the old veins often tough and persistent; peduncle leaves sessile, or shortly petiolate, bi- to rarely tripinnatisect, 1·0–3·0 × 0·3–1·5 cm, primary lobes in 1–6 subopposite pairs. *Inflorescence* a contracted corymbose cyme with individual creeping peduncles emerging from the centre of the caudex; each peduncle 6–30·0 cm long with 1–3 branches and terminal capitula, sparsely to densely villous, usually red, terete below the capitulum. *Involucre* 7·0–22·0 mm in diameter; involucral bracts in three rows, narrowly triangular, vivid green in the centre above, somewhat paler below with a distinct, but thin, dark-brown erose margin; receptacular scales obcuneate, carinate to canaliculate, the apices broadly obtrullate to cuspidate and overlapping the cypsela at maturity, somewhat membranous at the margin but extremely tough at the centre and above and often with a distinct central vein. *Ray florets* white, with a deep red stripe below; ligule 7·0–13·0 mm long, 3·0–4·5 mm wide, tube 3·0–5·0 mm long, 0·7–2·5 mm wide, anterior-dorsally compressed with narrow lateral wings, ♀-fertile but occasionally with vestigial anthers, articulating terminally on the ovary. *Disc florets* 3·0–5·0 mm long, anterior-dorsally compressed, lobes narrow triangular, somewhat cucullate and equal in size. *Styles c.* 3·5 mm long, the style arms 1·2–1·6 mm long. *Stamens* 3·9–4·1 mm long, anthers *c.* 2·0 mm long. *Cypselas* obcuneate to broadly ovate, 3·0–4·0 × 2·8–4·0 mm, pale grey to dark brown, sometimes purple, sphacelate; lateral wings thick, coriaceous, protruding apically with 2 ± acuminate auricles, 0·3–0·7 mm wide. *Pappus* absent.

Flowering period: Mainly May to August.

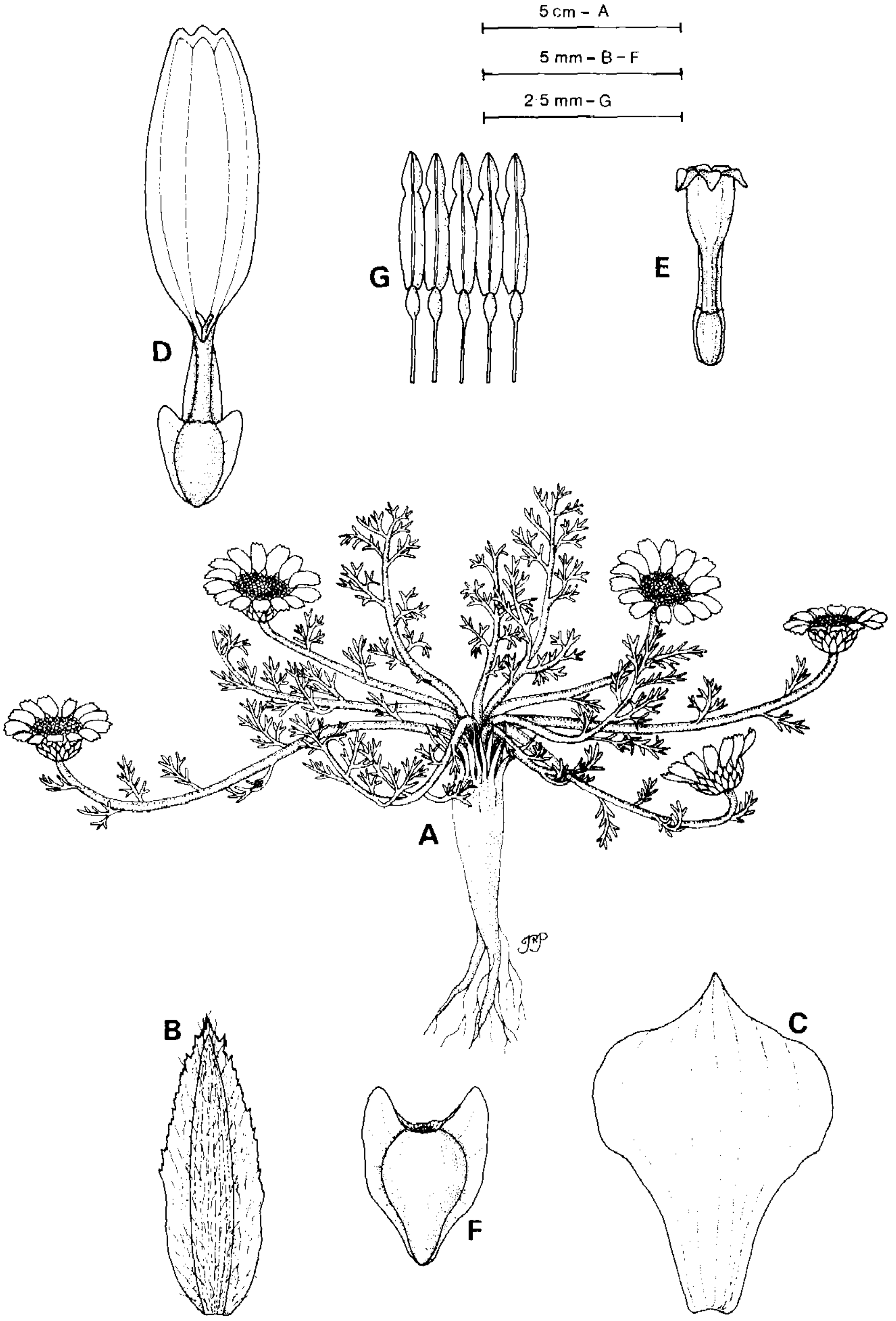

Fig. 12 *Anacyclus pyrethrum* var. *pyrethrum*: A – habit, B – involucral bract, C – receptacular scale, D – ray floret, E – disc floret, F – cypsela, G – anthers.

Chromosome number: 2n = 18.

Nomenclatural note: In Linnaeus's *Species Plantarum* the description of *Anthemis pyrethrum* remains unchanged from that given in *Hortus Cliffortianus* (1737 : 414). The type specimen, which should be in Herb. Cliff. (BM) is unfortunately missing. The only other specimens corresponding with elements in the protologue are those now kept at the Linnean Society of London (LINN). There are two specimens in this collection, genus 1016 – *Anthemis*, sheets 18 and 19 (Savage, 1945), of which the first, indicated by the name '*pyrethrum*', is an inflorescence fragment

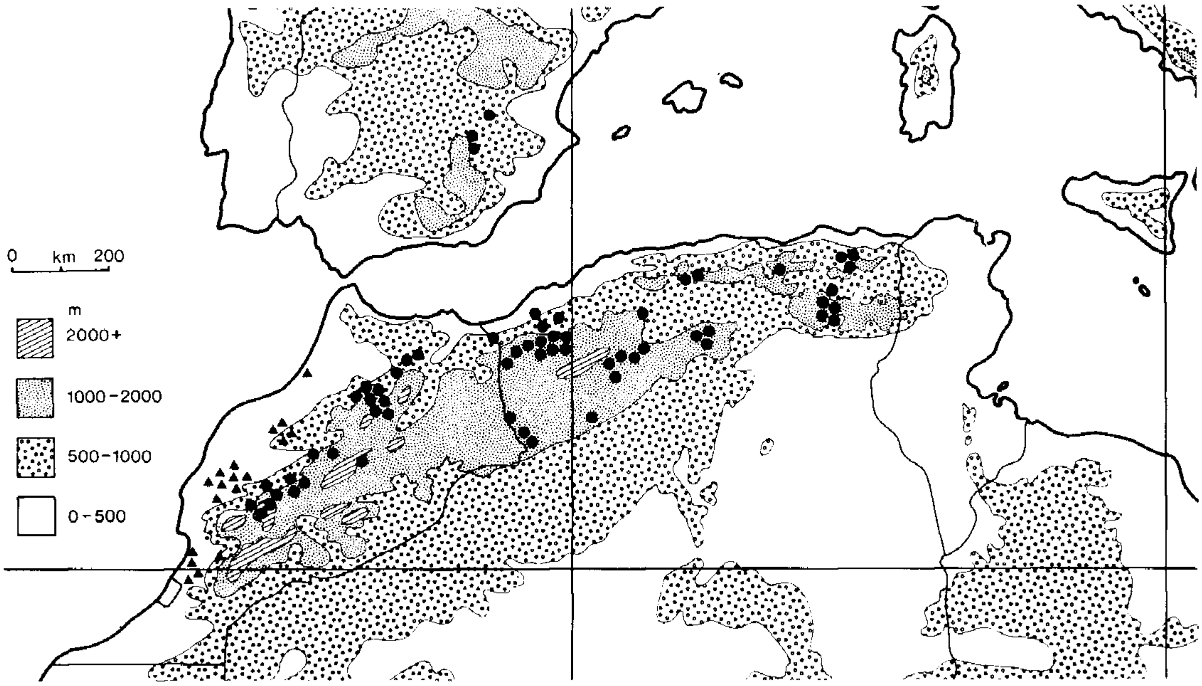

Fig. 13 Distribution of *Anacyclus pyrethrum* (●) and *A. maroccanus* (▲).

of *A. pyrethrum*. The second seems to be an aberrant cultivar. Therefore specimen 18 is chosen as the lectotype.

Variation: Anacyclus pyrethrum is perhaps the most distinctive species of the genus, since it possesses several morphological and biological features not shared by other species. Amongst the prominent morphological features are the submerged woody caudex, the heteromorphic leaves, the unusual prostrate inflorescence and the tough thickened cypselas. From a biological point of view, it appears to be the only species with a self-compatible breeding system (Uitz, 1970; Humphries, in press *a*) and occasionally has vestigial stamens in the normally female ligulate florets, suggesting its derivation from a homogamous hermaphrodite form. The cypselas are remarkably persistent at maturity and this, coupled with the fact that the receptacular scales overtop the cypselas so that they touch the next layer of bracts, makes the whole capitulum into a hard, round, almost woody head. Consequently it is often dispersed as a complete diaspore.

A. pyrethrum can be compared with the annual species *A. maroccanus*, since they share a number of plesiomorphous features, the most striking of which is the white ligules with the red stripe below. The hypothesis that they represent sister species should be tested as and when live material becomes available. The possibility that they have a recent common ancestry cannot be completely ruled out, especially in the light of their apparent vicariant distribution (Fig. 13).

A. pyrethrum is a very variable species, often occurring in small discrete montane populations. Formerly it was recognized as two species, *A. pyrethrum* and *A. depressus* Ball, the former usually being taken to comprise the more robust forms from Algeria and the eastern Moyen Atlas mountains of Morocco, which have longer stems, large capitula, longer ligules, harder fruits and generally larger vegetative parts, whereas the latter, variously called *A. feyni* Porta & Rigo, *A. pyrethrum* var. *subdepressus* Doumergue, var. *depressus* (Ball) Maire and var. *microcephalus* Maire, includes those shorter, less robust and occasionally hairier plants with small, but more numerous capitula, shorter ligules and smaller, softer cypselas, which occur in higher and drier habitats of western Algeria and the Sierra de Alcaraz, the Haut Atlas, the Anti-Atlas and the eastern Moyen Atlas. All the material of *A. pyrethrum* will fit into one of these form series; but since it is possible to find in the Moyen Atlas and parts of Algeria populations with plants which will fit into either series, to consider them as separate species or subspecies is artificial.

To emphasize the fact that there is a general reduction in various features in montane populations, two varieties are recognized.

Distribution and ecology: See Fig. 13. The distribution of *Anacyclus pyrethrum* covers a wide altitudinal range in all of the principal mountain ranges west of Guelma in Algeria in localities above 800 m. It occurs in Morocco in all exposed areas of the Moyen, Haut and Anti-Atlas and Algeria from all of the principal mountain ranges. In southern Spain all records refer to the Sierra de Alcaraz near Albacete.

The usual habitat is well drained stony ground or grassland between (800) 1100 and 3000 m, the species being particularly abundant around 1500 m.

Collections: 142 collections have been examined, mainly from the Haut and Moyen Atlas mountains and north-west Algeria.

a. Var. **pyrethrum**

Anacyclus pyrethrum var. *genuinum* Doumergue in *C.r. Ass. fr. Avanc. Sci.* **25** : 388 (1897), *nom. illeg.*
Anacyclus pyrethrum var. *typicus* Maire in *Mém. Soc. Sci. nat. Phys. Maroc* **15** : 39 (1926), *nom. illeg.*

Caudex robust. Leaf-bases persistent. Capitula 13·0–22·0 mm in diameter. Cypselas with thick wings.

Collections: Specimens mostly originate from Algeria but are common in Morocco in the more sheltered localities of the Moyen and Haut Atlas mountains.

b. Var. **depressus** (Ball) Maire

in Jahandiez & Maire, *Cat. Pl. Maroc.* **3** : 768 (1934).

Anacyclus depressus Ball in *J. Bot., Lond.* : 365 (1873); *J. Linn. Soc.* (Bot.) **16** : 503–504, t. 24 (1877). Orig. coll.: *Hooker & Ball s.n.* 'In regione superiore Atlantis majoris. In convalle Aït Mesan et in jugo Tagheret a 2200 m ad 2800 m' (K, holotypus).

Anacyclus feyni Porta & Rigo in *Atti J. R. Acad. Sci. Lett. Arli Nov.* 2 : 213 (1896) Orig. coll.: *Porta & Rigo* 721, 19–27/6/1891 (FI, holotypus, B, E, G, JE, M, S, W, U, Z, isotypi) [*Anacyclus freynianus* Porta & Rigo in sched. *A. freyni*(*i*) auct.].

Anacyclus pyrethrum var. *subdepressus* Doumergue in *C.r. Ass. fr. Advanc. Sci.* **25** 2 : 388 (1897). Orig. coll.: *Doumergue s.n.*, Bedeau, El Aricha (AL, holotypus).

Anacyclus pyrethrum var. *microcephalus* Maire in *Mém. Soc. Sci. nat. Phys. Maroc* **15** : 39 (1926). Orig. coll.: *Maire s.n.* 'Hab. in pascuis subalpinis Atlantis medii solo siliceo, ad alt. 1700–2000 m' (AL, holotypus, RAB, isotypus).

Caudex slender. Leaf bases not persistent. Capitula 7–12 mm n diameter. Cypselas with thin wings.

Collections: Specimens mostly originate from high alpine localities of the Atlas mountains, and also from exposed places in Spain and Algeria.

Anacyclus pyrethrum in **medicine and** the **origin of** *A. officinarum* Hayne

Pyrethrum, commonly known as pellitory, also as Spanish or Roman pellitory, Spanish chamomile, the πvpέθpv of Dioscorides and known in the east as Akurkurka, is the *Anacyclus pyrethrum* of modern writers. It owes its Greek and subsequent botanical names to the fiery and pungent flavour of the root (caudex) and the Latin name *Salivaria* because on chewing it causes a remarkable flow of saliva (Harley, 1876). In fact the caudex appears to be the only part which was widely used in medicine, because of its pungent efficacy in relieving toothache and promoting a free flow of saliva. Mary Grieve (1911) tells us that: 'the British Pharmacopoeia directs that it be used as a masticatory, and in the form of lozenges for its reflex action on the salivary glands in dryness of the mouth and throat. The tincture made from the dried root [caudex] may be applied to relieve the aching of a decayed tooth, applied on cotton wool, or rubbed along the gums, and for this purpose may with advantage be mixed with camphorated chloroform. It forms an addition to many dentifrices.

'A gargle of Pellitory infusion is prescribed for relaxed uvula and for partial paralysis of the tongue and lips. To make a gargle two or three teaspoonsful of Pellitory – to be obtained from any druggist – should be mixed with a pint of cold water and sweetened with honey if desired.' Amongst its other, less important uses, it has been prescribed for relief of neuralgia, rheumatism of the head and tongue palsy. Since it is a rubefacient and a local irritant when sliced and applied to the skin, it induces heat, tingling and redness. The powered root produced a good snuff to cure chronic catarrh of the head and nostrils and to clear the brain, by exciting a free flow of nasal mucous and tears. Culpepper's herbal (see Anon, 1814) notes that *A. pyrethrum* 'is one of the best purges of the brain that grows' and is not only 'good for ague and the falling sickness [epilepsy]' but is 'an excellent approved remedy in lethargy'. After stating that 'the powder of the herb or root snuffed up the nostrils procureth sneezing and easeth the headache', it goes on to mention that 'being made into an ointment with hog's lard it taketh away black and blue spots occasioned by blows or falls, and helpeth both the gout and sciatica'. All the uses described in Culpepper were obsolete by the turn of this century. The pellitory-of-Spain was well known in the thirteenth century and was a valuable remedy for toothache with Welsh physicians (Grieve, 1911). It was familiar to Arabian writers of medicine and was still a favourite herbal remedy in the east and western Europe until the First World War, having long been an article of export from Algeria and southern Spain by way of Egypt to India.

The activity of the root appears to be due to two active crystalline resiniferous alkaloids, pellitorine and pyrethrine. *A. pyrethrum* ceased a long time ago to be used in medicine, since pellitorine, with a melting point of 22 °C, has been identified as N-isobutylamide, a reasonably powerful, poisonous insecticide. It was originally identified as N-isobutyl-cis-2-trans-6-decadieneamide but is now known to contain a mixture of at least four isomers of this product (Metcalf, 1955).

Polyacetylenes and particular amides are important taxonomically and form a distinct group of natural products characteristic of the genus. Although their biogenesis is not sufficiently clarified, it appears that most of them are derived from C_{18}-diyne-ene acid and other compounds closely related to linoleic acid and dehydromatricaria ester (Greger, 1977).

During the eighteenth and nineteenth centuries, *A. pyrethrum* was widely cultivated in European botanic gardens, particularly for its medicinal properties. In his '*Getreue Darstellung und Beschreibung der in der Arzneykunde gebräuchlichen Gewdchse*, . . . part 9', Friedrich Hayne (1825) considered that Linnaeus's concept of *Anthemis pyrethrum* (subsequently *Anacyclus pyrethrum* Link) was a 'polytypic' species containing in reality two elements, the cultivated annual 'Bertram wurzel' from Magdeburg botanic garden and the true north African perennial *A. pyrethrum*. Hayne concluded that Linnaeus's phrase name referred to the common garden form of *A. pyrethrum* (i.e. var. *depressus*), and he therefore described the annual German cultivar as a distinct species, *A. officinarum*. There are very few herbarium specimens of the latter 'species' since it appears to have been extinct since the turn of this century. The Magdeburg apothecaries cultivated the Bertram wurzel to only a limited extent (Bischoff, 1847; Harley, 1876; Hayne, 1925); and their poor knowledge of this plant, which was variously known as the Bertram root, German pellitory, African pellitory and ringblume, has led to a certain amount of misapplication of the name so that today it is incorrectly used for various species, particularly for *Anthemis altissima* Jacq. but also for *Anacyclus pyrethrum*, *A. radiatus* and *A. clavatus*. Morphological examination of *A. officinarum* (see Table 2) suggests that it is either an unusual annual derivative of *A. pyrethrum* or a hybrid between the latter species and *A. radiatus* or *A. clavatus*, since all of these are commonly cultivated together. All attempts to artificially hybridize these three species (and any other annual species) with *A. pyrethrum* have so far met with failure (Humphries, in press, *a*), so therefore the first hypothesis is currently favoured.

Illustrations of Anacyclus officinarum: Hayne, 1825 : tab. 46; Schlectendal & Guimpal, 1833 : tab. 188; Petermann, 1849 : tab. 48, fig. 374; Berg & Schmidt, 1863 : tab. 34e; Bentley & Trimen, 1880: tab. 152;

Karsten, 1880–83: 1086; Hager, 1887 : 774; Schlechtendal, Langethal & Schenk, 1887 : tab. 3039, p. 264; Karsten, 1895 : 666; Garcke, 1898 : 320; Fedtschenko & Flerov, 1910 : 969.

Sect. 2. Anacyclus

Anacyclus sect. *Anacyclus*, sect. typ. gen.
Anacyclus sect. *Diorthordon* DC., *Prodr*. **6** : 16 (1838).
Anacyclus sect. *Cyrtolepidia* Pomel, *Nouv. Mat. Fl. Atl.* : 53 (1874).
Anacyclus sect. *Cyrtolepis* (Less.) Batt. & Trabut, *Fl. Algér*. **3** : 452 (1890).

Annuals; stems aerial; leaves homomorphic to heteromorphic, tripinnatisect to pinnatisect; radical leaves rarely present. Peduncles one to several, erect to rarely creeping, divaricately branching. Ray florets white or yellow, with or without a red stripe below, or completely absent.

2. **Anacyclus monanthos** (L.) Thell.

in *Mém. Soc. Nat. Sci. Cherbourg*, IV, 38 : 518 (1912); C. Christensen in *Dansk Bot. Ark*. **3** : 26 (1922).
[*Tanacetum monanthemum* Vaill. in *Hist. Acad. Sci. Paris* : 282 (1719).]
Tanacetum monanthos L., *Mantissa* **1** : 111 (1767). Orig. coll.: *Forskål*, Cult. hort. Uppsala, Herb. Linnaeus 987.8 (LINN, holotypus).

Annual; stems virtually absent, reduced to a short, erect or creeping protusion on a slender tap-root. *Leaves* heteromorphic; rosette leaves, when present petiolate, tripinnatisect, 3·0–10·0 × 0·5–3·0 cm, with slender to sometimes broad, fleshy, acuminate ultimate segments; primary lobes in 4–7 opposite or subopposite pairs; rhachis flat, cuneate at the base, with prominent veins; pedunculate leaves sessile to petiolate, bi- or more rarely tripinnatisect, 0·5–4·2 × 0·2–1·2 cm, primary lobes in 2–8 subopposite pairs. *Inflorescence* a contracted cyme with radiating creeping or ascending peduncles, emerging alternately from a reduced central stem; peduncles sometimes contracted to form a central synflorescence of 2–6 capitula or a single syncephalum (1·0–) 4·0–24·0 (–35·0) cm long, with 1–9 branches and 3–6 (–12) terminal capitula, sparsely to densely villous, often inflated and sometimes fasciate and tumescent. *Involucre* 6·0–20·0 mm in diameter or up to 25·0 mm in a syncephalum; involucral bracts in 3 rows, 2·5–5·2 × 0·5–2·5 mm, outer series triangular, inner series broadly triangular to obcuneate, usually densely villous, usually green to brown and scarious above, somewhat fleshy and thick below, with an acuminate apex and thin laciniate margins; receptacular scales 2·8–4·5 × 2·2 – 6·0 mm, transversely broadly obovate, the apex cuspidate, caniculate, overlapping the cypsela at the apex when mature, slightly membranous at the margin but tough at the centre and above, with an obvious central vein. *Florets* discoid, hermaphrodite, homomorphic, 3·0–4·0 mm long, actinomorphic to heteromorphic radiant, where 2 corolla lobes are longer than the other 3; corolla lobes slightly cucullate, tubes anterior-dorsally compressed with lateral wings slightly broader at the base. *Styles* 2·9–3·1 mm, style arms *c*. 0·6 mm long. *Stamens* 2·8–3·5 mm long, anthers *c*. 0·5 mm long. *Cypselas* broadly obovate, 1·8–2·5 × 1·0–2·7 mm, usually light brown to yellow, lateral wings narrow, 0·1–0·5 mm wide, but thick, with a distinct toothed margin. *Pappus* a marginal corona or absent.

Flowering period: Mainly February–April.

Variation: *Anacyclus monanthos* is a variable species comprised of two subspecies, subsp. *monanthos* and subsp. *cyrtolepidioides*, which look quite different from one another, but are vicariant sister taxa occurring as a stepped cline running from Egypt to central and southern Algeria. The western taxon, subsp. *cyrtolepidioides*, is the least distinct, since many populations look superficially very similar to the Iberian-Moroccan species *A. homogamos*. It is tempting to consider that these two taxa may have shared common ancestry, although the hard, almost epappose cypselas with narrow, dentate lateral wings, together with the somewhat leathery, obcuneate receptacular scales of subsp. *cyrtolepidioides*, are easily distinguishable from the pappose cypselas with broad, thin, entire wings and the scarious receptacular scales of *A. homogamos*. Subsp.

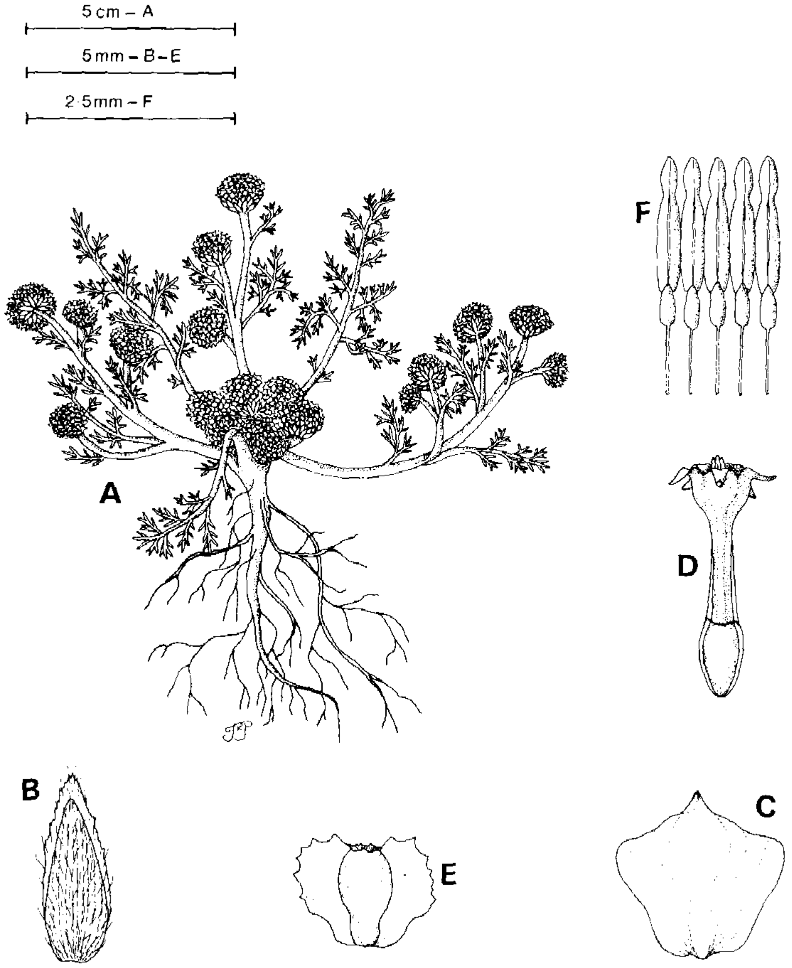

Fig. 14 *Anacyclus monanthos* subsp. *monanthos*: A – habit, B – involucral bract, C – receptacular scale, D – floret, E – cypsela, F – anthers.

monanthos, by contrast, is easily recognizable by a number of features and is usually known as *A. alexandrinus* Willd.

The habit, the type of inflorescence and the shape of the corolla lobes are the most important varying characters. Others include the hardness of the mature fruits and receptacular scales, and the size and number of capitula.

Subsp. *monanthos* is particularly well defined in both morphology and distribution. In the eastern part of its distribution it shows the most marked extremes in its acauline prostrate habit, the development of syncephalous and clustered capitula along with reduction and fasciation in the peduncles, the presence of prominent rosette leaves with very broad, cuneate rhachis bases, and the heaviest thickening in the mature fruits and receptacular scales. All these features appear to be adaptations to the extremely dry, hot conditions experienced in the desert. By contrast, subsp. *cyrtolepidioides* is less prostrate and even decumbent in Algerian and Tunisian collections, it does not have central basal clusters of capitula or syncephala, it rarely has fasciated peduncles and it sometimes has a short central stem. There is a marked absence of rosette leaves, the cypsela wings are thinner, and the cypselas are only slightly overtopped by the thickened cuspidate apices of the receptacular scales.

Both subspecies seem to occur in small discrete populations; but they come into contact in southern Tunisia and Tripolitania, where the differences between them are not quite as clear-cut as the above descriptions may suggest, several intermediate specimens having been found. Nevertheless, the vicariant, stepped-clinal variation between the extremes indicates a divergent allopatric speciation pattern.

Distribution and ecology: See Fig. 15. *Anacyclus monanthos* extends from the Nile delta in north-east Egypt to Ghardaia in the desert south of the Atlas Saharien in Algeria. Both subspecies are pioneers of sandy soils. In this context it is interesting that subsp. *cyrtolepidioides* is the dominant weed, replacing *A.* × *valentinus*, in the sandy wastelands of Biskra and Ghardaia in Algeria and around Gabes and Gafsa in Tunisia.

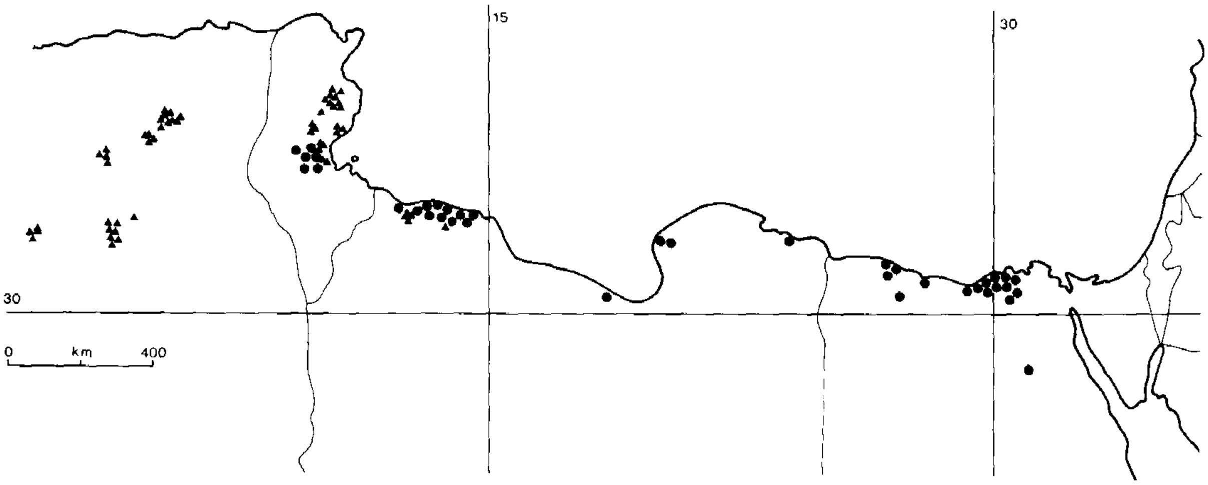

Fig. 15 Distribution of *Anacyclus monanthos* subsp. *monanthos* (●) and subsp. *cyrtolepidioides* (▲).

a. Subsp. **monanthos**

Santolina terrestris Forskål, *Fl. Aegypt.-Arab.* 147 (1775). Orig. coll.: *Forskål* (1762), Cent. 5, no. 72, Aegypto: Alexandria in vicinia columna Pompeyi (C, holotypus).
Anacyclus alexandrinus Willd., *Sp. Pl.* **3** : 2173 (1800). Orig. coll.: Herb. Willdenow 16307 (B, lectotypus).
Anthemis arabica Viv., *Fl. Lib.* : 56 (1824), non. L.
Hiorthia alexandrina (Willd.) Less., *Syn. Gen. Comp.* : 258 (1832).
Cyrtolepis alexandrina (Willd.) DC., *Prodr.* **6** : 17 (1838).
Cyrtolepis alexandrina (var.) β *glabra* DC., *Prodr.* 6 : 18 (1838).
Cyrtolepis alexandrina DC. var. nov. Coss. in *Bull. Soc. Bot. Fr.* **36** : 95 (1889).

Illustrations: Figs 2, 4, 14. Delile, 1814 : tab. 48; Gubb, 1913 : tab. 13; Quezel & Santa, 1963 : tab. 97, fig. 2850.
Common names: Sorret el Kebch.

Peduncles prostrate, emerging from the axils of the rosette leaves or from the axils of receptacular bracts of syncephalous capitula, frequently swollen and coalescing into groups of 2 or 3. Central capitula present, occasionally 2–4 coalescing into a syncephalum or forming a congested inflorescence.

Collections: 89 collections were examined, predominantly from the north desert areas of Libya and Egypt.

b. Subsp. **cyrtolepidioides** (Pomel) Humphries, **stat. nov.**

Anacyclus cyrtolepidioides Pomel, *Nouv. Mat. Fl. Atl.* : 54 (1874). Orig. coll.: *Kralik* 248, Gabes (BM, E, G, LE, Z, isotypi).
Anacyclus valentinus sensu Desf., *Fl. Atl.* **2** : 285 (1799) sphalm., non. L.
Cyrtolepis monanthos Less. in *Linnaea* 6 : 166 (1831).
Anacyclus mauritanicus Pomel, *Nouv. Mat. Fl. Atl.* : 55 (1874). Orig. coll.: *Pomel s.n.* Hautes steppes et montagnes des Ksous Mkraoula, El Beida, Aflou, Ksel (AL, holotypus; MPU, isotypus).

Anacyclus alexandrinus Boiss. in Batt. & Trabut, *Fl. Algér.* **3** : 452 (1890) sphalm, non Willd.
Anacyclus valentinus var. *tripolitanus* Borzi & Matthei in *Boll. Soc. bot. ital.* **1913** : 139 (1913).
Anacyclus cyrtolepidioides var. *mauritanicus* (Pomel) Batt. ex Jahandiez & Maire, Cat. *Pl. Maroc* **3** : 767 (1934).

Illustration: Gubb, 1913 : tab. 12.

Common names: Djerf, Sorret el Kebch, Rebiana.

Peduncles decumbent, emerging from a reduced, branched central stem, slender. Central capitulum absent.

Collections: 48 collections were examined, predominantly from Tunisia and Algeria.

3. **Anacyclus maroccanus** (Ball) Ball

in *J. Linn. Soc.* (Bot.) **16** : 504 (1878).
Anacyclus clavatus subsp. *maroccanus* Ball in *J. Bot. Lond.* **11** : 365 (1873). Orig. coll.: *J. Ball. s.n.* (31 May, 1871), ex provincia Shedma juxta Mskala, Insturia, Agadir, Marrakesh (K, holotypus, BM, LE, P).
Anacyclus valentinus var. *maroccanus* Ball ex Pitard, *Expl. Sci. Maroc. Bot.* **1** : 57 (1913), *nom. nud.*

Illustrations: Figs 2, 4, 16.

Common names: Chemt-el-fellous.

Annual; main stems extremely short, 1–2 cm long, or virtually absent, emerging from a simple taproot. *Leaves* alternate, sessile, oblong to spathulate in outline, 2·0–10·0 × 0·5–2·5 cm, tri-pinnatisect, sparsely to densely villous, especially when young. Primary lobes in 7–12 subopposite or alternate pairs, reduced at the base; ultimate segments long-acuminate; rhachis prominent, long-cuneate, broad at the base. *Inflorescence* a very contracted corymbose cyme; peduncles 2–12 erect, conspicuously spreading or decumbent, (2·0–) 5·0–30 cm long, emerging spirally from the axils of the stem leaves or basal rosette, ± glabrous to densely villous (especially towards the apex) and often tinged with red, distinctly clavate, up to 6·0 mm wide but narrowing slightly immediately below the capitulum. *Involucre* 5·0–12·0 (–15·0) mm; involucral bracts multiseriate 4·0–6·0 × *c.* 0·2 mm, triangular, herbaceous, green with a thin dark-brown margin, somewhat erose at the apex; receptacular scales ± oblong to obcuneate, 2·5–3·5 × 2·5–3·5 mm with tough, chartaceous centres and thinner, membranous wings, the apex cuspidate. *Ray-florets* white with a deep red stripe below; ligule 7·0–26·0 mm × 2·5–5·0 mm, usually minutely 3-lobed at the apex; tube 3·0–4·0 × *c.* 0·5 mm, anterior-dorsally compressed with a narrow, winged margin *Disc-florets* 3–4 × 0·5–0·7 mm, anterior-dorsally compressed with narrow winged margins; lobes narrow-triangular, cucullate, with extended heads on two of the lobes. *Styles c.* 3·5 mm long, style arms 0·5–0·8 mm long. *Stamens* 3·0–3·5 mm, anthers 1·5–2·0 mm. *Cypselas* 2·0–2·6 × 0·9–1·8 mm, obcuneate; wings 0·2–0·5 mm wide, thin, crenate, with two minute auricules; epicarp pale brown-grey, covered with long, longitudinally orientated myxogenic cells. *Pappus* either a minute crenate corona or occasionally absent.

Flowering period: Mainly March–April.

Observations: This distinctive species is generally a creeping or decumbent annual, with a markedly reduced main stem. Superficially, the habit and the white ligules with a red stripe of *Anacyclus maroccanus* are similar to *A. pyrethrum*. However, the fruit structure is entirely different, the crenate margins being similar to those of *A. monanthos*.

Distribution and ecology: See Fig. 13. An ephemeral annual of the Moroccan plain. Generally restricted to roadside habitats.

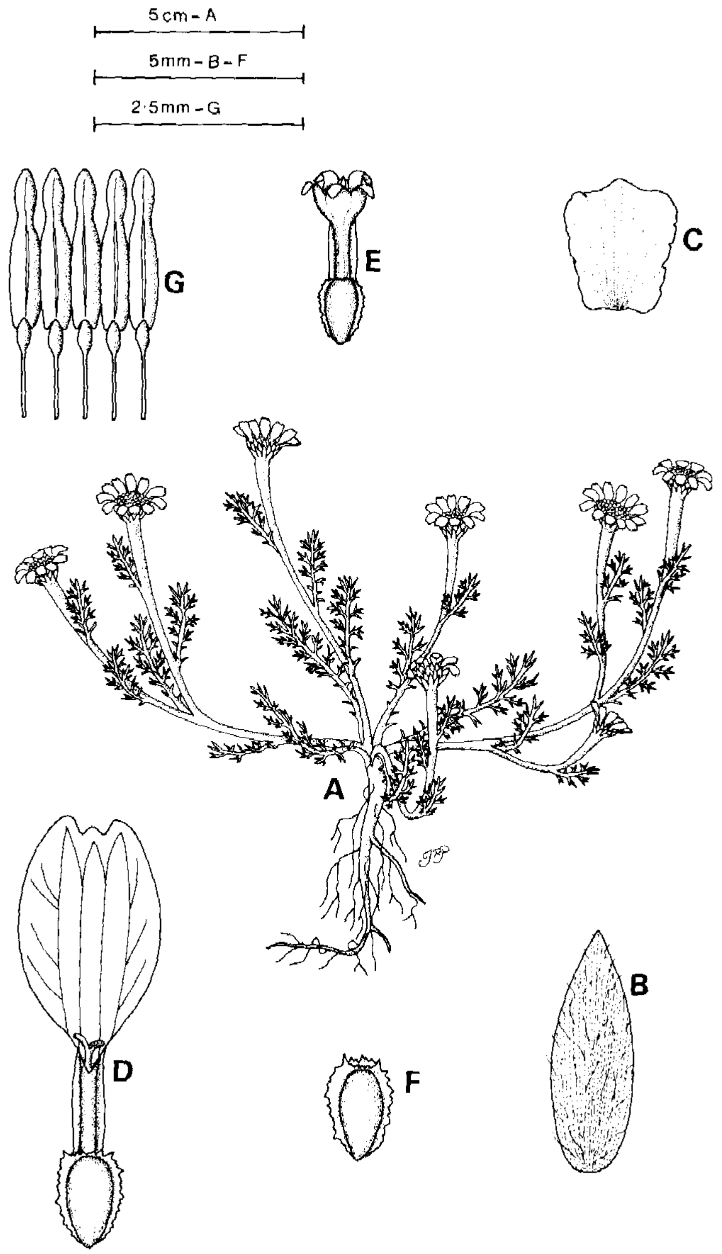

Fig. 16 *Anacyclus maroccanus*: A – habit, B – involucral bract, C – receptacular scale, D – ray floret, E – disc floret, F – cypsela, G – anthers.

Collections: 43 collections examined from the north-western plain of Morocco.

4. **Anacyclus radiatus** Loisel.

Fl. Gall. : 583 (1807). Orig. coll.: Herb. Loiseleur des Longchamps, 'Environs d'Hières (leg.) par M. Leon Dufour etc.' (AV, lectotypus).

Anthemis valentina L., *Sp. Pl.* : 895 (1753). Orig. coll.: Herb Cliff. '*Chrysanthemum folio matricariae latiori, flore aureo*' (BM, lectotypus).

Chamaemelum valentinum (L.) All., *Fl. Pedem.* **1** : 187 (1785).

Common names: Yellow Anacyclus.

Annual or short-lived biennial; stems erect, simple, 7·0–12·0 cm high, emerging from a vestigial basal rosette, glabrous or hairy, often tinged with red. *Leaves* alternate, sessile, crowded at the base, spathulate in outline, (2·5–) 4·0–16·0 × 2·0–5·0 cm, tripinnatisect; primary lobes in 6–14 subopposite or alternate pairs, reduced at the base; ultimate lobes short, simple, acuminate; rhachis broad, flattened at the base, slightly decurrent. *Inflorescence* a corymbose cyme; peduncles terminal, often clavate, hollow and up to 5 mm wide at the apex. *Involucre* (5·0–) 15·0–18·0 mm; involucral bracts in 2 or 3 rows; outer bracts triangular to linear-oblong, herbaceous, with a thin brown erose scarious margin; inner bracts oblong-obovate to spathulate, (4–) 5–8 × 1·5–3·0 mm, chartaceous, with a thin flabelliform laciniate membranous apex; receptacular scales 3·5–5·0 × 2·0–3·0 mm, chartaceous, obcuneate, mucronate, somewhat inwardly curved. *Ray florets* (4–) 8·0–17·0 (–22) mm long × (0·8–) 2·5–7·0 (–10·0) mm wide, yellow, cream or white, sometimes with a red-purple stripe below, ± truncate, shallowly emarginate to 3-lobed at the apex; tube 3·5–4·0 × 0·6–1·5 mm, anterior-dorsally compressed, with distinct, parallel-sided lateral wings. *Disc florets* 3·0–4·5 mm long, tube 0·3–1·4 mm wide, hypocrateriform; lobes triangular-ovate, acute, usually regularly cucullate, or with extended hoods on 2 of the lobes. *Styles* 3·0–4·0 mm, style arms *c.* 0·8 mm long. *Stamens* 3·4–3·8 mm, anthers *c.* 0·5 mm. *Cypselas* 2·5–4·0 × 1·0–3·0 (–3·8) mm, widely obovate to obcuneate, pale brown, covered with short, longitudinally orientated, striate myxogenic cells; lateral wings tough, hyaline when mature, 0·4–0·8 (–1·0) mm wide, terminating in an erect or slightly inwardly projecting point. *Pappus* a fimbriate corona, contiguous with the lateral wings, abaxially deeply emarginate to sometimes completely absent on the inner disc florets.

Flowering period: Mainly March–September; although occasional flowering specimens have also been recorded for January, February and October.

Chromosome number: 2n = 18.

Variation: Anacyclus radiatus is a robust annual herb easily distinguished from other species by the inner spathulate involucral bracts with expanded, membranous erose, hyaline apices. It is widespread over the western Mediterranean region and varies along the distribution range. As indicated by ligule colour it forms two fairly discrete taxa with distinct geographical distribution. Subsp. *radiatus*, found in north-west Morocco, the Atlantic coast of Portugal and the Mediterranean coasts of Algeria, Libya, France, Spain and Italy, and introduced in the eastern Mediterranean, is unique within the genus by the possession of yellow ligules (the remainder being white or rayless). In southern Morocco around the regions of Oueds Sous and Massa, the Sous valley towards Taroudant and in the Canary Islands, the white-rayed forms of subsp. *coronatus* completely replace subsp. *radiatus*. In various Atlantic coast localities of Morocco from Safi to Mogador there are several populations exhibiting intermediates between the two subspecies. Populations with pale yellow ligules have been called var. *ochroleucus* Ball. Various other colour morphs exist, particularly sulphur yellow forms known as var. *sulfureus* Braun-Blanquet & Maire and an unnamed form with pale yellow or whitish straps and deep yellow bases to the ray florets, which also occur in this region. None of these forms really warrants formal status. Both subspecies have sporadic individuals with red stripes on the lower side of the ligule (a plesiomorphous condition shared by *A. pyrethrum* and *A. maroccanus*), which for subsp. *radiatus* have been called *A. purpurascens* (Pers.) DC. or subvar. *purpurascens* (Pers.) Rouy.

In his protologue, Murbeck distinguishes subsp. *coronatus* (as a variety) not only by ligule colour but also by pappus shape: '. . . in facie interna pappo magno continuo lacero-fimbriato praeditis'. Although all material of this subspecies does seem to have an extremely large fimbriate pappus, the character is not restricted to this taxon but is also very common in individuals with yellow ray florets, particularly in northern Morocco and southern France.

Distribution and ecology: See Fig. 18. *Anacyclus radiatus* occupies a considerable area in lowland localities of the western Mediterranean from Ifni and the Canary Islands in the south to south central France and Italy in the north. Subsp. *radiatus* follows the coast and roadsides from Mogador in the south to around Tangier in north Morocco, occurring also inland around Fez.

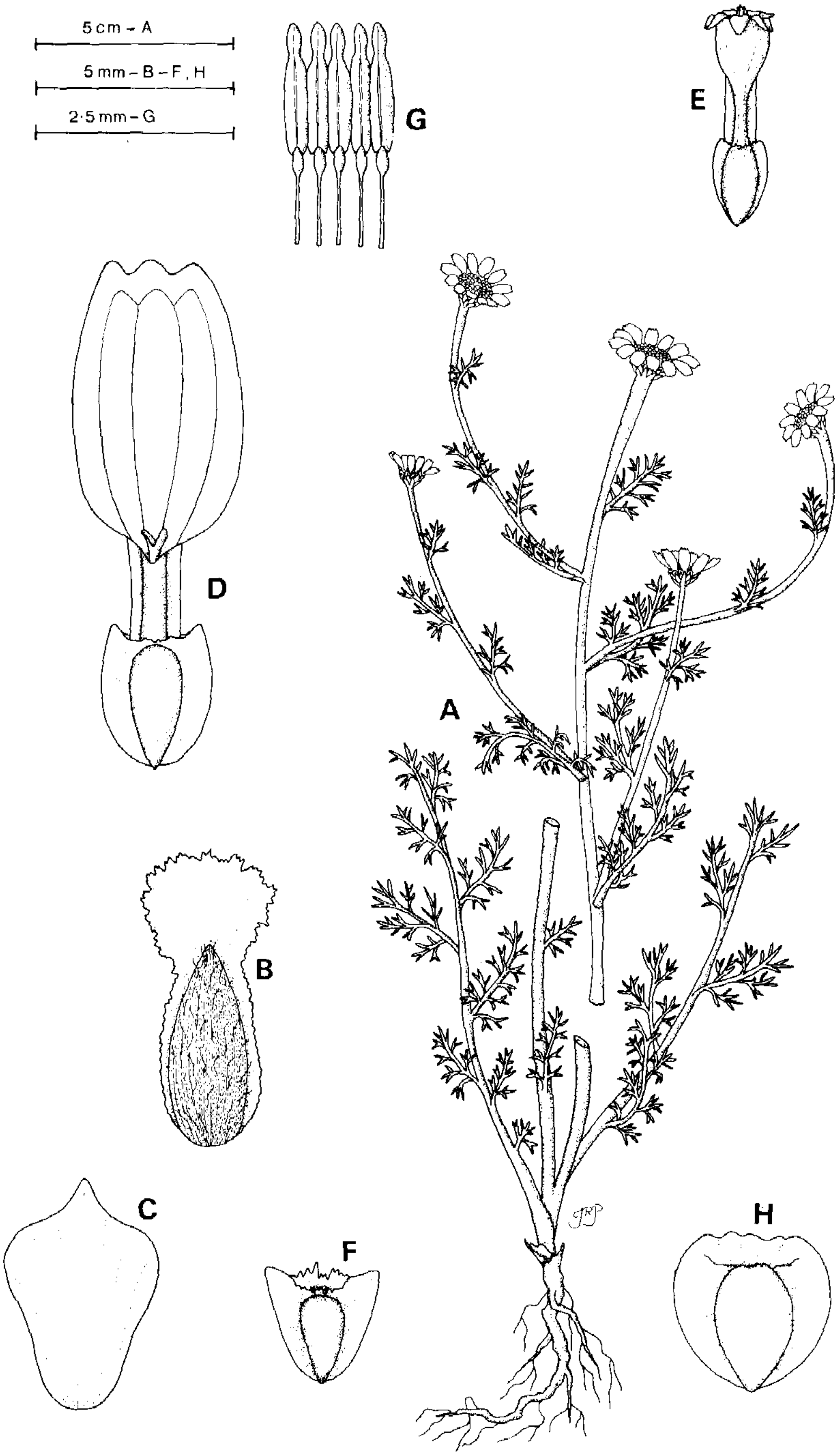

Fig. 17 *Anacyclus radiatus* subsp. *radiatus*: A – habit, B – inner involucral bract, C – receptacular scale, D – ray floret, E – disc floret, F – cypsela, G – anthers. Subsp. *coronatus*: H – cypsela.

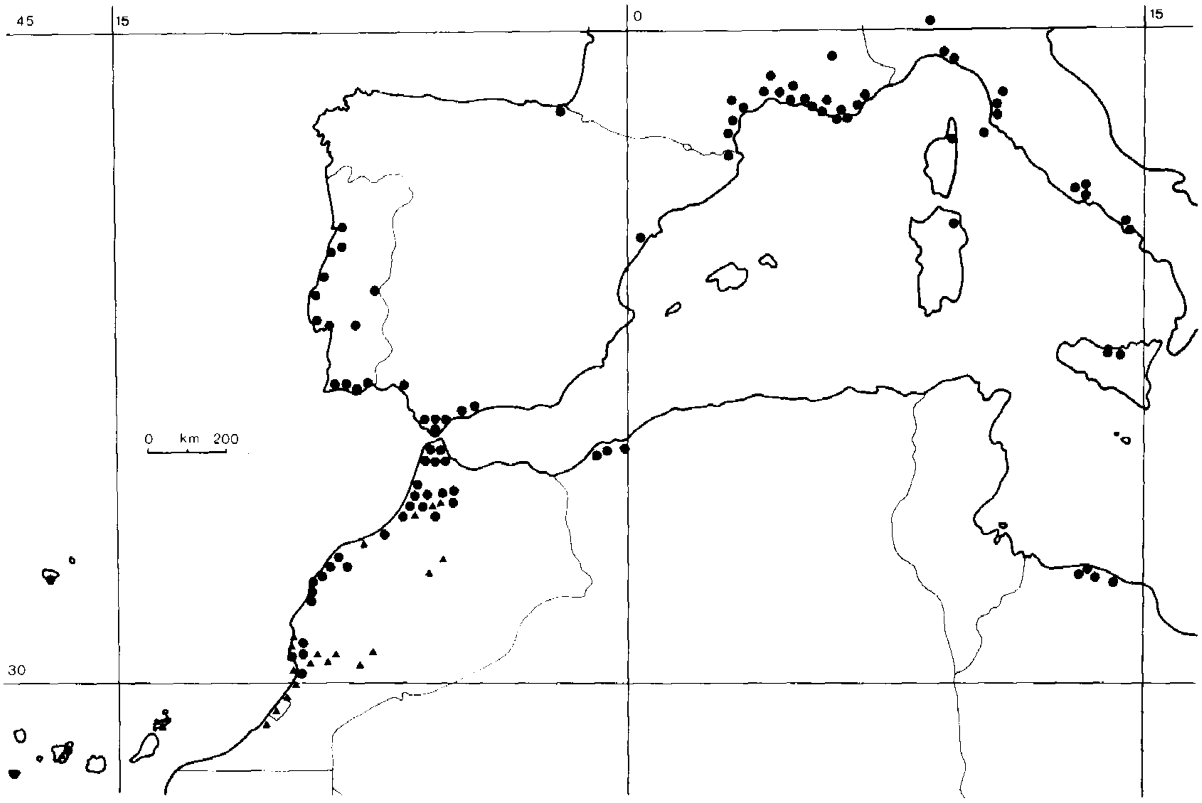

Fig. 18 Distribution of *Anacyclus radiatus* subsp. *radiatus* (●) and subsp. *coronatus* (▲).

Isolated collections have also been made from coastal regions around Oran in Algeria and Tripoli in Libya. Its European distribution is confined almost entirely to warm coastal places and around towns in Portugal, Spain, France, Italy, Sicily, Corsica and Sardinia. Subsp. *coronatus* occurs only in Morocco and the Canary Islands. It occurs most commonly in the Sous valley between the Haut Atlas and Anti-Atlas mountains, but occasional collections have been obtained as far north as the Marmora forest near Rabat.

Subsp. *radiatus* is mostly a ruderal of disturbed cultivated land but occurs on sand dunes and other shifting habitats in coastal localities. Subsp. *coronatus* occurs mostly on dry sandy soil or sand dunes, particularly in dried-up waddis.

a. Subsp. **radiatus**

Anacyclus aureus sensu Brot., *Fl. Lusit.* **1** : 363 (1804); DC. in Lam. *Fl. Fr.* 4 : 202, tab. 700, fig. 2 (1805) *pro parte quoad basionym.*

Anacyclus aureus (var.) β *radiatus* Pers., *Syn. Pl.* **2** : 465 (1807). Orig. coll.: Herb. Persoon in herb. Lugd. Bat. 900, 68-129 (L, lectotypus).

Anacyclus valentinus (var.) * (α) *bicolor* Pers., *Syn. Pl.* **2** : 465 (1807). Orig. coll.: Herb. Persoon in herb. Lugd. Bat. 900, 68-128 (L, lectotypus).

Anacyclus valentinus (var.) β *purpurascens* Pers., *Syn. Pl.* **2** : 465 (1807). Orig. coll.: Herb. Persoon in Herb. Lugd. Bat. 900, 68-137, Montpellier ad mare (L, lectotypus).

Anacyclus purpurascens (Pers.) DC. in Lam., *Fl. Fr.* **5** : 481 (1815).

Hiorthia aurea (L.) Less., *Syn. Gen. Comp.* : 258 (1832), *pro parte quoad basionym.*

Anacyclus radiatus (var.) β *purpurascens* (Pers.) DC. *Prodr.* **6** : 16 (1838).

Anacyclus pallescens Guss., *Fl. Sic. Syn.* **2** : 494 (1844). Orig. coll.: *Gussone s.n.* In herbosis maritimis Cefalu alla marina (Gasparrini) (not seen).

Anacyclus radiatus (var.) γ *pallescens* (Guss.) Arcangeli, *Comp. Fl. Ital.* : 359 (1882).

Anacyclus radiatus subvar. *purpurascens* (Pers.) Rouy, *Fl. Fr.* **8** : 239 (1903).

Anacyclus radiatus var. *sulfureus* Braun-Blanquet & Maire, in *Mém. Soc. Sci. nat. Phys. Maroc* **8** : 232

(1924) Orig. coll.: *Braun-Blanquet & Maire s.n.*(1921), Grande Île de Mogador. Pâturages sablonneux entre Tiflet et Camp Monod (AL, holotypus).

Anacyclus radiatus var. *typicus* Fiori, *Nuov. Fl. Anal. Ital.* 4 (2) : 650 (1927), *nom. illegit.*

Anacyclus radiatus var. *typicus* subvar. *concolor* Maire in Jahandiez & Maire, *Cat. Pl. Maroc.* 3 : 766 (1932), *nom. nud.*

Illustrations: Figs 2, 4, 17. Miller, 1760 : tab. 73; Reichenbach, 1854 : tab. 999, fig. III, 12–14; Cesati, Passer & Gibelli, 1867–86 : tab. 79, figs 5 b–e; Cusin & Ansberque, 1873 : tabs 147, 148; Regel 1882: tab. 1074; Coste, 1903 : p. 348, fig. 1961; Fiori & Paoletti, 1904 : 426; Cadevall & Sallent, 1917 : p. 278, fig. 1422; Bonnier, 1922 : tab. 297, fig. 1474; Bouloumoy, 1930 : tab. 217, fig. 4; Post, 1933 : p. 58, fig. 426; Nègre, 1962 : p. 285, tab. 124; Zhangeri, 1976 : tab. 143, figs 5237, 5239, 5240; Haslam, Sell & Wolseley, 1977 : tab. 45.

Common names: El-Guentouss, Marguerite des Doukkala.

Ligules yellow, or yellow with a red stripe below. Pappus 0·2–0·5 (–1·0) mm long on anterior, (adaxial) face.

Collections: 329 collections, predominantly from Spain, Morocco and France.

b. Subsp. **coronatus** (Murb.) Humphries, **stat. nov.**

Anacyclus radiatus var. *coronatus* Murb., *Contr. Fl. Maroc* 2 : 55 (1923). Orig. coll.: *Ibrahim* (20 May 1889), Oued Tizi (LD, lectotypus, LE).

Anacyclus radiatus var. *ochroleucus* Ball in *J. Linn. Soc.* (Bot.) 16 : 504 (1878). Orig. coll.: *Lowe s.n.* in arenosis maritimus prope Mogador (K, holotypus).

Anacyclus exalatus Murb. in *Bot. Notiser* **1923**: 61 (1923); *Contr. Fl. Maroc* 2: 55 (1923). Orig. coll.: *Ibrahim s.n.* (June, 1877), in herb. Cosson, prope oppidum Agadir imperii maroccani meridion alis (LD, lectotypus).

Anacyclus medians Murb. in *Bot. Notiser* **1923** : 60 (1923); *Contr. Fl. Maroc* 2: 53 (1923). Orig. coll.: *Murbeck s.n.* (23 April 1931), in herbosis ad Aguedal prope urbem Marrakech (LD, holotypus, MPU).

Anacyclus submedians Maire in *Mém. Soc. Sci. nat. Phys. Maroc* **15** : 39 (1927). Orig. coll: *Maire s.n.* (24 April 1925), Hab. in arvis argillaceo-humosis humidis planitei Gharb prope Sidi-Yaya, ubi martio et aprili floret (AL, holotypus, RAB, P, MPU).

Anacyclus ifniensis Caballero in *Trab. Mus. nac. Cienc. nat. Madr.* (Bot.) **28** : 24 (1935). Orig. coll.: *Caballero s.n.* (16 June 1934), en la plana de Ifni (M, holotypus, MPU).

Anacyclus ifniensis forma *viridis* Caballero, in *Trab. Mus. nac. Cienc. nat. Madr.* (Bot.) 28 : 25 (1935). Orig. coll.: *Caballero s.n.* (17 June, 1934), in umbrosis marginum flumine Ifni (M, holotypus).

Anacyclus radiatus var. *coronatus* Murb. subvar. *discolor* Maire in *Bull. Soc. Hist. nat. Afr. N.* 26 : 211 (1935). Orig. coll.: *Maire & Wilzeck s.n.* (1 April 1934), sables maritimes près du Cap Ghir (AL, holotypus, RAB, P).

Illustrations: Murbeck, 1923 : p. 54, figs a–h.

Ligules white, or rarely white with a red stripe below. Pappus (0·3–) 0·5–1·2 mm long on anterior (adaxial) face.

Collections: 51 collections, particularly from the Sous valley in south-west Morocco and Lanzarote in the Canary Islands.

5. **Anacyclus clavatus** (Desf.) Pers.

Syn. Pl. 2 : 465 (1807).

Anthemis clavata Desf., *Fl. Atl.* 2 : 287 (1799). Orig. coll.: Herb. Desf. (P, holotypus).

Anthemis tomentosa sensu Gouan, *Obs. Bot.* : 70 (1773), *pro parte quoad holotypus autem non L.* (= *Anthemis*).

Chamaemelum tomentosum sensu All., *Fl. Pedem.* **1** : 184 (1785).

Anthemis pedunculata Desf., *Fl. Atl.* **2** : 288 (1799). Orig. coll.: Herb. Desf. (P, holotypus).

Anthemis pubescens Willd., *Sp. Pl.* **3** (3) : 2177 (1800). Orig. coll.: Herb. Willd. 16246 (B, holotypus).

Anthemis biaristata DC. in Lam., *Fl. Fr.* 4 : 204 (1805); *Biv. Pl. Sic. Cent.* **2** : 7 (1807). Orig. coll.: Herb. DC., 'biaristata, les champs N.' (G–DC, holotypus).

Anacyclus pedunculatus (Desf.) Pers., *Syn. Pl.* **2** : (1807), *pro parte quoad basionym.*

Chamaemelum inodorum sensu Cup., *Pamph.* **2** : t. 69 (1807), non Vis.

Anacyclus divaricatus Cav. ex Balbis *Cat. Hort. Taur.* : 11 (1813); Steudel, *Nomencl. Bot.* 1st ed.: 41 (1821), *nom. nud.*

Anacyclus tomentosus sensu DC. in Lam., *Fl. Fr.* **5** : 481 (1815).

Chamaemelum incrassatum Hoffmanns. & Link, *Fl. Port.* **2** : 348 (1820). Orig. coll.: 'Frequent sur le bord de la rivière du Nabao près de Thomar' (? typus destructus).

Anthemis incrassata (Hoffmanns. & Link) Link, *Enum. Hort. Berol. Alt.* **2** : 345 (1822).

Anacyclus pubescens (Willd.) Reichb., *Fl. Germ. Excurs.* **2** : 225 (1831).

Bambagella clavata (Desf.) Ten., *Fl. Nap.* **5** : 235 (1835).

Anacyclus mucronulatus Hort. ex Steudel, *Nomencl. Bot.*, 2nd ed. : 82 (1840) *nom. nud.*, *non* Guss.

Anacyclus tomentosus var. β *marginatus* Guss., *Fl. Sic. Syn.* **2** (1); 495 (1844), *nom. illeg.*

Anacyclus candolii Nyman, *Syll.* : 8 (1854).

Anacyclus aristulatus Link ex Nyman, *Consp.* **2** : 363 (1879), *nom. nud.*

Anacyclus clavatus var. α *typicus* Fiori & Paol., *Fl. Anal. Ital.* **3** : 261 (1904), *nom. illeg.*

Anacyclus clavatus var. β *tomentosus* (L.) Fiori & Paol., *Fl. Anal. Ital.* **3** : 261 (1904).

Anacyclus tomentosus forma *glabrus* [sic] Huter, Porta & Rigo in Fiori, *Fl. Anal. Ital.* **3** : 261 (1904), *nom. nud. et illeg.*

Anacyclus capillifolius Maire in *Bull. Soc. Hist. nat. Afr. N.* **22** : 296 (1931). Orig. coll: *Font Quer & Maire s.n.* (25 June 1930) 'In Atlante rifano: in lapidosis calcareis montis Krâa, 1600 m' (MPU, holotypus).

Illustrations: Figs 2, 4, 19. Reichenbach, 1854 : tab. 999, fig. II, 4–11; Cesati, Passer & Gibelli, 1867–86; tab. 79, fig. 5a; Cusin & Ansberque, 1873 : tab. 146; Hoffman, 1894 : 269 fig. K; Acloque, 1894 : 374; Fiori & Paoletti, 1904 : tab. 426, fig. 3590; Merino, 1906 : 365; Lazaro é Ibiza, 1907 : 658; Adamović, 1911 : tab. 66 : Cadevall & Sallent, 1917 : p. 277, fig. 1421 ; Small, 1918 : p. 22, fig. K, M. : Bonnier, 1922 : tab. 297, fig. 1473 : Ponzo, 1927 : p. 563, fig. 24; Nègre, 1962 : p. 285, fig. 712 a–c: Zhangeri, 1976 : tab. 143 : figs 5238, 5241; Heywood & Humphries, 1977 : p. 865, fig. 7.

Common names: Rebiana, Beehibchou, Bouibicha, Bo Melal, Math-el-Djadja, Redjelet el Rh'orab, Oum-el-ali, White Anacyclus.

Annual; stems 7·0–30·0 (–40·0) cm, slender to stout, procumbent to erect, usually much branched from the base or branching from the middle, sparsely to densely appressed villous. *Leaves* (1·5–) 2·5–11·5 × (0·5–) –3·6 cm tri- to bipinnatisect, oblanceolate in outline, glabrescent to densely villous, usually sessile but occasionally long-petiolate; primary lobes in 3–12 subopposite or opposite pairs; ultimate segments linear-lanceolate 3·0–7·0 × *c.* 0·5 mm; rhachis flat, ± cuneate at the base with 3 or more prominent veins. *Inflorescence* a lax, corymbose cyme with up to 40 erect or ascending peduncles; peduncles markedly clavate near the apex at maturity, villous just below the capitulum. *Involucre* (0·5–) 8·0–1·8 mm in diameter, hemispherical; involucral bracts in three rows, 1·8–7·0 × 0·5–2·0 mm, outer series linear-triangular, inner series ± rectangular usually densely villous, pale brown or green and thicker towards the centre with thin, scarious, entire, pale yellow to dark brown margins; receptacular scales 1·7–5·0 × *c.* 2·5 mm, obovate or cuneate and mucronate, slightly caniculate towards the apex, somewhat membranous. *Ray florets* white; ligules dimorphic, 5·5–16·5 × 2·0–7·0 mm, white, trifid, usually somewhat rounded, creamy white; tube 3·5–5·5 × 0·5–1·0 mm, anterior-dorsally compressed with narrow, ± parallel-sided wings. *Disc florets* 3·5–5·0 × 0·5–1·3 mm, hypocrateriform with a distinct, campanulate corolla and a narrow basal tube; tubes anterior-dorsally compressed with broad, rounded wings towards the base, up to 1·0 mm wide in outer series, but narrower, *c.* 0·6 mm wide, towards the centre of the disc; lobes usually dimorphic, with three short lobes 0·5–0·6 mm long and two extended lobes, up to 2·0 mm long, especially towards the centre of the disc. *Styles* 3·0–4·0 mm long, style branches 0·3–0·6 mm long. *Stamens c.* 4·0 mm long, anthers 1·8–2·0 mm long. *Cypselas* (1·5–) 2·5–3·5 (–5·0) × (0·4) 1·5–4·7 mm, broadly obovate, those of the ray and outer disc with

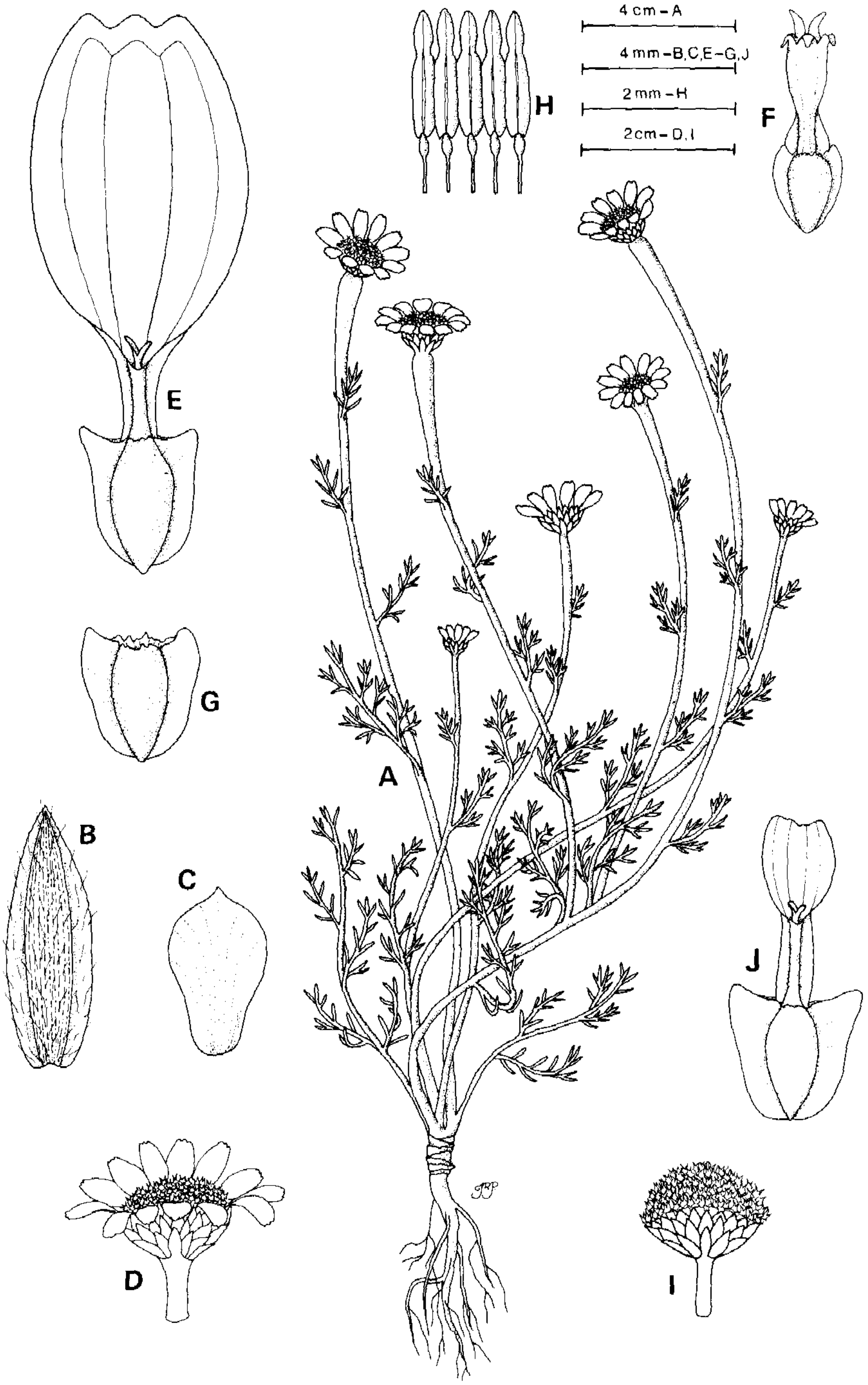

Fig. 19 *Anacyclus clavatus*: A – habit, B – involucral bract, C – receptacular scale, D – capitulum, E – ray floret, F – disc floret, G – cypsela, H – anthers. *A.* × *valentinus*: I – capitulum, J – ray florets.

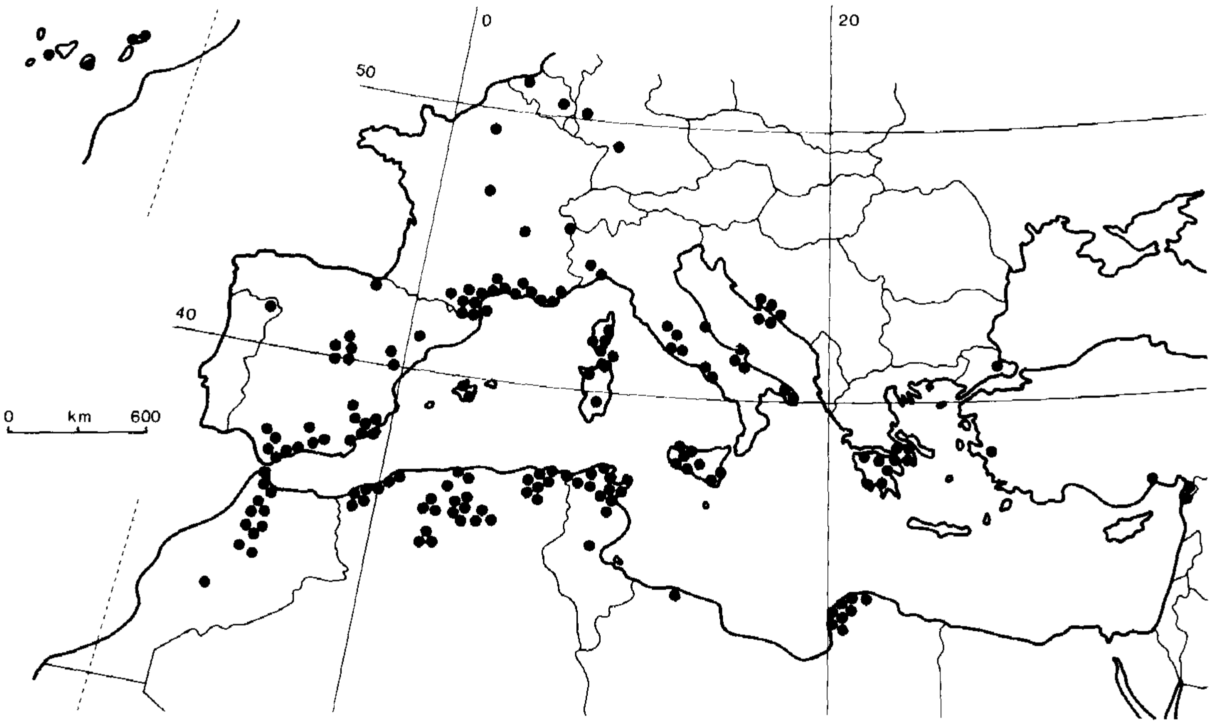

Fig. 20 Distribution of *Anacyclus clavatus.*

wings up to 1·2 mm, those from the centre of the disc with wings *c.* 0·3 mm in diameter, wings truncate or with bluntly pointed auricles. *Pappus* an anterior lacerate corona.

Flowering period: February–July.

Chromosome number: 2n = 18.

Observations: This species is most closely related to *Anacyclus homogamos* and *A. linearilobus.* They are similar in many respects, but *A. homogamos* can be readily distinguished by its generally smaller habit and hermaphrodite discoid capitula, and *A. linearilobus* by the greatly dissected leaves and longer spines on the receptacular scales.

Variation: *Anacyclus clavatus* varies considerably in habit, pubescence and ligule characters. As a consequence, different morphs have been given a variety of names. The name var. *tomentosus*, for example, is one of the most commonly used names, since many populations are densely pubescent. This character, as with habit and ligule length, is a continuously variable feature; so I find little reason to give formal taxonomic ranks to apparently distinctive populations.

Distribution and ecology: See Fig. 20. *Anacyclus clavatus* is a pernicious weed occupying a considerable range in Mediterranean Europe and Africa. It is a dominant plant in disturbed habitats of north Morocco, Algeria, Tunis and Libya and occurs abundantly in similar habitats in many coastal and inland places of Spain, France, Italy, Jugoslavia, Greece and Turkey. Also it often appears as a casual in various parts of Russia and northern Europe.

Collections: 386 collections have been examined, mainly from southern Europe and north Africa.

6. **Anacyclus homogamos** (Maire) Humphries, **comb. et stat. nov.**

Anacyclus valentinus subsp. *dissimilis* var. *homogamos* Maire in *Bull. Soc. Hist. nat. Afr. N.* **23** : 189–190 (1932). Orig. coll.: *Maire s.n.* (1929), 'In arvis et pascuis Imperii maroccani australis: prope

Tahanout ad radices Atlantis majoris it ditione Reraya, ad alt 900–1000 m' (RAB, holotypus, MPU, isotypus).

Anacyclus tomentosus (var.) c. *discoideus* Guss., *Fl. Sic. Syn.* : 495 (1844). Orig. coll.: *Gussone s.n.*, Italia Caltanisetta, Lentini Alicata (NAP, lectotypus) (not seen).

Anacyclus clavatus (var.) β *discoideus* Willk. & Lange, *Prodr. Fl. Hisp.* **2** : 84 (1865); Batt. & Trabut, *Fl. Algér.* : 452 (1890), *pro parte*.

Anacyclus valentinus sensu Briquet & Cavallier in Burnat, *Fl. Alp. Marit.* **6** : 165 (1916), non L.

Anacyclus dissimilis var. *australis* Maire in *Bull. Soc. Hist. nat. Afr. N.* **20** : 186 (1929) Orig. coll.: *Maire* 654, 'Hab in alveis arenoso-limosis torrentium in montibus Hoggar. Saharae centralis, ad alt. 1200–1450 m' (AL, lectotypus, MPU).

Anacyclus valentinus subsp. *eu-valentinus* Thell. in Jahandiez & Maire, *Cat. Pl. Maroc* **3** : 767 (1934), *nom. nud.*

Anacyclus valentinus subsp. *dissimilis* sensu Nègre, *Fl. Maroc Aride* **2** : 284 (1962), *quoad descr.*

Illustrations: Figs 2, 4, 21. Gaertner, 1791 : tab. 165; Lamarck, 1798 : tab. 700. fig. 1; Jaume St-Hilaire, 1808 : tab. 27; Nègre, 1962 : tab. 124, fig. 713.

Common names: Guerthoufa.

Annual; stems 5·0–40·0 (–50·0) cm, slender, ascending to erect, usually branched from the base, sparsely to densely appressed villous. *Leaves* (1·0–) 4·0–9·0 (–13·0) × 0·3–4·0 cm. tri- to bipinnatisect oblong or oblanceolate to obovate in outline, usually hairy, sessile. *Inflorescence* a lax corymb, with erect or ascending peduncles, emerging from a short stem; peduncles usually clavate at maturity, usually villous just below the capitulum. *Involucre* 5·0–18·0 mm in diameter, hemispherical; involucral bracts multiseriate, 3·0–7·0 × 1·8–3·0 mm; outer series linear-triangular, inner series rectangular, usually villous towards the centre and apex, brown or pale greenish with a thin brown scarious margin. Receptacular scales 3·0–4·5 × 1·1–1·7 mm, obovate or cuneate and mucronate, slightly caniculate towards the apex, somewhat membranous. Capitula discoid, all florets monoecious discoid. *Florets* 2·5–4·6 mm long, hypocrateriform with a distinct campanulate upper part; tube slender, anterior-dorsally compressed with broad, rounded wings towards the base; wings up to 1·2 mm wide in the outer series, *c.* 0·7 mm wide towards the centre of the capitulum, lobes irregularly dimorphic, particularly in central florets with three short lobes, 0·3–0·9 mm long and 2 long lobes up to 1·6 mm long. *Styles c.* 4·0 mm long, style branches 0·2–0·5 mm long. *Stamens* 3·8–4·0 mm long, anthers 1–2 mm long. *Cypselas* 1·5–4·2 × 1·4–3·8 mm, broadly ovate, with thin membranous wings; wings somewhat heteromorphic, those of the outer series with broad wings 0·7–1·8 mm wide with rounded or slightly pointed diverging auricles, those of the inner series with narrow wings 0·4–0·6 mm wide and less prominent auricles. *Pappus* a fimbriate corona contiguous with the wings, particularly developed on the anterior side of the apex.

Flowering period: March–July.

Chromosome number: 2n = 18.

Observations: This species is easily recognized by its broad, more or less parallel-sided, cypsela wings and the somewhat rounded wings at the base of the corolla tube. It is very closely related to *Anacyclus clavatus* and is considered in this revision to be its sister-species (see p. 108). However, it is a much less robust species, the capitula are obviously discoid with homogamous hermaphrodite disc-florets, and the cypselas have more delicate, but broader wings.

Many apparently discoid specimens of *Anacyclus* have been identified as *A. valentinus* L. when in fact they are not homogamous discoid but heterogamous with structurally reduced female ligules in the outer floret series of the capitulum (Fig. 19). There seem to be two possible reasons for this phenomenon: (i) either the short-liguled forms represent an intermediate stage in the evolution of discoid monoecious forms from gynomonoecious radiate taxa or (ii) the short-liguled plants are hybrids between discoid and radiate taxa.

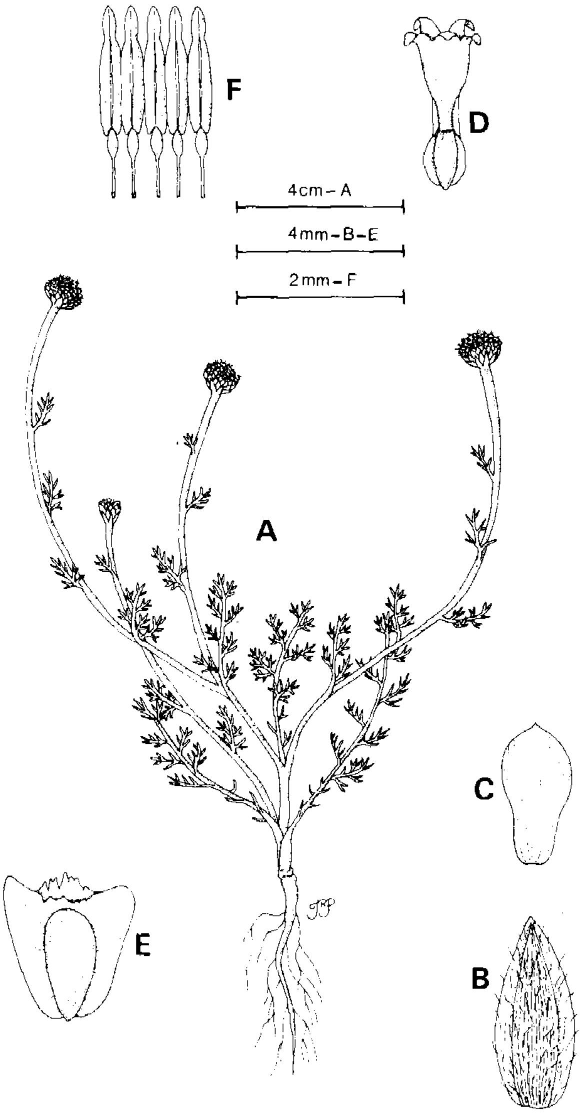

Fig. 21 *Anacyclus homogamos*: A – habit, B – involucral bract, C – receptacular scale, D – disc floret, E – cypsela, F – anthers.

The evidence will not be presented here since the details form part of a critical experimental study (Humphries, in press, *a*). However, the principal reasons for accepting the second hybrid hypothesis are that: (a) In almost all herbarium specimens, the ligules are extremely short and are frequently masked entirely by the involucral bracts. They fall into one particular size class and do not form a gradual series between rayed and rayless forms. There are fewer ligules in short-rayed morphs than can ever be found in a radiate plant, and these are irregularly arranged at the periphery of each capitulum. (b) This condition can readily be synthesized in artificial F_1 hybrids, especially in crosses involving *A. homogamos*, *A. clavatus* and *A. radiatus* (Humphries, in press, *a*). (c) In most herbarium specimens it is extremely difficult to identify ligule colour, but it is possible to show that in a number of cases both white and yellow short-rayed morphs exist. (d) The short-rayed plants are often found in mixed populations with the putative parents and invariably have sympatric distributions with one or both of them. (e) There are numerous citations in European literature (see synonyms) of collections believed to be rayless forms of *A. clavatus* and *A. radiatus* found in Europe. However, truly rayless forms are extremely rare in Europe and occur in abundance only in north Africa (Fig. 22).

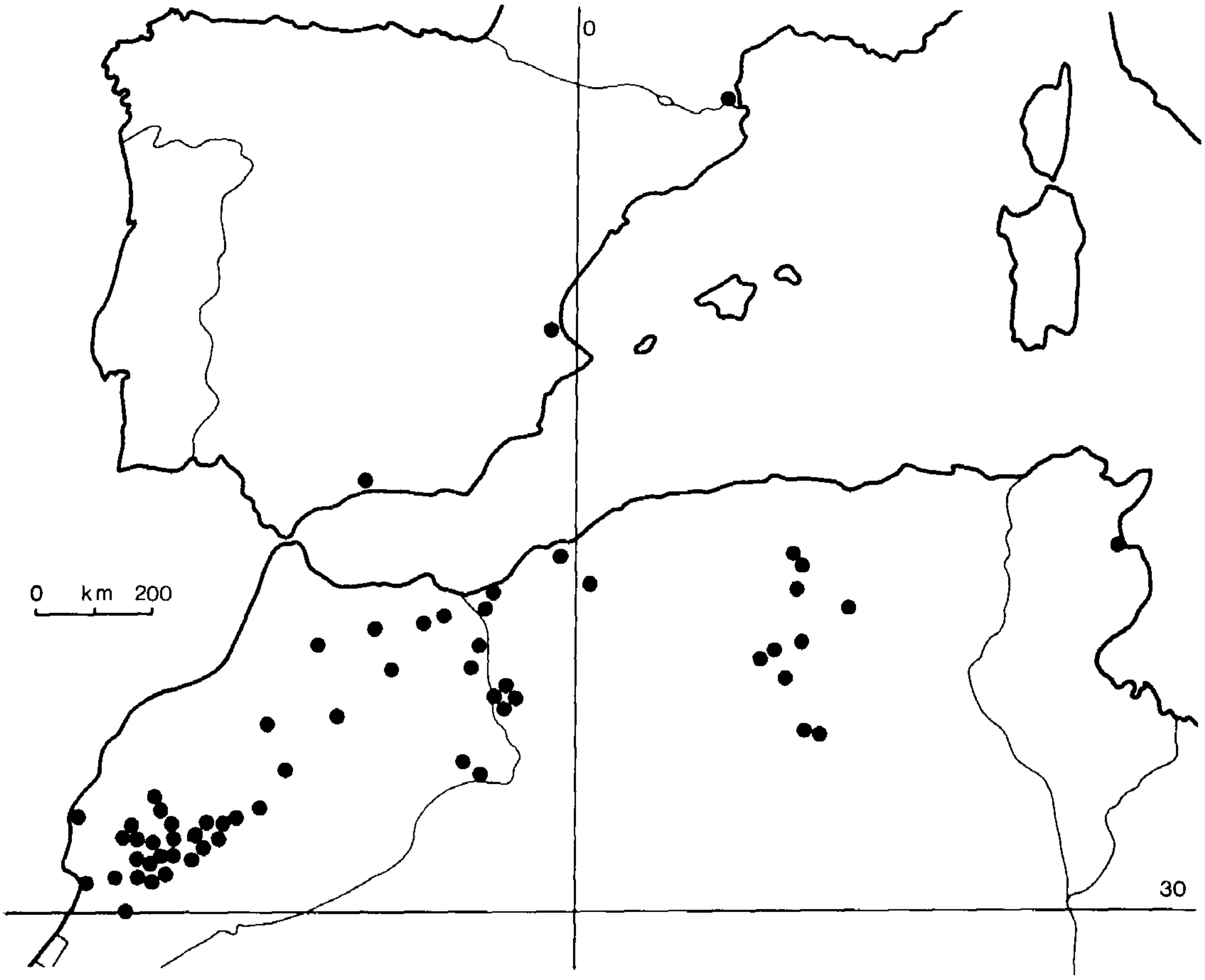

Fig. 22 Distribution of *Anacyclus homogamos.*

From these points it is possible to suggest that the short-rayed plants are established hybrids of *A. homogamos* × *radiatus* and *A. homogamos* × *clavatus*. Observations on habit and cypsela morphology support this interpretation, particularly in the variation of overall plant size, cypsela size, wing structure and auricle shape.

A. homogamos was not previously unrecognized but was considered to be only a variety of *A. valentinus* L. A new name had to be found for the homogamous plants, as Linnaeus's type for *A. valentinus* is a Spanish specimen of one of the hybrids *A. homogamos* × *radiatus* (see p. 109).

Collections: 75 collections were examined, mostly from Morocco.

a. **Anacyclus** × **inconstans** Pomel

Nouv. Mat. Fl. Alt. : 52 (1874).

(*A. homogamos* × *clavatus*). Orig. coll.: *Pomel s.n.*, Algeria Oued Dahra (MPU, holotypus).

Anacyclus clavatus var. *inconstans* (Pomel) Batt. & Trabut, *Fl. Algér* : 452 (1889); Fiori & Paol., *Fl. Anal Ital.* 3 : 261 (1903).

Illustrations: Small, 1918 : 22, fig. L.

Capitula incompletely radiate to apparently discoid, (5·0–) 10·0–22·0 mm in diameter. Outer florets ♀, ± tubular to truncate-ligulate, white, 2·0–3·0 (–11·0) mm long. Cypselas 3·0–4·0 × 2·0–4·0 mm, broadly ovate with thin, but broad-membranous wings with pointed to obtuse auricles.

b. **Anacyclus × valentinus** L.

Sp. Pl. : 892 (1753) (*A. homogamos × radiatus*). (Lectotypus, see p. 109).
Anacyclus lanuginosus Moench., *Meth.* : 581 (1794) Orig. coll.: typus destructus.
Anacyclus clavatus (var.) β *discoideus* Willk. & Lange, *Prodr. Fl. Hisp.* **2** : 84 (1865), *pro parte*.
Anacyclus valentinus (var.) β *microcephalus* Costa in Willk. & Lange, *Prodr. Fl. Hisp.* **2** : 84 (1865); Sennen in Sennen & Mauricio, *Cat. Fl. Rif. Or.* : 59 (1933). Orig. coll.: *Costa Pl.* catal exs. (M, holotypus) (not seen).
Anacyclus dissimilis Pomel, *Nouv. Fl. Atl.* : 53 (1874). Orig. coll.: *Pomel s.n.* (1 April 1862),Terrains Sablonneux du Sahara, Mzab, Metlili (Al, holotypus, MPU).
Anacyclus prostratus Pomel, *Nouv. Mat. Fl. Atl.* : 52–53 (1874). Orig. coll.: *Pomel s.n.*, 'Lieux herbeux des montagnes elevées d l'interieur (Al, holotypus) (not seen).
Anacyclus radiatus (var.) β *valentinus* (L.) Arcangeli, *Comp. Fl. Ital.* : 359 (1882).
Anacyclus radiatus (var.) β *discoideus* Chiov. in Fiori & Paol., *Fl. Anal. Ital.* **3** : 261 (1903) Orig. coll.: *Chiovenda*, 'Lit. del Lazio tra Furbana e S. Severa (Fl, holotypus) (not seen).
Anacyclus valentinus var. *ligulata* Sennen in Anvari, *Jta Cienc. Nat. Barc.* **2** : 647 (1917), *nom. nud.*
Anacyclus valentinus subsp. *dissimilis* var. *typicus* Maire in *Bull. Soc. Hist. nat. Afr. N.* **20** : 186 (1929), *nom. illeg.*
Anacyclus valentinus var. *eriolepis* Maire in *Bull. Soc. Hist. nat. Afr. N.* **20** : 186 (1929), *nom superfl.*
Anacyclus valentinus subsp. *dissimilis* (Pomel) Thell. in Jahandiez & Maire, *Cat. Pl. Maroc.* **3** : 767 (1934).
Anacyclus valentinus subsp. *dissimilis* var. *eudissimilis* Maire in Jahandiez & Maire, *Cat. Pl. Maroc.* **3** : 767 (1934), *nom. illeg.*

Illustrations: Fig. 19 I, J. Schkuhr, 1808 : tab. 254 6; Reichenbach, 1854 : tab. 999, fig. 4; Cusin & Ansberque, 1873 : tab. 148 : Coste 1903 : 348; Cadevall & Sallent, 1917 : fig. 1423; Bonnier, 1922 : tab. 297, fig. 1475; Quezel & Santa, 1963 : tab. 975, fig. 2854.

Capitula apparently discoid or subradiate, 12·0–18·0 mm in diameter. Outer florets ♀, tubular to ligulate, yellow, 3·5–8·0 mm long. Cypselas *c.* 4·0 × 3·4 mm, obovate with broad wings and usually pointed auricles.

Hybrid collections (*Anacyclus × inconstans* and *A. × valentinus*): 171 collections, mostly from north Morocco, north Algeria and Spain.

Distribution and ecology: See Fig. 23. *Anacyclus homogamos* and its hybrids, *A. × inconstans* and *A. × valentinus*, are amongst the commonest roadside and field weed species of the western Mediterranean region, particularly in Morocco. The normal habitat is disturbed ground, especially in sandy and rocky places, particularly in montane regions of south-west Morocco but extending into north Morocco, Algeria, Tunisia and Spain.

It is not possible to demonstrate to any great extent, from herbarium material, the origin and spread of hybrids except to report that they have a sympatric distribution with either or both of the parental species. Along the eastern coast of Spain and the Mediterranean coast of France, some populations consist almost entirely of *A. × valentinus* L. Mixed populations of *A. × valentinus*, *A. clavatus* and *A. discoideus* occur around Oran in north-west Algeria, as is shown particularly by the collection of Faure, and in the Moyen Atlas Mountains, as is shown in the collections of Humphries, Jury, Mullin and Richardson.

7. **Anacyclus linearilobus** Boiss. & Reuter

Pugillus : 52 (1852). Orig. coll.: *Reuter s.n.*, Algér: Oran, inter la Stidia et Mostaganem in arenosis (G, holotypus).
Anacyclus acutilobus Durieu ex Boiss. & Reuter, *Pugillus* : 52 (1852). Orig. coll.: *Balansa* 689 (27 June 1852), Algér: Sables a voisinant la Batterie espagnole, pres d'Oran (MPU, holotypus, BM, C, E, G, K, LE, P).
Anacyclus rubricantes Durieu ex Boiss. & Reuter, *Pugillus* : 52 (1852).

Illustrations: Figs 2, 4, 24. Quezel & Santa, 1963 : 975, fig. 2853.

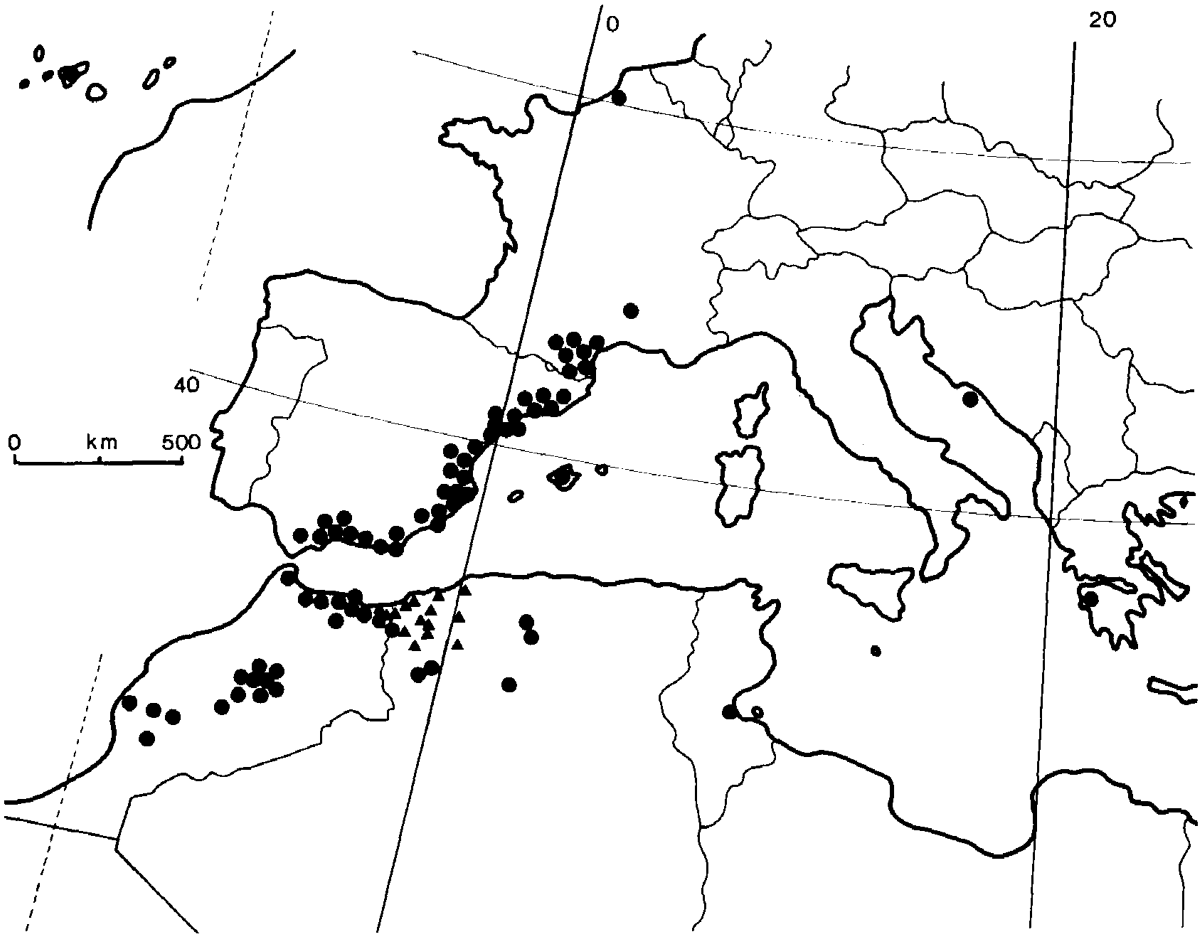

Fig. 23 Distribution of *Anacyclus* × *valentinus* (●) and *A.* × *inconstans* (▲).

Annual; stems 15·0–70·0 cm, erect, usually divaricately branching above, but occasionally from the axil of a 'rosette' leaf, rather striate, deep red, glabrous below to lightly pubescent above. *Leaves* 4·0–12·0 (–15·0) × 1·5–5·0 (–7·0) cm, ovate in outline, bi- to more rarely tripinnatisect, usually sessile above to long petiolate below; primary lobes in 4–9 opposite to subopposite pairs, with internodes up to 3 cm long; ultimate segments broad, acuminate, fleshy, rhachis narrow; peduncle leaves (bracts) 2–4·0 × 0·5–1·0 cm, pinnatisect, sessile, segments linear-acuminate. *Inflorescence* a lax, corymbose cyme, usually with 2–4 capitula; peduncles erect, branching from the middle of the stem, 7–23 cm long, distinctly clavate and hollow at the apex, pubescent (especially when young) to sometimes glabrous at maturity. *Involucre* 8·0–17·0 mm in diameter; involucral bracts in three rows, 4·5–7·0 × 1·5–2·5 mm, narrow-triangular to rectangular or ovate-oblong, acute, somewhat membranous, but with a thick, pale green to brown centre vein and narrow, scarious margins, invested with fairly long white hairs; receptacular scales 4·0–6·5 × 2·8–3·2 mm, obtrullate to narrowly obovate, cuspidate at the apex, with sharp spines at maturity, ± canaliculate above, flat below, usually pale-brown, glabrous. *Ray florets* white, reflexed at anthesis; ligules (5·0–) 8·0–16·0 × (3·0) 3·5–7·0 mm, acuminate to bifid, tube 1·8–2·5 × 1·0–1·3 mm, anterior-dorsally compressed, with broad ovate wings, female fertile. *Disc florets* 4·5–5·2 × *c.* 1·0 mm, infundibiliform, lobes ± equal in the outer series, but two distinctly longer than the rest in the inner series, wings broad, the basal part enlarged into an anterior circular appendage up to *c.* 1 mm wide, extending over the cypsela. *Styles* 3·5–3·8 mm long, branches 0·5–0·8 mm long. *Stamens* 3·5–4·0 mm long, anthers *c.* 1·8 mm long. *Cypselas* dimorphic, anterior dorsally compressed but subrectangular with thin hyaline wings, those of the ray florets broadly ovate, 3·5–4·0 × 3·0–3·5 mm, the wings with rounded auricles 1–1·3 mm wide, those of the disc florets

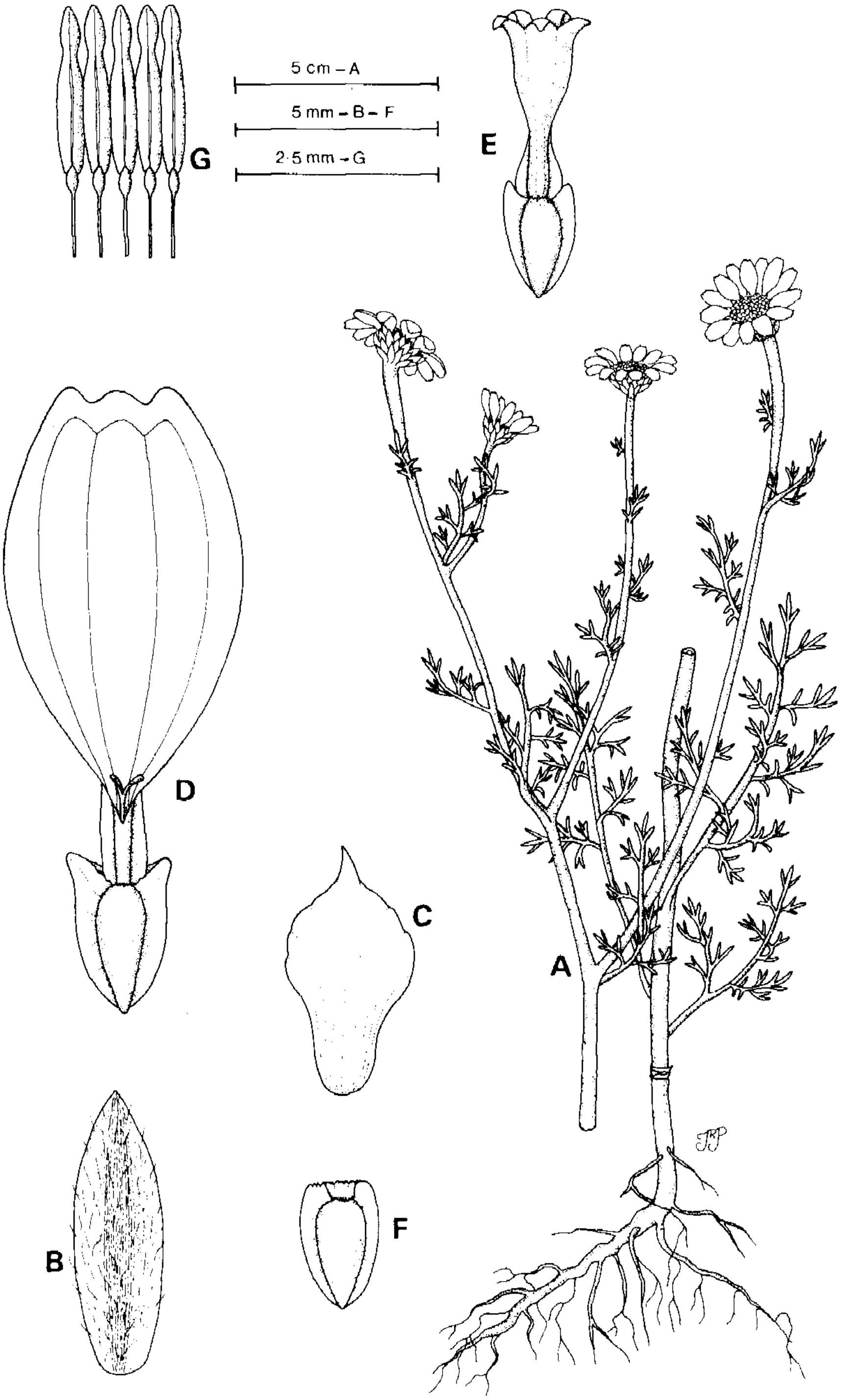

Fig. 24 *Anacyclus linearilobus*: A – habit, B – involucral bract, C – receptacular scale, D – ray floret, E – disc floret, F – cypsela, G – anthers.

obovate, 2·8–3·2 × 1·5–2·2 mm, with narrow truncate wings, 0·3–0·5 mm wide. *Pappus* a marginal corona or ± absent.

Flowering period: May–June.

Observations: This species is one of the most distinctive annuals in the genus, characterized by numerous vegetative and capitulum characters. The leaves are very fleshy, differing from the

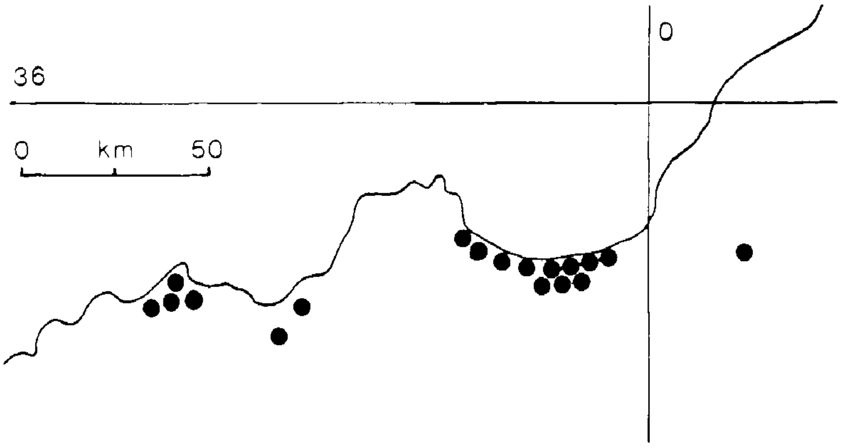

Fig. 25 Distribution of *Anacyclus linearilobus.*

closely related *Anacyclus clavatus* and *A. homogamos* by the wider internodes of the rhachis between the primary lobes, the broad fleshy retinate lobes, and the long red rhachis of the lower leaves. It shows an advanced disc corolla structure, similar to that of *A. nigellifolius*, where the lateral wings are expanded at the base into an anterior disc overlapping the cypsela, and is unique in the genus by the possession of long spiny receptacular scales.

Distribution and ecology: See Fig. 25. This species is endemic to Algeria. It grows on sand dunes and disturbed sandy ground up to about 50 m around Mostaganem, La Macta, Oran and Cap Falcon.

Collections: 30 collections were examined, all from coastal areas around Mostaganem, Oran and La Macta.

8. **Anacyclus latealatus** Hub.-Mor.

in *Feddes Reprium Spec. nov. veg.* **48** : 291 (1940). Orig. coll.: *A. Huber-Morath* 5664, Turkey: C2 Burdur zwischen Tefenni und Burdur, 18 Km nach Tefenni, 1100 (BASL, holotypus).

Illustrations: Huber-Morath, 1940 : tab. 327.

Annual; stems erect to ascending, up to 25 cm, divaricately branching from the base, often striate, tinged with red, sparsely villous to glabrescent. *Leaves* oblanceolate in outline, bipinnatisect, 2·0–4·0 × *c.* 1·0 cm, petiolate; primary lobes in 2–4 subopposite pairs; ultimate segments linear-lanceolate, 3·0–5·0 × *c.* 0·25 mm; rhachis narrow; peduncle leaves 2·0–3·0 × 0·5–1·0 cm, pinnatisect, often dilated at the base; segments linear. *Inflorescence* a protracted corymbose cyme; peduncles erect-ascending, 2·0–5·0 cm long only slightly thickened below the capitulum, ± densely villous. *Involucre* 10·0–13·0 mm in diameter, turbinate-hemispherical, involucral bracts in 3 rows 4·0–9·0 × 1·5–3·0 mm, lanceolate-acute, covered in dense white hairs, midrib green, apex and margins brown-scarious; receptacular scales lanceolate-acuminate, 7·0–8·0 × *c.* 1·5 mm, flat, hyaline, slightly green above, scarious, lightly villous. *Ray florets* white; ligules 8·0–9·0 × 2·0–3·0 mm, 2–3 lobed at the apex; tube 3·0–4·0 × *c.* 2·5 mm, anterior-dorsally compressed with very narrow wings, female fertile. *Disc florets* 3·0–4·0 × 2·5–3·0 mm, infudibuliform, lobes ± equal. *Styles c.* 3·5 mm long, branches *c.* 0·6 mm long. *Stamens c.* 4·0 mm long, anthers *c.* 1·8 mm long. *Cypselas* slightly dimorphic, broadly obovate (in disc florets) to obcuneate-auriculate (in ray florets), 4·0–6·0 × 5·0–8·0 mm, pale brown; lateral wings extremely thin, scarious, 2·5–2·75 mm wide, with pointed auricles. *Pappus* a fimbriate corona, contiguous with the auricles.

Flowering period: Virtually unknown, but flowering holotype was collected in June.

Observations: This species is easily recognized by its characteristic broadly winged, scarious cypselas. It can be distinguished from its sister-species, *Anacyclus nigellifolius*, by the truncate base of the corolla tube, the broader cypsela wings and the broad rhachis of the upper leaves.

Distribution and ecology: See Fig. 27. *Anacyclus latealatus* grows in fallow fields and steppic communities around 1100 m. It is known from only the south-west Turkish vilayet of Burdur. According to Grierson (1975) the species is endemic and probably Irano-Turanian.

Collections: Known only from the holotype.

9. **Anacyclus nigellifolius** Boiss.

Diagn. Pl. Or. I, 2 (11) : 13, t. 14 p. 267 (1849) ; Bois., *Fl. Or.* **3** : 322 (1875). Orig. coll.: *Haussknecht s.n.* (April 1867), Mesopotamia, in gracuis, Dara (G, holotypus, BM, JE, Z).

Anacyclus nigellifolius subsp. *orientalis* Grierson in *Notes R. bot. Gdn. Edinb.* **33** : 411 (1975) ; Grierson in Davis, *Fl. Turk.* **5** : 223 (1975). Orig coll.: *Sintenis* 817, Turkey: Urfa, Nemrut Dagh (LD, holotypus, BM).

Illustrations: Figs 2, 4, 26. Bouloumoy, 1930 : tab. 212, fig. 1; Davis, 1975 : 267, fig. 14, no. 13.

Annual; stems erect, slender, 10·0–20·0 cm long, simple or sparsely branched from, or above the middle, rarely much branched from below, ± glabrous. *Leaves* ± sessile, sparsely villous, bipinnatisect to pinnatisect, 1·5–3·0 × 0·3–1·5 cm; primary lobes in 5–6 subopposite pairs; ultimate segments 2·0–12·0 × 0·3–10 mm, acute; rhachis cuneate, thickened towards the base. *Inflorescence* monocephalic or a very loose corymbose cyme, peduncles usually emerging from or above the middle of the stem, clavate below the capitulum at maturity, distinctly villous above. *Involucre* 5·0–13·0 mm, turbinate-hemispherical; involucral bracts in three series, ovate acute in outer series to obovate obtuse in inner series, 4·5–7·0 × *c*. 2 mm, villous, distinctly centrally veined, green-brown towards apex, scarious, hyaline at the margin; receptacular scales obovate, acuminate, 5·0–7·0 × 2·0–2·8 mm, slightly caniculate, scarious, but thickened slightly above, glabrous. *Ray florets* white, ligule 4·5–6·0 × 1·0–3·0 mm, 2–3 fid; tube 3·5–4·8 × 1·0–1·2 mm, anterior-dorsally compressed with narrow wings, persistent at maturity. *Disc florets* 3·5–4·0 mm, base broadened into large circular appendage 2·5–3·0 mm wide covering top of cypsela on the anterior side, lobes equal. *Styles* 3·5–3·8 mm long, style branches 0·5–0·8 mm long. *Stamens c*. 4·0 mm, anthers 1·8–2·0 cm long. *Cypselas* ± monomorphic, somewhat rounded to obovate, 4·2–4·8 × 3·0–3·6 mm, pale brown; lateral wings extremely thin, transparent, scarious, 1·0–2·0 mm wide, with rounded auricles. *Pappus* coroniform to virtually absent, contiguous with wings.

Flowering period: May–June.

Observations: This species is similar in habit to *Anacyclus latealatus* and is its sister species, but it has more erect stems, less elaborate leaves, and rounded auricles on the cypselas. It differs from its congeners by the curious overlapping lobe at the base of the disc corollas, which is akin to that found in the monotypic *Leucocyclus formosus* Boiss., in which the two overlapping lobes clasp the top of the cypselas.

Variation: Stem size, stem branching, size of involucre and florets are subject to considerable variation. Grierson (1975*b*) distinguishes two subspecies, *nigellifolius* and *orientalis*, which differ in these characters, the generally more reduced form occurring in Hatay in southern Turkey. This variation, however, is continuous and not distinctly geographical, since plants with all the size-differences can be found in the Antilebanon, especially on Mount Hermon. The species is polymorphic, with each population differing slightly in genetic constitution. I do not think that this variation is worthy of taxonomic recognition.

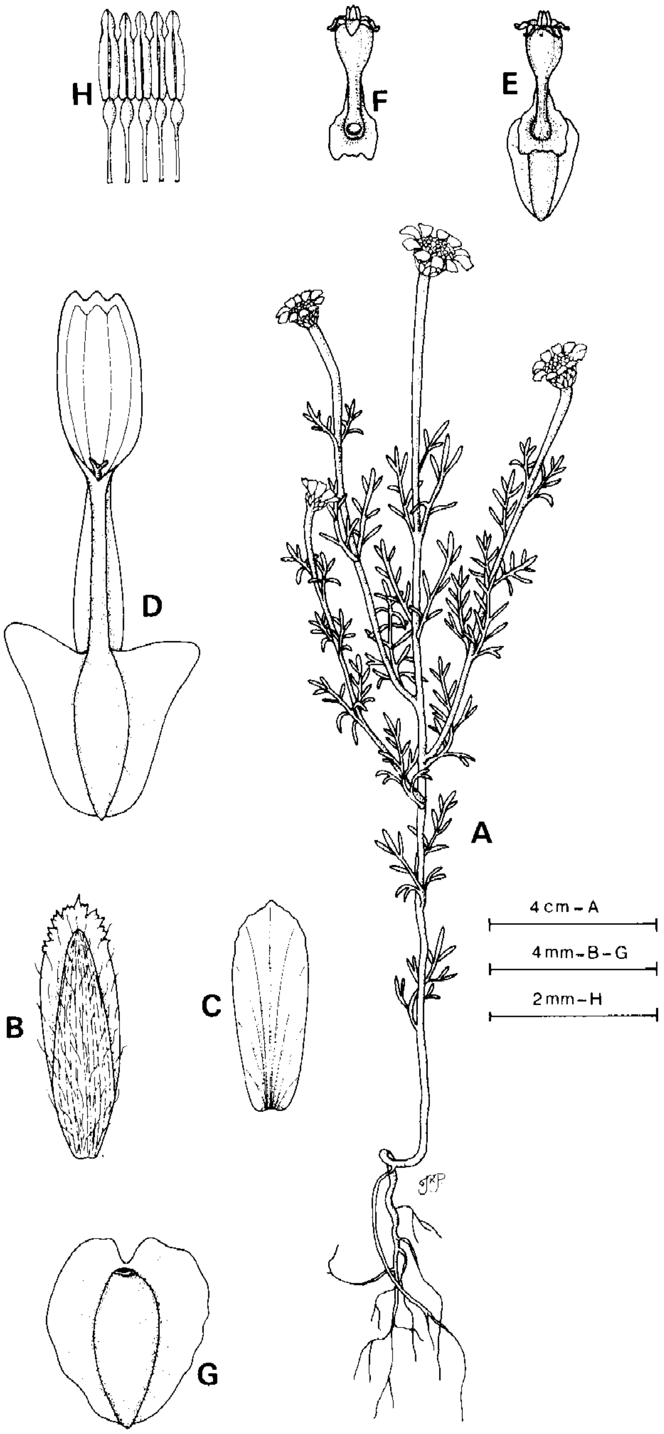

Fig. 26 *Anacyclus nigellifolius*: A – habit, B – involucral bract, C – receptacular scale, D – ray floret, E – disc floret (dorsal surface), F – disc floret (anterior surface), G – cypsela, H – anthers.

Distribution and ecology: Fig. 27. *Anacyclus nigellifolius* grows on rocky steppes and calcareous mountain slopes, between 1000 and 1500 m. It is restricted to the eastern Mediterranean region, from southern Anatolia and Syria to northern Iraq.

Collections: 18 collections were examined.

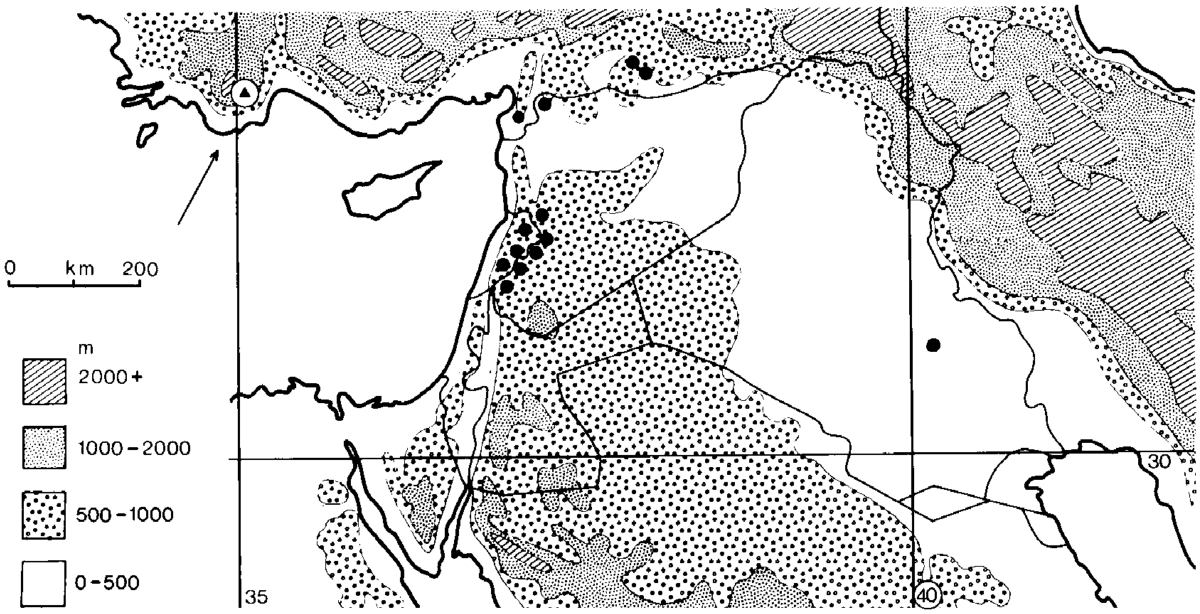

Fig. 27 Distribution of *Anacyclus nigellifolius* (●) and *A. latealatus* (▲).

Excluded taxa

- *Anacyclus* sect. *Hiorthia* (Necker) DC., *Prodr.* **6** : 17 (1838).
  - *altissimus* (L.) G. Samp. in *Ann. Acad. Polyt. Port.* **14** : 162 (1920) = *Anthemis altissima* L.
  - *anomalus* Gay ex Boiss., *Fl. Or.* **3** : 283 (1875)= *Anthemis palestina* Reuter.
  - *anthemoides* (L.) Lag. ex Sprengel., *Syst. Veg.* **3** : 497 (1826)= *Anthemis abrotanifolia* (Willd.) Guss.
  - *atlanticus* Litard & Maire in *Mém. Soc. Sci. nat. Phys. Maroc* **4** (1) : 13 (1924)= *Heliocauta atlantica* (Litard & Maire) Humphries.
  - *australis* Sieber ex Sprengel, *Syst. Veg.* **3** : 497 (1826)= *Cotula australis* (Sieber ex Sprengel) Hook. f.
  - *austriacus* (Jacq.) G. Samp. in *Ann. Acad. Polyt. Port.* **14** : 162 (1920)= *Anthemis austriaca* Jacq.
  - *barrelieri* (Ten.) Guss., *Pl. Rar.* : 357 (1826)= *Achillea barrelieri* (Ten.) Schultz Bip.
  - *ciliatus* Trautv., in *Bull. Soc. Nat. Moscou* **41** (1) : 461 (1868)= *Anthemis ciliata* (Trautv.) Boiss.
  - *creticus* L., *Sp. Pl.* : 892 (1753)= *Anthemis rigida* (Sibth. & Sm.) Boiss. & Heldr.
  - *formosus* Fenzl ex Boiss., *Diag. Pl. Or. Nov.* II, **11** : 14 (1849)= *Leucocyclus formosus* Boiss.
  - *inflatus* Lehm. ex Steudel, *Nomencl. Bot.* 2nd ed. **1** : 82 (1840)= *Anthemis* sp.
  - *membranacea* Labill., *Icones Pl. Syr.* **3** : tab. 9 (1809)= *Leucocyclus formosus* Boiss.
  - *mucronulatus* (Bertol.) Guss., *Pl. Rar.* : 356 (1826)= *Achillea barrelieri* (Ten.) Schultz Bip.
  - *nobilis* L. ex Jackson, *Index Linn. Herb.* : 33 (1912)= *Chamaemelum nobile* (L.) All.
  - *orientalis* L., *Sp. Pl.* : 892 (1753)= *Anthemis orientalis* (L.) Degen.
  - *pectinatus* Bory & Chaub., *Nouv. Fl. Pelop.* : 59, tab. 30 (1838)= *Anthemis orientalis* (L.) Degen.
  - *pyrethraria* (L.) Sprengel, *Syst. Veg.* **3** : 497 (1826)= *Cotula pyrethraria* L.
  - *tinctorius* (L.) G. Samp. in *Ann. Acad. Polyt. Port.* **14**: 162 (1920)= *Anthemis tinctoria* L.
  - *triumfetti* (L.) G. Samp., in *Ann. Acad. Polyt. Port.* **14** : 162 (1920)= *Anthemis triumfetti* (L.) DC.
- *Hiorthia* Necker, *Elem.* **1** : 97 (1790) pro parte= *Anthemis* L.
- *Lyonnetia* Cass., *Dict. Sci. Nat.* : 102 (1825)= *Anthemis* L.

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Taxonomic index

Extant names are given in roman and synonyms in italic; new names are in bold, as are principal references.