Christoph Oberprieler

The Systematics of *Anthemis* L. *(Compositae, Anthemideae)* in W and C North Africa

Abstract

Oberprieler, Ch.: The Systematics of *Anthemis* L. *(Compositae, Anthemideae)* in W and C North Africa. – Bocconea 9: 1-328. 1998. – ISSN 1120-4060.

Anthemis L., a mainly Mediterranean and SW Asian genus of the *Compositae-Anthemideae*, is revised for the W and C North African part (Morocco, Algeria, Tunisia, Libya) of its distribution range. On the basis of detailed morphological studies all species are fully described and illustrations of habit, leaves, involucral bracts, and pales are presented, along with photographs of mature achenes under SEM and of transverse sections of achenes under LM. Keys for the determination of all species, subspecies, and varieties are provided. Complete synonymies are given, including the typification of the names as far as possible. Distribution maps of all taxa studied are presented. Chromosome numbers and karyotypes for most taxa are provided and discussed.

In the area covered, *Anthemis* is represented by 25 species belonging to two subgenera, four sections, and four series. Three taxa are described as new to science: *A. maritima* subsp. *pseudopunctata* Oberprieler, *A. stiparum* subsp. *intermedia* Oberprieler, and *A. zaianica* Oberprieler. The following ten new combinations are established: *A. abylaea* (Font Quer & Maire) Oberprieler, *A. maroccana* subsp. *aguilarii* (Maire & Sennen) Oberprieler, *A. mauritiana* subsp. *faurei* (Maire) Oberprieler, *A. pedunculata* subsp. *atlantica* (Pomel) Oberprieler, *A. pedunculata* subsp. *clausonis* (Pomel) Oberprieler, *A. pedunculata* var. *discoidea* (Boiss.) Oberprieler, *A. pedunculata* subsp. *turolensis* (Pau ex Caballero) Oberprieler, *A. punctata* subsp. *kabylica* (Battand.) Oberprieler, *A. stiparum* subsp. *sabulicola* (Pomel) Oberprieler, *A. tenuisecta* subsp. *jahandiezii* (Maire) Oberprieler.

Multivariate statistical methods (principal component analysis) and/or analyses of random amplified polymorphic DNAs (RAPD) were used to assess morphological and genetic variation and to address problems of species delimitation in the *Anthemis boveana* group and the *A. pedunculata* - *A. punctata* complex.

Contents

1. Introduction

The genus *Anthemis* belongs to the family *Compositae* Giseke, alternatively named *Asteraceae* Dumort. It is the name-giving genus of the *Anthemideae* Cass., a tribe which presently consists of 109 genera (Bremer & Humphries 1993; adding *Castrilanthemum* recently described by Vogt & Oberprieler 1996) and shows an extratropical, mainly Old-World-centred distribution. According to the most recent phylogenetic reconstruction of the family (Bremer 1996), the *Anthemideae* are a member of the subfamily *Asteroideae* and form the sister group to the *Astereae*. While Heywood & Humphries (1977) indicate around 130 species in the genus, more recent estimates give a total of c. 210 annual, biennial, or perennial species (Bremer & Humphries 1993).

Since Candolle's account of *Anthemis* in his *Prodromus* (Candolle 1838), the genus has never again been subject to a complete revisionary treatment. However, quite comprehensive regional treatments like Boissier's (1875) *Flora orientalis* account and Eig's (1938) studies on the oriental species of *Anthemis,* along with revisions made in the course of the large flora projects of the last 40 years, have resulted in our up-to-date understanding of the genus over a large part of its distributional range, viz. Europe (Fernandes 1975a, 1975b, 1976, 1983), E Europe and W Asia (Fedorov 1961), Turkey (Grierson & Yavin 1975), the Near East (Feinbrun-Dothan 1978), the *Flora iranica* area (Iranshahr 1986), and Saudi Arabia (Ghafoor & Al-Turki 1997). Additional information was contributed by revisionary treatments of defined infrageneric groups (*A. ammanthus* group, Greuter 1968; *A.* sect. *Maruta,* Yavin 1970; *A.* sect. *Anthemis,* Yavin 1972; *A. tomentosa* group, Geôrgiou 1990) and by geographically limited biosystematic revisions (Bulgaria: Kuzmanov & al. 1981 and Thin 1983; Spain: Benedí i González 1987).

In N Africa, as compared to other regions within the distributional range of *Anthemis,* the taxonomy of the genus is poorly understood, and a critical revision is lacking. While there are flora treatments available for Algeria (Quézel & Santa 1963), Tunisia (Pottier-Alapetite 1981), Libya (Alavi 1986), and Egypt (Täckholm 1974), for Morocco there is only a checklist (Jahandiez & Maire 1934). The main aim of the present study was to fill this gap by elaborating a complete taxonomic treatment of the genus for the area covered by Maire's *Flore de l'Afrique du Nord* (Maire & al. 1952-1987), i.e. the territories of Morocco, Algeria, Tunisia, and Libya.

2. Material and methods

This revision is based partly on plant material collected during field trips to Morocco and Tunisia in 1992-1995, which is deposited at the herbarium of the Botanic Garden & Botanical Museum Berlin-Dahlem (B). In June 1992, the study and collection of *Anthemis* in N Morocco was enabled by the participation in the "Iter Mediterraneum V" sponsored by the Organization for the Phyto-Taxonomic Investigation of the Mediterranean Area (OPTIMA). Further collections in Morocco (April-May 1993, May 1995) and Tunisia (May 1994) were made during field trips organised by the Botanic Garden and Botanical Museum Berlin-Dahlem.

Additionally, the study is based on herbarium material from the following public herbaria, abbreviated as in Holmgren & al. (1990) and Holmgren & Holmgren (1996), and private collections:

B	Botanischer Garten & Botanisches Museum Berlin-Dahlem
BC	Institut Botánic de Barcelona
BC-Sennen	Institut Botánic de Barcelona (Herbarium F. Sennen)
BM-Clifford	The Natural History Museum, London (Herbarium G. Clifford; microfiche)
C-Vahl	Botanical Museum and Library, University of Copenhagen (Herbarium M. Vahl; microfiche)
FI	Museo di Storia Naturale, Museo Botanico, Firenze
G	Conservatoire et Jardin botaniques de la ville de Genève
GOET	Systematisch-Geobotanisches Institut der Universität Göttingen
K	Royal Botanic Gardens, Kew (London)
LINN	The Linnean Society of London (Herbarium C. Linné; microfiche)
MA	Real Jardín Botánico, Madrid
MPU-AfN	Institut de Botanique Montpellier (Herbier de l'Afrique du Nord)
MPU-Braun-Blanquet	Institut de Botanique Montpellier (Herbarium J. Braun-Blanquet)
MPU-Dubuis	Institut de Botanique Montpellier (Herbarium A. Dubuis)
MPU-Weiller	Institut de Botanique Montpellier (Herbarium M. Weiller)
MPU-Sauvage	Institut de Botanique Montpellier (Herbarium Ch. Sauvage)
MSB	Institut für Systematische Botanik der Ludwig-Maximilians-Universität, München
P	Muséum National d'Histoire Naturelle - Laboratoire de Phanérogamie Paris

P-DESF	Muséum National d'Histoire Naturelle - Laboratoire de Phanérogamie Paris (Herbarium R. L. Desfontaines)
P-LA	Muséum National d'Histoire Naturelle - Laboratoire de Phanérogamie Paris (Herbarium J. B. P. A. de Monet de Lamarck)
RNG	University of Reading, School of Plant Sciences
SEV	Departamento de Biología Vegetal y Ecología, Universidad de Sevilla
UPS-Burser	Botanical Museum at Uppsala University (Herbarium J. Burser; microfiche)
Herb. Bayreuth	Universität Bayreuth, Lehrstuhl für Pflanzengeographie
Herb. Oberprieler	private collection of Ch. Oberprieler (Jena)
Herb. Vogt	private collection of R. Vogt (Berlin)

Specimens were examined with a stereo-microscope (Wild M5A), measurements being performed using the camera-lucida device to slot in a millimetric scale in the corresponding magnification.

The description of taxa is based on measurements made on dried plants. The variation ranges cited cover the total observed variation exhibited by a particular taxon. Extreme values have been placed in parentheses, while main range values relate to the interval covered by the mean ± 1 standard deviation of a particular character distribution.

A list of specimens seen is presented under each species. Localities are given countrywise from W to E in the following order: Spain (N African part), Morocco, Algeria, Tunisia, and Libya. Within each country, administrative districts (Morocco: Province; Algeria: Wilaya; Tunisia: Gouvernorat; Libya: Baladiyah) are listed in alphabetic order. Within each district, specimens are listed from N to S. Most of the specimens are given with longitude and latitude of the collecting locality, written as stated by the collector(s), or taken from various maps [when they are cited in square brackets]. Distribution maps were drawn using the public domain map projection program MICROCAM by S. A. Loomer (ftp://ftp.usma.edu/g&ene/gsl/microcam/).

For comparative carpological studies, achenes were taken from herbarium specimens and soaked for two days in a mixture (6 : 1) of 10 % aqueous solution of dioctyl sodium sulfosuccinate and 96 % ethanol (Peterson & al. 1978). Following dehydration through a 1 : 1, 3 : 7, 1 : 9 incremental series of sulfosuccinate/ethanol, with changes every 24 hours, and a final step in pure 96 % ethanol for 45 min, achenes were subsequently soaked for 4-6 weeks in a pretreatment solution of Kulzer Technovit 7100® and solidifier no. 1 at 4°C. After final embedding in a 1 : 15 mixture of the pretreatment solution and Kulzer solidifier no. 2, median-transverse and median-longitudinal sections of achenes were made using a rotary microtome. 3-5 µm thick sections from the middle half of the achenes were stained with toluidine blue and mounted in Vitroclud (Langenbrinck).

For scanning electron microscopy (SEM) achenes were taken from herbarium specimens, mounted on preparation stubs, and coated with a gold-palladium layer 2 nm thick in a Polaron sputter-coater. The observations and photography were performed with a Philips SEM 515 at the Botanical Museum Berlin-Dahlem.

3. Taxonomic history

Though mentioned already in *Genera plantarum* (Linnaeus 1737a) and *Hortus Cliffortianus* (Linnaeus 1737b), the generic name *Anthemis* was validated by Linnaeus (1753) in the first edition of *Species plantarum.* By doing so, Linnaeus preferred the generic name already used by Micheli (1729) over the name *Chamaemelum* which had been used by Bauhin (1623) and Tournefort (1700) for most of the Linnean *Anthemis* species.

In contrast to definitions given in *Genera plantarum* (Linnaeus 1737a: 256; 1754: 381) where *Anthemis* and *Anacyclus* are described to differ in the shape of achenes which are stated to be compressed in *Anacyclus* and terete in *Anthemis*, Linneaus (1753) arranged the species of these two genera according to the rather artificial character of presence vs. absence of ray florets in *Species plantarum.* This led to decades of uncertainty about the correct demarcation of the two genera which was still apparent in Willdenow's fourth edition of *Species plantarum* (Willdenow 1803) and Persoon's *Synopsis plantarum* (Persoon 1807) where both mentioned authors stressed the essential fruit characters as diagnostic for *Anacyclus* and *Anthemis* but ignored them when assigning the species to genera.

Shortly after Linnaeus' *Species plantarum* (Linnaeus 1753), Miller (1754) validated the generic name *Chamaemelum* (Druce 1914) to comprise some *Anthemis* species cultivated in English gardens. In Miller (1768), however, *Anthemis* is adopted and *Chamaemelum* treated as a synonym. A few decades later, Necker (1790), Gaertner (1791), and Moench (1794) revived the name *Chamaemelum* to accommodate some former *Anthemis* species with apically rounded achenes in a separate genus. Though initially refraining from the recognition of these two entities on a level higher than subgenus (Cassini 1817: 83), Cassini (1823) contributed to the excessive dismemberment of *Anthemis* into a number of genera by accepting *Anthemis* and its meanwhile described segregates *Chamaemelum, Maruta, Ormenis, Cladanthus,* and *Lepidophorum* as members of his "Anthémidées-Prototypes vraies", later (Cassini 1825) adding the monotypic genus *Lyonnetia* for *Anacyclus creticus* L. (*L. pusilla* Cass.; currently recognized as *Anthemis rigida* Sm.).

Lessing and Candolle were considerably influenced by the work of Cassini when they provided their synthetic classifications for the genera of *Compositae.* Lessing (1832) placed *Anthemis* species, which, on the basis of discoid capitula, had been assigned to Necker's *Hiorthia* (*H. orientalis* = *Anacyclus orientalis* L.) or Cassini's *Lyonnetia* in the subtribe *Artemisiinae,* far apart from the radiate representatives in subtribe *Anthemidinae.* This extremely unnatural dismembering of *Anthemis* species was overcome by Candolle (1838) who included *Lyonnetia,* along with *Anthemis, Maruta, Anacyclus, Ormenis, Cladanthus,* and *Lepidophorum* in his *"Euanthemideae"*.

Moris (1840-1843) was the first to note that the basally saccate disc florets observed by Cassini in his *Ormenis mixta* are also found in *Maruta fuscata* and *Anthemis nobilis.* He united them all under the generic name *Maruta,* foreshadowing to some extent the present circumscription of the genus *Chamaemelum,* except by also including *Anthemis cotula,* the type of *Maruta*.

A further step toward a natural arrangement of *Anthemis* species was made by Gay, the designated *Anthemis* monographer of his period, when he contributed an account of the genus in the appendix to the second volume of Gussone's *Synopsis* (Gussone 1844: 866-872). Here, Gay created the new genus *Cota* to accommodate four *Anthemis* species with dorso-ventrally compressed and indistincly ribbed achenes, while leaving the species with terete achenes and 10 distinct ribs in *Anthemis*. He also included *A. fuscata* and *A. cotula* in *Anthemis,* while noting their similarity with *A. mixta* which he left in *Ormenis*.

Problems relating to the correct demarcation of *Ormenis* against *Anthemis* owe their solution to Schultz's revised taxonomy of the *Anthemideae* (in Schnitzlein 1854: 69-70; Schultz 1860). Schultz proposed a subdivision of the tribe into six subtribes, mainly on carpological grounds, with members of *Anthemis* assigned to *Cotinae* and *Anthemidinae* and members of *Ormenis (O. fuscata, O. mixta, O. nobilis),* along with the unispecific *Cladanthus* forming subtribe *Ormenidae*.

Bentham & Hooker (1873) and Hoffmann (1891-1892) reacted to the excessive splitting of *Anthemis* by more or less re-establishing the Linnean circumscription of the genus, in which they merged such rather unrelated genera as *Ormenis, Lepidophorum,* or the N African *Rhetinolepis* described by Cosson (1856), while keeping separate other segregates of *Anthemis,* e.g. *Ammanthus* (described in Boissier 1849) and *Hiorthia* (containing the poorly understood *Anacyclus orientalis* L.). By that time, however, Boissier (1875) had already worked out a taxonomy of *Anthemis* that corresponds almost completely with our present circumscription and supraspecific taxonomy of the genus. Only *Ammanthus* was still to face a long period of generic independence, or misplacement in *Chrysanthemum,* until Greuter (1968) proposed its inclusion in *Anthemis,* thus completing our present notion of the genus.

4. Generic relationships

Anthemis provides the type of the name *Anthemideae,* used by Cassini (1819: 192) to designate his eleventh tribe of *Compositae.* Cassini (1823) divided the tribe into two major groups: "Anthémidées-Chrysanthémées" and "Anthémidées-Prototypes", based on the absence vs. presence of pales. These two subtribes, later-on validly named *Chrysantheminae* Less. and *Anthemidinae* Dumort., were used by most systematists concerned with the infratribal taxonomy in the following decades (e.g. Candolle 1838, Boissier 1875, Hoffmann 1891-1892, Hegi 1928). The artificiality of this subdivision clearly stated by Merxmüller (1954) and Wagenitz (1964) and demonstrated by Greuter (1968) when he found that in *Ammanthus,* up till then classified with *Chrysantheminae,* the presence or absence of scales "does not even necessarily suffice to distinguish species", which led him to transfer its species to *Anthemis.* Hybridisation experiments among members of *Anthemideae* made by Mitsuoka & Ehrendorfer (1972) have shown that the inheritance of pales is probably under simple oligogenic control. Further evidence came from the ambiguous position of the unispecific genus *Lepidophorum,* usually placed in the vicinity of *Anthemis* due to the presence of pales, but in morphological, phytochemical (Bohlmann & al. 1973, Harborne & al. 1976), and embryological features (Harling 1960) closely resembling pale-lacking members of the tribe. Observations of sporadic paleate capitula in *Chrysanthemum* (Napp-Zinn & Eble 1978) and inclusion of paleate and epaleate species into *Athanasia* by Källersjö (1991) point in the same direction.

Owing to the artificiality of a classification based on the presence vs. absence of pales, numerous attempts have been made in the last forty years to elaborate a more satisfactory taxonomy of the tribe. Thorough embryological studies of representatives of *Anthemideae* by Harling (1950, 1951, 1960) contributed to a natural delimitation and grouping of genera. Features of embryo sac formation can be used to set off *Anthemis* against other genera that have, at one time or another, been treated as synonymous or closely related. While all members of *Anthemis* were found to have a tetrasporic embryo sac development, members of the paleate genera *Chamaemelum* (sub *Ormenis*), *Lepidophorum, Anacyclus,* and *Cladanthus* showed monosporic embryo sac formation (Harling 1950, 1960). Further findings (Harling 1951) suggest close relationships of *Anthemis* with genera that had been considered to be unrelated due to their epaleate receptacles: A tetrasporic embryo sac development war found in representatives of *Tanacetum* (sub *Chrysanthemum parthenium, C. millefolium*), *Tripleurospermum* (sub *Matricaria maritima, M. oreades*), *Heteranthemis* (sub *C. viscidehirtum*), and, in an older embryological contribution by Martinoli (1940), also in *Nananthea.*

Cytological (Uitz 1970) and carpological surveys (Reitbrecht 1974) yielded a subdivision of *Anthemideae* into seven provisional groups. *Anthemis* was considered to hold a somewhat central position in the so-called *Matricaria* group, also including *Chamaemelum, Cladanthus, Tripleurospermum, Matricaria, Anacyclus, Otospermum, Daveaua,* and the S African *Pentzia.* In contrast to embryological findings mentioned above, Reitbrecht (1974) thought of the generic relationships of *Anthemis* to lie in two directions: with *Anacyclus,* due to the dorso-ventrally flattened achenes in *Anthemis* subg. *Cota*, and with *Chamaemelum* and *Tripleurospermum.* Outside the *Matricaria* group, additional relationships of *Anthemis* were suggested to exist with *Tanacetum* which was treated as the central member of the so-called *Chrysanthemum* complex.

In Heywood & Humphries's (1977) account of *Anthemideae* the so-called *Anthemis* assemblage was but a slight modification of Reitbrecht's (1974) *Matricaria* group, with the exclusion of *Pentzia* and related S hemisphere genera. The close relationship of *Anthemis* and *Chamaemelum* that had been suggested by crossing data (Mitsuoka & Ehrendorfer 1972) was considered by Heywood & Humphries (1977) to be obscured by differences in fruit and corolla structure (Briquet 1916), embryo sac development (Harling (1960), and phytochemical data (Bohlmann & al. 1965, Bohlmann & Zdero 1966). Further achene morphological and anatomical studies by Humphries (1977, 1979) revealed the suggested close relationship between *Anthemis* subg. *Cota* and *Anacyclus* to be rather superficial: While achenes of *Anacyclus* species were found to have only two vascular bundles in the pericarp wall, those of *Anthemis* species, though having ten or even more epicarpic ribs, invariably had five. Cyanogenic glycoside and flavonoid profiles (Greger 1977, 1978) also suggest a closer relationship of *Anacyclus* with *Achillea* than with *Anthemis*.

Bremer & Humphries (1993) elaborated a subtribal classification of *Anthemideae* using all morphological, embryological, and phytochemical information available at that time in a cladistic analysis. They classified *Anthemis* together with the unispecific *Nananthea* as the only members of the subtribe *Anthemidinae.* The subtribe *Chrysantheminae* with four genera *(Argyranthemum, "Chrysanthemum", Ismelia,* and *Heteranthemis)* was sister to the *Anthemidinae.* However, Bremer & Humphries (1993: 131) state that *Nananthea* was included only provisionally due to its tetrasporic embryo sac development and that "the immediate relatives of *[Anthemis]* are unknown". Also, the sister group relationship of *Anthemidinae* and *Chrysantheminae* remains rather uncertain since the analysis of the interrelationships of the 12 proposed subtribes yielded a number of equally parsimonious solutions and the strict consensus tree of these solutions collapsed completely (Bremer & Humphries 1993: 90).

Chloroplast restriction site studies in *Anthemideae* by Francisco-Ortega & al. (1995) and Watson (1996) contributed little to the solution of the problem of the position of *Anthemis* within the tribe, due to the restricted sampling of genera or the absence of *Anthemis* representatives in the data set, respectively. Francisco-Ortega & al. (1997), using sequence data of the internal transcribed spacer (ITS) regions of the nuclear ribosomal repeat to assess the intergeneric relationships of *Argyranthemum,* provide molecular information on 32 genera of eight subtribes of *Anthemideae.* Phylogenetic analyses of ITS data showed that most of the subtribes suggested by Bremer & Humphries (1993) are not resolved as monophyletic clades. *Anthemis* was found to be sister to *Tanacetum vulgare* within a rather basal clade grouping genera with predominantly Eurasian and Mediterranean distribution. However, low bootstrap values for many of the nodes of the cladogram suggest that caution is needed when interpreting the tree presented.

As Bremer & Humphries (1993) pointed out, our further understanding of the phylogeny of the tribe depends on a better resolution of non-monophyletic taxa, e.g. *Tanacetum* and *Tanacetinae.* Solutions for these problem taxa may also have positive bearings on positioning *Anthemis* within the tribe. At present, information on additional interesting features (e.g. calcium-oxalate crystals in epicarp cells) are too sparse to allow an improved cladistic analysis of the tribe. It is nevertheless promising to compare the results of the cladistic analysis of morphological data given by Bremer & Humphries (1993) with cytological data given by Uitz (1970) and Mitsuoka & Ehrendorfer (1972). As discussed later (see chapter 10), karyotype similarities appear to indicate relationships between the subtribes *Anthemidinae, Tanacetinae, Chrysantheminae, Achilleinae,* and *Matricariinae* through their predominantly perennial and (morphologically) basal genera *Anthemis, Tanacetum, Argyranthemum, Achillea,* and *Tripleurospermum.* In such a scheme, *Anthemis* would hold a rather central (basal) position within the tribe, with most of the mentioned subtribes showing sister-group relationships to it.

5. Supraspecific taxonomy

In the presently accepted circumscription, *Anthemis* comprises c. 211 species (Bremer & Humphries 1993). Traditionally, and mainly on carpological grounds, two main subgroups are distinguished within the genus (Wagenitz 1968): *A.* subg. *Anthemis* is characterised by actinomorphic achenes which are round or tetragonal in cross-section, usually have 10 longitudinal epicarpic ribs and epicarpic cells filled with sand of calcium-oxalate crystals; *A.* subg. *Cota* exhibits disymmetrical achenes which are dorso-ventrally flattened, usually have 8-22 ribs and epicarpic cells that either lack crystals or contain single, large crystals (Fig. 3). Since Gay's treatment in Gussone (1844), the latter subgenus was sometimes considered as an independent genus on morphological and phytochemical (Reitbrecht 1974) or cytogenetical grounds (Mitsuoka & Ehrendorfer 1972). However, as discussed in the previous chapter, there is hardly any evidence for a para- or polyphyletic nature of *Anthemis* that would necessitate the acknowledgement of the two entities in a rank higher than subgenus.

The species of the former genus *Ammanthus,* which were transferred to *Anthemis* by Greuter (1968), were (at least partly) considered to be sufficiently deviating by Fernandes (1975b, 1976) to merit recognition as a third subgenus, *A.* subg. *Ammanthus*. However, acknowledgement of this subgenus will likely cause *A.* subg. *Anthemis* to become paraphyletic. Yavin's (1972) treatment of this group as a series within *A.* sect. *Anthemis* is therefore preferred.

The classification of *Anthemis* subg. *Anthemis* traditionally follows the common pattern, with recognition of a number of apomorphic sections in addition to more plesiomorphic and presumably paraphyletic ones. Representatives of *A.* sect. *Hiorthia* (including *A.* sect. *Rumata*), which are characterised by suffruticose or pleiocormous perennial habit, were often considered to form the most basal group of the subgenus (Meusel & Jäger 1992). Here, in contrast to the other sections of *Anthemis,* polyploidy has played a significant role in the evolution of species and species groups. Mitsuoka & Ehrendorfer (1972) and Kuzmanov & al. (1981) suggested that perennial habit may enable plants to overcome the setbacks of reduced fertility caused by polyploidisation. Infrasectional taxonomies proposed by Fedorov (1961) and Thin (1983) have to be considered preliminary since they concern restricted geographical areas and are based on rather arbitrary selections of representative species.

In contrast to *Anthemis* sect. *Hiorthia, A.* sect. *Anthemis* has received a comprehensive assessment of its infrasectional taxonomy by Yavin (1972). In addition to two series accepted by Fedorov (1961), Yavin (1972) defined 14 new series, each with one to 12 species, segregated 12 species with extremely slender achenes into an independent section *A.* sect. *Rascheyanae,* and the fruit-anatomically deviating *A. chia* into the unispecific *A.* sect. *Chiae.* However, since besides the annual habit no other synapomorphy for members of *A.* sect. *Anthemis* is presently known and sister-group relationships of *A.* sect. *Rascheyanae* and sect. *Chiae* with species or species groups of *A.* sect. *Anthemis* are rather probable, the acknowledgement of these two annual sections would cause *A.* sect. *Anthemis* to become paraphyletic. In the case of *A.* sect. *Rascheyanae,* sister-group relationships may exist with *A.* ser. *Scariosae,* ser. *Melampodinae,* ser. *Haussknechtianae,* or ser. *Cornucopiae* due to shared apomorphies (hairy tubes of ray florets and hairy disc florets) in some of their members.

Anthemis sect. *Maruta* is characterised by the apomorphic feature of subulate pales. This morphologically rather distinct section is presumably nested within *A.* sect. *Anthemis* since it shows some similarities with *A. scariosa,* a species grouped within *A.* sect. *Anthemis* by Yavin (1972) but considered to hold a transitional position between the two sections by Grierson & Yavin (1975). *A.* sect. *Maruta* was subdivided into three series by Fedorov (1961): ser. *Cotulae,* ser. *Microcephalae,* and ser. *Odontostephanae.* When presenting a revision of the section, Yavin (1970) found the latter series distinct enough to exclude it from *A.* sect. *Maruta* and proposed its acknowledgement as a separate section, or even genus.

Anthemis subg. *Cota* is traditionally subdivided into two sections, *A.* sect. *Cota* and sect. *Anthemaria* (e.g. Fernandes 1975b, 1976, Benedí i Gonzáles 1987). The main difference between the two sections relates to life span: members of *A.* sect. *Anthemaria* are characterised by a perennial, suffruticose to pleiocormously herbaceous habit, *A.* sect. *Cota* consists of annual to biennial herbs. Fedorov (1961) proposed a different classification, subdividing the subgenus (his *A.* sect. *Cota*) into five series. Pending a comprehensive morphological and cladistic study, no deliberate choice is made here between the two proposed scenarios, but for practical purposes the classification proposed by Fernandes (1975b, 1976) is provisionally followed.

6. Phytogeography

The total geographical range of *Anthemis* encompasses almost the whole western Eurasia, the Mediterranean, and a small part of E Africa. According to Meusel & Jäger (1992) the distribution range is very similar to those of *Daucus, Cichorium,* and *Filago*. While C Europe is inhabited by few archaeophytic species only, the main centre of diversity is found in SW Asia where about 150 of the c. 210 described species occur and all of the presently accepted subgenera and sections are found. The W and C North African part of the distribution area, which is covered by the present revision, hosts a markedly lower number of species and certainly has played a rather peripheral role in the evolution of the genus.

Anthemis sect. *Hiorthia,* formed by perennial herbs and subshrubs of predominantly mountainous habitats and often considered to be the most primitive section of *Anthemis,* shows a marked centre of diversity in SW Asia (Turkey and the adjacent Caucasus countries) and the mediterranean and submediterranean parts of SE Europe. According to Kuzmanov & al. (1981), Asia Minor is considered the primary evolutionary centre of the genus in general and of *A.* sect. *Hiorthia* in particular, since diploid representatives of this section, in which polyploidy occurs, are concentrated here. While most of the SW Asian and SE European species of *A.* sect. *Hiorthia* are restricted to small areas, the highly polymorphic *A. cretica* (including *A. carpatica* and *A. saxatilis*) which is represented in Turkey by not less than 12 subspecies (Grierson & Yavin 1975) extends to C and even W southern Europe, and *A. cretica* subsp. *columnae*, a subspecies which is centred on the Balkan Peninsula and Italy, even occurs in Algeria in an extremely restricted area. The distribution range of three other N African members of *A.* sect. *Hiorthia, A. maritima, A. pedunculata,* and *A. abylaea,* contrasts markedly with the pattern just described for *A. cretica*. *A. maritima* is restricted to the W Mediterranean area and, due to its deviating ecology, presumably represents a evolutional lineage quite independent from the remainder of the section. Additionally, diploid plants are found scattered throughout the distribution range of the species (Menorca, Benedí i Gonzáles 1987; Algeria, *A. maritima* subsp. *bolosii*, present paper). Similarly, the Ibero-Maghrebine *A. pedunculata* is also restricted to the W Mediterranean region and occurs at the diploid and tetraploid level. The deviating fruit morphology, with achenes circular instead of rhombic in cross-section, again suggests that *A. pedunculata* and its close tetraploid relative *A. abylaea* evolved independently from the remainder of the section. An obvious pattern of vicariance within *A.* sect. *Hiorthia* thus emerges, with a main centre of diversity in SW Asia and a minor centre formed by the lineages of *A. maritima, A. pedunculata,* and the Spanish diploid *A. alpestris* in the W Mediterranean area. The tetraploid NE Algerian and N Tunisian *A. punctata,* the fifth N African species of *A.* sect. *Hiorthia,* geographically links *A. pedunculata* with the *A. cretica* group (the Sicilian endemic species *A. cupaniana* and *A. cretica* subsp. *columnae*), being restricted to the area where the two lineages overlap.

Additionally, it shows a clinal morphological variation mediating between two extremes: strongly tuberculate achenes which are round in cross-section (as in *A. pedunculata*) in plants from the western part of the species' distribution area and weakly tuberculate achenes tending to be rhombic in cross-section (as in *A. cretica*) in its eastern part.

Anthemis sect. *Anthemis* which according to the preliminary list given by Yavin (1972) comprises c. 60 annual species, shows an originally Mediterranean-Oriental-Submediterranean-Pontic distribution area that was enlarged palaeosynanthropically in an Atlantic-W-Sarmatic-Scandinavian direction (Meusel & Jäger 1992). The main concentration of species is in the E Mediterranean and SW Asian region, where 11 of Yavin's (1972) 14 series are found. The individual species of the section are often restricted to rather small areas, and even the series, usually, grow only in a small portion of the section's total range. In the area covered by the present revision four series occur: *A.* ser. *Anthemis,* ser. *Bourgaeinianae,* ser. *Chrysanthae,* and ser. *Secundirameae,* whose members show distinct vicariant distribution patterns.

In *Anthemis* ser. *Anthemis,* the closely related species *A. arvensis* and *A. ruthenica* provide a good example of vicariance. *A. arvensis* is considered an originally iberic-centromediterranean-hellenic species *(A. arvensis* subsp. *incrassata)* which enlarged its areal synanthropically into the Oceanic-Suboceanic parts of W and C Europe (subsp. *arvensis*); *A. ruthenica* is restricted to the adjacent, dryer, Pontic-Balkanic-Pannonic area (Meusel & Jäger 1992); and the third species of this series, *A. auriculata,* occupies a comparably small area in the S parts of the Balkan Peninsula and the N Aegean region. N Africa is reached only by the Mediterranean-Submediterranean *A. arvensis* subsp. *incrassata,* restricted here to the rather humid regions of the Tangier peninsula and the adjacent W and C parts of the Rif mountains.

Anthemis ser. *Bourgaeinianae* consists of five allopatric species growing in the SW-Mediterranean and N-Saharic region. *A. bourgaei* is known only from a small area in SW Spain, and *A. mauritiana, A. zaiànica,* and *A. monilicostata* occur locally in Morocco and Algeria. The polymorphic *A. stiparum* is more widespread, being distributed throughout the arid areas of W Morocco and Algeria. *A. stiparum* subsp. *stiparum* and subsp. *intermedia* grow among steppe vegetation on the High Plains between Tell Atlas and Sahara Atlas. *A. stiparum* subsp. *sabulicola* in the even more xeric, semi-desert habitats of the northern fringe of the Algerian Sahara.

Vicariant distribution patterns are also observed in the two other species groups, which are largely centred on N Africa: *Anthemis* ser. *Chrysanthae* and ser. *Secundirameae*. The five species of the Moroccan and NW Algerian *A.* ser. *Chrysanthae* show allopatric areas of distribution arranged in a well marked more or less linear sequence spanning NW Algeria *(A. boveana, A. chrysantha),* N Morocco *(A. maroccana, A. gharbensis),* and SW Morocco *(A. tenuisecta)*. Like its mirror image, the N African members of *A.* ser. *Secundiramea* are distributed allopatrically between N Tunisia and N Egypt. The northernmost member of the series, *A. secundiramea,* covers a larger geographic area than the other species and shows a C Mediterranean distribution with some outposts in S Europe (Menorca, S France, Corsica, Sardinia). The closely related, discoid species *A. muricata* is endemic to Sicily and, in contrast to *A. secundiramea,* is only found in inland habitats. The sequence of allopatric N African endemics of the series starts with *A. ubensis* in NE Algeria and N Tunisia, followed by *A. confusa* in C and S Tunisia, *A. glareosa* in W Libya, *A. kruegeriana, A. cyrenaica,* and *A. taubertii* in E Libya, and *A. retusa* in N Egypt, while *A. rigida* is found in the Aegean archipelago.

Anthemis sect. *Maruta* consists of 14 species and, according to Meusel & Jäger (1992), inhabits an E Mediterranean-SW Iranian area with one species *(A. cotula,* incl. *A. lithuanica)* being archeophytically distributed throughout Europe and SW Asia. Two representatives of the section, *A. cotula* and *A. pseudocotula,* reach N Africa, the former is presumably introduced by Man into N Morocco (Tangier peninsula, Rif mountains, Melilla peninsula) and the vicinity of cities like Oran (Algeria), Sfax, and Gabès (Tunisia), the latter reaching the SW limit of its natural distribution in Cyrenaica.

Anthemis subg. *Cota*, like sect. *Anthemis* and sect. *Hiorthia,* shows a concentration of its species in the SE European and SW Asian part of its distributional range. Most of its species are restricted to small areas in the submediterranean parts of Turkey and the adjacent Caucasus countries. However, some perennial members of *A.* sect. *Anthemaria* (e.g. *A. tinctoria, A. triumfetti*), along with monocarpic representatives of *A.* sect. *Cota* *(A. altissima, A. austriaca),* penetrate C and SW Europe. Since *A. austriaca* is known to occur synanthropically in ruderal plant communities of C Europe, its occurrence in N Africa, which is demonstrated in the present paper for the first time, is likely due to human activity.

7. Modes of speciation within *Anthemis* in N Africa

The N African representatives of the genus *Anthemis* offer an interesting insight into the evolutionary patterns realised in this genus. Most of the observed mechanisms also occur in groups of related taxa in other parts of the generic range, and in other genera of *Anthemideae*. As Ehrendorfer (1970) has pointed out, main changes of evolutionary patterns and strategies in this tribe are observed in connection with the switch from perennial to annual life form.

New data on N African taxa, along with published records by Uitz (1970), Ehrendorfer (1970), Mitsuoka & Ehrendorfer (1972), and Kuzmanov & al. (1981), show that *Anthemis* sect. *Hiorthia* is the only section of the genus where polyploidy has played a significant evolutionary role. All of the N African representatives of this section were found to exist at the tetraploid level. While *A. abylaea, A. cretica* subsp. *columnae,* and *A. punctata* are restricted to this level, in the widespread *A. pedunculata,* and according to pollen dimensions in some N African populations of *A. maritima* (in *A. maritima* subsp. *bolosii*) as well, diploids are found. These populations, along with the discoid *A. alpestris* which is endemic to the Iberian Peninsula, are the only diploid representatives of the section in the W Mediterranean area.

While in *Anthemis maritima* morphological differences between (presumably) diploid and tetraploid representatives were found to be marked enough to recognise the two entities as separate subspecies, there seems to exist but little correlation between ploidy level and morphology in *A. pedunculata*. Multivariate statistical analyses of morphological variation along with results of molecular studies (see chapter 13) indicate that most of the tetraploids have to be considered to be of autotetraploid origin. Though the difference in ploidy level may act as a rather effective crossing barrier, most of the tetraploid populations have not developed conspicuously deviating morphological characters yet that would permit their acknowledgement at any taxonomic level. As alone exception, tetraploid populations of the limestone mountains in the E parts of the Tangiers peninsula were found to deviate morphologically from other diploid and tetraploid representatives of *A. pedunculata* and are considered to represent an independent species, *A. abylaea*.

As multivariate statistical analyses in the *A. pedunculata* - *A. punctata* complex (chapter 13) and in the *A. boveana* group (chapter 12) indicate, the geographical pattern of morphological variation in perennial and annual representatives of *Anthemis* in N Africa shows some marked differences. Variation in perennials occurs on a larger geographical scale, morphologically divergent forms are geographically isolated but connected by morphological intermediates, resulting in a clinal pattern of morphological variation. In contrast, annual taxa show more restricted distribution areas, morphological variation within taxa is rather small as compared to these between taxa. Evolutionary divergence appears to be more rapid in the annual representatives of the genus than in the perennial ones. As Wright (1940) and Stebbins (1952) pointed out, the population structure most favourable for rapid evolution is that of a large or medium-sized population divided into many small subunits which are largely isolated from each other, but can occasionally interchange genes. In such a set-up, the small subunits permit new genotypes to become stabilised through natural selection or genetic drift, while migration between colonies prevents the subunit's genetic stagnation and ensure genetic coherence of the large population for a certain period of time. Since such a population structure occurs more frequently in arid or semiarid regions than in areas with abundant moisture, Stebbins (1952) considers aridity to be a stimulus for plant evolution.

A further acceleration of genetic and morphological divergence may be caused by the switch from self-incompatibility and allogamy in perennials towards self-compatibility and autogamy in annuals. The combination of annual life form and autogamy enables plants to rapidly occupy unstable or pioneer habitats and to survive unfavourable seasons as diaspores. Populations of annuals have to be built up every year from a seed-bank and, as a consequence, are affected by rapid natural selection or genetic drift through a so-called bottleneck effect (Runemark 1970, Nei & al. 1975), since only part of the gene pool of the parent population will be maintained in the next one when conditions are suboptimal. The repeated contraction of populations narrows down genetic and morphological variability within populations and increases discontinuities between them, because inbreeding and genetic drift may lead to the fixation of alleles different from those found in the parental populations, or at least to deviating allele frequencies.

In contrast to the allopolyploid mode of speciation, the frequency of hybrid speciation on the diploid level, as hypothesised for *Anthemis ubensis* on morphological grounds in the present paper, is less well known (Rieseberg & Brouillet 1994) and its occurrence is often questioned (Grant 1981), although there is positive evidence for it in some plant groups (e.g. *Helianthus,* Rieseberg 1991; *Iris,* Arnold & al. 1990, 1991; *Stephanomeria,* Gallez & Gottlieb 1982). Since even intergeneric crosses between *Anthemis* species and representatives of *Chamaemelum, Matricaria,* and *Tripleurospermum* may produce fertile or semifertile offspring (Mitsuoka & Ehrendorfer 1972), the existence of fertile or semifertile hybrids involving two *Anthemis* species is plausible, even if they belong to different sections, as in the case of *A. pedunculata* and *A. secundiramea*, the presumed parent species of *A. ubensis*. As Grant (1981) set out, the central problems with diploid hybrid speciation are genotype segregation in the hybrid progeny as well as backcrossing, introgression, and consequent resorption of the hybrid genotype. Grant (1981) lists seven strategies that may overcome segregation of a hybrid genome and enhance its stability. Only two such strategies, however, are connected with sexual propagation and the homoploid nature of hybrids: speciation by recombination and isolation of the hybrids from the parent species by external factors. Speciation by recombination may occur in the progeny of a sterile or semisterile hybrid formed by hybridisation of two parent species which differ by two or more chromosomal rearrangements, when recombination types evolve that are homozygous for these rearrangements; the resulting hybrid descendants are fertile and diploid, but genetically isolated from the parent species due to a chromosomal sterility barrier. Isolation may occur when new combinations of characters lead to a mechanical, ethological, or ecological crossing barrier between descendants and their parent species. In the case of *A. ubensis*, both possibilities exist, but evidence, which would require thorough molecular and cytological studies, is lacking.

8. Delimitation of taxa - Concepts of species, subspecies, and varieties

In the present revision of *Anthemis* in W and C North Africa the taxonomic categories of species, subspecies, and variety are used to classify the encountered patterns of morphological variation at and below the species level.

As noted by Jansen (1985), "much debate and little consensus exists among biologists concerning the definition of species." A number of different species concepts exist (see Rieseberg & Brouillet 1994: 24 for a comprehensive list), based on biological (e.g. the biological, better termed reproductive, species concept of Mayr 1969, 1970), phenetic (Cronquist 1988), ecological (Van Valen 1976), and phylogenetic criteria (the phylogenetic species concept of Cracraft 1989 and the autapomorphic species concept of Mishler & Brandon 1987).

A primarily morphological or phenetic species concept has been used in the present study. As discussed in the previous chapter, morphological discontinuities are assumed to be due to genetic differences and, together with cytological and molecular information in some taxa groups, to a certain degree are taken to reflect speciation processes and phylogenetic relationships. Since patterns of morphological variation show marked differences between different subgroups of the genus, the resulting species may not be equivalent. As noted by Lewis (1955, cited in Stuessy 1990:179), "the pattern of morphological differentiation may differ from one group of plants to another and is a reflection of the diversity of evolutionary processes. Consequently, species and subspecies are not necessarily equivalent in different genera or different sections of the same genus." As discussed above, the prevailing modes of speciation in perennials of *Anthemis* sect. *Hiorthia* are hybridisation and polyploidy, while in annuals of *A.* sect. *Anthemis* allopatric speciation and local (founder effect) speciation (Levin 1993) is usually encountered. Therefore, species acknowledged in the former section tend to be wide-spread, polymorphic, and often exhibit clinal variation of morphological characters; while those of the latter section tend to be more local and less polymorphic.

Both subspecies and variety were used as infraspecific categories to describe patterns of infraspecific morphological variation. Since little is known on genetic divergence and reproductive behaviour, only geographical information was used to decide on the rank of morphologically defined infraspecific taxa. Following suggestions made by Stuessy (1990), subspecies rank is used for a cohesive series of morphologically similar individuals forming allopatric or parapatric neighbour populations to other cohesive series of morphologically deviating populations, when morphologically intermediate individuals or populations occur along the contact zones. This subspecies concept, based on phenetics and geography, dates back to Wettstein (1898) who found that similar and closely related young taxa (subspecies) show allopatric distribution patterns, since their ecological demands are too similar to allow their sympatric co-existence. Only after a further divergence involving ecological demands (and often correlated with further genetic and morphological divergence) taxa (species) will be able to sympatrically co-exist. Subspecies, therefore, are considered by Wettstein (1898) to represent intermediate stages in an allopatric speciation process, which modern evolutionary biologists (e.g. Stebbins 1950, Grant 1981, Ehrendorfer 1984) still consider to be the prevalent mode of speciation in plants. According to Rieseberg & Brouillet (1994), allopatric speciation by subdivision (or vicariance) rather results in monophyletic (sub)species pairs, while allopatric founder effect speciation may lead to a monophyletic derivative (sub)species and leave a paraphyletic or metaphyletic progenitor behind. As Crisp & Chandler (1996) have demonstrated, the avoidance of paraphyletic or metaphyletic taxa at and below the species level is neither realistic nor reasonable and may be theoretically impossible. Over and above, the occurrence of reticulate evolution in *Anthemis* due to polyploidization and homoploid hybrid speciation also argues against a strict cladistic species concept.

While subspecies have often been regarded as regional facies of a species, varieties were considered to represent a local facies (Du Rietz 1930, Stuessy 1990). In the present revision the rank of variety is used for morphologically deviating populations or population groups when all individuals are uniform but do not form a geographically cohesive population or population series. For example, varietal status was used for discoid representatives of *Anthemis pedunculata* subsp. *pedunculata* which occur nearly throughout the range of the subspecies but show no geographical integrity because they are usually neighboured by uniformly radiate representatives. Since morphological distinctions are few and presumably under a simple genetic control, one may assume that discoid plants have evolved in different populations in parallel. The resulting variety, *A. pedunculata* var. *discoidea*, is therefore quite likely of polyphyletic origin.

The rank of forma, perhaps best applied to morphologically deviating individuals appearing sporadically within normal populations of a taxon (Stuessy 1990), has not been used in the present work. Some do formally name such minor differences to draw attention to populational variation (Valentine 1975), others (Burtt 1970, Jansen 1985) consider this unnecessary nomenclatural clutter. I agree with the latter authors and will refer to minor morphological variants in the discussion of taxa while denying them formal acknowledgement.

9. Morphological features

Duration and life form

The majority of N African representatives of *Anthemis* are annuals belonging to *A.* sect. *Anthemis,* sect. *Maruta,* and sect. *Cota*. The annual habit may be interpreted as an adaptation to the dry semi-desert and steppe habitats of the adjacent areas of the Sahara, and to disturbed habitats or arable fields. *A. stiparum, A. confusa,* or *A. glareosa* are prostrate annuals with reduced main axes and procumbent stems with small leaves, found in natural stony and sandy habitats of the deserts. The vigorous growth of *A. gharbensis* and *A. cotula,* found as weeds in arable fields and along field margins in more humid areas, forms the opposite extreme habit of therophytic *Anthemis* in N Africa.

Anthemis sect. *Hiorthia* contains short- to long-lived perennial herbs which are restricted in N Africa to the humid areas of the coasts *(A. maritima)* or to the mountains of the Atlas ranges of Morocco, Algeria, and Tunisia *(A. abylaea, A. pedunculata, A. punctata, A. cretica* subsp. *columnae).* At least *A. pedunculata* is capable to flower and set fruit already in the first year, and especially diploid plants are often found growing as weeds in arable fields, so that the differences between annual and perennial life form seem not to be too clear-cut in this species. However, in better growing conditions *A. pedunculata* is clearly a short-lived perennial, with annual shoots arising from a woody stock (pleiocorm) formed by the bases of the primary and subsequent annual shoots. Tetraploid plants of *A. pedunculata,* along with representatives of *A. abylaea, A. punctata,* and *A. cretica* subsp. *columnae,* also grow as pleiocormous hemicryptophytes. Observations in the field and herbarium suggest that most representatives of these species have life spans of three to five years.

Roots and rhizomes

The root system type is closely correlated with habit and duration. In all annuals of *Anthemis* sect. *Anthemis,* sect. *Maruta,* and sect. *Cota,* taproots are found. The perennials in *A.* sect. *Hiorthia* are characterized by a woody caudex formed by the lignified bases of previous years' shoots fused with the basal taproot. In younger individuals the caudex may be unbranched and only partly subterranean, in older ones branched and completely subterranean caudices (pleiocorms) may be found. In the perennial species, especially in *A. maritima,* accessory roots borne at the basal stem nodes are frequently observed which are missing in annuals, even if procumbent.

Growth habit, stems and capitulescence

The most simple condition in the organisation of stem and disposition of capitula found in *Anthemis* is shown in Fig. 1A: the main axis is erect and ends in a cymose capitulescence characterised by a terminal capitulum which flowers first. This type of capitulescence organisation is found in most N African annuals, e.g. *A. austriaca, A. ubensis,* or *A. monilicostata*. Unsuitable growing conditions like drought or malnutrition may considerably reduce the number of developing branches and lead to poor capitulescences of few or a single capitulum.

A more complicated condition of stem and capitulescence organisation results when side axes are added beneath the main capitulescence (Fig. 1B). Troll (1964) and Panero (1992) use the term paracladia to designate these accessory flowering branches, each of which resembles the main structural axis of the capitulescence. The number of paracladia depends on growth conditions. In very robust annual species it is not uncommon that the main axis produces a paracladium from every leaf axil of the main axis, down to the basal nodes (Fig. 1C; e.g. *A. cotula*). In some species, e.g. *Anthemis gharbensis,* a more or less

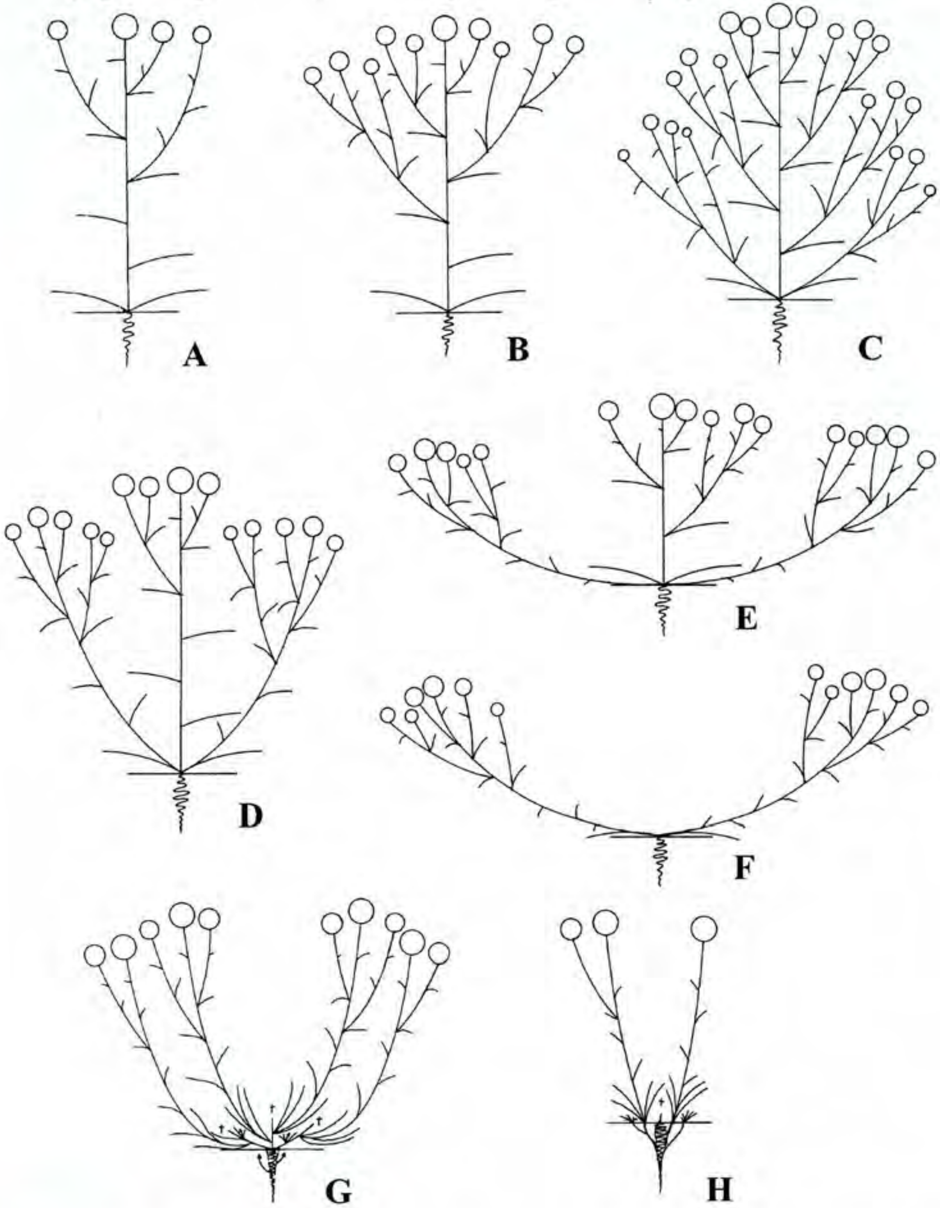

Fig. 1. Growth forms and capitulescence types in N African representatives of *Anthemis* (see text for explanation).

conspicuous inhibition zone is found beneath the capitulescence of the main axis, and side axes will arise from the basal nodes of the main axis after its capitulescence has flowered (Fig. 1D). For convenience, such side axes are termed stems in the present revision.

Some annual N African representatives of *Anthemis* (e.g. *A. tenuisecta, A. confusa,* or *A. glareosa*) are characterised by a prostrate habit. Their main axis is reduced and its basal internodes are extremely short (Fig. 1E). Reduction of the main axis is often so complete that branching occurs directly from the taproot (Fig. 1F). The larger and usually petiolate lower cauline leaves that normally make up the basal rosette are almost totally missing; most leaves are sessile and resemble upper cauline leaves of plants with a normally developed main axis. This character may be used to distinguish between N Tunisian *A. ubensis* and the closely related C Tunisian *A. confusa:* While *A. ubensis* has an erect habit with a main axis and leaves that successively decrease in size and dissection from base to top, *A. confusa* is characterised by prostrate habit and poorly dissected leaves.

In perennial N African representatives of the genus, the trend towards reduction of the main axis is well marked, but realised in a different way. The current year's shoots arise from the lignified bases of primary and subsequent shoots of the last years (Fig. 1G). Sometimes the main axis is basally more or less completely fused with the taproot to form a ± subterranean rootstock (caudex) that often bears both non-flowering and flowering shoots (Fig. 1H). The capitulescences are often reduced to a single capitulum, and rarely more than three (up to 10) capitula.

The stems are usually herbaceous in their distal part but conspicuously lignified basally, particularly in perennials. Stems formed by the main axis are usually straight basally, while those corresponding to side branches or borne on a rootstock are basally bent upwards. In species with a procumbent habit, only the capitulescence or single peduncles are lifted above the ground. In all cases, the stems are round in cross-section and somewhat sulcate. They are usually green, often tinged with red in the lower half.

In *Anthemis maritima* in particular, and to a lesser extent in the other perennial representatives of *A.* sect. *Hiorthia*, the lower stem nodes may be beset with accessory roots.

Stem length varies considerably with growth conditions: in the perennials of *Anthemis* sect. *Hiorthia* it is 20-40 cm, in representatives of *A.* sect. *Anthemis* and sect. *Maruta* usually up to 25 cm, but under favourable conditions sometimes much more (e.g. in *A. gharbensis* 60 cm, *A. cotula* 90 cm). Accordingly, the diameter of stem bases may vary between less than 1 mm in poorly developed plants up to 3 or occasionally 6 mm in vigorously growing annuals and some perennials.

Indumentum

The indumentum in most N African representatives of *Anthemis* consists of biseriate glands and medifixed covering hairs, as already found by Napp-Zinn & Eble (1980).

Medifixed hairs are usually borne on a stalk formed by 2-4 (sometimes even up to 7) more or less isodiametic cells and a large, strongly elongated apical cell that is symmetrically or asymmetrically suspended at the tip of the stalk. While the stalks may reach a length of c. 50-80 µm, the length of the apical cell is usually found to be 400-1000 µm. In some species, extremely asymmetrically medifixed apical cells are found. Sometimes, especially on peduncles and involucral bracts, asymmetry is so marked that the apical cell is no longer medifixed and an uniseriate flagellar covering hair is formed. These hairs are referred to as basifixed hairs in the descriptions. However, their presence seems to have little taxonomic relevance.

Glands are usually found on all overground parts of plants, even on pales, ray florets, disc florets and achenes. Their structure and shape is very similar in all species studied. They are formed by two parallel series of 3-4 isodiametrical cells and have a knob-like appearance. They are found in all N African representatives of *Anthemis* and do not have taxonomic significance.

Covering hairs are usually found on stems, leaves, peduncles, involucres, and sometimes on the peripheral pales *(Anthemis mauritiana, A. monilicostata).* Covering hairs on disc florets and tubular parts of ray florets occur in some species of *Anthemis,* but none were found N African representatives of the genus.

In most N African *Anthemis* species, the stems are sparsely to densely appressed-hairy, with medifixed hairs and interspersed glands. However, in *A. maritima, A. pedunculata, A. punctata* subsp. *kabylica, A. secundiramea,* and *A. cotula* completely glabrous stems were encountered.

In leaves, biseriate glands are sunk in pits on the upper and lower surface. The density of the non-glandular leaf indumentum is extremely variable and has little taxonomic significance. Completely glabrous leaves were encountered in *Anthemis maritima, A. pedunculata, A. punctata* subsp. *kabylica, A. confusa,* and *A. secundiramea*. All other species have sparsely to rarely densely hairy leaves. *A. cretica* subsp. *columnae* is characterized by an extremely dense, sericeous leaf indumentum.

Peduncles are always furnished with at least some covering hairs, except in *Anthemis maritima* subsp. *bolosii* where even peduncles are devoid of covering hairs.

The involucral bracts (at least the outer and middle ones) of most species studied are covered with long hairs, but are completely glabrous in *Anthemis maritima* subsp. *bolosii* and subsp. *pseudopunctata* (those of *A. maritima* subsp. *maritima* are usually sparsely to densely hairy), and, contrary to the other members of *A.* ser. *Bourgaeinianae*, also in *A. monilicostata.* Interspersed biseriate glands are present in all taxa. Inside, the of involucral bracts are usually glabrous, except in some plants of *A. ubensis* where some hairs were found.

Leaves

The leaves are consistently alternate, though sometimes forming basal rosettes. The shape, size and dissection of the leaves may vary considerably depending on their position. Rosette leaves and leaves from the basal parts of erect stems are usually narrowly elliptical to narrowly obovate in outline, while leaves from the upper parts of erect stems and leaves of prostrate stems tend to be more ovate in outline. This is correlated with the tendency of basal and lower cauline leaves to be petiolate, while the upper cauline leaves are usually sessile.

In most of the species studied, the base of the petiole bears several pairs of lateral teeth. In basal leaves primary lobes differ markedly from the basal teeth in size and dissection: basal teeth are rather small, entire or pinnatisect; primary leaf lobes are larger, 1-3-pinnatisect or -pinnatipartite. Also, basal teeth and leaf lobes are well spaced and separated by the petiole. In the upper half of the stem leaf petioles become more and more reduced, basal teeth and leaf lobes become closer to each other, and as basal teeth are larger and leaf-lobes less dissected, upper leaves are sessile in appearance. While teeth at the leaf base are found in all perennial and most annual species, they tend to be absent in *Anthemis boveana, A. chrysantha,* and *A. gharbesis* of *A.* ser. *Chrysanthae,* and in most of the members of *A.* ser. *Bourgaeinianae.*

Leave texture is usually herbaceous, but succulent leaves are common in species from maritime habitats (e.g. *Anthemis maritima, A. secundiramea, A. chrysantha, A. mauritiana*).

Dimensions of leaves are variable and depend on growth conditions. However, in the *Anthemis pedunculata - A. punctata* group of species they may help in the determination of taxa: basal leaves in *A. pedunculata* are usually up to 45(-75) mm long and up to 20(-30) mm wide, those of *A. punctata* are conspicuously longer (up to 115 mm) and wider (up to 53 mm). *A. abylaea* is also characterized by rather long (up to 80 mm) and wide (up to 35 mm) basal leaves.

The dissection of leaf blades proves to be taxonomically relevant, its degree depending on the position of the leaf on the stem. As a rule, the most basal leaves are less strongly dissected than the lower cauline ones, and further upward leaf dissection is again gradually reduced. Therefore, differences in leaf dissection are particularly important in the lower cauline leaves. In most N African *Anthemis* taxa the lower leaves are pinnatisect with primary lobes cut right to the axis, but in *A. maritima* subsp. *bolosii* and some plants of *A. punctata* subsp. *kabylica* they are pinnatifid or pinnatipartite.

2- to 3-pinnatisect or -pinnatipartite leaves are found in most species. The shape of ultimate leaf segments may vary within taxa from broadly triangular to narrowly elliptical or even linear, and their dimensions also varies. No clear-cut discontinuities between taxa could be observed, but some tendencies are sufficiently marked to be used as distinguishing features. For example, *Anthemis pedunculata* usually has 1.0-5.5 mm long and 0.3-1.8 mm wide ultimate leaf segments, but those of *A. punctata* (1.4-9.0 mm x 0.6-2.3 mm) and *A. cretica* var. *columnae* (1.7-20.0 mm x 0.6-2.0 mm) are considerably larger. In most species, ultimate leaf segments end in a mucro of 0.1-0.3 mm length. No mucronate leaf segments were observed in some populations of *A. secundiramea.*

Peduncles

In the present study, the peduncle is defined as the distal portion of the stem subtending a capitulum, from the most distal leaf on this axis to the base of the involucre. While peduncle length was found to be very variable in all species examined and therefore unhelpful for the characterisation of taxa, the inflation of peduncles at maturity proved to be relevant. In the N African representatives of *Anthemis* subg. *Cota (A. austriaca)* and of *A.* sect. *Hiorthia* the peduncles usually remain slender or become only slightly inflated at maturity. In *A.* sect. *Anthemis* and sect. *Maruta,* strongly inflated peduncles are found in *A. arvensis* subsp. *incrassata* of *A.* ser. *Anthemis* and in *A. chrysantha* of *A.* ser. *Chrysanthae.* In *A. secundiramea* of *A.* ser. *Secundirameae,* this character is used to distinguish the two N African varieties of that species, var. *secundiramea* with and var. *cossyrensis* without conspicuously inflated peduncles. A further representative of this series, *A. ubensis,* and some populations of *A. glareosa* also show incrassate peduncles. In contrast, all representatives of *A.* ser. *Bourgaeinianae* have peduncles remaining slender at maturity. In *A.* sect. *Maruta,* this character can be used to distinguish *A. cotula* (slender peduncles) from *A. pseudocotula* (inflated peduncles).

Capitula

Most species are gynomonoecious, with a single row of female ray florets and a central mass of perfect, hermaphrodite disc florets. Monoecious plants with all florets tubular and hermaphrodite are found in *Anthemis pedunculata* var. *discoidea, A. cyrenaica,* and *A. kruegeriana*. In the latter two taxa, however, radiate capitula are also found, sometimes on the same plant as discoid ones. In these cases, ray florets are minute (up to c. 5 mm long) but still fertile, and have sometimes been called hemiligules (e.g. Benedí i González 1987).

The diameter of capitula (including ray florets) is a useful criterion in the *Anthemis pedunculata - A. punctata* group of species where in radiate representatives of *A. pedunculata* it is 6-37 mm, while *A. abylaea* (30-50 mm) and *A. punctata* (30-55 mm) have larger and more showy capitula.

The number of ray florets is correlated with the dimensions of capitula. In small-headed species it often scatters around the Fibonacci numbers 8 and 13, while in other species even numbers between 13 and 21 are preferred. In *A. abylaea* and *A. punctata* capitula with up to 23 ray florets were observed.

Involucre and involucral bracts

The involucres of N African representatives of *Anthemis* usually have the shape of hemispherical cups. Only in *A. austriaca* and *A. secundiramea* a tendency towards a more conical shapes was observed. The dimensions of involucres are usually correlated with the diameter of capitula and are very variable within taxa. Taxonomically relevant differences in the diameter of involucres may be observed in the *A. pedunculata - A. punctata* complex *(A.* sect. *Hiorthia): A. pedunculata* is characterised by smallish involucres with diameters of 6-14 mm, the closely related *A. abylaea* and *A. punctata* have involucres with 13-21 mm and (10-)14-22 mm in diameter, respectively. In all other N African representatives of the genus the dimension of involucres fall within the rânge indicated for *A. pedunculata*.

In most species studied, involucres, most conspicuously in *Anthemis punctata, A. chrysantha, A. cyrenaica,* and *A. kruegeriana,* become umbonate at maturity. However, taxa with conspicuously inflated peduncles and/or conical involucres like *A. arvensis* subsp. *incrassata, A. secundiramea* var. *secundiramea,* or *A. austriaca* usually have attenuate or only very slightly umbonate involucres.

The involucre consists of free involucral bracts (sometimes called phyllaries). In all species, the involucral bracts are unequal in size and shape and arranged in 3-4 imbricate layers and in a series of spiral parastiches (here referred to as "rows"). In *Anthemis cretica* subsp. *columnae* and *A. cyrenaica* up to 5 layers of involucral bracts may be observed. For convenience, involucral bracts of different positions in the parastiches will be referred to as "outer", "middle" and "inner" involucral bracts.

The involucral bracts are variable in texture, but there is always a central, conspicuously thickened portion that is several cell layers thick and a marginal, membranous portion of only one cell layer, referred to as "membranous margin". The central part may be rather thin and almost membranous in texture in *Anthemis cotula,* thickish and somewhat fleshy as in *A. maritima,* or hard and tough as in *A. austriaca,* and usually consists of a green longitudinal strip surrounding the midvein of the bract and laterally adjacent stramineous portions. At maturity, at least the base of this central part of the involucral bract becomes indurated, and sometimes, as in *A. austriaca, A. maritima,* or *A. chrysantha,* the whole bract is sclerified.

While the outer involucral bracts are invariably triangular or ovate in outline, the middle and inner ones show differences in shape between the different taxa, ranging from narrowly elliptical to narrowly obovate. Such differences are particularly useful to discriminate between the subspecies of *Anthemis pedunculata* and *A. punctata: A. pedunculata* subsp. *pedunculata* and subsp. *clausonis,* along with *A. punctata* subsp. *kabylica* have narrowly elliptical inner involucral bracts, those of *A. peducnulata* subsp. *atlantica* and *A. punctata* subsp. *punctata* are conspicuously broader and narrowly obovate in outline. This is mainly due to the membranous margins being narrow in narrowly elliptical but wider in narrowly obovate involucral bracts.

Although variable in some taxa (e.g. *Anthemis confusa*), the colour of the membranous margins of involucral bracts is a good criterion in others. In *A. maritima* subsp. *maritima* and subsp. *bolosii* the membranous margin is usually pale and only at the tip it is sometimes tinged with brown or black, while in *A. maritima* subsp. *pseudopunctata* it is brown or black throughout. In *A. pedunculata* subsp. *pedunculata* involucral bracts usually have brown and in *A. pedunculata* subsp. *clausonis* invariably pale membranous margins, in *A. pedunculata* subsp. *atlantica* the margins are brown or black in the outer but pale in the inner involucral bracts, causing a somewhat two-coloured appearance of the involucre. *A. ubensis* is easily distinguished from the rather similar *A. secundiramea* var. *cossyrensis* by its involucral bracts with brown, as opposed to pale, membranous margins.

As a matter of course, dimensions of involucral bracts correlate with those of the involucre and capitulum. The longest middle and inner involucral bracts are therefore found in *Anthemis abylaea* (to 8.0 mm) and *A. punctata* (to 8.2 mm) and may be used to distinguish these species from the related *A. pedunculata*. In the *A. boveana* group of species, bract size was also found to have some taxonomic importance (see chapter 12).

Receptacle

The receptacles of N African *Anthemis* taxa are usually slightly convex to hemispherical in flower, but considerable variation between taxa is found in mature capitula. In *A. austriaca,* the sole N African member of *A.* subg. *Cota,* the receptacle remains slightly convex during maturation, whereas in most members of *A.* subg. *Anthemis* receptacles elongate, the degree of elongation characterising the different sections. The perennials of *A.* sect. *Hiorthia* usually have hemispherical to ovate or conical receptacles, in *A.* sect. *Anthemis* receptacles elongate more strongly at maturity and usually become conical or even, in some species, narrowly conical to narrowly cylindrical in shape (e.g. in *A. confusa, A. secundiramea,* and *A. glareosa* of *A.* sect. *Secundirameae).* In *A. arvensis* subsp. *incrassata, A. secundiramea* var. *secundiramea,* or *A. ubensis*, where peduncles become strongly inflated at maturity, this also affects the shape of the receptacles which become basally broadened and somewhat pyriform in outline. The two studied representatives of *A.* sect. *Maruta, A. cotula,* and *A. pseudocotula,* are also characterised by very slender and elongated, conical to narrowly conical or even cylindrical-fusiform receptacles.

Receptacles are paleate throughout in all species of the present revision, i.e. each disc floret is subtended by a bract (pale, receptacular scale), with the lone exception of *An-*

themis cotula where pales are restricted to the apical half of the receptacle, while the peripheral disc florets are devoid of subtending bracts.

In all representatives of *Anthemis* in N Africa, receptacles were found to be filled with spongy tissue with large intercellulars; hollow receptacles as found in *Matricaria* are absent.

Pales

The pales or receptacular scales offer a number of characters that are diagnostic of single taxa, species groups, series, or sections. In all N African taxa, pales were found to have a single vascular bundle. The shape of pales varies conspicuously between taxa: *Anthemis cotula* and *A. pseudocotula* of *A.* sect. *Maruta,* like all other members of this section, have very narrow, subulate pales (up to 0.2-0.3 mm wide) comprising little more than the vascular bundle and the adjacent sclerenchymatous tissue. In all other species, the midvein of the pale is bordered by a flimsy and scarious membrane formed by strongly elongate cells. Usually, this membrane is only one cell-layer thick and stramineous (red-tinged in some populations of *A. confusa, A. glareosa,* and *A. kruegeriana*). In *A. pedunculata* and *A. punctata* the shape of the pales is diagnostic of subspecies: pales are narrowly linear to almost subulate in *A. pedunculata* subsp. *pedunculata* but narrowly elliptical to narrowly obovate in *A. pedunculata* subsp. *atlantica;* in *A. punctata* subsp. *punctata* pales are narrowly obovate, and in *A. punctata* subsp. *kabylica* narrowly linear. The width of pales also contributed to the circumscription of subspecies in *A. stiparum,* where subsp. *intermedia* and subsp. *sabulicola* have rather narrow (0.2-0.6 mm) and subsp. *stiparum* broader (0.4-1.2 mm) pales. The broadest pales were observed in *A. maritima* subsp. *maritima* (1.2-1.7 mm), *A. chrysantha* (1.1-1.8 mm), *A. punctata* subsp. *punctata* (0.75-1.5 mm), and *A. ubensis* (0.8-1.6 mm). In these taxa, pales are usually narrowly elliptical to narrowly obovate.

A further valuable character diagnostic of taxa is the shape of the tip of the pales. In most species it is formed by the protruding midrib, but in some species of *Anthemis* ser. *Chrysanthae* and ser. *Secundirameae* the midrib does not reach the apex, which is usually membranous, often tinged with yellow and somewhat hooded owing to the slightly inrolled margin. In *A.* ser. *Chrysanthae* this character is useful to discriminate between the Algerian taxa (*A. boveana* and *A. chrysantha,* with a protruding midrib) and the Moroccan ones (*A. maroccana, A. gharbensis,* and *A. tenuisecta,* with membranous tips). In *A.* ser. *Secundiramea* the Libyan *A. kruegeriana* and *A. glareosa* are easily distinguished by the same character from their Tunisian relatives *A. secundiramea, A. ubensis,* and *A. confusa.* Pales with a membranous tip are acuminate to bluntly rounded, in *A. gharbensis* and *A. glareosa* they even may be truncate or emarginate.

There are two types of pales with excurrent midrib among the N African representatives of *Anthemis* sect. *Hiorthia: A. abylaea, A. pedunculata* subsp. *pedunculata* and subsp. *clausonis, A. maritima* subsp. *pseudopunctata,* and *A. punctata* subsp. *kabylica* have pales which gradually taper into the tip, whereas the pales of *A. pedunculata* subsp. *atlantica, A. maritima* subsp. *maritima* and subsp. *bolosii,* and *A. punctata* subsp. *punctata* taper rather abruptly into a tip that may be tricuspidate due to the apical projecting lateral margins. In some cases the lateral tips are even overtopping the central tip. In *A. cretica* subsp. *columnae, A. arvensis* subsp. *incrassata,* and *A. cyrenaica* the tips are often abruptly acuminate and erose.

A further character of some taxonomic importance is the colour of the pale tips. In taxa of *A.* sect. *Hiorthia* they are often tinged with dark brown or even black (e.g. *A. pedunculata, A. cretica* subsp. *columnae, A. punctata*), but such tinge is lacking in populations of *A. maritima* and some plants of *A. punctata* subsp. *punctata.* Pales of *A. monilicostata* and some populations of *A. ubensis* also end in blackish tips.

The strength of attachment of pales on the receptacles is also a useful character. In most of the species studied, at least the peripheral pales persist on the receptacles even after the dissemination of achenes. In *A.* sect. *Bourgaeinianae,* however, pales fall off very easily, so that after dissemination receptacles are left completely naked.

The hypothesis of Stuessy & Spooner (1988), that one of the functions of pales may be the protection of flowers, ovaries, and achenes from apical and lateral insect attack, is plausible though the adaptive significance may be less obvious in *Anthemis* than in the *Heliantheae* they had studied.

Ray florets

Ray florets of N African *Anthemis* have few taxonomically relevant characters. Corollas are divided into a lower tubular part and an upper, flat corolla limb. The tubular part is usually flattened dorso-ventrally but may get somewhat inflated and winged at maturity. In most species the tubular part and the abaxial face of the limb bear biseriate glands. Four vascular bundles are found in the tubular part of the ray florets. In the proximal region of the limb, several minor traces that end blindly split off from these main bundles which continue up to the 3-lobed apex of the limb where they anastomose. Baagøe (1977) studied four representatives of the genus and found that the adaxial epidermis of their ray florets corresponds to her "helianthoid type", consisting of more or less isodiamterical and papillose cells without thickened walls. Contrary to her indications, the corolla glands are not one-celled but correspond to the typical biseriate glands formed by usually eight cells that are found all over the vegetative and floral parts of all *Anthemis* species.

The length and the colour of ray floret limbs may be taxonomically relevant. Most radiate species are characterised by white ray florets, but those of *Anthemis* ser. *Chrysanthae* are yellow, ranging from a saturated canary yellow (9A in Anon. 1966) in *A. boveana, A. chrysantha, A. maroccana,* and *A. tenuisecta* to a pale yellow (3A in Anon. 1966) in *A. gharbensis*. White ray florets are usually monochromous during flowering, but tend to a brownish tinge at the base of the limb when withered. Limb length is diagnostic for some closely related taxa, for instance *A. maritima* subsp. *maritima* (7.5-12.0 mm) and subsp. *bolosii* (3.8-8.0 mm); *A. boveana* (7.0-14.0 mm) and *A. chrysantha* (2.1-7.0 mm); and *A. stiparum* subsp. *stiparum* (7.2-11.5 mm) or subsp. *intermedia* (7.0-10.5 mm) and subsp. *sabulicola* (4.5-8.5 mm). The width of ray floret limbs being fairly constant, variation in length usually also affects the shape of the limb, which ranges from nearly circular to narrowly elliptical or narrowly oblong.

Usually the florets are female and furnished with a style. In contrast to disc florets, the style branches are often laterally enlarged and devoid of sweeping hairs, having lost their function for pollen presentation. In *Anthemis cotula,* however, some plants with sterile ray florets lacking a style were observed, along with others in which they are pistillate and even fertile. Occasionally, in most species anther rudiments can be found in the tubular part of the ray florets.

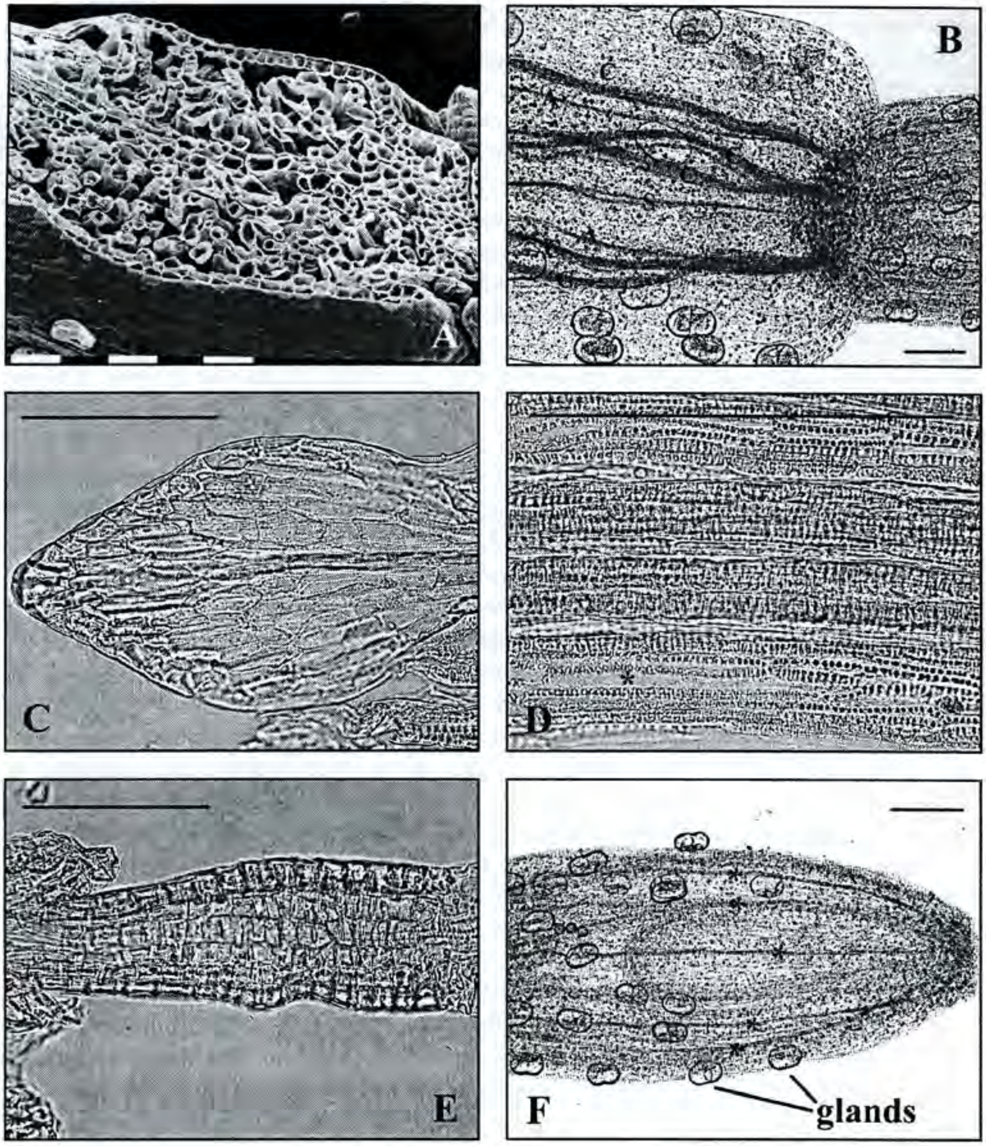

Fig. 2. Micrographs of details from *Anthemis* flowers. – A: *A. tenuisecta* subsp. *tenuisecta,* longisection through the basal part of a disc floret showing long and interwoven cell rows causing the inflated and spongy appearance at maturity *(Podlech 45076;* cult. in HB Berlin No. 049-26-93-10). B: *A. gharbensis,* vascularisation of basal part of disc floret: A = anther trace, C = corolla trace, S = style trace *(Vogt 10161 & Oberprieler 4609).* C: *A. gharbensis,* apical anther appendage *(Vogt 10161 & Oberprieler 4609).* D: *A. gharbensis,* endothecial tissue; an asterisk denotes a cell with evenly arranged wall thickenings *(Vogt 10161 & Oberprieler 4609).* E: *A. gharbensis,* filament collar *(Vogt 10161 & Oberprieler 4609).* F: *A. gharbensis,* vascularisation of an immature achene; asterisks denote the five vascular bundles *(Vogt 10161 & Oberprieler 4609).* – Scale bars = 0.1 mm (SEM, top left, and LM).

The styles are also very uniform throughout the genus. The base of the style becomes usually swollen and hardened due to enlarged and sclerified cells. Two vascular bundles run through the cylindrical and glabrous style shaft and end in the stigmatic branches, which are truncate-penicillate, bearing two separate lines of stigmatic papillae on the inside and obtuse sweeping hairs at their apex. Usually the stigmatic branches contain elongate resin ducts with a brown or orange content.

Achenes

Like the vast majority of *Compositae, Anthemis* has dry, monospermous fruits developed from a bicarpellate coenocarpic inferior ovary, with the seed testa adhering to but not coalescent with the pericarp. Although the ovary of *Compositae* is inferior, the fruit wall is generally termed pericarp, and its structures usually been described in the terms of epi-, meso- and endocarp, by analogy to the fruit wall in a superior ovary. Following Wagenitz (1976) and Roth (1977), the term "achene" as defined by Candolle (1813) is used in the present work for this type of fruits. The term "cypsela" was introduced by Mirbel (1815) and is frequently used in Anglo-Saxon and Nordic synantherological literature (e.g. Humphries 1979, Källersjö 1991, Anderberg 1991a, b, c, Bremer & Humphries 1993, Bremer 1994). However, exceptions are found (e.g. Hansen 1991), and in Anglo-American literature the term "achene" still prevails (e.g. Stuessy 1968, Funk 1982, Jansen 1985, Panero 1992).

Dating back to the thorough studies of Briquet (1916), the paramount importance of achene morphology and anatomy for the taxonomy of *Anthemideae* and for the delimitation of genera in this tribe is well known. In *Anthemis* the achenes provide some very important diagnostic features for the subdivision of the genus and the circumscription of species groups.

Achenes of ray florets were found to be rather similar in most studied representatives of *Anthemis* subg. *Anthemis*. They are usually subcylindrical or fusiform in shape and slightly bent inward. Being tightly confined to the trigonal space between the achenes of peripheral disc florets and their pales and the flat inner surface of the inner involucral bracts, they are roundish to triangular in cross section, with a flattish abaxial and a rounded or edged adaxial face. The achenes of ray florets usually have (8-)9(-10) ribs which are rather indistinct on the adaxial but more prominent and in some species even tuberculate on the abaxial face. Like the achenes of disc florets, they are usually beset with mucilage cells on their ribs and by glands in the intercostal furrows. The apical plate is usually bordered with a ridge that in some species is adaxially protracted into a membranous auricle up to 0.3 mm long. The achenes of ray florets in *A. austriaca (A.* subg. *Cota),* unlike those in *A.* subg. *Anthemis,* strongly resemble achenes of disc florets in being conspicuously flattened dorso-ventrally.

The achenes of disc florets provide a greater number of characters of use for species delimitation and supraspecific classification than the achenes of ray florets. While essentially homomorphic, the achenes of disc florets tend towards heteromorphy in most of the species due to overall structural reduction from the larger peripheral to the smaller central achenes. In some species, the differences between achenes of marginal and central disc florets are particularly well marked: In *Anthemis mauritiana* and *A. arvensis* the achenes of peripheral disc florets are extremely stout and subcylindrical or obconical, while the central achenes are much more slender and obconical-obovoidal. In most N African *An-*

themis taxa the peripheral disc achenes persist on the receptacles at maturity, while the central ones fall off readily. In *A. pseudocotula* even the central achenes persist, and the whole capitulum forms a compact, cone-like dispersal unit (synaptospermy).

Achenes of *Anthemis austriaca* differ markedly from those of all other representatives of the genus in N Africa. As in other species of *A.* subg. *Cota,* they are dorso-ventrally flattened and rhombic in cross section. While the lateral ribs are very pronounced and acutely angled, the 3-5 ribs on the adaxial and abaxial faces are inconspicuous. In *A.* subg. *Anthemis* disc achenes are never dorso-ventrally flattened but more or less terete and provided with (9-)10(-11) conspicuous, longitudinal ribs (except in *A. maritima, A. cretica* subsp. *columnae,* and *A. punctata* subsp. *punctata* where they are usually tetragonal in cross section and inconspicuously ribbed). The ribs may be sharply angled as in *A. gharbensis* or rounded and shallow as in *A. cyrenaica* and *A. taubertii.*

The sculpturing of the achene surface is a very important character taxonomically. Most of the N African representatives of *Anthemis* have tuberculate achenes, and the degree of tuberculation may vary considerably within most taxa. Nevertheless, this character may be of use in several species groups. Achenes of *A. maritima* subsp. *maritima, A. punctata* subsp. *punctata,* and *A. cretica* subsp. *columnae* are usually smooth, those of *A. maritima* subsp. *bolosii* and *A. punctata* subsp. *kabylica,* as in the other N African representatives of *A.* sect. *Hiorthia,* are tuberculate. In *A.* ser. *Chrysanthae, A. gharbensis, A. tenuisecta* subsp. *jahandiezii,* and some populations of *A. tenuisecta* subsp. *tenuisecta* have rather smooth achenes, in all other taxa of this series achenes are strongly tuberculate. *A. taubertii* and *A. cyrenaica* of *A.* ser. *Secundiramea* have smooth to feebly tuberculate achenes, those of the superficially very similar *A. glareosa* and *A. kruegeriana* are prominently tuberculate. *A. cotula* of *A.* sect. *Maruta* has strongly tuberculate achenes, those of *A. pseudocotula* are smooth or moderately tuberculate. Extremely tuberculate achenes are sometimes found in *A. pedunculata,* but other populations of this species have moderately tuberculate or nearly smooth achenes.

An important character observed in all species is the shape and size of mucilage cells of the achene surface. These specialised epidermal cells are usually confined to the ribs or tubercle tips (Fig. 3A). In most species mucilage cells are small, isodiametrical or only moderately elongate longitudinally, but in *Anthemis monilicostata* they are drastically enlarged and protrude from the achene surface (Fig. 39). Achenes of *A. gharbensis* are characterised by strongly elongate mucilage cells that form continuous slime ribbons on the ridges of the ribs (Fig. 3B). Additionally, in most species with ribbed achenes sessile, biseriate glands are found in the intercostal furrows (Fig. 2F, 3B, 3C).

In most species the apical plate is flat or slightly convex, circular or quadrangular in outline, and bears a relatively large, bowl-shaped discus ("coronet" in Kynčlová 1970, "Nektarium" in Vogt 1991, "stylopodium" in Bremer & Humphries 1993 and Källersjö 1991) in its centre. In *Anthemis tenuisecta* subsp. *jahandiezii* the apical plate is strongly convex, in *A. austriaca* it is rhombic. The apical plate is bordered by a corona ("border" in Kynčlová 1970), which in some species (e.g. *A. arvensis, A. cotula, A. pseudocotula*) may be an inconspicuous, rounded and crenulate rim formed by the apically protruding ribs of the achene, but in others is adaxially protracted into an up to 1 mm long, membranous auricle.

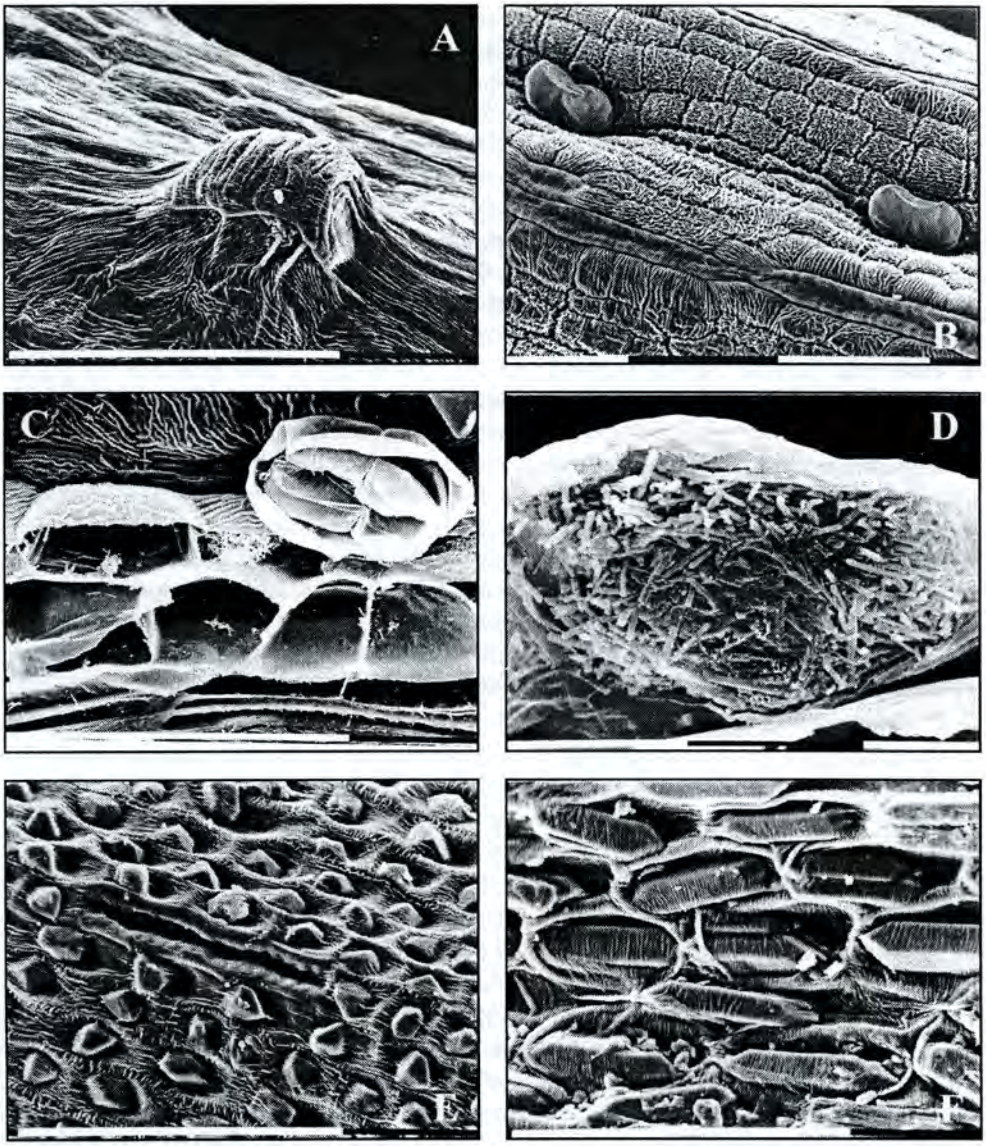

Fig. 3. SEM micrographs from *Anthemis* achenes. – A: *A. maroccana* subsp. *maroccana,* epicarp with mucilage cell *(Jahandiez 159).* B: *A. gharbensis,* epicarp with glands and extremely elongated mucilage cells (*Podlech 43409,* cult. in HB Berlin No. 049-27-93-10). C: *Anthemis tenuisecta* subsp. *tenuisecta,* longisection of achene wall showing epicarpic cells with a strongly wrinkled cuticula and a longisectioned gland (*Podlech 45076;* cult. in HB Berlin No. 049-26-93-10). D: *A. mauritiana* subsp. *faurei,* epicarpic cell filled with sand of needle-like calcium oxalate crystals *(Vogt 10872 & Oberprieler 5320).* E: *A. austriaca,* epicarpic cells with single, large, octahedral crystals *(Vogt 13151 & Oberprieler 7456).* F: *A. altissima,* epicarpic cells with single, large, prismatic crystals (HB Liège, cult. in HB Berlin No. 194-17-92-10). – Scale bars = 100 µm (A-C, E-F) or 10 µm (D).

The epicarpic cells (i.e. the epidermis of the pericarp) of N African species usually have strongly cutinised outer walls and wide cell lumina. In transverse section the cells are isodiametric, while they are usually elongate and rectangular in longisection. In all cases studied, the epicarpic cells remain unsclerified and parenchymatous. Often they were found to collapse during maturation. Marked differences in shape and number of calcium oxalate crystals in the epicarpic cells were observed. In *Anthemis austriaca,* the single studied representative of *A.* subg. *Cota,* cells contain single, large, octahedral crystals (Fig. 3E); in all species of *A.* subg. *Anthemis,* epicarpic cells contain crystal sand formed by large numbers of needle-like crystals (Fig. 3D). While in the case of *A. austriaca* the crystals are responsible for the minutely punctulate macroscopic appearance of achenes, the crystal sand in the other subgenus causes an more or less intensive whitish tinge of achenes.

The mesocarp exhibits considerable variation, its thickness and degree of sclerification showing specific differences. The sclerenchymatic tissue is formed by two kinds of elements, libriform fibre cells and sclereids, which can be best distinguished in longisection. Libriform fibre cells are strongly elongate longitudinally, have strongly sclerified cell walls with small pits, and extremely restricted cell lumina with large calcium oxalate crystals at maturity. Sclereids are usually much larger, more or less isodiametric in cross section, moderately elongate longitudinally, and less sclerified. Initially parenchymatous, these cells become progressively sclerified during maturation due to continuous thickening of their walls, so that sclereids eventually have thick, concentrically multi-layered cell walls, but retain large pits and cell lumina not as restricted as in fibre cells, which only occasionally contain calcium oxalate crystals.

Vascularisation of the achene wall is very similar in all species studied. About 10 *(Anthemis* subg. *Anthemis)* or more *(A.* subg. *Cota)* sclerenchymatic ribs are formed in the mesocarp of the achenes, but only 5 vascular bundles can be found (Fig. 2F), contrary to the indications of Wagenitz (1968), Kynčlová (1970), and Reitbrecht (1974) who assumed that each rib of the achenes has its vascular strand, but in accordance with the findings of Humphries (1979). Especially in young, immature achenes it is easy to observe that only every second sclerenchymatic bundle in the pericarp contains one or several vessel elements with spirally arranged wall thickenings.

In most species studied, libriform fibre cells, in cross sections of achenes, form a continuous ring at the inner side of the mesocarp. This ring is 1-5 cell layers thick between the ribs, but conspicuously thicker in the vascularised and non-vascularised ribs. Between this inner layer of sclerenchyma, formed by fibre cells, and the exocarp, the mesocarp usually consists of 1-5(-10) cell layers of sclereids. The scereid layer may either be continuous or restricted to the ribs, when in the furrows the epicarp is in direct contact with the mesocarpic fibre cell layer.

In *Anthemis austriaca* the sclereids are regularly rectangular in transverse section and form a continuous, palisade-like layer under the exocarp. In the rather smooth and inconspicuously ribbed achenes of *A. cretica* subsp. *columnae, A. maritima* subsp. *maritima,* and *A. punctata* subsp. *punctata* the furrows between the ribs formed by the mesocarpic fibre cell layer are filled out by the sclereid layer. Here, sclereids are often found to be radially elongate and somewhat pyriform, separated by large intercellulars and propping the somewhat lifted-off epicarp. In most other cases, when achenes are conspicuously ribbed, the large sclereids are found on top of and/or along the sides of the internal ribs of the fibre cell layer, accentuating the external ribs and their sculpturing with tubercles. However, achenes of *A. arvensis* and related species of *A.* ser. *Anthemis* display a quite differently patterned mesocarp: The inner cylinder of libriform fibre cells is conspicuously ribbed, as in all other species of *A.* sect. *Anthemis,* but the external ribs of the achene are placed on top of the internal furrows. This is caused by a parenchymatous outer mesocarpic layer of cells that divide intensively during maturation. Since the parenchyma is thicker above the internal furrows of the sclerenchymatic cylinder than above its ribs, the latter will eventually coincide with the furrows of the achene.

From peripheral disc achenes to central ones, one may note a trend to reduction of sclerenchymatic mesocarp tissue. This trend is particularly obvious in some representatives of *Anthemis* ser. *Chrysanthae* and ser. *Bourgaeinianae*. Unlike other taxa in *A.* sect. *Chrysanthae, A. tenuisecta* subsp. *tenuisecta* has achenes that usually lack a continuous layer of sclerenchymatic mesocarp tissue. Libriform fibre cells are confined to bundles in the ribs, and the outer mesocarpic cell layer remains parenchymatous. Same is true for all achenes of *A. monilicostata* and the central achenes of *A. stiparum* and *A. mauritiana* of *A.* sect. *Bourgaeinianae.*

The cells of the endocarp remain parenchymatous and soon become compressed during achene maturation. In ripe achenes they cannot usually be identified. The testa consists of an epidermis and 2-3 layers of large, parenchymatous cells that soon disintegrate during maturity. Cells of the testa epidermis are characterised by curved and conspicuously thickened radial walls. The testa epidermis and the endosperm layer surrounding the cotyledons are still visible in mature achenes.

10. Chromosomes

Material and methods

For the study of pollen mother cell (PMC) meiosis, buds of capitula were fixed in 96 % ethanol/glacial acetic acid (3 : 1) in the field and stored in a refrigerator after return to Berlin. For chromosome staining several buds of disc florets were removed from the capitula, coarsely crushed, and squashed in aceto-orcein.

For the study of mitosis, root tips were obtained either by growing plants in the Botanic Garden Berlin-Dahlem or by germinating achenes in petri dishes. In both cases root tip meristems were pre-treated with hydroxyquinoline (0.002 molar aqueous solution) for 4 hours, fixed in 96 % ethanol/glacial acetic acid (3 : 1) and refrigerated. Hydrolysis was performed with 1-2n hydrochloric acid for 10 minutes at 60°C. For chromosome staining root tips were squashed in aceto-orcein.

Camera lucida drawings of chromosomes were made with a Zeiss Standard 16 microscope and measured with an ocular micrometer of a Wild M5A stereomicroscope for arm lengths. The PC program CHROMEX described by Voss & al. (1994) was used to transfer measurements to a karyological database, to sort chromosomes automatically according to their length and arm ratios, to find homologous chromosomes interactively, to construct idiograms, and to calculate means of multiple probes. For the description of karyotypes the ribbed, the large sclereids are found on top of and/or along the sides of the internal ribs of the fibre cell layer, accentuating the external ribs and their sculpturing with tubercles. However, achenes of *A. arvensis* and related species of *A.* ser. *Anthemis* display a quite differently patterned mesocarp: The inner cylinder of libriform fibre cells is conspicuously ribbed, as in all other species of *A.* sect. *Anthemis,* but the external ribs of the achene are placed on top of the internal furrows. This is caused by a parenchymatous outer mesocarpic layer of cells that divide intensively during maturation. Since the parenchyma is thicker above the internal furrows of the sclerenchymatic cylinder than above its ribs, the latter will eventually coincide with the furrows of the achene.

From peripheral disc achenes to central ones, one may note a trend to reduction of sclerenchymatic mesocarp tissue. This trend is particularly obvious in some representatives of *Anthemis* ser. *Chrysanthae* and ser. *Bourgaeinianae*. Unlike other taxa in *A.* sect. *Chrysanthae, A. tenuisecta* subsp. *tenuisecta* has achenes that usually lack a continuous layer of sclerenchymatic mesocarp tissue. Libriform fibre cells are confined to bundles in the ribs, and the outer mesocarpic cell layer remains parenchymatous. Same is true for all achenes of *A. monilicostata* and the central achenes of *A. stiparum* and *A. mauritiana* of *A.* sect. *Bourgaeinianae*.

The cells of the endocarp remain parenchymatous and soon become compressed during achene maturation. In ripe achenes they cannot usually be identified. The testa consists of an epidermis and 2-3 layers of large, parenchymatous cells that soon disintegrate during maturity. Cells of the testa epidermis are characterised by curved and conspicuously thickened radial walls. The testa epidermis and the endosperm layer surrounding the cotyledons are still visible in mature achenes.

10. Chromosomes

Material and methods

For the study of pollen mother cell (PMC) meiosis, buds of capitula were fixed in 96 % ethanol/glacial acetic acid (3 : 1) in the field and stored in a refrigerator after return to Berlin. For chromosome staining several buds of disc florets were removed from the capitula, coarsely crushed, and squashed in aceto-orcein.

For the study of mitosis, root tips were obtained either by growing plants in the Botanic Garden Berlin-Dahlem or by germinating achenes in petri dishes. In both cases root tip meristems were pre-treated with hydroxyquinoline (0.002 molar aqueous solution) for 4 hours, fixed in 96 % ethanol/glacial acetic acid (3 : 1) and refrigerated. Hydrolysis was performed with 1-2n hydrochloric acid for 10 minutes at 60°C. For chromosome staining root tips were squashed in aceto-orcein.

Camera lucida drawings of chromosomes were made with a Zeiss Standard 16 microscope and measured with an ocular micrometer of a Wild M5A stereomicroscope for arm lengths. The PC program CHROMEX described by Voss & al. (1994) was used to transfer measurements to a karyological database, to sort chromosomes automatically according to their length and arm ratios, to find homologous chromosomes interactively, to construct idiograms, and to calculate means of multiple probes. For the description of karyotypes the

Table 1. Summary of karyotype asymmetry analyses. Intrachromosomal and interchromosomal asymmetry were calculated as defined by Romero Zarco (1986: A_1 and A_2) and Barghi & al. (1989: AsI and R).

	Taxon	Origin	Collection	2*n*	A_1	A_2	AsI	R
	Anthemis sect. *Hiorthia*							
1	*A. maritima* subsp. *maritima*	Ga: Narbonne	HB Liège	36	.370	.166	60.0	1.80
2	—	Co: Alistro	HB Liège	36	.361	.139	59.4	1.75
3	*A. pedunculata* var. *pedunculata*	Ma: Tazzeka	*Vogt & Oberprieler 3937*	37	.397	.119	60.4	1.63
4	—	Ma: Taza	*Vogt & Oberprieler 3945*	18	.388	.132	60.9	1.55
5	var. *discoidea*	Ma: Tidighin	*Deil 4867*	18	.397	.135	61.4	1.59
	Anthemis sect. *Anthemis*							
6	*A. arvensis* subsp. *incrassata*	Ma: Bab Taza	*Vogt 9652 & Oberprieler 4088*	18	.395	.107	60.4	1.42
7	—	Hs: Sierra de las Nieves	*Vogt 9229*	18	.341	.133	58.6	1.52
8	—	Ma: Tidirhine	*Vogt 9592 & Oberprieler 4028*	18	.388	.109	60.9	1.35
9	*A. confusa*	Tn: Tataouine	*Vogt 13131 & Oberprieler 7436*	18	.433	.133	62.4	1.57
10	—	Tn: Remada	*Vogt 13049 & Oberprieler 7354*	20	.416	.136	61.7	1.64
11	*A. gharbensis*	Ma: Mamora	*Podlech 43489*	18	.388	.143	60.7	1.58
12	*A. melampodina*	Eg: El Arish	*Podlech 49968*	18+1B	.435	.131	62.9	1.58
13	*A. secundiramea* var. *cossyrensis*	Tn: Cap Blanc	*Vogt 13791 & Oberprieler 8096*	18	.391	.125	60.7	1.56
14	*A. tenuisecta*	Ma: Tiznit	*Podlech 45076*	18	.402	.118	61.3	1.34
15	*A. ubensis*	Tn: Kesra	*Vogt 13524 & Oberprieler 7829*	19	.351	.116	59.2	1.46
	Anthemis sect. *Maruta*							
16	*A. cotula*		HB Dijon	18	.327	.119	57.7	1.53
17	*A. pseudocotula*	Cy: Paphos	*Vogt 9000*	18+1B	.362	.112	60.8	1.42
	Anthemis sect. *Cota*							
18	*A. altissima*	Ga: Alzonne	HB Liège	18	.350	.148	59.8	1.53
19	—	Ga: Montolieu	HB Liège	18	.355	.157	60.1	1.53
20	—	Ga: Sigean	HB Liège	18	.339	.158	59.3	1.76
21	—	Ga: Villedubert	HB Liège	18	.342	.152	59.5	1.49
22	—	It: Perinaldo	HB Genua	18	.348	.144	59.5	1.55
23	—	Ga: Montolieu	HB Liège	18	.342	.135	59.6	1.69
	Anthemis sect. *Anthemaria*							
24	*A. tinctoria*	Au: Persenberg	HB Univ. Salzburg	18	.373	.148	60.2	1.61

Table 2. Data on karyotype asymmetry (as defined by Barghi & al. 1989) used in our analysis of *Anthemideae,* in addition to the original data of Table 1.

	Taxon	AsI	R	Source
	Chrysantheminae			
25	*Argyranthemum frutescens* (L.) Schultz-Bip.	60.5	1.65	Uitz (1970: Table 7)
26	*Chrysanthemum segetum* L.	56.2	1.69	Uitz (1970: Table 8)
27	*C. coronarium* L.	54.7	1.46	Uitz (1970: Table 8)
28	*Ismelia vesicolor* Cass.	53.7	1.33	Uitz (1970: Table 8, sub *Chrysanthemum carinatum)*
	Achilleinae			
29	*Achillea asplenifolia* Vent.	60.8	1.55	Uitz (1970: Table 5)
30	*A. setacea* Wildst. & Kit.	60.2	1.41	Uitz (1970: Table 5)
31	*Anacyclus clavatus* (Desf.) Pers.	57.7	1.44	Uitz (1970: Table 5)
32	*A. radiatus* Loisel.	59.9	1.37	Uitz (1970: Table 5)
33	*A. pyrethrum* (L.) Lagasca	56.5	1.33	Uitz (1970: Table 5)
34	*Chamaemelum nobile* (L.) All.	57.7	1.21	Uitz (1970: Table 10, sub *Ormenis nobilis)*
35	*C. fuscatum* (Brot.) Vasc.	58.9	1.60	Uitz (1970: Table 10, sub *Ormenis fuscata)*
36	*C. mixtum* (L.) All.	59.9	1.63	Uitz (1970: Table 10, sub *Ormenis mixta)*
37	*Cladanthus arabicus* (L.) Cass.	55.1	1.45	Uitz (1970: Table 8)
	Tanacetinae			
38	*Tanacetum vulgare* L.	59.3	1.53	Uitz (1970: Table 11)
39	*T. parthenium* (L.) Schultz-Bip.	58.0	1.23	Uitz (1970: Table 11)
40	*T. annuum* L.	60.8	1.93	Uitz (1970: Table 11)
	Matricariinae			
41	*Tripleurospermum perforatum* (Merat) Laínz	62.6	1.56	Uitz (1970: Table 11, sub *T. inodorum)*
42	*T. maritmum* (L.) K. Koch	60.7	1.47	Uitz (1970: Table 12)
43	*T. disciforme* (C. Meyer) Schultz-Bip.	60.4	1.63	Uitz (1970: Table 11)
44	*Matricaria recutita* (L.) Rauschert	60.7	1.68	Uitz (1970: Table 10)
45	*M. matricarioides* Porter ex Britton	56.1	1.93	Uitz (1970: Table 10)
	Leucantheminae			
46	*Rhodanthemum arundanum* (Boiss.) Wilcox & al.	56.4	1.51	Vogt (1991: 67, sub *Leucanthemum arundanum)*
47	*Leucanthemum vulgare* Lam.	59.3	1.24	Uitz (1970: Table 9)
48	*L. vulgare* subsp. *pujiulae* Sennen	54.1	1.24	Vogt (1991: 67)
49	*Coleostephus myconis* (L.) Reichenb. f.	57.3	1.30	Uitz (1970: Table 9, as *Leucanthemum myconis)*
50	*Lepidophorum repandum* (L.) DC.	54.1	1.51	Uitz (1970: Table 9)
51	*Nivellea nivellei* (Br.-Bl. & Maire) Wilcox & al.	57.7	1.48	Vogt & Oberprieler (1996: 124)

terminology of Levan & al. (1964) is used. Arm ratios of single chromosomes are expressed by the ratio long arm to short arm. Karyotype asymmetry was assessed using the indices (A_1, A_2) proposed by Romero Zarco (1986).

Alternatively, for purposes of comparison of karyotype asymmetries of the present study with measurements given by Uitz (1970), the asymmetry indices AsI and R as defined by Barghi & al. (1989) were computed. Here, intrachromosomal asymmetry (AsI) is expressed by the ratio of long arms in chromosome set to total chromosome length in the set multiplied by 100, and interchromosomal asymmetry (R) by the ratio of longest pair to shortest pair in the chromosome set.

In the following lists, specimens used for karyotype analysis are marked with an asterisk. Results of karyotype analyses are summarised in Table 1, and morphometric chromosome data for each karyotype studied are given in Tables 3-16, where n is the number of different metaphase plates studied.

Results

Anthemis (subg. *Anthemis*, sect. *Anthemis*) ser. ***Anthemis***

Anthemis arvensis subsp. *arvensis*

$2n = 18$

- Ge, Sachsen-Anhalt, Brachwitz, *HB Halle* (cult. in HB Berlin No. 153-02-93-10).

Numerous counts of the cosmopolitan *Anthemis arvensis* have been published, most of them without a mention of subspecies. Counts relating to *A. arvensis* subsp. *arvensis* were given by Kuzmanov & al. (1980) and Kuzmanov & al. (1981) for Bulgarian, Fernandes & Queirós (1971, sub *A. arvensis* var. *arvensis*) for Portuguese, and Benedí i González (1987) for Spanish plants. All counts yielded a diploid chromosome number of $n = 9$ or $2n = 18$. Kuzmanov & al. (1981) found the karyotype of this subspecies to consist of 2 metacentric, 12 submetacentric and 4 satellited subtelocentric chromosomes (2m + 12sm + 4st-sat).

Anthemis arvensis subsp. *incrassata*

$n = 9$

- Ma, Rif, Djebel Tassaot, 1600m, 25 Jun 1992, *Vogt & Oberprieler 4078*.
- Ma, Rif, Souk-Tleta-Taghramet - Ceuta, 450-500 m, 17 Apr 1993, *Vogt 9854 & Oberprieler 4302* (Fig. 4A).
- Ma, Rif, Monts de Beni Hosmar, 1200 m, 21 Apr 1993, *Vogt 10001 & Oberprieler 4449*.
- Ma, Rif, Chefchaouene, 730 m, 30 May 1993, *Vogt 12037*.
- Ma, Rif, Monts de Beni Hosmar, 1200 m, 30 May 1993, *Vogt 12038*.

$2n = 18$

*– Ma, Rif, Djebel Tidirhine, 1550 m, 20 Jun 1992, *Vogt 9592 & Oberprieler 4028*.
- Ma, Rif, Bab Berret, 1450 m, 25 Jun 1992, *Vogt 9632 & Oberprieler 4068*.

*– Ma, Rif, Bab Taza - Djebel Talamssantane, 1420 m, 26 Jun 1992, *Vogt 9652 & Oberprieler 4088* (Fig. 4B).

*– Hs, Málaga, Sierra de las Nieves, 900-1250 m, 26 May 1992, *Vogt 9229*.
- Hs, Cádiz, El Puerto de Sta. Maria - Jerez de la Frontera, 30 m, 17 Apr 1993, *Vogt 9711 & Oberprieler 4159*.
- Hs, Cádiz, Benolup, 20 m., 16 Apr 1989, *Deil 3603*.
- Si, Palermo, Scillato - Collesano, 520-800 m, 25 May 1994, *Vogt 13885 & Oberprieler 8190*.
- It, Grosseto, Monte Labbro, 1 Sep 1992, *Marchetti* (HB Siena) (cult. in HB Berlin No. 103-02-93-10).

Table 3. Chromosomes of *Anthemis arvensis* subsp. *incrassata*

Chromosome pair	Long arm (µm)	Short arm (µm)	Total length (µm)	Relative length (%)	Arm ratio	Chromosome type
OTU 6 (n = 4)						
I	3.43	2.62	6.05	13.8	1.30	m
II	3.06	2.33	5.39	12.3	1.31	m
III	2.74	2.27	5.01	11.4	1.20	m
IV	3.12	1.71	4.83	11.0	1.82	sm
V	3.12	0.91	4.81	11.0	3.42	st-sat
VI	2.71	1.98	4.69	10.7	1.36	m
VII	3.13	1.36	4.49	10.3	2.30	sm
VIII	2.42	1.94	4.36	10.0	1.24	m
IX	2.76	0.72	4.26	9.7	3.83	st-sat
OTU 7 (n = 3)						
I	3.97	3.11	7.08	13.9	1.27	m
II	3.44	2.95	6.39	12.6	1.16	m
III	3.28	2.83	6.11	12.0	1.15	m
IV	3.23	2.52	5.75	11.3	1.28	m
V	3.47	2.16	5.63	11.1	1.60	m
VI	3.59	0.93	5.30	10.4	3.86	st-sat
VII	2.97	2.29	5.26	10.4	1.29	m
VIII	2.67	2.02	4.69	9.2	1.32	m
IX	3.19	0.68	4.65	9.2	4.69	st-sat
OTU 8 (n = 3)						
I	4.02	2.97	6.99	13.3	1.35	m
II	3.57	2.97	6.54	12.4	1.20	m
III	4.16	1.19	6.13	11.6	3.49	st-sat
IV	3.32	2.76	6.08	11.5	1.20	m
V	3.95	2.13	6.08	11.5	1.85	sm
VI	3.06	2.51	5.57	10.6	1.21	m
VII	3.81	0.80	5.39	10.2	4.76	st-sat
VIII	3.51	1.67	5.18	9.8	2.10	sm
IX	2.75	2.08	4.83	9.2	1.32	m

Anthemis arvensis subsp. *incrassata* was studied cytologically by Brullo & al. (1978b) from Sicily and Benedí i Gonzalez (1987) from Spain, who found $n = 9$ or $2n = 18$, respectively. Additionally, many counts published for *A. arvensis* concern this subspecies, e.g. those of Dahlgren & al. (1971) for Balearic or Pavone & al. (1981) for Sicilian plants because *A. arvensis* subsp. *arvensis* is missing there. Counts on N African plant material of *"A. arvensis"* were made by Humphries & al. (1978) who found $2n = 18$ chromosomes, but the identity of the plants, originating from "Jbel Ayachi, cirque de Jaffar" in the High Atlas mountains where *A. arvensis* was never found to grow, is questionable.

A deviating and presumably wrong count of $n = 8$ was published by Blanché & al. (1985) for plants from the Sierra Nevada in S Spain identified as *A. granatensis* which according to Benedí i González (1987) is a synonym of *A. arvensis* subsp. *arvensis* and in my opinion, of *A. arvensis* subsp. *incrassata*. A triploid chromosome number of $2n = 27$ was found in Bulgarian plants by Kuzmanov & al. (1981), who found the karyotype of this population to consist of 7 metacentric, 14 submetacentric and 6 satellited subtelocentric chromosomes. A further karyotype analysis was performed by Benedí i González (1987) who indicates the chromosome formula 12m + 2M + 2st-sat + 2t-sat for plants from near Barcelona. Karyotype analyses performed for the present study yielded a chromosome formula of 10m + 4sm + 4st-sat for two Moroccan populations and a more symmetric karyotype with 14m + 4st-sat for a S Spanish population (Table 3).

Anthemis arvensis subsp. *sphacelata*

n = 9

–It, Reggio Calabria, Montalto, 1600 m, 27 May 1994, *Vogt 13983 & Oberprieler 8288.*

This interesting biennial to perennial subspecies of *Anthemis arvensis* endemic to the mountains of Sicily and S Italy, had been studied cytologically only once, by Brullo & al. (1978a) who found a diploid chromosome set of 2*n* = 18 chromosomes (12m + 4sm + 2t-sat) in a Sicilian population. The present count from the Calabrian mountains corroborates this data.

Anthemis (subg. *Anthemis,* sect. *Anthemis*) ser. ***Chrysanthae***

Anthemis gharbensis

n = 9

–Ma, Arbaoua - Moulay Bousselham, 10 m, 24 Apr 1993, *Vogt 10161 & Oberprieler 4609.*

–Ma, Forêt de la Mamora, 120 m, 27 Apr 1993, *Vogt 10259 & Oberprieler 4707.*

2*n* = 18

*–Ma, Forêt de la Mamora, 120 m, 2 May 1987, *Podlech 43489.*

The haploid and diploid chromosome numbers mentioned above were already reported earlier (Oberprieler 1994). The karyotype was found to be very symmetrical, consisting of 5 pairs of metacentic, 2 pairs of submetacentric, and 2 pairs of satellited subtelocentric chromosomes (10m + 4sm + 4st-sat, Table 4).

Table 4. Chromosomes of *Anthemis gharbensis* (OTU 11; n = 8).

Chromosome pair	Long arm (µm)	Short arm (µm)	Total length (µm)	Relative length (%)	Arm ratio	Chromosome type
I	4.54	3.60	8.14	14.4	1.26	m
II	3.95	3.18	7.13	12.6	1.24	m
III	4.63	2.28	6.91	12.2	2.03	sm
IV	3.44	2.93	6.37	11.2	1.17	m
V	4.33	1.00	6.11	10.8	4.33	st-sat
VI	3.32	2.65	5.97	10.5	1.25	m
VII	3.69	1.94	5.63	9.9	1.90	sm
VIII	3.02	2.31	5.33	9.4	1.30	m
IX	3.55	0.84	5.17	9.1	4.22	st-sat

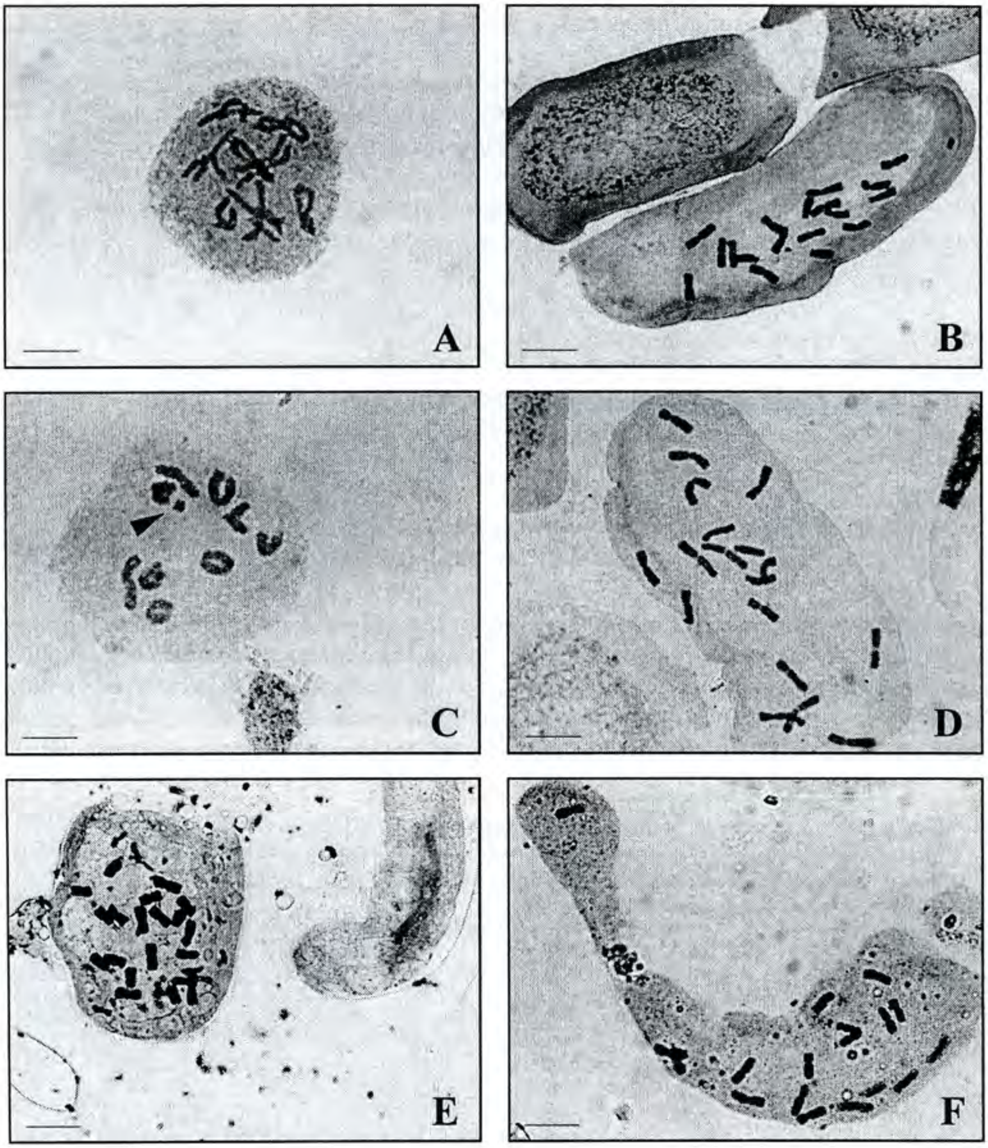

Fig. 4. Metaphase plates in *Anthemis*. – A: *A. arvensis* subsp. *incrassata,* PMC meiosis, $n = 9$ *(Vogt 9854 & Oberprieler 4302).* B: *A. arvensis* subsp. *incrassata,* root tip mitosis, $2n = 18$ *(Vogt 9652 & Oberprieler 4088).* C: *A. maroccana* subsp. *maroccana,* PMC meiosis, $n = 9 + 1$B, arrowhead indicating B chromosome *(Vogt 10181 & Oberprieler 4729).* D: *A. tenuisecta* subsp. *tenuisecta,* root tip mitosis, $2n = 18$ *(Podlech 45076).* E: *A. confusa,* root tip mitosis, $2n = 20$ *(Vogt 13049 & Oberprieler 7354).* F: *A. secundiramea* var. *secundiramea,* root tip mitosis, $2n = 18$ *(HB Catania).* – Scale bars = 10 µm.

Anthemis maroccana subsp. *maroccana*
$n = 9 + 0\text{-}1B$
- Ma, Aïn-Cheggag, 620 m, 27 Apr 1993, *Vogt 10181 & Oberprieler 4729*. (Fig. 4C).
- Ma, Middle Atlas, Sefrou, 1060 m, 27 Apr 1993, *Vogt 10284 & Oberprieler 4732*.
- Ma, Middle Atlas, Sefrou, 1150m, 28 Apr 1993, *Vogt 10296 & Oberprieler 4744*.

Anthemis maroccana had never been investigated cytologically before. The three populations studied here all belong to subsp. *maroccana* and proved to be diploid with n = 9 chromosomes.

Anthemis tenuisecta subsp. *tenuisecta*
$n = 9$
- Ma, Agadir, Tiznit - Agadir, 180 m, 19 May 1993, *Vogt 11905 & Oberprieler 6353*.
- Ma, Agadir, Agadir - Essaouira, 160m, 21 May 1993, *Vogt 11924*.

$2n = 18$
* – Ma, Agadir, Tiznit - Agadir, 25 Apr 1989, *Podlech 45076*. (Fig. 4D).
- Ma, Agadir, Agadir - Essaouira, 120 m, 22 May 1993, *Vogt 11930*.

The chromosome number of *Anthemis tenuisecta,* a species closely related to *A. gharbensis*, is reported here for the first time. As in *A. gharbensis* and *A. maroccana,* a diploid chromosome set was found, with n = 9 and $2n$ = 18, respectively. The karyotype is a little more asymmetrical than in *A. gharbensis* due to the occurrence of an additional pair of submetacentric instead of metacentric chromosomes (8m + 6sm + 4st-sat, Table 5).

Table 5. Chromosomes of *Anthemis tenuisecta* (OTU 14; n = 11).

Chromosome pair	Long arm (µm)	Short arm (µm)	Total length (µm)	Relative length (%)	Arm ratio	Chromosome type
I	4.16	3.58	7.74	13.7	1.16	m
II	4.55	2.60	7.15	12.7	1.75	sm
III	3.64	3.12	6.76	12.0	1.16	m
IV	3.99	2.27	6.26	11.1	1.75	sm
V	3.40	2.68	6.08	10.8	1.26	m
VI	4.05	1.02	5.85	10.4	3.97	st-sat
VII	3.87	1.92	5.79	10.3	2.01	sm
VIII	3.08	2.42	5.50	9.8	1.27	m
IX	3.93	0.71	5.42	9.6	5.53	st-sat

Anthemis (subg. *Anthemis,* sect. *Anthemis*) ser. ***Melampodinae***

Anthemis melampodina
$2n = 18 + 1B$
* – Eg, Sinai, Nizzana - El Arish, 130 m, 2 May 1991, *Podlech 49968*.

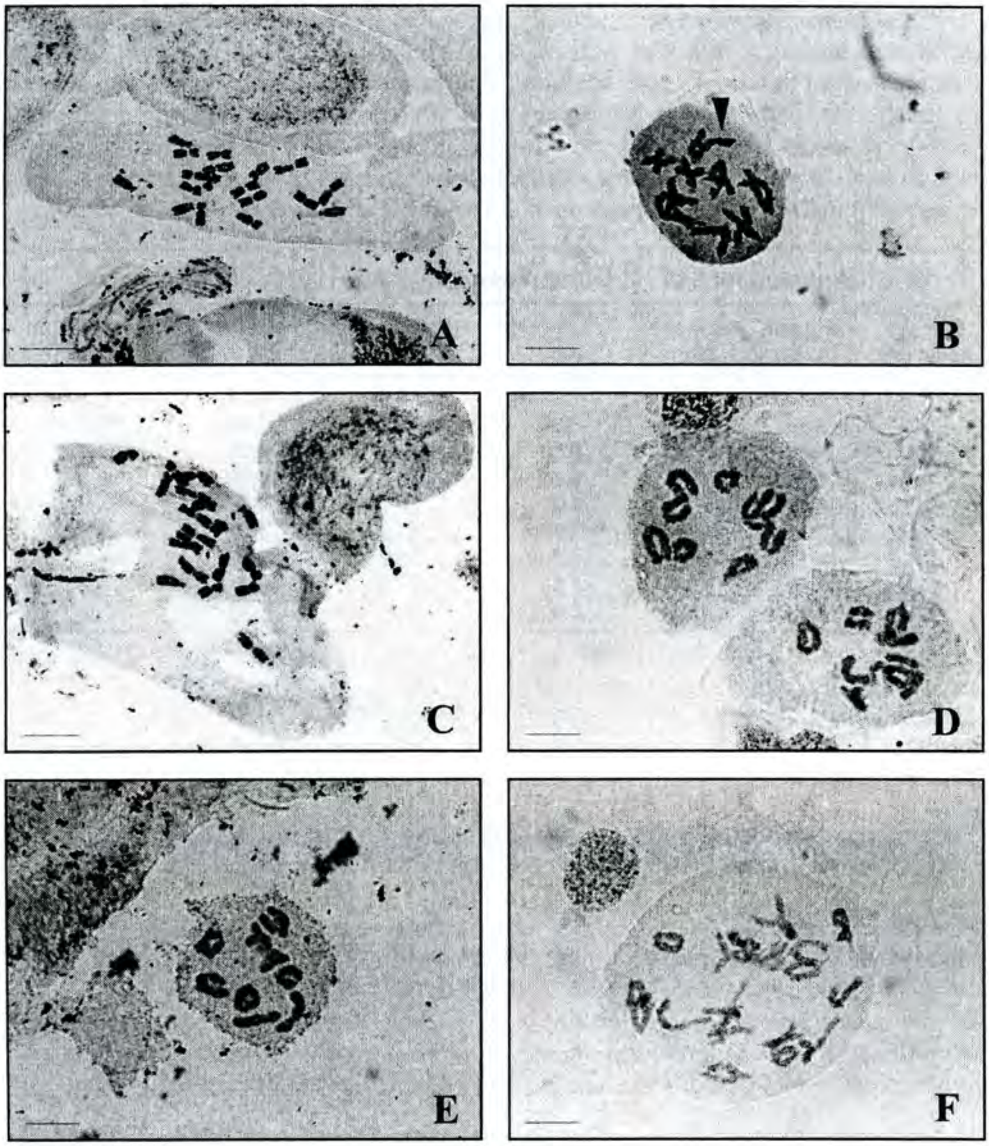

Fig. 5. Metaphase plates in *Anthemis*. – A: *A. secundiramea* var. *cossyrensis*, root tip mitosis, $2n$ = 18 *(Vogt 13791 & Oberprieler 8096)*. B: *A. ubensis*, PMC meiosis, n = 9, arrowhead indicating a bivalent formed by chromosomes differing markedly in length *(Vogt 12216 & Oberprieler 6521)*. C: *A. ubensis*, root tip mitosis, $2n$ = 19 *(Vogt 13524 & Oberprieler 7829)*. D: *A. mauritiana* subsp. *faurei*, PMC mitosis, n = 9 *(Vogt 10927 & Oberprieler 5375)*. E: *A. zaianica*, PMC meiosis, n = 9 *(Vogt 14840 & Oberprieler 9149)*. F: *A. abylaea*, PMC meiosis, n = 18 *(Vogt 10023 & Oberprieler 4471)*. – Scale bars = 10 µm.

This seems to be the first count not only for this species but for *Anthemis* ser. *Melampodinae* as a whole. It coincides with nearly all records for *A.* sect. *Anthemis*. All cells checked proved to have a small accessory B-chromosome. The karyotype resembles that of other species of the section, with 5 pairs of metacentric, 2 pairs of submetacentric, and 2 pairs of satellited subtelocentric chromosomes (Table 6). The intrachromosomal asymmetry index A_1 yielded the highest value of all species studied here. A comparably high value was found only in one population of *A. confusa* from S Tunisia.

Table 6. Chromosomes of *Anthemis melampodina* (OTU 12; n = 5).

Chromosome pair	Long arm (µm)	Short arm (µm)	Total length (µm)	Relative length (%)	Arm ratio	Chromosome type
I	4.20	3.57	7.77	13.9	1.17	m
II	3.89	2.97	6.86	12.3	1.30	m
III	4.49	2.19	6.68	12.0	2.05	sm
IV	4.86	0.96	6.60	11.8	5.06	st-sat
V	3.48	2.50	5.98	10.7	1.39	m
VI	3.32	2.41	5.73	10.3	1.37	m
VII	4.11	0.81	5.70	10.2	5.07	st-sat
VIII	3.79	1.79	5.58	10.0	2.11	sm
IX	2.98	1.94	4.92	8.8	1.53	m

Anthemis (subg. *Anthemis,* sect. *Anthemis*) ser. **Secundirameae**

Anthemis confusa

$n = 9$

–Tn, Gafsa, Redeyef - Tamerza, 680 m, 9 May 1994, *Vogt 12747 & Oberprieler 7052.*
–Tn, Sidi-Bouzid, Jelma, 370 m, 17 May 1994, *Vogt 13333 & Oberprieler 7638.*

$2n = 18$

–Tn, Gafsa, Tozeur - El Oued, 45 m, 9 Apr 1980, *Podlech 34145.*
*–Tn, Tataouine - Ghomrassen, 340 m, 14 May 1994, *Vogt 13131 & Oberprieler 7436.*

$2n = 20$

*–Tn, Tataouine - Remada, 450 m, 13 May 1994, *Vogt 13049 & Oberprieler 7354* (Fig. 4E).

This seems to be the first report of chromosome numbers for this species. The indications of $n = 9$ and $2n = 18$ agree with all previous reports for members of *Anthemis* ser. *Secundirameae*. Plants from a population in S Tunisia were found to have an aneuploid chromosome number of $2n = 20$, but other plants from that area had the normal chromosome set with $2n = 18$ chromosomes (Table 7). As discussed in the taxonomic part of the present work, Le Houérou (1962) considered plants from this area to be morphologically intermediate between his *A. pedunculata* var. *decumbens* [= *A. confusa*] and the W Libyan *A. glareosa*. However, in the present revision they are assigned to *A. confusa* not to *A. glareosa*. The aneuploid chromosome number found in one of these plants may be due to the past or recent interbreeding of the two closely related species in SE Tunisia.

Table 7. Chromosomes of *Anthemis confusa*.

Chromosome pair	Long arm (µm)	Short arm (µm)	Total length (µm)	Relative length (%)	Arm ratio	Chromosome type
OTU 9 (n = 2)						
I	3.37	2.54	5.91	14.1	1.32	m
II	3.64	0.66	5.08	12.1	5.51	st-sat
III	2.81	2.23	5.04	12.0	1.26	m
IV	2.58	2.13	4.71	11.2	1.21	m
V	3.16	1.55	4.71	11.2	2.03	sm
VI	3.18	0.58	4.54	10.8	5.48	st-sat
VII	2.46	1.94	4.40	10.5	1.26	m
VIII	2.79	1,.07	3.86	9.2	2.60	sm
IX	2.23	1.53	3.76	9.0	1.45	m
OTU 10 (n = 5)						
I (3x)	3.60	2.91	6.51	14.3	1.23	m
II	3.08	2.42	5.50	12.1	1.27	m
III	3.68	1.76	5.44	11.9	2.09	sm
IV	3.76	0.80	5.34	11.7	4.69	st-sat
V	2.88	2.22	5.10	11.2	1.29	m
VI	3.25	0.67	4.70	10.3	4.85	st-sat
VII	3.09	1.54	4.63	10.2	2.00	sm
VIII (3x)	2.60	1.92	4.52	9.9	1.35	m
IX	2.29	1.69	3.98	8.7	1.35	m

Anthemis secundiramea var. *secundiramea*

$2n = 18$

- –Si, Noto, Vendicari, 16 Jun 1990, HB Catania (cult. in HB Berlin No. 301-04-92-10 & 298-06-91-10) (Fig. 4F).

The chromosome number presented here for this variety of *Anthemis secundiramea* agrees with indications by Capineri & al. (1976, sub *A. secundiramea*) for Sicilian material and Benedí i González (1987) for plants from Menorca. One pair of satellite chromosomes was found in the studied plants of *A. secundiramea* var. *secundiramea,* whereas Brullo (in Bartolo & al. 1979) found none, and *A. secundiramea* var. *cossyrensis* (see below) has two. No Algerian or Tunisian plant material was available for cytological investigations.

Anthemis secundiramea var. *cossyrensis*

$n = 9$

–Tn, Bizerte, Cap Blanc, 10-30 m, 22 May 1994, *Vogt 13791 & Oberprieler 8096.*

$2n = 18$

*–Tn, Bizerte, Cap Blanc, 10-30 m, 22 May 1994, *Vogt 13791 & Oberprieler 8096* (Fig. 5A)
–Si, Isole Egadi, Fariguana, 15 Sep 1990, HB Catania (cult. in HB Berlin No. 298-05-91-10 & 301-02-92-10).

The finding of $n = 9$ and $2n = 18$ chromosomes for this variety of *Anthemis secundiramea* agrees with a report by Brullo & al. (1977, sub *A. secundiramea* subsp. *intermedia*). Brullo (in Bartolo & al. 1979) later found two pairs of satellited chromosomes in plants from Lampedusa which he considered to represent a separate subspecies, *A. secundiramea* subsp. *lopadusana*, on account of its karyogram (12m + 2sm + 4st-sat), as he had found that *A. secundiramea* subsp. *secundiramea* lacked satellites. The Tunisian plant material studied here shows two pairs of satellited subtelocentric chromosomes (Table 8), exactly as the morphologically similar plants from Lampedusa. This supports the inclusion of *A. secundiramea* subsp. *lopadusana* in *A. secundiramea* var. *cossyrensis* described from Pantellaria.

Table 8. Chromosomes of *Anthemis secundiramea* var. *cossyrensis* (OTU 13; n = 6).

Chromosome pair	Long arm (µm)	Short arm (µm)	Total length (µm)	Relative length (%)	Arm ratio	Chromosome type
I	3.38	2.76	6.14	14.0	1.22	m
II	2.98	2.36	5.34	12.2	1.26	m
III	3.58	0.76	5.12	11.7	4.71	st-sat
IV	2.67	2.34	5.01	11.4	1.14	m
V	3.29	1.67	4.96	11.3	1.97	sm
VI	3.24	0.59	4.61	10.5	5.49	st-sat
VII	2.51	2.04	4.55	10.4	1.23	m
VIII	2.73	1.52	4.25	9.7	1.79	sm
IX	2.29	1.64	3.93	9.0	1.39	m

Anthemis secundiramea var. *urvilleana*
$n = 9$
–Me, Paradise Bay, 27 Feb 1994, *Mevert & Seifert s.n.* (Herb. Oberprieler).

This taxon, endemic to Malta, had been studied cytologically by Brullo & al. (1997). The chromosome number reported here is in agreement with their findings.

Anthemis ubensis
$n = 9$
–Tn, Beja, Djebel Goraa, 730 m, 3 May 1994, *Vogt 12216 & Oberprieler 6521* (Fig. 5B).
–Tn, Beja, Djebel Goraa, 960 m, 3 May 1994, *Vogt 12291 & Oberprieler 6596.*
–Tn, Beja, Djebel Goraa, 960 m, 3 May 1994, *Vogt 12305 & Oberprieler 6610.*
–Tn, El Kef, Djebel Dyr, 1000 m, 4 May 1994, *Vogt 12352 & Oberprieler 6657.*
–Tn, El Kef, Table de Jughurta, 1200-1270 m, 5 May 1994, *Vogt 12467 & Oberprieler 6772.*

$2n = 19$
*–Tn, Forêt de Kesra, 18 May 1994, *Vogt 13524 & Oberprieler 7829* (Fig. 5C).
–Tn, Zaghouan, Djebel Zaghouan, 23 May 1994, *Vogt 13824 & Oberprieler 8129.*

This interesting species from E Algeria and N Tunisia had not yet been studied cytologically. In morphological respects it holds a somewhat intermediate position between *Anthemis pedunculata* and *A. secundiramea*. The occurrence of accessory chromosomes in two of the seven plants studied (Table 9) may be a consequence of hybrid speciation. Meiosis, studied in five other plants, was found to be regular, with the formation of nine bivalents. In one such population I was able to observe the formation of a bivalent by two chromosomes differing markedly in length (Fig. 5B). This again suggests that the chromosome set of this species is relatively unbalanced.

Table 9. Chromosomes of *Anthemis ubensis* (OTU 15; n = 3).

Chromosome pair	Long arm (µm)	Short arm (µm)	Total length (µm)	Relative length (%)	Arm ratio	Chromosome type
I	3.60	2.80	6.40	13.5	1.28	m
II	3.18	2.57	5.75	12.2	1.23	m
III	3.75	1.12	5.65	12.0	3.34	st-sat
IV	3.58	1.95	5.53	11.7	1.83	sm
V	2.91	2.43	5.34	11.3	1.19	m
VI	2.82	2.17	4.99	10.6	1.29	m
VII	3.10	0.98	4.86	10.3	3.16	st-sat
VIII	2.47	2.00	4.47	9.5	1.23	m
IX (3x)	2.65	1.73	4.38	9.3	1.53	m

Anthemis (subg. *Anthemis*, sect. *Anthemis*) ser. ***Bourgaeinianae***

Anthemis mauritiana subsp. *faurei*
n = 9
– Ma, Saidia, 10 m, 5 May 1993, *Vogt 10872 & Oberprieler 5320*.
– Ma, Ras-el-Ma, 40 m, 5 May 1993, *Vogt 10927 & Oberprieler 5375* (Fig. 5D)

This seems to be the first report of a chromosome number for this species endemic to the Mediterranean coast of E Morocco. Bivalent formation in pollen mother cell meiosis was found to be regular.

Anthemis stiparum subsp. *sabulicola*
2*n* = 18
– Ag, Laghouat, Ghardaia - El Golea, 400 m, 28 Mar 1981, *Podlech 35529*.
– Ag, Laghouat, Zelfana, 360 m, 30 Mar 1981, *Podlech 35571*.

This subspecies of *Anthemis stiparum* was studied by Podlech (1986, sub *A. monilicostata* subsp. *stiparum*) who found the same chromosome number of 2*n* = 18 using one of the specimens *(Podlech 35571)* of the present study.

Anthemis zaianica
n = 9
– Ma, Oulmès, 1310 m, 12 May 1995, *Vogt 14840 & Oberprieler 9149*. (Fig. 5E).

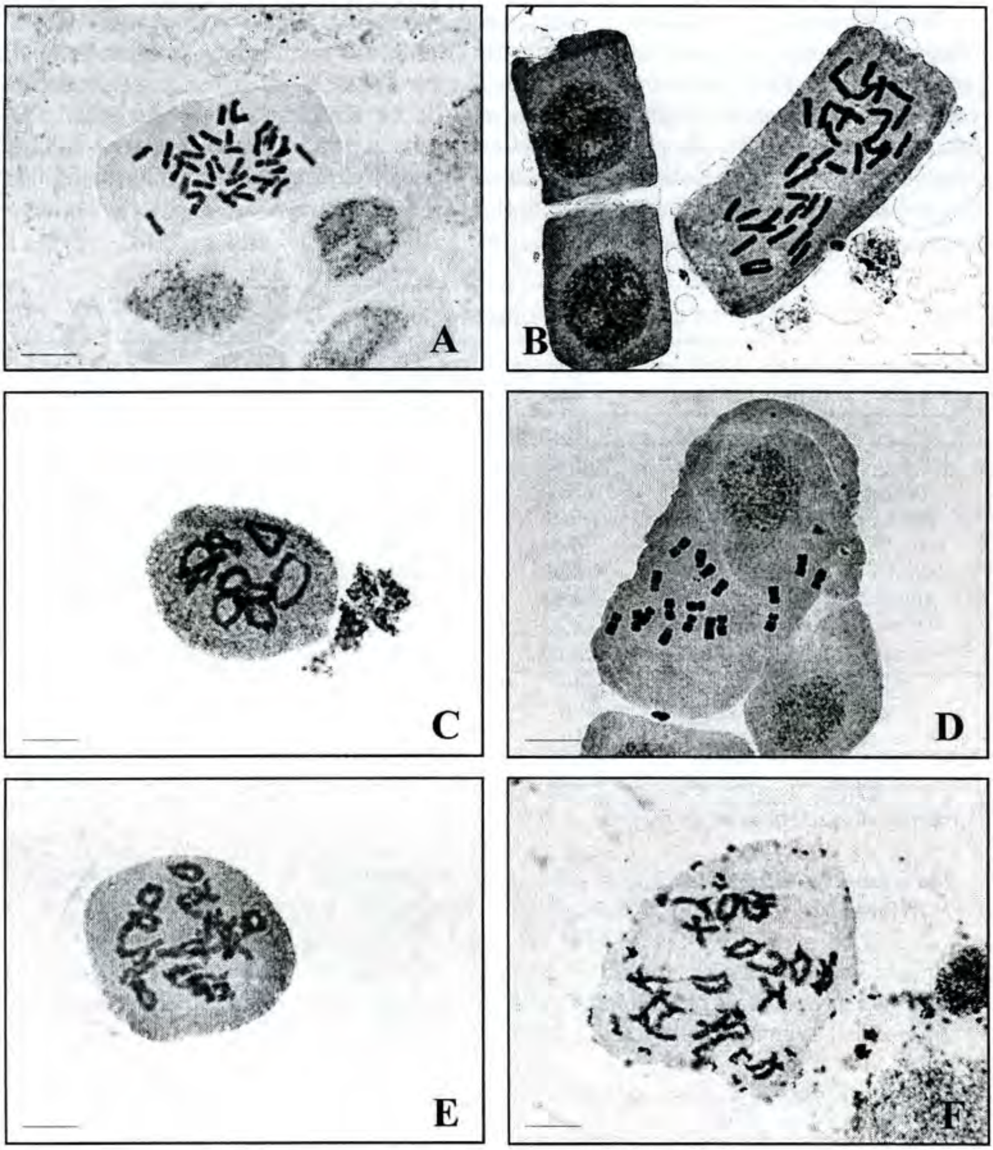

Fig. 6: Metaphase plates in *Anthemis*. – A: *Anthemis abylaea,* root tip mitosis, $2n = 36$ *(Vogt 12045)*. B: *A. maritima* subsp. *maritima,* root tip mitosis, $2n = 36$ *(HB Liège)*. C: *A. pedunculata* var. *pedunculata,* PMC meiosis, $n = 9$ *(Vogt 9414 & Oberprieler 3852)*. D: *A. pedunculata* var. *pedunculata,* root tip mitosis, $2n = 18$ *(Vogt 9414 & Oberprieler 3852)*. E: *A. pedunculata* var. *pedunculata,* PMC meiosis, $n = 18$ *(Vogt & Oberprieler 4026)*. F: *A. pedunculata* var. *pedunculata,* PMC meiosis, $n = 18$ *(Vogt 14962 & Oberprieler 9271)*. – Scale bars = 10 µm.

No previous report of a chromosome number for this species newly described exists. The number of $n = 9$ chromosomes reported here agrees with that found in other species of *Anthemis* ser. *Bourgeinianae* and most members of *A.* sect. *Anthemis*.

Anthemis (subg. *Anthemis*) sect. ***Hiorthia***

Anthemis abylaea

$n = 18$

- –Ma, Djebel Fahies, 550-660 m, 20 Apr 1993, *Vogt 9897 & Oberprieler 4345*.
- –Ma, Monts de Beni Hosmar, 1200 m, 21 Apr 1993, *Vogt 10023 & Oberprieler 4471* (Fig. 5F).
- –Ma, Monts de Beni Hosmar, 1200 m, 30 May 1993, *Vogt 12039*.

$2n = 36$

- –Ma, Djebel Fahies, 550-660 m, 31 May 1993, *Vogt 12045* (Fig. 6A).

The chromosome number for this species endemic to the limestone mountains of the Tangier peninsula is reported here for the first time.

Anthemis cretica subsp. *columnae*

$2n = 36$

- –It, Avellino, Monte Vergine, 1220 m, 28 May 1994, *Vogt 14004 & Oberprieler 8309*.

It was not possible to study N African plant material of this taxon cytologically, so a chromosome count from the locus classicus of this subspecies in S Italy is provided instead. The tetraploid level found confirms counts by Strid & Franzén (1983, sub *Anthemis carpatica*) and Papanicolaou (1984, sub *A. cretica*) on Greek plants that were later assigned to *A. cretica* subsp. *columnae* by Franzén (1986).

Anthemis maritima subsp. *maritima*

$n = 18$

- –Tn, Bizerte, Cap Blanc, 10-30 m, 22 Jun 1994, *Vogt 13792 & Oberprieler 8097*.
- –Ga, Col de Tende, 270 m, 23 May 1995, *Vogt 15352 & Oberprieler 9661*.

$2n = 36$

- –Tn, Bizerte, Cap Blanc, 20 m, 22 May 1994, *Vogt 13813 & Oberprieler 8118*.
- –Hs, Cabo Roche, 5-10m, 17 Apr 1993, *Vogt 9733 & Oberprieler 4181*.
- *–Ga, Aude, Narbonne, HB Liège (cult. in HB Berlin No. 194-25-92-10).
- *–Co, Alistro, HB Liège (cult. in HB Berlin No. 194-27-92-10) (Fig. 6B).

The tetraploid chromosome numbers found in Tunisian, Spanish and French material (Table 10) confirms counts of $n = 18$ or $2n = 36$, respectively, made on plants of the same taxon from the Mediterranean coasts of France (Larsen 1954, Rashid 1974), Italy (Capineri & al. 1976), Sicily (Brullo & Pavone 1978, Brullo & al. 1988), and Mallorca (Benedí i González 1987), and from the Atlantic coasts of Portugal (Fernandes & Queirós 1970, 1971) and Spain (Luque 1984, Benedí i González 1987).

Deviating, diploid chromosome numbers for *Anthemis maritima* were given by Harling (1950) and Mitsuoka & Ehrendorfer (1972) who studied plant material from botanical gardens, without documented provenance. Aneuploid chromosome numbers of $n = 10$ and $2n = 20$ for a population of *A. maritima* from Menorca were reported by Benedí i González (1987), which suggests that diploid chromosome numbers can indeed be found in natural populations of *A. maritima*.

Table 10: Chromosomes of *Anthemis maritima* subsp. *maritima*.

Chromosome pair	Long arm (µm)	Short arm (µm)	Total length (µm)	Relative length (%)	Arm ratio	Chromosome type
OTU 1 (n = 1)						
I	4.07	3.91	7.98	14.6	1.04	m
I	4.38	3.41	7.79	14.2	1.28	m
II	4.77	2.71	7.48	13.6	1.76	sm
II	4.19	2.95	7.14	13.0	1.42	m
III	3.88	2.83	6.71	12.2	1.37	m
III	3.76	2.67	6.43	11.7	1.40	m
IV	3.60	2.64	6.24	11.4	1.36	m
IV	3.60	2.48	6.08	11.1	1.45	m
V	3.10	2.91	6.01	11.0	1.06	m
V	3.37	2.52	5.89	10.7	1.33	m
VI	3.99	1.28	6.05	11.0	3.11	st-sat
VI	3.99	0.85	5.62	10.3	4.69	st-sat
VII	3.84	1.90	5.74	10.5	2.02	sm
VII	3.06	2.48	5.54	10.1	1.23	m
VIII	3.72	0.78	5.28	9.6	4.76	st-sat
VIII	3.26	0.74	4.78	8.7	4.40	st-sat
IX	2.33	2.09	4.42	8.1	1.11	m
IX	2.83	1.63	4.46	8.1	1.73	sm
OTU 2 (n = 4)						
I	3.53	2.64	6.17	14.7	1.33	m
I	3.56	1.85	5.41	12.9	1.92	sm
II	2.99	2.42	5.41	12.9	1.23	m
II	2.95	2.18	5.13	12.2	1.35	m
III	3.31	1.15	5.24	12.5	2.87	sm-sat
III	3.34	0.93	5.05	12.0	3.59	st-sat
IV	2.68	2.20	4.88	11.6	1.21	m
IV	2.65	2.13	4.78	11.4	1.24	m
V	2.55	2.01	4.56	10.9	1.26	m
V	2.96	1.76	4.72	11.2	1.68	m
VI	2.96	0.89	4.63	11.0	3.32	st-sat
VI	2.49	0.86	4.13	9.8	2.89	sm-sat
VII	2.73	1.64	4.37	10.4	1.66	m
VII	2.36	1.91	4.27	10.2	1.23	m
VIII	2.19	1.84	4.03	9.6	1.19	m
VIII	2.51	1.37	3.88	9.2	1.83	sm
IX	2.08	1.76	3.84	9.1	1.18	m
IX	2.03	1.49	3.52	8.4	1.36	m

Anthemis pedunculata (subsp. *pedunculata*) var. *pedunculata*

$n = 9$

- –Ma, Middle Atlas, Azrou - Aïn Leuh, 1585 m, 11 Jun 1992, *Vogt 9414 & Oberprieler 3852 bis* (Fig. 6C).
- –Ma, Middle Atlas, Azrou - Aïn Leuh, 1580 m, 11 Jun 1992, *Oberprieler 3849*.
- –Ma, Middle Atlas, Foum Kheneg, 1880 m, 12 Jun 1992, *Vogt 9440 & Oberprieler 3878*.
- –Ma, Djebel Tazzeka, Gouffe de Friovato, 1200 m, 15 Jun 1992, *Vogt 9468 & Oberprieler 3905*.
- –Ma, Rif, Djebel Tizirene, 1700 m, 24 Jun 1992, *Vogt 9628 & Oberprieler 4064*.
- –Ma, Rif, Djebel Lakraa, 1900-2000 m, 26 Jun 1992, *Vogt & Oberprieler 4115*.
- –Ma, Monts des Beni Snassen, Tanezzert - Taforalt, 900-950 m, 9 May 1993, *Vogt 11448 & Oberprieler 5896*.
- –Ma, Middle Atlas, Source de l'Oum-er-Rbia, 1630 m, 28 May 1993, *Vogt 12002*.
- –Ma, Middle Atlas, Aïn-Leuh - Azrou, 1900 m, 13 May 1995, *Vogt 14949 & Oberprieler 9258 bis*.
- –Ma, Middle Atlas, Aïn-Leuh - Azrou, 1980 m, 13 May 1995, *Vogt 14927 & Oberprieler 9236*.
- –Ma, Monts des Beni-Snassen, Djebel Foughal, 1280 m, 16 May 1995, *Vogt 15264 & Oberprieler 9573*.

$2n = 18$

- –Ma, Taza, Ahermoumou (Ribat-el-Kheyr) - Jebel Bou Iblane, 1430-1550 m, 25 Jun 1989, *Podlech 46964*.
- –Ma, ibid., 1680 m, 25 Jun 1989, *Oberprieler 1908*.
- –Ma, Middle Atlas, Azrou - Aïn Leuh, 1585 m, 11 Jun 1992, *Vogt 9414 & Oberprieler 3852 bis* (Fig. 6D).
- –Ma, Middle Atlas, Foum Kheneg, 1880 m, 12 Jun 1992, *Vogt 9440 & Oberprieler 3878*.
- –Ma, Middle Atlas, Col du Zad, 2100 m, 12 Jun 1992, *Vogt 9442 & Oberprieler 3880*.
- –Ma, Djebel Tazzeka, Gouffe de Friovato, 1200 m, 15 Jun 1992, *Vogt 9468 & Oberprieler 3905*.
- *–Ma, Djebel Tazzeka, Taza - Bab-Bou-Idir, 1420 m, 17 Jun 1992, *Vogt & Oberprieler 3945*.
- –Ma, Rif, Djebel Tizirene, 1700 m, 24 Jun 1992, *Vogt 9628 & Oberprieler 4064*.

$n = 18$

- –Ma, Djebel Tazzeka, 1900 m, 16 Jun 1992, *Vogt 9487 & Oberprieler 3923*.
- –Ma, Rif, Ketama - Djebel Tidirhin, 1750 m, 20 Jun 1992, *Vogt & Oberprieler 4026* (Fig. 6E).
- –Ma, Rif, Talembote - Djebel Tassaot, 1565 m, 25 Jun 1992, *Vogt 9647 & Oberprieler 4083*.
- –Ma, Rif, Djebel Talamssantane, 1765-1900 m, 26 Jun 1992, *Vogt 9668 & Oberprieler 4105*.
- –Ma, Monts des Beni Snassen, Tanezzert - Taforalt, 900 m, 9 May 1993, *Vogt 11466 & Oberprieler 5914*.
- –Ma, Anti-Atlas, Djebel Lekst, 1500 m, 15 May 1993, *Vogt 11766 & Oberprieler 6214*.
- –Ma, Anti-Atlas, Djebel Lekst, 1550-1570 m, 16 May 1993, *Vogt 11829 & Oberprieler 6277*.
- –Ma, Middle Atlas, Col du Zad, 2125 m, 26 May 1993, *Vogt 11988*.
- –Ma, Tahout-ou-Fillali, 1990 m, 26 May 1993, *Vogt 11948*.
- –Ma, Middle Atlas, Aïn-Leuh - Source de l'Oum-er-Rbia, 1790 m, 28 May 1993, *Vogt 12006*.
- –Ma, Middle Atlas, Aïn-Leuh - Azrou, 1900 m, 13 May 1995, *Vogt 14949 & Oberprieler 9258*.
- –Ma, Middle Atlas, Aïn-Leuh - Azrou, 1900 m, 13 May 1995, *Vogt 14949 & Oberprieler 9258 ter*.
- –Ma, Middle Atlas, Aïn-Leuh - Azrou, 1830 m, 13 May 1995, *Vogt 14962 & Oberprieler 9271* (Fig. 6F).
- –Ma, Middle Atlas, Aïn-Leuh - Azrou, 1720 m, 14 May 1995, *Vogt 15005 & Oberprieler 9314*.
- –Ma, Middle Atlas, Aïn-Leuh - Azrou, 1700 m, 14 May 1995, *Vogt 15010 & Oberprieler 9319*.

Table 11. Chromosomes of *Anthemis pedunculata* var. *pedunculata*.

Chromosome pair	Long arm (µm)	Short arm (µm)	Total length (µm)	Relative length (%)	Arm ratio	Chromosome type
OTU 3 (n = 5)						
I	2.90	2.33	5.23	13.4	1.24	m
I	2.53	2.29	4.82	12.3	1.10	m
II	2.67	1.96	4.63	11.8	1.36	m
II	2.46	2.03	4.49	11.5	1.21	m
III	3.03	0.77	4.58	11.7	3.93	st-sat
III	2.74	0.66	4.18	10.7	4.15	st-sat
IV	2.78	1.52	4.30	11.0	1.82	sm
IV	2.65	1.40	4.05	10.4	1.89	sm
V	2.44	1.83	4.27	10.9	1.33	m
V	2.29	1.79	4.08	10.4	1.27	m
VI	2.49	0.62	3.89	10.0	4.01	st-sat
VI	2.66	0.54	3.98	10.2	4.92	st-sat
VII	2.13	1.81	3.94	10.1	1.17	m
VII	2.13	1.59	3.72	9.5	1.33	m
VIII	2.00	1.54	3.54	9.1	1.29	m
VIII	2.07	1.40	3.47	8.9	1.47	m
IX	2.54	1.12	3.66	9.4	2.26	sm
IX	2.22	0.97	3.19	8.2	2.28	sm
+ (V)	2.50	1.66	4.16	10.6	1.50	m
OTU 4 (n = 14)						
I	3.90	3.28	7.18	14.2	1.18	m
II	4.13	2.14	6.27	12.4	1.92	sm
III	3.39	2.72	6.11	12.1	1.24	m
IV	2.99	2.53	5.52	11.0	1.18	m
V	3.96	0.78	5.52	11.0	5.07	st-sat
VI	3.46	1.75	5.21	10.3	1.97	sm
VII	2.88	2.26	5.14	10.2	1.27	m
VIII	3.42	0.72	4.92	9.8	4.75	st-sat
IX	2.60	2.03	4.63	9.2	1.28	m

- Ma, Middle Atlas, Azrou - Ifrane, 1750 m, 14 May 1995, *Vogt 15016 & Oberprieler 9325*.
- Ma, Monts des Beni-Snassen, Gorge du Zegzel - Aïn-Almou, 800-900 m, 15 May 1995, *Vogt 15123 & Oberprieler 9432*.
- Ma, Monts des Beni-Snassen, Aïn Almou, 1180 m, 16 May 1995, *Vogt 15188 & Oberprieler 9497*.
- Ma, Monts des Beni-Snassen, Djebel Foughal, 1200 m, 16 May 1995, *Vogt 15227 & Oberprieler 9536*.
- Ma, Monts des Beni-Snassen, Oulad Jabein-Fouaga, 1180 m, 16 May 1995, *Vogt 15280 & Oberprieler 9589*.

$2n = 36$

- Ma, Taza, Ahermoumou (Ribat-el-Kheyr) - Jbel Bou-Iblane 1680 m, 25 Jun 1989, *Oberprieler 1895*.
- Ma, Jebel Bou Iblane, Tizi Bouzabel, 2040 m, 26 Jun 1989, *Oberprieler 1967*.
- Ma, Tizi-n-Tahout-ou-Fillali, 2070 m, 4 Jul 1989, *Podlech 47622*.

- –Ma, Middle Atlas, Foum Kheneg, 1880 m, 12 Jun 1992, *Vogt 9440 & Oberprieler 3878bis.*
- –Ma, Djebel Tazzeka, 1780 m, 16 Jun 1992, *Vogt & Oberprieler 3937.*
- –Ma, Rif, Talembote - Djebel Tassaot, 1600 m, 25 Jun 1992, *Vogt 9638 & Oberprieler 4074* (Fig. 7A).
- –Ma, Rif, Talembote - Djebel Tassaot, 1565 m, 25 Jun 1992, *Vogt 9647 & Oberprieler 4083.*
- –Ma, Rif, Talembote - Djebel Tassaot, 1565 m, 25 Jun 1992, *Vogt & Oberprieler 4084.*
- –Ma, Rif, Djebel Talamssantane, 1765-1900 m, 26 Jun 1992, *Vogt 9668 & Oberprieler 4105.*

2n = 37
*–Ma, Djebel Tazzeka, 1780 m, 16 Jun 1992, *Vogt & Oberprieler 3937* (Fig. 7B).

Vogt & Oberprieler (1993, sub *Anthemis pedunculata* subsp. *tuberculata*) were the first to find tetraploid chromosome numbers in *A. pedunculata*. Before, only diploid numbers had been reported, both for N African (Galland 1985, sub *A. pedunculata;* Galland 1991, sub *A. pedunculata* subsp. *pedunculata*) and Spanish populations (Aparicio & Silvestre 1985; Blanché & al. 1985, sub *A. tuberculata;* Benedí i Gonzaléz 1987, sub *A. tuberculata* subsp. *tuberculata*). The counts listed above demonstrate that in Morocco both cytotypes grow not only in the same geographical region but in close proximity, even in the same locality (Table 11).

Anthemis pedunculata (subsp. *pedunculata*) var. *discoidea*
n = 9
–Ma, Rif, Djebel Tidirhin, 2200 m, 20 Jun 1992, *Vogt & Oberprieler 4012* (Fig. 7C, D).

2*n* = 18
–Ma, Rif, Bab Bagla, 2000 m, 8 Jun 1987, *Deil 2648* (Fig. 7E).
*–Ma, Rif, Djebel Tidighin, 2000 m, 10 Jul 1989, *Deil 4867* (Fig. 7F).

This is the first report of a chromosome number for this variety, found in the W parts of the Betic Range in S Spain as well as in the C Rif and C High Atlas mountains of Morocco. Unlike *Anthemis pedunculata* var. *pedunculata,* only diploid chromosome numbers were found (Table 12).

Table 12. Chromosomes of *Anthemis pedunculata* var. *discoidea* (OTU 5; n = 3).

Chromosome pair	Long arm (µm)	Short arm (µm)	Total length (µm)	Relative length (%)	Arm ratio	Chromosome type
I	4.99	4.16	9.15	13.4	1.19	m
II	5.75	3.05	8.80	12.9	1.88	sm
III	4.59	3.85	8.44	12.4	1.19	m
IV	5.37	2.57	7.94	11.6	2.08	sm
V	4.25	3.15	7.40	10.9	1.34	m
VI	5.27	1.14	7.19	10.5	4.62	st-sat
VII	4.06	3.06	7.12	10.4	1.32	m
VIII	3.69	2.85	6.54	9.6	1.29	m
IX	4.02	0.97	5.77	8.5	4.14	st-sat

Anthemis pedunculata subsp. *atlantica*

$n = 9$

- Tn, Kasserine, Djebel Chambi, 1540 m, 7 May 1994, *Vogt 12606 & Oberprieler 6911.*

$n = 18$

- Tn, Siliana, Forêt de Kesra, 1030-1100 m, 18 May 1994, *Vogt 13510 & Oberprieler 7815.*
- Tn, Siliana, Forêt de Kesra, 1040-1100 m, 18 May 1994, *Vogt 13523 & Oberprieler 7828.*

This is the first report of a chromosome number for this taxon, endemic to the mountainous areas of E Algeria and N Tunisia.

Anthemis pedunculata subsp. *turolensis*

$n = 9$

- Hs, Cuenca, Beteta, 1350 m, 20 May 1995, *Vogt 15350 & Oberprieler 9659.*

This taxon, endemic to the mountains of C Spain, had been studied cytologically only once (Benedí i González 1987), and found to be diploid. The present count corroborates these data.

Anthemis punctata subsp. *punctata*

$n = 18$

- Tn, Beja, Djebel Goraa, 780 m, 3 May 1994, *Vogt 12238 & Oberprieler 6543.*
- Tn, El Kef, Djebel Dyr, 1000 m, 4 May 1994, *Vogt 12353 & Oberprieler 6658.*
- Tn, El Kef, Table de Jughurta, 1200-1270 m, 5 May 1994, *Vogt 12466 & Oberprieler 6771.*
- Tn, Zaghouan, Djebel Zaghouan, 750-850 m, 23 May 1994, *Vogt 13823 & Oberprieler 8128.*

$2n = 36$

- Tn, El Kef, Djebel Dyr, 1000 m, 4 May 1994, *Vogt 12353 & Oberprieler 6658.*

This species, confined to the mountains of NE Algeria and N Tunisia, had not been studied cytologically. The four specimens studied were all found to be tetraploid, same as the closely related *Anthemis cupaniana* from Sicily (see below).

Anthemis cupaniana

$2n = 36$

- Si, Madonie, Collesano - Petralia, 1590 m, 26 May 1994, *Vogt 13938 & Oberprieler 8243.*
- Si, Madonie, Quacella, 28 Jul 1990, HB Catania (cult. in HB Berlin No. 298-04-91-10).

The findings of a tetraploid chromosome number confirms earlier reports by Brullo & al. (1978a), Brullo & al. (1988), and Devesa & al. (1988). Though no locality is given, it is probable that Capineri's (1968) report of $2n = 36$ for "*A. punctata*" was based on Sicilian material and also relates to *A. cupaniana.*

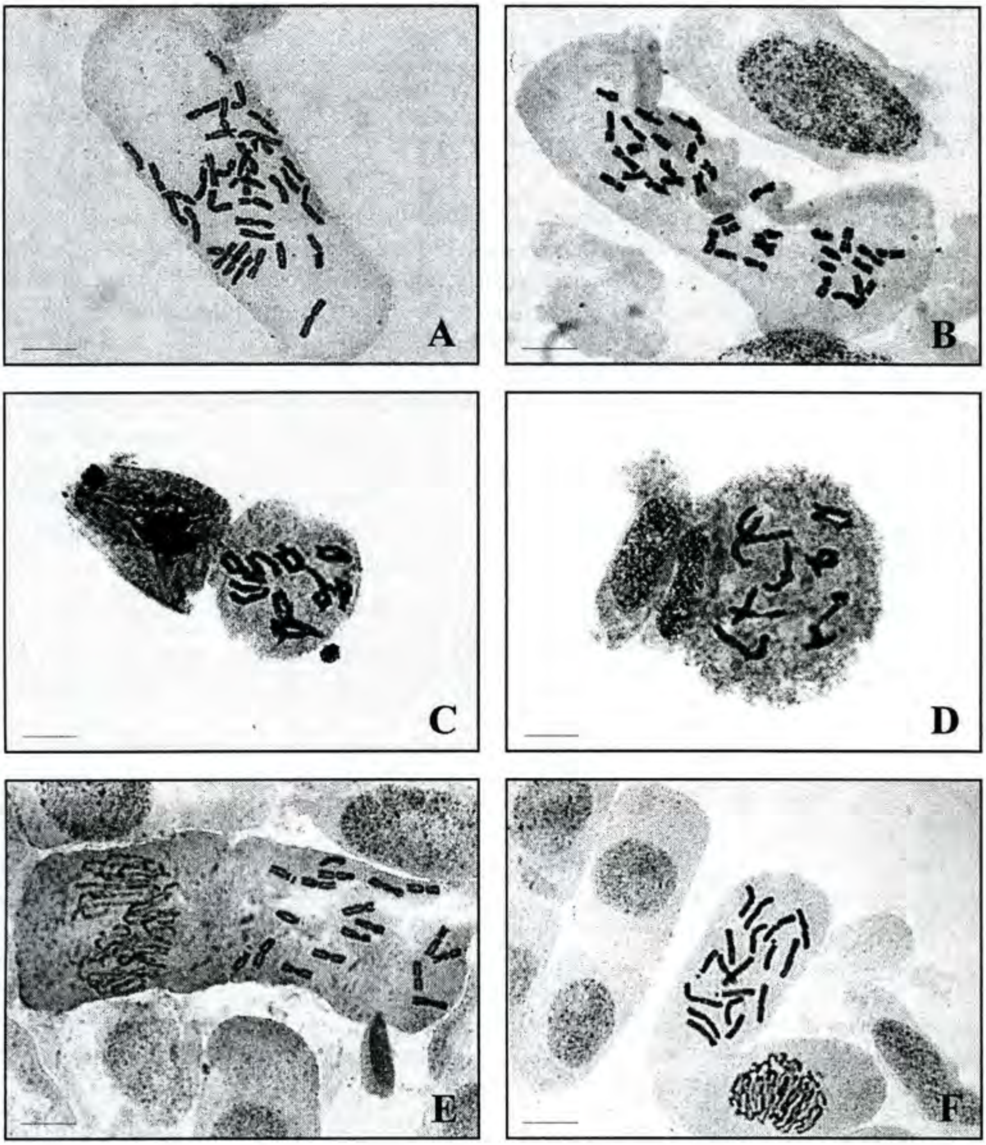

Fig. 7. Metaphase plates in *Anthemis*. – A: *A. pedunculata* var. *pedunculata*, root tip mitosis, $2n = 36$ *(Vogt 9638 & Oberprieler 4074)*. B: *A. pedunculata* var. *pedunculata*, root tip mitosis, $2n = 37$ *(Vogt & Oberprieler 3937)*. C: *A. pedunculata* var. *discoidea*, PMC meiosis, $n = 9$ *(Vogt & Oberprieler 4012)*. D: *A. pedunculata* var. *discoidea*, PMC meiosis, $n = 9$ *(Vogt & Oberprieler 4012)*. E: *A. pedunculata* var. *discoidea*, root tip mitosis, $2n = 18$ *(Deil 2648)*. F: *A. pedunculata* var. *discoidea*, root tip mitosis, $2n = 18$ *(Deil 4867)*. – Scale bars = 10 µm.

Anthemis (subg. *Anthemis*) sect. ***Maruta***

Anthemis cotula
$2n = 18$
*–Ga, HB Dijon (cult. in HB Berlin No. 116-02-93-10).

The report of $2n = 18$ chromosomes for *Anthemis cotula* fits the numerous previous counts published for this wide-spread species. 1-2 accessory B-chromosomes were observed by Yavin (1970) on Greek and Yugoslavian material. The French plants studied here were found to have two pairs of satellited subtelocentric chromosomes, which agrees with observations by Yavin (1970), Mitsuoka & Ehrendorfer (1972), Bartolo & al. (1978), Kuzmanov & al. (1981), and Benedí i González (1987). In Portuguese populations, Fernandes & Queirós (1971) found karyotypes with tandem satellites but also one population with only one pair of satellited chromosomes; while Uitz (1970) figures a karyotype without any satellites. The karyotype found in the present study consists of 6 pairs of metacentric, 1 pair of submetacentric, and 2 pairs of satellited subtelocentric chromosomes (Table 13). Interchromosomal asymmetry (A_1) has the lowermost value of all samples of the present study. No plants from N Africa were available for study.

Table 13. Chromosomes of *Anthemis cotula* (OTU 16; n = 14).

Chromosome pair	Long arm (µm)	Short arm (µm)	Total length (µm)	Relative length (%)	Arm ratio	Chromosome type
I	2.71	2.19	4.90	13.8	1.23	m
II	2.42	1.97	4.39	12.4	1.22	m
III	2.69	0.75	4.22	11.9	3.58	st-sat
IV	2.22	1.82	4.04	11.4	1.21	m
V	2.44	1.40	3.84	10.8	1.74	sm
VI	2.06	1.71	3.77	10.6	1.20	m
VII	2.24	0.66	3.68	10.4	3.39	st-sat
VIII	1.97	1.57	3.54	10.0	1.25	m
IX	1.77	1.43	3.20	9.0	1.23	m

Anthemis pseudocotula
$2n = 18 + 1B$
*–Cy, Paphos-Harbour, 3-20 m, 2 May 1991, *Vogt 9000*.

Same as Yavin (1970) who studied plants from Palestine, we found a chromosome number of $2n = 18$ plus a small accessional B-chromosome on a Cyprian representative of this species. N African plants of Libyan provenance were studied by Brullo & al. (1990), who found no B-chromosome. The karyotype of *Anthemis pseudocotula* had not yet been studied. Unlike *A. cotula,* only one of its two subtelocentric chromosome pairs is satellited (Table 14), but as discussed above for *A. cotula,* this character may show considerable variation.

Table 14. Chromosomes of *Anthemis pseudocotula* (OTU 17; n = 3).

Chromosome pair	Long arm (µm)	Short arm (µm)	Total length (µm)	Relative length (%)	Arm ratio	Chromosome type
I	3.49	2.71	6.20	13.4	1.28	m
II	3.16	2.69	5.85	12.62	1.17	m
III	2.98	2.47	5.45	11.7	1.20	m
IV	3.47	1.06	5.31	11.4	3.27	st-sat
V	3.58	1.51	5.09	11.0	2.37	sm
VI	2.75	2.26	5.01	10.8	1.21	m
VII	3.66	1.14	4.80	10.3	3.21	st
VIII	2.82	1.60	4.42	9.5	1.76	sm
IX	2.38	2.00	4.38	9.4	1.19	m

Anthemis (subg. *Cota*) sect. ***Cota***

Anthemis altissima
$2n = 18$
*–Ga, Aude, Alzonne, HB Liège (cult. in HB Berlin No. 194-17-92-10).
*–Ga, Aude, Montolieu, HB Liège (cult. in HB Berlin No. 194-18-92-10).
*–Ga, Aude, Sigean, HB Liège (cult. in HB Berlin No. 194-19-92-10).
*–Ga, Aude, Villedubert, HB Liège (cult. in HB Berlin No. 194-20-92-10).
*–Ga, Aude, Montolieu, HB Liège (cult. in HB Berlin No. 152-07-93-10).
*–It, Imperia, Perinaldo, 520 m, HB Genova (cult. in HB Berlin No. 268-01-92-10).

My chromosome counts for *Anthemis altissima* agree with all previous indications, by Delay (1971) for French, Capineri & al. (1978) for Italian, Stephanou & Georgiadis (1982) for Greek, Kuzmanov & Georgieva (1977) and Kuzmanov & al. (1980) for Bulgarian, Strid (1980) for Turkish, and Podlech & Dieterle (1969) for Afghanian material. Karyotypes have been reported by Uitz (1970) and Kuzmanov & al. (1981). As they correctly indicate, the karyotype of *A. altissima* differs markedly from those of the other *Anthemis* species studied by me (Table 15): The two pairs of satellite chromosomes are not subtelocentric but submetacentric, the arm ratio being on average 2.48 (vs. 4.03) for the long and 2.68 (vs. 4.36) for the short pair of satellited chromosomes. With relative lengths of (on average) 12.5 % for the long and 11.6 % for the short satellited pair they are among the long or medium chromosomes of the set, not among the medium to short ones (11.2% and 9.8% on average, respectively) as in the other *Anthemis* species

Anthemis austriaca
$2n = 18$
–Au, Niederösterreich, Erlauftal, 220 m, HB Salzburg (cult. in HB Berlin No. 007-11-93-10).

No N African plants were available for study. The diploid chromosome number of $2n = 18$ chromosomes found on material of Austrian provenance agrees with most previous reports for this species, e.g. by Kuzmanov & Kožuharov (1970), Kuzmanov & al. (1980), and Kuzmanov & al. (1981) for Bulgarian, Stephanou & Georgiadis (1982) for Greek, and

Váchová & Májovský (1980) for Slovakian plants. Uitz (1970) reports diploid chromosome numbers for several garden provenances of *Anthemis austriaca,* along with a tetraploid number for material from Turkey. Although *A. austriaca* supposedly belongs to the same section as *A. altissima,* both Uitz (1970) and Kuzmanov & al. (1981) found its satellited chromosomes to be subtelocentric not submetacentric.

Table 15. Chromosomes of *Anthemis altissima.*

Chromosome pair	Long arm (µm)	Short arm (µm)	Total length (µm)	Relative length (%)	Arm ratio	Chromosome type
OTU 18 (n = 4)						
I	4.95	4.04	8.99	14.4	1.22	m
II	4.99	2.20	7.97	12.7	2.26	sm-sat
III	5.11	1.88	7.77	12.4	2.71	sm-sat
IV	3.82	3.31	7.13	11.4	1.15	m
V	3.71	3.02	6.73	10.8	1.22	m
VI	3.31	2.85	6.16	9.9	1.16	m
VII	3.53	2.61	6.14	9.8	1.35	m
VIII	3.87	2.03	5.90	9.4	1.90	sm
IX	4.20	1.68	5.88	9.4	2.50	sm
OTU 19 (n = 13)						
I	5.35	4.16	9.51	14.7	1.28	m
II	5.45	2.06	8.29	12.8	2.64	sm-sat
III	4.24	3.59	7.83	12.1	1.18	m
IV	5.06	1.75	7.59	11.7	2.89	sm-sat
V	3.84	3.15	6.99	10.8	1.21	m
VI	4.24	2.26	6.50	10.0	1.87	sm
VII	3.42	2.86	6.28	9.7	1.19	m
VIII	4.22	2.00	6.22	9.6	2.10	sm
IX	3.26	2.52	5.78	8.9	1.29	m
OTU 20 (n = 6)						
I	4.78	4.09	8.87	15.0	1.16	m
II	4.66	1.79	7.23	12.2	2.60	sm-sat
III	3.72	3.17	6.89	11.7	1.17	m
IV	4.52	2.31	6.83	11.6	1.95	sm
V	4.16	1.59	6.53	11.1	2.61	sm-sat
VI	3.50	2.81	6.31	10.7	1.24	m
VII	3.24	2.51	5.75	9.7	1.29	m
VIII	3.76	1.97	5.73	9.7	1.90	sm
IX	2.73	2.31	5.04	8.5	1.18	m
OTU 21 (n = 12)						
I	4.98	4.02	9.00	14.5	1.23	m
II	4.94	2.19	7.91	12.8	2.25	sm-sat
III	3.99	3.40	7.39	11.9	1.17	m
IV	4.77	1.81	7.36	11.9	2.63	sm-sat
V	3.67	2.97	6.64	10.7	1.23	m
VI	4.05	2.20	6.25	10.1	1.84	sm
VII	3.29	2.75	6.04	9.8	1.19	m
VIII	4.24	1.79	6.03	9.7	2.36	sm
IX	3.03	2.45	5.48	8.8	1.23	m

Table 15 (continued).

Chromosome pair	Long arm (µm)	Short arm (µm)	Total length (µm)	Relative length (%)	Arm ratio	Chromosome type
OTU 22 (n = 12)						
I	4.58	3.78	8.36	14.6	1.21	m
II	4.48	1.87	7.13	12.4	2.39	sm-sat
III	3.69	3.12	6.81	11.9	1.18	m
IV	4.26	1.59	6.63	11.6	2.67	sm-sat
V	3.44	2.85	6.29	11.0	1.20	m
VI	3.84	1.97	5.81	10.1	1.94	sm
VII	3.18	2.53	5.71	10.0	1.25	m
VIII	3.74	1.67	5.41	9.4	2.23	sm
IX	2.95	2.35	5.30	9.3	1.25	m
OTU 23 (n = 3)						
I	5.04	3.94	8.98	14.4	1.27	m
II	4.90	1.78	7.46	11.9	2.75	sm-sat
III	3.89	3.46	7.35	11.8	1.12	m
IV	4.78	2.34	7.12	11.4	2.04	sm
V	3.71	3.20	6.91	11.1	1.15	m
VI	4.37	1.72	6.87	11.0	2.54	sm-sat
VII	3.49	2.85	6.34	10.1	1.22	m
VIII	4.17	2.14	6.31	10.1	1.94	sm
IX	2.97	2.35	5.32	8.5	1.26	m

Anthemis (subg. *Cota*) sect. ***Anthemaria***

Anthemis tinctoria
$2n = 18$
* – Au: Niederösterreich, Persenberg, 200 m, HB Salzburg (cult. in HB Berlin No. 007-14-93-10).

The present count agrees with the many previous reports for this species, e.g. by Strid (1980) for Turkish, Strid & Franzén (1981) for Greek, Capineri (1971) for Italian, Kuz-

Table 16. Chromosomes of *Anthemis tinctoria* (OTU 25; n = 4).

Chromosome pair	Long arm (µm)	Short arm (µm)	Total length (µm)	Relative length (%)	Arm ratio	Chromosome type
I	5.23	4.30	9.53	14.5	1.21	m
II	4.60	3.99	8.59	13.1	1.15	m
III	4.08	3.49	7.57	11.5	1.16	m
IV	4.10	3.17	7.27	11.1	1.29	m
V	4.74	2.29	7.03	10.7	2.06	sm
VI	4.79	1.39	6.96	10.6	3.44	st-sat
VII	3.76	3.06	6.82	10.4	1.22	m
VIII	4.04	2.04	6.08	9.3	1.98	sm
IX	4.24	0.89	5.91	9.0	4.76	st-sat

manov & Kožuharov (1970) and Van Loon & Van Setten (1982) for Bulgarian, and Rostovceva (1983) for Sibirian plant material. The karyotype was described by Kuzmanov & al. (1981) to consist of one pair of metacentric, six pairs of submetacentric, and two pairs of satellited subtelocentric chromosomes. I found 5 pairs of metacentric, 2 pairs of submetacentric, and 2 pairs of satellited subtelocentric chromosomes (Table 16).

Discussion

Karyotypes proved to be rather uniform throughout the genus. Most species have five pairs of metacentric, two pairs of submetacentric, and two pairs of satellited subtelocentric chromosomes in the diploid chromosome sets. The most deviating karyotype was found in *Anthemis altissima* of *A.* sect. *Cota,* where satellited chromosomes are submetacentric rather than subtelocentric. Following Stebbins's (1971) classification of karyotypes with respect to interchromosomal and intrachromosomal asymmetry, all species studied, even *A. altissima,* fall into class 2A. As Romero Zarco (1986) has shown using karyotypes of representatives of *Aveneae (Gramineae),* Stebbins's classification is rather coarse when taxa with minute differences in karyotype asymmetry are studied. He therefore proposed a more sensitive method to assess interchromosomal and intrachromosomal asymmetry, using two indices. The results for the 24 OTUs studied are shown in Fig. 8. The x axis is formed by Romero's A_1 and indicates intrachromosomal asymmetry increasing from left to right, while Romero's A_2 is reported on the y axis and shows interchromosomal (karyotype) asymmetry increasing from bottom to top. In this diagram we find *A. altissima* well separated from the other representatives of the genus, which is caused by the combination of low A_1 and high A_2 values, i.e. high intrachromosomal and low interchromosomal symmetry. *A.* sect. *Anthemis* proves to be very variable in respects to karyotype symmetry: While populations of *A. confusa* and *A. melampodina* show a pronounced intrachromosomal asymmetry, chromosomes are much more symmetrical in *A. ubensis* (OTU 15) and the Spanish population of *A. arvensis* (OTU 7), which reach the same values of intrachromosomal symmetry as *A. altissima*. The karyotypes of *A.* sect. *Hiorthia* are less variable in their intrachromosomal but more variable in interchromosomal symmetry. The plants of *A. pedunculata* (OTU 3, 4, 5) and one of *A. maritima* (OTU 2) fall within the range of *A.* sect. *Anthemis,* but the other population of *A. maritima* (OTU 1) has a karyotype with a very high interchromosomal asymmetry. The perennial representative of *A.* subg. *Cota, A. tinctoria* (OTU 24), is well nested within the group of the perennials of *A.* subg. *Anthemis* (OTUs 1-5). The annuals of *A.* sect. *Maruta, A. pseudocotula* and *A. cotula* (OTUs 16 and 17), show rather low interchromosomal and interchromosomal asymmetry, but are still close to the representatives of *A.* sect. *Anthemis*.

According to Heywood & Humphries (1977) and Bremer & Humphries (1993), $x = 9$ is the commonest base number in the *Anthemideae*. Other base numbers occur only in a few genera. Descending dysploidy is found in *Cancrinia* ($x = 7$) of the *Cancriniinae, Pentzia* ($x = 8$, 6) of the *Matricariinae, Ursinia* ($x = 8$, 7) and *Athanasia* ($x = 8$, Källersjö 1991) of the *Ursiniinae*, and *Artemisia* ($x = 9$, 8, 7, 6) of the *Artemisiinae*. Ascending dysploidy is reported for *Lasiospermum* ($x = 9$, 10), *Osmitopsis, Inezia,* and *Thaminophyllum* ($x = 10$) of the *Thaminophyllinae,* and *Hilliardia, Cotula* sect. *Cotula, Soliva* ($x = 10$), *Leptinella* ($x = 13$), and *Cotula* sect. *Strongylosperma* ($x = 17$) of the *Cotula* group in *Matricariinae* (Bremer & Humphries 1993). Until now, approximately 280 chromosome number reports had been published for *Anthemis* species. All indicate that the base chromosome number in this genus is $x = 9$ and most chromosome counts in the present study are in agreement with this assumption. The deviating counts of $2n = 19, 20, 37$ reported for plants of *Anthemis ubensis*, *A. confusa*, and *A. pedunculata*, respectively, are interpreted as resulting from aneuploid changes.

Polyploidy is common in the tribe. Extensive polyploid complexes are found in *Achillea* (2-10x), *Artemisia* (2-12x), *Dendranthema* (2-10x), *Leptinella* (-12x), and *Leucanthemum* (2-22x, Vogt 1991). Polyploid series in *Anthemis* are less marked, and only members of the *A. cretica* group reach the hexaploid (*A. carpatica*, Küpfer 1974, Baltisberger 1993; *A. cretica* subsp. *pontica*, Oberprieler unpubl.) or octoploid level (*A. carpatica*, Küpfer 1974). Polyploidy is almost exclusively found in the perennials of *A.* sect. *Hiorthia*. Reports of polyploids in the other sections are sparse and confined to triploids in *A. arvensis* (Kuzmanov & al. 1981) and *A. triumfetti* (González Zapatero & Elena Rosselló 1986) and one reported occurrence of a tetraploid in *A. austriaca* (Uitz 1970). Five N African taxa of *Anthemis*, all members of *A.* sect. *Hiorthia*, were found to be tetraploid: *A. abylaea*,

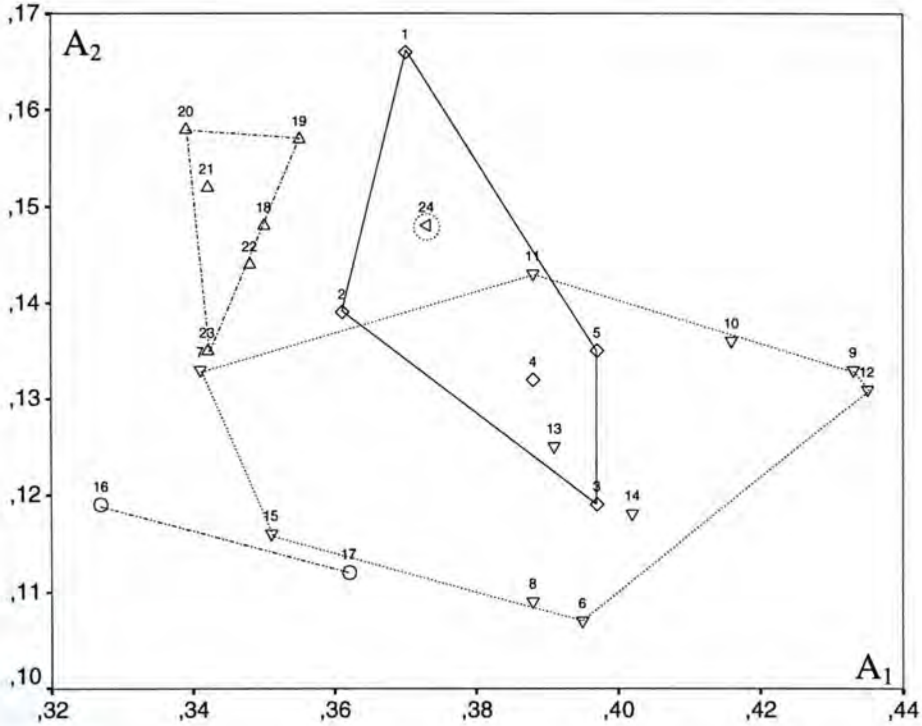

Fig. 8. Intrachromosomal (A_1) and interchromosomal (A_2) asymmetry in representatives of five sections of *Anthemis* (Δ = *A.* sect. *Anthemis;* ◇ = *A.* sect. *Hiorthia;* ○ = *A.* sect. *Maruta;* ◁ = *A.* sect. *Anthemaria;* Δ = *A.* sect. *Cota*). OTU numbers are explained in Table 1. Indices A_1 and A_2 were assessed using the formulae of Romero Zarco (1986).

A. punctata, and *A. cretica* subsp. *columnae* consistently so, *A. pedunculata* (present study) and *A. maritima* (Benedí i González 1987) comprising both diploid and tetraploid cytotypes. All other N African representatives of *Anthemis* studied cytologically are diploids.

Aneuploid changes in the chromosome number were observed in three N African species. Plants from two populations of *Anthemis ubensis* were found to have $2n = 19$ chromosomes, $2n = 20$ chromosomes were counted in a population of *A. confusa,* and $2n = 37$ chromosomes were found in plants from a tetraploid population of *A. pedunculata* in Morocco. In all cases, the accessory chromosomes were metacentric or submetacentric. The occurrence of aneuploidy on a diploid level contrasts with Vogt's (1991) observations on Spanish *Leucanthemum,* that aneuploid chromosome numbers occur only at the tetraploid and higher polyploid levels but never among diploids. Aneuploidy on a diploid level in *Anthemis,* however, had already been reported by Uitz (1970; *A. ruthenica,* $2n = 20$), Kuzmanov & al. (1981; *A. orbelica,* $2n = 22$; *A. stribrnyi,* $2n = 21$), and Benedí i González (1987; *A. maritima,* $2n = 20$). Hypertetraploid chromosome numbers, found once in the present study, had been reported also by Kuzmanov & al. (1981; *A. hinkovae,* $2n = 39$) and Küpfer (1974; *A. saxatilis,* $2n = 37, 38, 39$). It is plausible that ascending aneuploid changes are better tolerated than descending ones, since the gain of an extra chromosome affects viability less serious than a loss (Grant 1981: 363). Hypodiploids (monosomics or nullisomics), therefore, are unlikely to be found under natural conditions. Unlike in diploids, however, aneuploidy at higher ploidy levels may also be due to the loss of chromosomes. Hypotetraploid numbers were reported by Benedí i González (1987; *A. saxatilis,* $2n = 35$) and Küpfer (1974; *A. saxatilis,* $2n = 35$). Hypohexaploidy was found by Baltisberger (1993; *A. carpatica,* $2n = 53$), and hypo-octoploidy by Küpfer (1974; *A. carpatica,* $2n = 66, 68, 70$). According to Grant (1981: 363) this "polyploid drop", i.e. the loss of one or more chromosomes in a polyploid, is often tolerated because of the duplication of genetic material in the homologous chromosomes. Gottschalk (1976: 356) and Khush (1973: 11) explained aneuploid chromosome numbers by uneven distribution of chromosomes during mitotic or meiotic cell divisions. When non-disjunction events in the germ line of somatic tissues or during meiosis affects the chromosome number of gametes, the accessory chromosome(s) will be found in all cells of the offspring. In higher polyploids, especially autopolyploids, the uneven distribution of chromosomes during meiosis is likely enhanced by the formation of multivalents, whereas in diploids it may be caused by distorted pairing of homologous chromosomes and the formation of univalents during meiosis, consequent to hybridisation. It is hardly a fortuitous coincidence that the two hyperdiploid chromosome numbers reported here were found in populations which belong to species likely to be of hybrid origin *(A. ubensis)* or supposedly influenced by hybridisation in the corresponding area *(A. confusa).*

B chromosomes are accessory chromosomes that differ from the basic chromosomal complement (A chromosomes) by their smaller size, varying number, and greater degree of heterochromatisation (Stebbins 1971). They are considered to be fragments homologous to parts of A chromosomes, and suspected to originate from them through disturbance during cell divisions, but they do not pair with the homologous A chromosomes during meiosis (Nagl 1980). B chromosomes may vary in number during ontogeny or in different tissues of the same plant and are considered to have but limited taxonomic significance (Stuessy 1990). In the present study, B chromosomes were observed in *Anthemis* *maroccana*, *A. melampodina*, and *A. pseudocotula*. B chromosomes in *Anthemis* species had been reported previously by Yavin (1970) for *A. cotula* (1-2 B) and *A. pseudocotula* (1 B), Uitz (1970) for *A. carpatica* (1-4 B), Benedí i González (1987) for *A. pedunculata* var. *pedunculata* (1 B; sub *A. tuberculata* var. *tuberculata*) and *A. pedunculata* subsp. *turolensis* (1 B; sub *A. tuberculata* subsp. *turolensis*), and Geôrgiou (1990) for *A. werneri* subsp. *werneri* (1 B) and *A. peregrina* subsp. *peregrina* (1-4 B).

Karyotypes were studied comprehensively in the present work. Comparable surveys were made previously only by Uitz (1970) who studied 8 and Kuzmanov & al. (1981) who studied 21 *Anthemis* species. Mitsuoka & Ehrendorfer (1972) also presented detailed analyses of karyotypes and furthermore studied experimental hybrids and their meiotic chromosome pairing. Uitz (1970) found prominent differences in structure and total size of karyotypes among *Anthemideae*, in parallel to phylogenetic relationships between species, sections and genera as deduced from other characters.

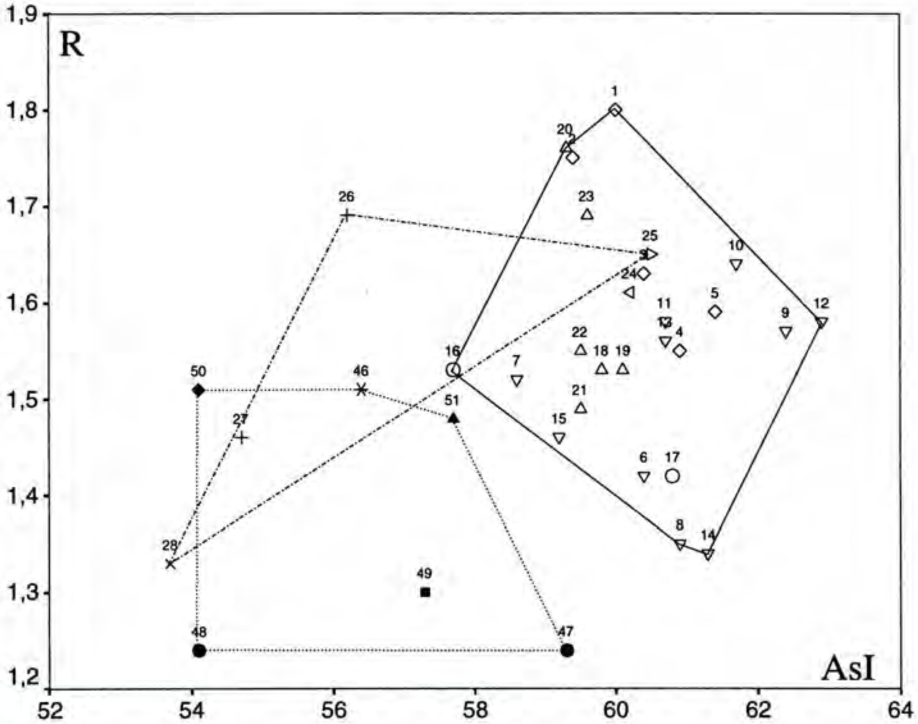

Fig. 9. Intrachromosomal (AsI) and interchromosomal (R) asymmetry in representatives of *Anthemidinae* (solid line; ▽ = *Anthemis* sect. *Anthemis*, ◇ = *A.* sect. *Hiorthia*, ○ = *A.* sect. *Maruta*, ◁ = *A.* sect. *Anthemaria*, △ = *A.* sect. *Cota*), *Chrysantheminae* (broken line; ▷ = *Argyranthemum*, + = *Chrysanthemum*, × = *Ismelia*) and *Leucantheminae* (dotted line; ✶ = *Rhodanthemum*, ● = *Leucanthemum*, ■ = *Coleostephus*, ◆ = *Lepidophorum*, ▲ = *Nivellea*). OTU numbers and data sources are explicited in Tables 1 and 2. The Indices AsI and R were assessed using the formulae of by Barghi & al. (1989).

When compared with other genera of the *Anthemideae* (Fig. 9, 10), the sections of *Anthemis* cluster together due to their asymmetrical chromosomes (intrachromosomal asymmetry, AsI) and moderately bimodal karyotype (interchromosomal asymmetry, R). Most other genera have a more symmetrical karyotype, but in some representatives of *Matricaria* and *Tanacetum* even greater asymmetry is found.

Some interesting patterns emerge when one compares karyotype differentiation in the different subtribes of *Anthemideae,* as defined by Bremer & Humphries (1993) on morphological grounds.

The *Chrysantheminae,* which Bremer & Humphries (1993) considered to be the sister group of *Anthemidinae,* are represented by three genera (Fig. 9). While the perennial *Argyranthemum* (OTU 25) was found to have quite similar symmetry values to *Anthemis,* the annual *Chrysanthemum* (OTUs 26 and 27) and *Ismelia* (OTU 28) show very low intrachromosomal asymmetry.

The *Achilleinae,* as defined by Bremer & Humphries (1993), also exhibit a considerable increase of chromosomal symmetry from perennial to annual life form (Fig. 10): The perennial species of *Achillea* (OTUs 29 and 30) fall within the range of *Anthemis,* the perennial (OTU 33) and annual species (OTUs 31 and 32) of *Anacyclus* and the unispecific annual genus *Cladanthus* (OTU 37) stand apart, with *Chamaemelum* (OTUs 34-36) linking *Anthemis* to *Anacyclus* and exhibiting considerable intrageneric variation. Of the three *Chamaemelum* species studied, the perennial *C. nobile* (OTU 34) has the karyotype least similar to *Anthemis,* although Mitsuoka & Ehrendorfer (1972) reported that it is easily crossed with *A. cotula,* and found frequent chromosome pairing during meiosis and high pollen fertility in the resulting hybrid. They therefore considered the two genera to be closely related. However, since only a single intergeneric cross was made, and bearing in mind that crossability is considered a primitive trait and the formation of reproductive barriers progressive (Funk 1985, but see discussion in Stuessy 1990: 201), crossability of *C. nobile* and *A. cotula* may be a symplesiomorphic feature rather than reflecting true phylogenetic affinity.

In the *Leucantheminae* (Fig. 9), a considerable shift is detectable from the moderately asymmetrical karyotype of the long-lived perennial *Rhodanthemum* (OTU 46) to the very symmetrical karyotypes of the short-lived perennials of *Leucanthemum* (OTU 47 and 48) and the annual *Coleostephus myconis* (OTU 49). *Lepidophorum* (OTU 50), a unispecific annual genus considered by Bremer & Humphries (1993) to be a basal member of their *Leucantheminae,* shows largely symmetrical chromosomes and on karyological, but also on fruit morphological grounds (Uitz 1970), may rather belong to the *Chrysantheminae.*

Tanacetum, as the only representative of Bremer & Humphries's (1993) provisional subtribe *"Tanacetinae",* was represented in Uitz's (1973) studies by three species, the perennials *T. vulgare* (OTU 38) and *T. parthenium* (OTU 39) and the annual *T. annuum* (OTU 40). They show similar intrachromosomal symmetry values (Fig. 10) but differ markedly from each other in their interchromosomal asymmetry, the two perennials having a moderately to extremely symmetrical karyotype, the annual an extremely bimodal one.

The same trend is noted in Bremer & Humphries's (1993) subtribe *Matricariinae* (Fig. 10), represented by the perennials of *Tripleurospermum* (OTUs 41-43) and the annuals of *Matricaria* (OTUs 44 and 45): *Tripleurospermum* falls within range of *Anthemis, Matricaria* (at least the species *M. recutita* OTU 44) shows highly symmetrical chromosomes but a very asymmetrical karyotype.

The relatively similar karyotypes found in the predominantly perennial genera *Anthemis, Achillea, Argyranthemum, Tanacetum,* and *Tripleurospermum* led both Uitz (1970) and Mitsuoka & Ehrendorfer (1972) to consider these genera as rather central (basal) within the *Anthemideae.* From these, progressive karyotype divergence led to mostly more symmetrical, but sometimes to more asymmetrical (e.g. *Matricaria*) karyotypes. This assumption is supported by morphology. The mentioned genera all belong to different subtribes in Bremer & Humphries's (1993) classification, and it is more parsimonious to consider similarities of karyotypes as the symplesiomorphic condition rather than suppose an independent origin of similar karyotypes from quite dissimilar ones within each subtribe. *Anthemis,* therefore, would belong to the basal stock of genera in the *Anthemideae,* showing relations to *Tanacetum* as well as to *Achilleinae, Chrysantheminae,* and *Matricariinae* through their basal genera *Achillea, Argyranthemum,* and *Tripleurospermum,* respectively.

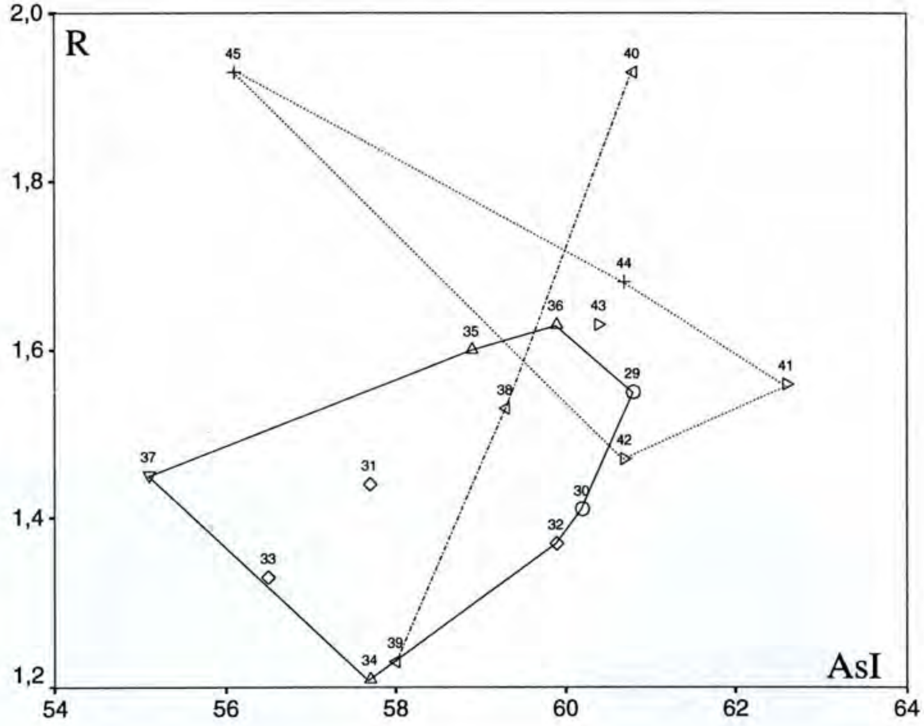

Fig. 10. Intrachromosomal (AsI) and interchromosomal (R) asymmetry in representatives of *Achilleinae* (solid line; ○ = *Achillea,* ◇ = *Anacyclus,* △ = *Chamaemelum,* ▽ = *Cladanthus*), *Tanacetinae* (broken line; ◁ = *Tanacetum*), and *Matricariinae* (dotted line; ▷ = *Tripleurospermum,* + = *Matricaria*). OTU numbers and data sources are expicited in Table 1 and 2. The indices AsI and R were assessed using the formulae of Barghi & al. (1989).

Indications of gross structural differences in the karyotypes of *Anthemideae* are very sparse. Small structural changes, along with karyotype differentiation due to hybridisation, are considered as the main mechanism underlying karyotype divergence (Mitsuoka & Ehrendorfer 1972). As Nagl & Ehrendorfer (1974) found, karyotype differentiation is more rapid in annuals than in perennials perhaps because annuals show shorter cell cycles and enhanced cell elongation, thus a more rapid development.

Mitsuoka & Ehrendorfer (1972) stated that structural differentiation of chromosomes in the *Anthemideae,* already occurs at the infraspecific level. They gave *Anthemis cotula* as an example of a species in which the number and formation of satellites is very variable. The same is observed in *A. secundiramea* where Brullo (in Bartolo & al. 1979) found a Sicilian population of *A. secundiramea* var. *secundiramea* to lack satellited chromosomes, our own material from Sicily revealed one pair, and plants of *A. secundiramea* var. *cossyrensis* from Tunisia, two pairs of satellited chromosomes. In *A. arvensis* subsp. *incrassata,* considerable differences in karyotype symmetry between N African and S Spain populations were detected in the present study.

11. Pollen morphology

First detailed light microscopic studies of *Anthemideae* pollen were made by Wodehouse (1926, 1935) on *Anthemis cotula* and *Chamaemelum nobile.* He described the pollen as echinate, having a coarse-granular, two-layered exine. The thicker inner layer appeared to him to be built of coarse radial striae, while the outer, much thinner layer was found to have very fine radial striae. He considered the exine sculpturing as a main difference within the tribe, with echinate pollen grains with sharply pointed spines characterising *Anthemis* together with other insect-pollinated genera *(Leucanthemum, Chrysanthemum, Tanacetum)* and non-echinate pollen grains with vestigal or entirely absent spines being typical for wind-pollinated genera like *Artemisia* (Woodhouse 1935).

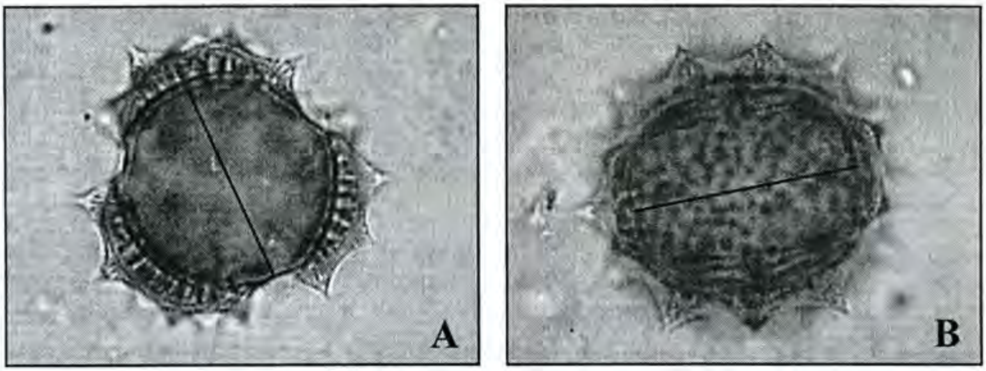

Fig. 11. *Anthemis gharbensis (Vogt 10161 & Oberprieler 4609).* – A: Acetolysed pollen grain in polar view; equatorial inside diameter (E) as measured for the comparative analysis of pollen size indicated. B: Acetolysed pollen grain in equatorial view; inside length of polar axis (P) indicated.

Stix (1960), in her comprehensive light microscopical work on pollen morphology of *Compositae,* described her "*Anthemis* type", to which she also assigned representatives of *Achillea, Chamaemelum, Chrysanthemum, Leucanthemum, Cotula,* and *Matricaria,* as having a tegillate sexine. She found the inner, coarsely striate layer of the sexine to consist of rather thick and distally branched infrategillary baculae, while the outer, finely striate layer is formed of fine pila with heads mostly fused together (intertegillary baculae). Her findings were later corroborated by transmission electron microscopy (TEM) and scanning electron microscopy (SEM) (e.g. Skvarla & al. 1977, Vezey & al. 1994; the latter authors use the term "double tectum" for the outer layer of baculae which they misleadingly call "infratectal columellae", while the infrategillary baculae are called "basal columellae").

Besides the mentioned authors, pollen of *Anthemis* was studied by Čigurjaeva & Tereškova (1983), Benedí i González (1987), Fedorončuk & Savitskii (1988), and De Leonardis & al. (1991). In all species studied, pollen grains were found to be rather uniformly spheroidal, trizonocolporate and spiny, with tenuimarginate, sharply pointed colpi and lalongate, tenuimarginate, sharply pointed ora. No qualitative features were found to define subgroups. However, pollen dimensions vary markedly between species. Benedí i Gonzaléz (1987) found annual representatives of *A.* subg. *Anthemis* to have conspicuously smaller pollen than the perennial representatives of this subgenus.

Vogt (1991) has demonstrated that dimensions of pollen grains are correlated with ploidy level in *Leucanthemum.* I therefore aimed to find out whether diploids and tetraploids in *Anthemis* as well can be separated by pollen measurements, i.e. whether pollen dimensions can help to assess of chromosome numbers, e.g. for types and other herbarium specimens, especially from presently inaccessible areas. For that purpose, it was thought desirable to exclude variation of exine thickness and spine length by using inside measures of equatorial diameter and length of polar axis rather than total equatorial diameter and total length of polar axis (Fig. 11).

Material and methods

A total of 104 pollen samples (Table 17) were taken from herbarium specimens representing 35 N African *Anthemis* taxa. All 25 species accepted in the present revision were included in the survey. Pollen was treated with the acetic anhydride/sulfuric acid (acetolysis) mixture of Erdtman (1960), washed with destilled water, mounted in glycerine jelly, and the slides were sealed with Paraplast. The material was studied with an Leitz Dialux 20 microscope, and measurements were made using an eyepiece micrometer. Equatorial inside diameter (E) of pollen grains was measured in polar view in at least 50 grains per sample; inside length of the polar axis (P) was measured in equatorial view in at least 30 grains per sample. In both cases, the inner boundary of the nexine was used as starting and ending points for the measurements (Fig. 11).

Results and discussion

Pollen grains of all studied representatives of the genus were found to be uniformly spiny, spheroidal, and trizonocolporate. Dimensions of pollen grains vary conspicuously. Equatorial inside diameters (E) were found to range between 12.5 μm and 25.4 μm, and the inside length of polar axis (P), between 13.3 μm and 27.5 μm. The index of equatorial diameter and polar axis (P/E), however, was found to be fairly constant and usually falls

Table 17. Pollen grain dimensions (mean ± standard deviation) in *Anthemis*. – E: Equatorial inside diameter; P: Inside length of polar axis; ploidy, when inferred from pollen measurements, is given in square brackets.

OTU	specimen	ploidy	E (μm)	P (μm)	P/E
Anthemis* sect. *Hiorthia					
A. abylaea					
1	Ma: Beni Hosmar, *29.6.1930, Maire* (P)	[4*x*]	19.51 ± 0.92	21.15 ± 1.04	1.08
A. cretica subsp. *columnae*					
2	Ag: Dj. Tamesguida, *6.1890, Battandier* (G) [Type of *A. numidica*]	[?]	19.61 ± 0.84	20.31 ± 1.04	1.04
A. maritima subsp. *maritima*					
3	Hs: Cabo Roche, *Vogt 9733 & Oberprieler 4181* (B)	4x [?]	18.83 ± 0.69	18.86 ± 0.61	1.00
4	Tn: Cap Blanc, *Vogt 13792 & Oberprieler 8097* (B)	4*x*	22.01 ± 1.50	21.29 ± 1.27	0.97
5	Ga: Col du Tende, *Vogt 15352 & Oberprieler 9661* (B)	4*x*	20.67 ± 0.55	22.36 ± 1.14	1.08
6	Ag: La Calle, *2.5.1914, Clavé* (G)	[?]	18.18 ± 0.73	19.38 ± 0.96	1.07
7	Ag: Bône, *14.5.1906, Romieux* (G)	[4*x*]	20.21 ± 0.83	22.24 ± 0.89	1.10
8	Sa: Su Palloon, *31.5.1983, Charpin* (G)	[?]	18.60 ± 1.50	19.57 ± 1.54	1.05
A. maritima subsp. *bolosii*					
9	Ag: Philippeville, *11.5.1853, Cosson* (P)	[2*x*]	17.50 ± 0.62	17.68 ± 0.58	1.01
10	Ag: Stora, *23.6.1930, Maire* (P)	[2*x*]	17.01 ± 0.70	18.14 ± 0.91	1.07
11	Ag: Philippeville, *5.1858, Choulette* (MPU)	[2*x*]	16.77 ± 0.67	18.50 ± 0.56	1.10
12	Ag: Stora, *5.1913, Battandier* (MPU)	[2*x*]	16.58 ± 0.77	17.00 ± 0.77	1.03
A. maritima subsp. *pseudopunctata*					
13	Ag: Cap Aokas, *5.1896, Reverchon* (B) [Type]	[?]	19.31 ± 0.76	20.50 ± 1.01	1.06
A. pedunculata var. *pedunculata*					
14	*Herb. Desfontaines* (P) [Type]	[2*x*]	16.12 ± 0.62	18.99 ± 0.72	1.18
15	Hs: Sierra Nevada (G)	[4*x*]	19.66 ± 0.69	20.81 ± 0.97	1.06
16	Ag: Tiaret, *Pomel* (P) [Type of *A. granulata*]	[?]	17.90 ± 1.03	19.56 ± 1.13	1.09
17	Ag: Miliana, *6.1856, Pomel* (MPU) [Type of *A. tenuisecta*]	[2*x*]	17.21 ± 1.07	17.97 ± 0.97	1.04
18	Ma: Tazzeka, *6.1925, Maire* (P) [Type of *A. laeviscula*]	[?]	18.43 ± 0.55	18.90 ± 0.71	1.03
19	Hs: Sierra Nevada (G) [Type of *A. tuberculata* var. *microcephala*]	[2*x*]	19.27 ± 0.81	16.74 ± 0.66	0.87
20	Ma: Dj. Touchka, *1876, Ibrahim* (MPU) [Type of *A. punctata* var. *maroccana*]	[?]	19.51 ± 0.71	20.07 ± 0.83	1.03
21	Ag: Bossuet, *6.6.1927, Faure* (MPU) [Type of *A. punctata* var. *microcephala*]	[?]	18.58 ± 0.86	20.13 ± 0.83	1.08
22	Hs: Sa. de los Filabres, *28.7.1995, Rico* (SALA 59886)	[2*x*]	18.58 ± 0.93	18.26 ± 1.22	0.98
23	Ag: Yakouren, *Podlech 39294* (G)	[2*x*]	16.37 ± 0.45	16.13 ± 0.55	0.99
24	Ag: Aurès, *Podlech 38937* (MSB)	[2*x*]	17.75 ± 0.60	18.17 ± 0.57	1.02
25	Ag: Tizi N´Kouilal, *Podlech 39137* (MSB)	[?]	18.94 ± 0.85	18.63 ± 0.81	0.98
26	Ag: Takerbouzt, *Podlech 38994* (MSB)	[2*x*]	15.84 ± 0.66	15.72 ± 0.49	0.99
27	Ag: Dj. Babor, *5.6.1980, Dubuis* (MSB)	[2*x*]	16.37 ± 0.65	16.32 ± 0.59	1.00
28	Ag: Djurdjura, *Podlech 39060* (MSB)	[?]	18.79 ± 0.60	18.85 ± 0.76	1.00
29	Ag: Djurdjura, *Podlech 39007* (MSB)	[2*x*]	17.33 ± 0.70	17.83 ± 0.60	1.03
30	Ag: Dj. Babor, *21.6.1880, Cosson* (P)	[?]	18.15 ± 1.06	20.25 ± 0.89	1.12
31	Ag: Dj. Babor, *20.6.1880, Cosson* (P)	[2*x*]	15.90 ± 0.75	16.14 ± 0.78	1.02
32	Ag: Col de Tirourda, *26.6.1875, Duhamel* (G)	[2*x*]	17.13 ± 1.12	18.08 ± 1.08	1.06
33	Ag: Col de Telmet, *Davis 52583* (RNG)	[2*x*]	17.98 ± 0.61	17.60 ± 0.88	0.98
34	Ag: Dj. Tougour, *22.5.1853, Cosson* (P)	[4*x*]	23.18 ± 1.57	23.58 ± 1.65	1.02
35	Ma: Dj. Foughal, *Vogt 15264 & Oberprieler 9573* (B)	2*x* [?]	19.10 ± 0.86	20.57 ± 0.81	1.08
36	Ma: Dj. Bou Iblane, *Oberprieler 1908* (B)	2*x*	17.48 ± 1.30	18.76 ± 1.04	1.07
37	Ma: Foum Kheneg, *Vogt 9440 & Oberprieler 3878a* (B)	2*x*	16.11 ± 0.69	16.29 ± 1.23	1.01
38	Ma: Taforalt, *Vogt 11448 & Oberprieler 5896* (B)	2*x*	17.68 ± 1.38	17.57 ± 1.50	0.99
39	Ma: Aïn Leuh, *Vogt 14949 & Oberprieler 9258b* (B)	2*x*	17.72 ± 0.83	17.88 ± 0.59	1.01
40	Ma: Aïn Leuh, *Vogt 14962 & Oberprieler 9271* (B)	4*x*	21.80 ± 1.16	21.81 ± 1.31	1.00
41	Ma: Dj. Tazzeka, *Vogt 9487 & Oberprieler 3923* (B)	4*x*	20.48 ± 0.71	20.07 ± 1.00	0.98

Table 17. (continued)

OTU	specimen	ploidy	E (µm)	P (µm)	P/E
42	Ma: Foum Kheneg, *Vogt 9440 & Oberprieler 3878b* (B)	4*x*	18.44 ± 0.65	23.90 ± 0.93	1.30
43	Ma: Tahout-ou-Fillali, *Vogt 11948* (B)	4*x*	18.67 ± 0.87	22.39 ± 0.97	1.20
44	Ma: Dj. Lekst, *Vogt 11829 & Oberprieler 6277* (B)	4*x*	20.47 ± 1.08	20.43 ± 1.33	1.00
45	Ma: Col du Zad, *Vogt 11988* (B).	4*x*	18.64 ± 0.75	23.50 ± 0.89	1.26
46	Ma: Aïn Leuh, *Vogt 14949 & Oberprieler 9258* (B)	4*x*	21.12 ± 0.91	21.38 ± 0.90	1.01
47	Ma: Azrou - Ifrane, *Vogt 15016 & Oberprieler 9325* (B)	4*x*	21.99 ± 0.95	25.07 ± 1.06	1.14
48	Ma: Aïn Leuh, *Vogt 14927 & Oberprieler 9236* (B)	2*x* [4*x*]	20.83 ± 1.42	22.79 ± 1.37	1.09
A. pedunculata var. *discoidea*					
49	Ma: Rif, Azrou, *26.6.1926, Maire* (MPU) [Type of *A. pedunculata* f. *eradiata*]	[2*x*]	17.00 ± 0.77	16.92 ± 0.79	1.00
50	Hs: Sa. de las Nieves (G) [Type]	[4*x*]	20.24 ± 0.78	20.65 ± 0.95	1.02
51	Ma: Assif-n-Arous, *Crane 170* (RNG)	[2*x*]	18.23 ± 0.94	17.99 ± 0.99	0.99
A. pedunculata subsp. *atlantica*					
52	Ag: Dj. Tougour, *Balansa 967* (G)	[?]	17.68 ± 1.08	19.54 ± 1.23	1.11
53	Ag: Kenchala, *Pomel* (MPU) [Type]	[?]	18.24 ± 0.88	21.14 ± 1.29	1.16
54	Ag: Dj. Babor, *Podlech 39380* (MSB)	[2*x*]	16.47 ± 1.07	16.42 ± 1.01	1.00
55	Ag: Dj. Gouffi, *10.7.1861, Cosson* (P)	[2*x*]	16.44 ± 0.56	17.62 ± 0.66	1.07
56	Ag: Dj. Gouffi, *10.7.1861, Cosson* (P)	[2*x*]	16.42 ± 0.68	18.25 ± 1.00	1.11
57	Ag: Dj. Babor, *20.7.1880, Cosson* (P)	[4*x*]	19.86 ± 1.26	21.64 ± 1.15	1.09
58	Ag: Dj. Babor, *7.1897, Reverchon* (P)	[2*x*]	17.48 ± 0.76	18.85 ± 0.86	1.08
59	Ag: Roumel, *Reboud 1677* (G)	[?]	18.38 ± 0.47	19.11 ± 0.72	1.04
60	Ag: Oued Zenati, *27.5.1911, Clay* (P)	[4*x*]	20.02 ± 0.92	20.94 ± 0.86	1.05
61	Ag: Rummel, *28.5.1840, Durieu* (P)	[?]	18.75 ± 0.99	19.15 ± 1.63	1.02
62	Ag: Dj. Chelia, *Podlech 38760* (MSB)	[2*x*]	17.95 ± 1.34	18.94 ± 1.04	1.06
63	Ag: Oued Abdi, *4.6.1853, Cosson* (P)	[2*x*]	17.77 ± 0.85	18.44 ± 0.64	1.04
64	Ag: Dj. Cheliah, *11.6.1853, Cosson* (P)	[4*x*]	21.20 ± 1.12	21.32 ± 0.97	1.01
65	Ag: Adghar Amellal, *1.7.1880, Cosson* (P)	[2*x*]	15.27 ± 0.65	16.08 ± 0.91	1.05
66	Tn: Dj. Semata, *21.5.1887, Letourneux* (P)	[?]	19.67 ± 0.84	20.19 ± 0.76	1.03
67	Tn: Souk el Djema, *28.5.1887, Letourneux* (P)	[?]	19.92 ± 0.69	20.01 ± 0.83	1.00
68	Tn: Dj. Meghila, *16.5.1887, Letourneux* (P)	[4*x*]	20.63 ± 1.22	22.03 ± 1.25	1.07
A. pedunculata subsp. *clausonis*					
69	Ag: Castiglione, *Clauson* (MPU) [Type]	[?]	18.61 ± 1.17	18.39 ± 1.38	0.99
70	Ag: Zeralda, *Battandier* (MPU)	[2*x*]	16.66 ± 0.75	17.08 ± 1.09	1.03
A. pedunculata subsp. *turolensis*					
71	Hs: Beteta, *Vogt 15350 & Oberprieler 9659* (B)	2*x*	15.98 ± 0.53	15.72 ± 0.74	0.98
A. punctata subsp. *punctata*					
72	Ag: Tamesguida, *Battandier* (P) [Type of *A. punctata* var. *baborensis*]	[?]	18.33 ± 0.70	19.03 ± 0.66	1.04
73	Tn: Dj. Zaghouan, *Vogt 13823 & Oberprieler 8128* (B)	[?]	19.05 ± 0.68	18.10 ± 0.71	0.95
74	Tn: Dj. Dyr *Vogt 12353 & Oberprieler 6658* (B)	[?]	18.67 ± 0.59	18.76 ± 1.11	1.00
75	Ag: Mecid Sidi Aïcha, *8.1880, Reboud* (P)	[?]	18.10 ± 0.75	19.17 ± 0.93	1.06
A. punctata subsp. *kabylica*					
76	Ag: Tirourda, *6.1882, Battandier* [Type]	[?]	18.41 ± 0.67	19.24 ± 0.62	1.05
77	Ag: Tala Guilef, *Davis 53190* (RNG)	[?]	18.73 ± 0.96	18.61 ± 1.10	0.99
78	Ag: Tirourda, *7.1896, Reverchon* (G)	[?]	19.76 ± 0.66	20.47 ± 0.66	1.04
79	Ag: Tirourda, *9.7.1909, Saint-Lager* (G)	[2*x*]	17.95 ± 0.98	18.10 ± 1.31	1.01
Anthemis* sect. *Anthemis					
Anthemis* ser. *Anthemis					
A. arvensis subsp. *incrassata*					
80	Ma: Tetouan, *Vogt 10061 & Oberprieler 4509* (B)	[2*x*]	16.42 ± 0.90	16.35 ± 0.69	1.00
Anthemis* ser. *Chrysanthae					
A. boveana					
81	Ag: Oran, *9.5.1907, Faure* (B)	[2*x*]	16.83 ± 0.76	17.22 ± 0.73	1.02

Table 17. (continued).

OTU	specimen	ploidy	E (µm)	P (µm)	P/E
A. chrysantha					
82	Ag: Bou-Sfer, *Dubuis n° 10733* (MSB)	[?]	18.95 ± 1.38	19.32 ± 0.86	1.02
A. gharbensis					
83	Ma: Arbaoua, *Vogt 10161 & Oberprieler 4609* (B) [Type]	[2*x*]	17.48 ± 0.88	16.93 ± 0.82	0.97
A. maroccana subsp. *maroccana*					
84	Ma: Sefrou, *Vogt 10296 & Oberprieler 4744* (B)	[2*x*]	16.22 ± 0.73	16.01 ± 0.65	0.99
A. maroccana subsp. *aguilarii*					
85	Ma: Azib de Ktama, *Font Quer 441* (G)	[2*x*]	17.04 ± 0.90	17.07 ± 0.83	1.00
A. tenuisecta subsp. *tenuisecta*					
86	Ma: Essaouira, *Vogt 11930* (B)	[2*x*]	16.75 ± 1.09	17.99 ± 0.99	1.07
87	Ma: Tiznit, *Vogt 11905 & Oberprieler 6353* (B)	[2*x*]	15.26 ± 1.78	16.56 ± 2.19	1.09
A. tenuisecta subsp. *jahandiezii*					
88	Ma: Safi, *Jahandiez 115* (B)	[2*x*]	15.04 ± 0.56	15.39 ± 0.75	1.02
Anthemis* ser. *Secundirameae					
A. confusa					
89	Tn: Gabès, *Kralik 356* (G) [Type]	[2*x*]	16.94 ± 0.97	16.44 ± 0.64	0.97
90	Tn: Gafsa, *Vogt 12712 & Oberprieler 7017* (B)	[2*x*]	16.22 ± 1.31	16.01 ± 1.06	0.99
A. cyrenaica					
91	Li: Benghasi, *Ruhmer 182* (GOET)	[2*x*]	16.11 ± 0.68	16.12 ± 0.67	1.00
A. glareosa					
92	Li: Misurata, *Davis 49829* (RNG)	[2*x*]	15.33 ± 0.83	15.50 ± 0.59	1.01
A. secundiramea var. *secundiramea*					
93	Tn: La Haouaria, *Davis 56896 & Lamond* (RNG)	[?]	19.42 ± 1.45	19.90 ± 1.22	1.03
A. taubertii					
94	Li: Baiada, *Davis 49985* (RNG)	[2*x*]	16.23 ± 0.72	16.00 ± 0.69	0.99
A. ubensis					
95	Tn: Kesra, *Vogt 13524 & Oberprieler 7829* (B)	2*x*	17.22 ± 1.22	16.56 ± 0.98	0.96
Anthemis* ser. *Bourgaeinianae					
A. mauritiana subsp. *faurei*					
96	Ma: Saidia, *Vogt 10872 & Oberprieler 5320* (B)	2*x* [?]	19.88 ± 1.04	19.89 ± 0.95	1.00
A. monilicostata					
97	Ag: Saïda, *20.3.1872, Warion* (G)	[?]	19.58 ± 1.07	20.79 ± 1.14	1.06
A. stiparum subsp. *stiparum*					
98	Ag: Aflou, *Podlech 34022* (MSB)	[?]	18.67 ± 0.89	18.60 ± 0.75	1.00
A. stiparum subsp. *sabulicola*					
99	Ag: Ghardaia, *Podlech 35529* (MSB)	[2*x*]	17.58 ± 1.28	17.32 ± 1.19	0.99
A. stiparum subsp. *intermedia*					
100	Ag: Aïn Ben Khelil, *Kralik n° 194* (GOET) [Type]	[2*x*]	16.93 ± 0.95	16.65 ± 0.98	0.98
A. zaianica					
101	Ma: Tougroulmès, *Vogt 14840 & Oberprieler 9149* (B).	2*x*	18.21 ± 0.93	18.04 ± 0.94	0.99
Anthemis* sect. *Maruta					
A. cotula					
102	Ma: Imasinen, *13.6.1929, Maire* (P)	[2*x*]	16.58 ± 0.75	16.17 ± 0.64	0.98
A. pseudocotula					
103	Li: Timimi, *Davis 50308* (RNG)	[2*x*]	17.09 ± 0.99	16.96 ± 1.02	0.99
Anthemis* sect. *Cota					
A. austriaca					
104	Tn: Tataouine, *Vogt 13151 & Oberprieler 7456* (B)	[2*x*]	16.13 ± 0.96	16.28 ± 0.80	1.01

within the range of 0.9-1.1 (see Table 17). Deviating, prolate-spheroidal pollen grains with indices of 1.2-1.3 were observed only in three tetraploid populations of *Anthemis pedunculata* var. *pedunculata* from the Middle Atlas mountains of Morocco (OTUs 42, 43, 45).

Pollen size differences between diploids and tetraploids are well marked: equatorial inside diameter (E) is (12.5-)15.3-19.9(-22.5) µm in diploids, (16.7-)18.4-22.0(-25.4) µm in tetraploids. (Values in brackets denote the range of single pollen grains, non-bracketed values, the range of means.) The inside length of the polar axis (P) was found to be (13.3-)15.7-20.6(-22.5) µm in diploids and (16.6-)18.1-25.1(-27.5) µm in tetraploids. In spite of considerable overlap of values, the combination of both measures makes it possible to discriminate between diploids and tetraploids (Fig. 12). The overlap zone corresponds to three representatives of tetraploid *Anthemis maritima* (OTU 3) and *A. punctata* (OTUs 73-74) and two diploid representatives of *A. pedunculata* (OTU 35) and *A. mauritiana* (OTU 96). Within this overlap zone pollen measurements do not permit to assess with confidence the ploidy level of the OTUs. Another exceptional case is OTU 48, found to have a diploid chromosome number but whose pollen dimensions fall fully within the range of tetraploid representatives of *A. pedunculata*. This is explained by the fact that at the locality in question – as in many places in Morocco – one finds a mixture of diploid

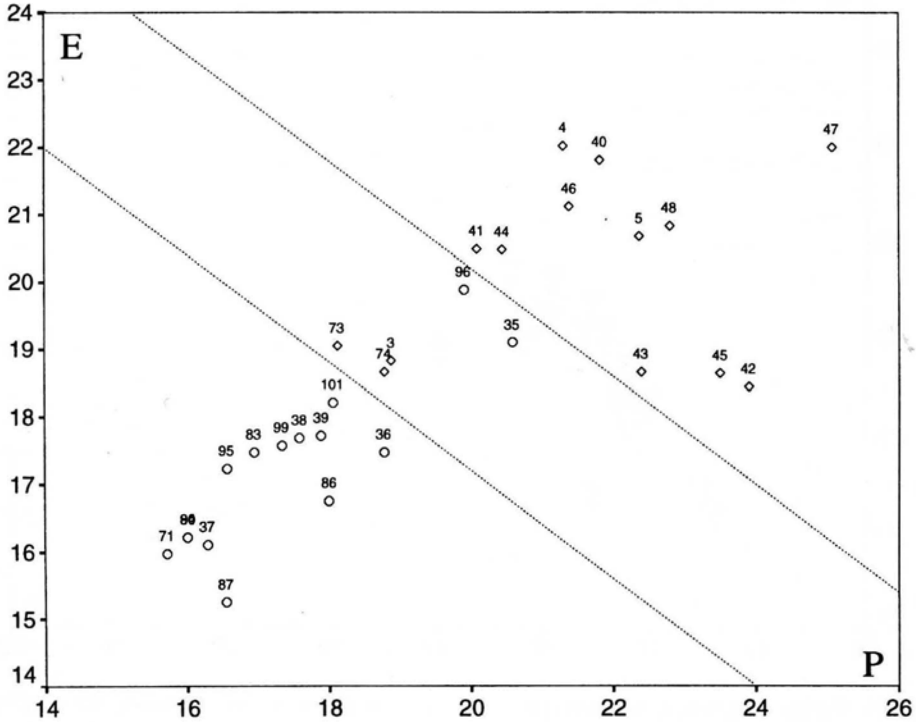

Fig. 12. Pollen dimensions of OTUs with known chromosome number (○ = diploids; ◇ = tetraploids). E = equatorial inside diameter (µm); P = inside length of polar axis (µm). Numbers of OTUs refer to numbers given in Table 17.

and tetraploid plants of *A. pedunculata,* and the plant studied palynologically was not the same individual studied cytologically. In the following, the range of pollen dimensions of known diploids and tetraploids was used to assess ploidy levels in cytologically unchecked specimens.

In contrast to Benedí i González (1987), who had studied Spanish representatives of *Anthemis,* I could detect no difference between pollen sizes of annual and perennial diploids. Since Benedí i González (1987) included spines in his measurements of equatorial diameter and length of polar axis, this seeming contradiction obviously reflects differences in the thickness of the exine or the length of spines, between the annuals and perennials. Further measurements of exine thickness and spine length in annuals and perennials of *Anthemis* are needed to confirm this assumption. However, since the annual representatives of *Anthemis* are usually considered to be autogamous while the perennial representatives are allogamous, the reduction of exine thickness and, moreover, the reduction of spine length in annuals is plausible.

Fig. 13 displays pollen dimensions of annuals of *Anthemis* sect. *Anthemis,* sect. *Maruta,* and sect. *Cota.* All representatives of the two latter sections and most of sect. *Anthemis*

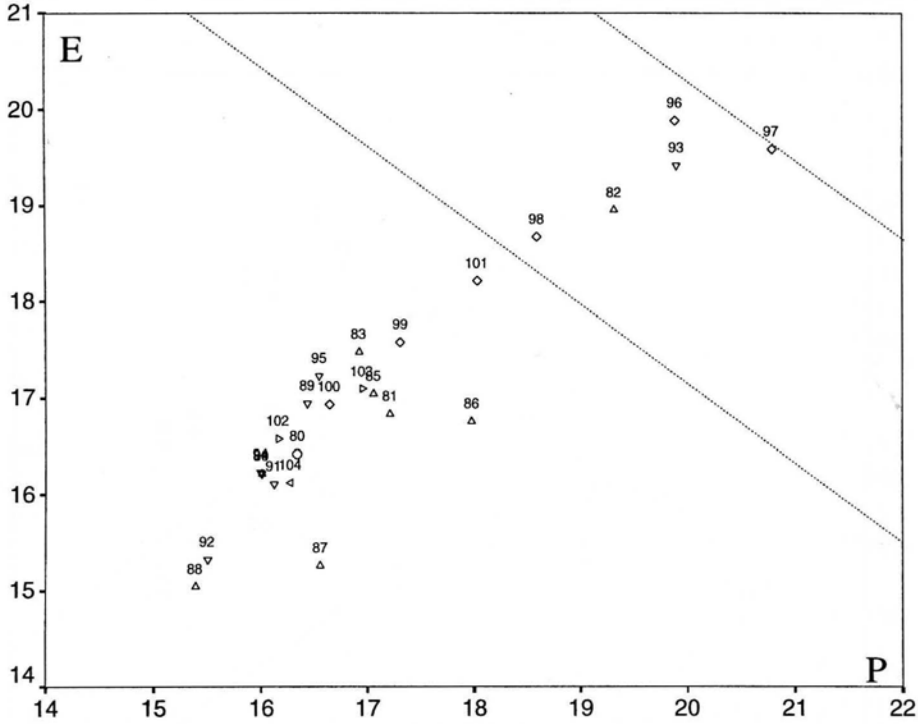

Fig. 13. Pollen dimensions in *Anthemis* sect. *Anthemis* (○ = *A.* ser. *Anthemis;* ◇ = *A.* ser. *Bourgaeinianae;* △ = *A.* ser. *Chrysanthae;* ▽ = *A.* ser. *Secundirameae*), *A.* sect. *Cota* (◁), and *A.* sect. *Maruta* (▷). E = equatorial inside diameter (µm); P = inside length of polar axis (µm). Dotted lines delimit the area of overlap between diploid (bottom left) and tetraploid (top right) OTUs (see Fig. 12).

clearly fall within the range of typical diploids, but five OTUs are found in the overlap zone between diploids and tetraploids: *A. secundiramea* var. *secundiramea* (OTU 93) of *A.* ser. *Secundirameae, A. chrysantha* (OTU 82) of *A.* ser. *Chrysanthae,* and *A. mauritiana* (OTU 96), *A. monilicostata* (OTU 97), and *A. stiparum* subsp. *stiparum* (OTU 98) of *A.* ser. *Bourgaeinianae*. The last mentioned series seems to be characterised by distinctly larger pollen grains than most other annual representatives of the genus.

In *Anthemis maritima* (Fig. 14), representatives of *A. maritima* subsp. *maritima* and subsp. *pseudopunctata* were found to fall within the pollen size range of tetraploids or in the overlap zone between diploids and tetraploids, while the four studied specimens of *A. maritima* subsp. *bolosii* have conspicuously smaller pollen grains. Since this subspecies also has smaller achenes, capitula, ray florets, etc. than *A. maritima* subsp. *maritima* and subsp. *pseudopunctata,* it is reasonable to assume that *A. maritima* subsp. *bolosii* is a diploid taxon. Diploid chromosome numbers in *A. maritima* have been indicated by Benedí i González (1987) from Menorca (Balearic Islands) and by Harling (1950) and Mitsuoka & Ehrendorfer (1972) for plants of unstated provenance.

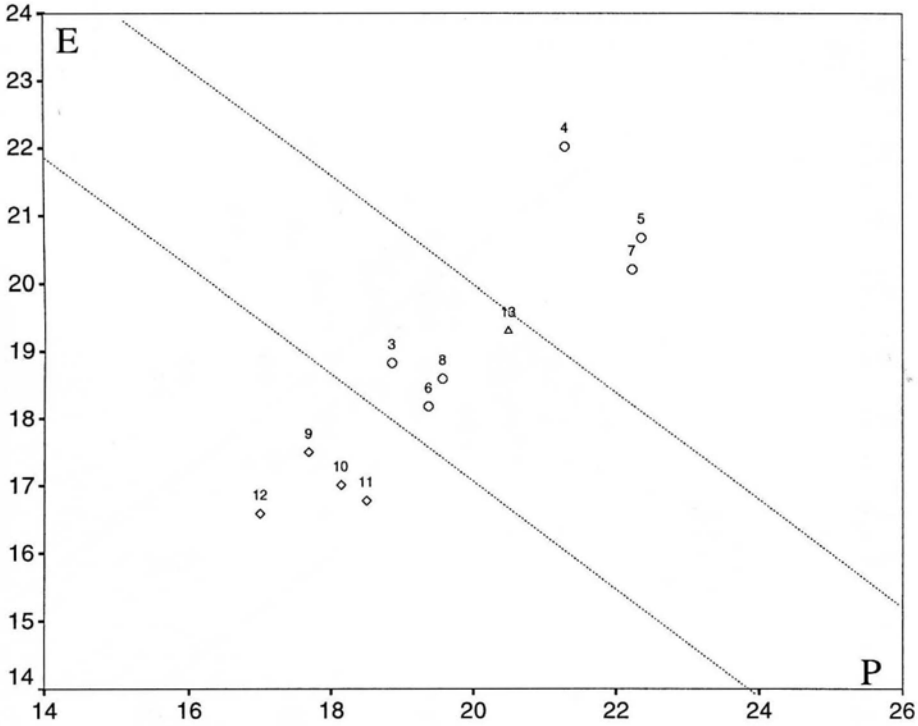

Fig. 14. Pollen dimensions in *Anthemis maritima* subsp. *maritima* (○), subsp. *bolosii* (◇), and subsp. *pseudopunctata* (△).E = equatorial inside diameter (μm); P = inside length of polar axis (μm). Dotted lines delimit the area of overlap between diploid (bottom left) and tetraploid (top right) OTUs (see Fig. 12).

Fig. 15 and Fig. 16, plotting pollen dimensions found in the perennial *Anthemis pedunculata - A. punctata* complex and *A. cretica* subsp. *columnae,* suggest ploidy levels for some of the studied herbarium specimens. As found by cytological study, *A. pedunculata* var. *pedunculata* is represented by diploids and tetraploids. The type specimens of *A. pedunculata* (OTU 14) and *A. tuberculata* var. *microcephala* (OTU 19) definitively fall within the group of diploids by their pollen size. The type specimens of *A. granulata* (OTU 16), *A. laeviuscula* (OTU 18), *A. punctata* var. *maroccana* (OTU 20), and *A. punctata* var. *microcephala* (OTU 21) were found to have intermediate pollen dimensions, so that no suggestion on their ploidy level is possible. A specimen from the Sierra Nevada (OTU 15), labelled as "neotype" of *A. tuberculata* by Benedí i González in 1984 (but not designated neotype in Benedí i González 1987), has rather large pollen suggesting tetraploidy. No concrete data on tetraploidy in Spanish representatives of *A. pedunculata* (= *A. tuberculata*) yet exist, but counts for this taxon are very scarce (Aparicio & Silvestre 1985, Blanché & al. 1985, Benedí i González 1987), and further cytological studies of Spanish plants may well yield similar results as for Morocco, where both cytotypes were found to grow side by side in most populations studied. The same may apply for *A. pedunculata* var. *discoidea,* since the pollen dimensions of the type of that name from the Sierra

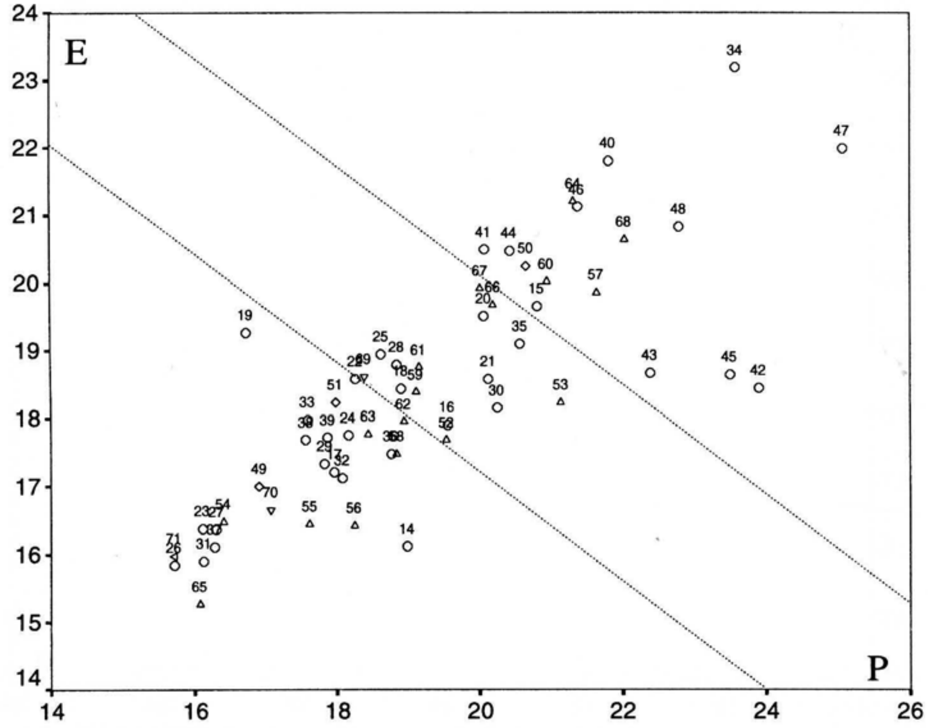

Fig. 15. Pollen dimensions in *Anthemis pedunculata* var. *pedunculata* (○), var. *discoidea* (◇), subsp. *atlantica* (△), subsp. *clausonis* (▽), and subsp. *turolensis* (◁). E = equatorial inside diameter (µm); P = inside length of polar axis (µm). Dotted lines delimit the area of overlap between diploid (bottom left) and tetraploid (top right) OTUs (see Fig. 12).

de Grazalema in S Spain (OTU 50), also fall within the range of the tetraploids, although no tetraploid chromosome count yet exists for this taxon, all its studied Moroccan representatives being unequivocally diploid. Pollen dimensions suggest that *A. pedunculata* subsp. *atlantica* (OTUs 52-68) similarly occurs on two ploidy levels, but all representatives of *A. pedunculata* subsp. *clausonis* (OTUs 69-70) and subsp. *turolensis* (OTU 71) fall within the pollen size range of the diploids, which in the latter case confirms the results of cytological studies by Benedí i González (1987) and myself.

In *Anthemis punctata, A. abylaea,* and *A. cretica* subsp. *columnae,* even in plants suspected to be tetraploid due to their morphological characteristics, or known to be tetraploid (OTUs 73-74), pollen dimensions did not normally reach the dimensions typical for tetraploids, but fell within the overlap zone between diploids and tetraploids, or even within diploid values (OTU 79). Obviously, pollen dimensions are not unrestrictedly comparable between different species groups of *Anthemis*.

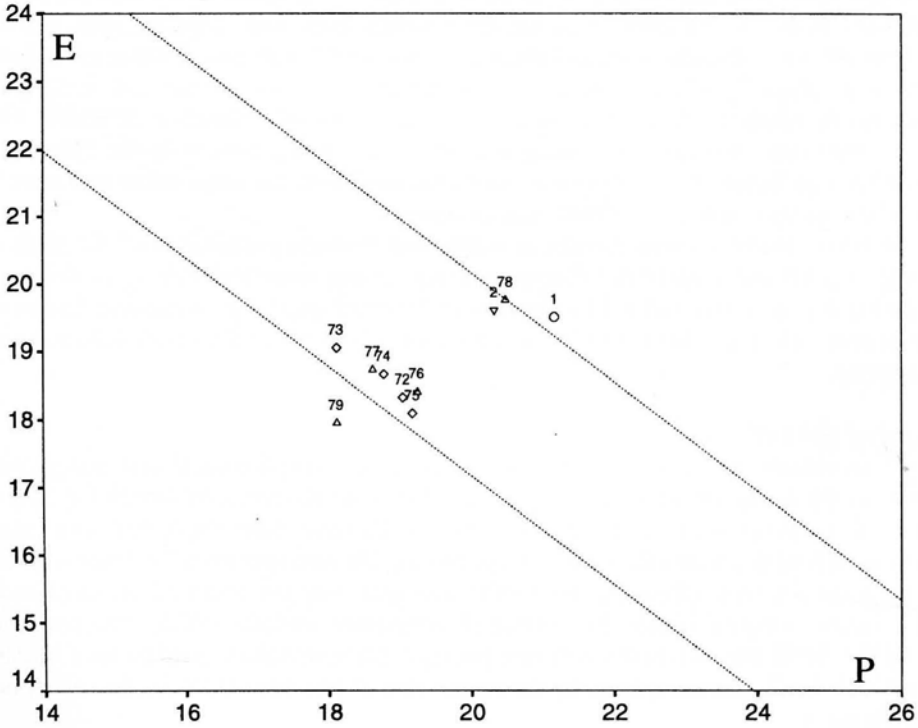

Fig. 16. Pollen dimensions in *Anthemis abylaea* (○), *A. cretica* subsp. *columnae* (▽), *A. punctata* subsp. *punctata* (◇), and subsp. *kabylica* (△). E = equatorial inside diameter (μm); P = inside length of polar axis (μm). Dotted lines delimit area of overlap between diploid (bottom left) and tetraploid (top right) OTUs (see Fig. 12).

12. Species delimitation in the *Anthemis boveana* group

The *Anthemis boveana* group, together with the more remote species *A. chrysantha,* forms *A.* ser. *Chrysanthae* within sect. *Anthemis,* being characterised by the yellow colour of the ray florets and endemic to the W Mediterranean region. While *A. chrysantha* is restricted to the surroundings of Oran (Algeria) and Cartagena (Spain), the *A. boveana* group – formerly treated as a single species, *A. boveana* – is also found in the vicinity of Oran but is furthermore scattered throughout Morocco, especially in the N and W parts of the country. The species group varies considerably throughout its range, which has led to the description of several species, varieties and forms. Gay (in Bory & Durieu 1848-1850) described *A. boveana* from the coastal areas around Oran. Ball (1873: 365) added *A. tenuisecta* from the N foothills of the High Atlas S of Marrakech in Morocco. Battandier & Pitard (in Pitard 1918, 1931) considered plants collected in the surroundings of Fès in N Morocco to be rather similar to *A. boveana* but distinct enough to deserve the status of a new species, *A. maroccana.* Maire (1923) found it impossible to separate the Moroccan taxa from the Algerian ones on the specific level and, together with his new *A. boveana* var. *jahandiezii,* treated them as varieties of *A. boveana.* Further infraspecific taxa were added by Maire & Sennen (in Maire 1933: *A. boveana* var. *aguilarii*) to accommodate plants from the Rif mountains, and Maire (in Jahandiez & Maire 1934: *A. boveana* [var. *tenuisecta*] f. *elongata*) for deviating populations in the Fôret de la Mamora near Rabat. Anticipating the result presented here, the latter taxon was raised to specific rank by Oberprieler (1994) as *A. gharbensis.*

To assess morphological variability within and between populations of the *Anthemis boveana* group and to assist in defining taxonomic limits, numerical techniques were used. Additionally, attention was paid to qualitative morphological and anatomical features of the achene, which are known to be of considerable importance for taxon delimitation in this group.

Material and methods

33 specimens (OTUs) representative of the entire morphological and geographical range of the *Anthemis boveana* group (Table 18) were measured or scored for 26 morphological characters (Table 19, Fig. 17). The OTUs were either single herbarium specimens or sets of duplicates from the same gathering. On each specimen 3-10 measurements were made for each character, the results averaged, and the mean values used in the multivariate analysis (Table 20). Principal component analysis (PCA) was performed using the SPSS FOR WINDOWS software package. Missing values (marked by a question mark in Table 20) were replaced by the mean value of all other OTUs for the corresponding character.

Results and discussion

Principal component analysis (PCA) based on the complete data set (Table 20) yielded six components with eigenvalues higher than 1, accounting for 77.6 % of the total variance in the data set. Loadings of characters on the first three components, which explain 58.8 % of the total variance, are presented in Table 21. The first principal component (PC 1; 28.6 % of the total variance) is dominated by variables describing the dimensions of involucres (invol, oibl, mibl, iibl), ray and disc florets (rayl, rayw, discl, discm), and the shape of pale

Table 18. OTUs used in the multivariate analysis of the *Anthemis boveana* group.

No.	Location	Specimen
A. boveana		
1	Ag: Oran, au Cagneret.	9/30 May 1907, *Faure* (B)
2	Ag: Oran, Cap Canastel, 100 m.	*Maire n° 7489* (B)
3	Ag: Broussailles avoisinant le pont de la Macta.	*Balansa n° 13* (GOET; P; G)
4	Ag: Pelouses rocailleuses à Gambetta.	13 May 1909, *Faure* (G)
5	Ag: Oran.	May 1889, *s. coll.* (Herb. Girod) (G)
6	Ag: Oran, au Cagneret.	9/30 May 1907, *Faure* (G)
7	Ag: Canastel, près Oran.	13 May 1936, *Faure* (G)
8	Ag: [...] ad promontorium Canastel, 100 m.	23 Apr 1934, *Maire* (B, G)
A. maroccana subsp. *aguilarii*		
9	Ma: Atlas Rifain, Azib de Ketama, 1600 m.	20 Jun 1934, *Sennen & Mauricio n° 9406* (MPU-AfN, G)
10	Ma: Rif SW: Suberain de Rhomara, 1450 m.	11 Jul 1959, *Sauvage* (MPU-AfN)
11	Ma: Atlas Rifain, à Isaguen, 1650 m.	6 Jul 1932, *Sennen & Mauricio* (MPU-AfN)
A. maroccana subsp. *maroccana*		
12	Ma: Middle Atlas, Massif du Kandar S Sefrou.	*Vogt 10296 & Oberprieler 4744* (B)
13	Ma: Meknès, vers D'Khissa, bords des champs.	*Jahandiez 159* (G)
14	Ma: entre Kasbet el Hadjeb et Dar Caïd Ito.	*Benoist 550* (P)
15	Ma: In lapidosis calcareis prope jugum Zegotta.	21 Apr 1926, *Maire* (P)
A. gharbensis		
16	Ma: Casablanca.	May 1887, *Méllerio* (P)
17	Ma: Mamora, 5km N Sidi-Allal-Bahraoui.	*Podlech 43489* (MSB, G)
18	Ma: Mamora.	15 May 1939, *Sauvage* (MPU-Sauvage)
19	Ma: La Mamora.	23 Apr 1928, *Braun-Blanquet* (MPU-Braun-Blanquet)
20	Ma: Mamora, Sidi-Allal-el-Babraui.	*Vogt 10259 & Oberprieler 4707* (B)
21	Ma: Rharb, Arbaoua - Moulay Bousselham.	*Vogt 10161 & Oberprieler 4609* (B)
22	Ma: c. El Araix.	*Font Quer n° 666* (G)
23	Ma: circa Tingidem: Charf-el-Agab.	27 Apr 1924, *Maire* (MPU-AfN, P, G)
A. tenuisecta subsp. *jahandiezii*		
24	Ma: entre l'Oued Tensift & Souk et Tleta.	*Romieux 1348* (G)
25	Ma: Safi.	*Jahandiez 115* (B, G)
A. tenuisecta subsp. *tenuisecta*		
26	Ma: Djebileh, au N de Marrakech.	21 Apr 1921, *Wilczek* (G)
27	Ma: c. 10km N Tamri.	*Vogt 11930* (B)
28	Ma: Safi, Tamanar, loco dicto Tamri.	*Fernandez Casas & al. 9171* (B, G)
29	Ma: 6 km S Ait-ou-Mribeta.	*Podlech 42958* (MSB)
30	Ma: 15 km N Tiznit.	*Podlech 45076* (MSB)
31	Ma: c. 14.3 km N Tiznit.	*Vogt 11905 & Oberprieler 6353* (B)
32	Ma: route d'Agadir à Tiznit.	*Maire & Wilczek 551* (G)
33	Ma: à l'embouchure de l'O. Massa.	*Sauvage 3998 & al.* (MPU-Sauvage)

tips (palet), whereas PC 2 (21.1 % of total variance) is dominated by variables describing the length/width ratio of involucral bracts (oibi, mibi, iibi) and leaves (leafi), and the number of ray florets (rayno). On PC 3, which explains only 9.0 % of the total variance (and therefore strongly falls back behind the first two principal components), there are only few variables with high loadings describing length and shape of ultimate leaf segments (ulsl, ulsi) and dimensions of achenes (achel, achew).

Table 19. Characters used in the numerical analysis of the *Anthemis boveana* group (leafl and coron not used) and the *A. punctata – A. pedunculata* complex (rayw and discm omitted). See Fig. 17 for details of measurements.

Symbol	Characters (unit of measure / character states)
Leaves	
leafl	length of basal leaves (mm)
leafi	length-width ratio of basal leaves (leafl / leafw)
ulsl	length of ultimate leaf segments of basal leaves (mm)
ulsi	length-width ratio of ultimate leaf segments of basal leaves (ulsl / ulsw)
Capitula	
invol	diameter of involucrum (mm)
rayno	number of ray florets per capitulum
Involucral bracts	
oibl	length of outer involucral bracts (mm)
oibi	length-width ratio of outer involucral bracts (oibl / oibw)
oibs	shape of outer involucral bracts (1 = ovate, 2 = elliptical, 3 = obovate)
mibl	length of middle involucral bracts (mm)
mibi	length-width ratio of middle involucral bracts (mibl / mibw)
mibs	shape of middle involucral bracts (1 = ovate, 2 = elliptical, 3 = obovate)
iibl	length of inner involucral bracts (mm)
iibi	length-width ratio of inner involucral bracts (iibi / iibw)
iibs	shape of inner involucral bracts (1 = ovate, 2 = elliptical, 3 = obovate)
Pales	
palel	length of pales (mm)
palei	length-width ratio of pales (palel / palew)
pales	shape of outer pales (1 = ovate, 2 = elliptical, 3 = obovate)
palet	shape of tip of pales (1 = tricuspidate, 2 = acute, 3 = acuminate, 4 = blunt, 5 = emarginate)
Ray florets	
rayl	length of ray florets, including tubular part (mm)
rayw	width of ray florets (mm)
rayi	length-width ratio of ray floret limbs (raylb / rayw)
Disc florets	
discl	total length of disc florets (mm)
disci	ratio total length / basal part of disc florets (discl / discb)
discm	length of distal appendages of corolla lobes (mm)
Achenes of peripheral disc florets	
achel	length of achenes, excluding corona (mm)
achew	width of achenes (mm)
coron	maximal length of corona (mm)

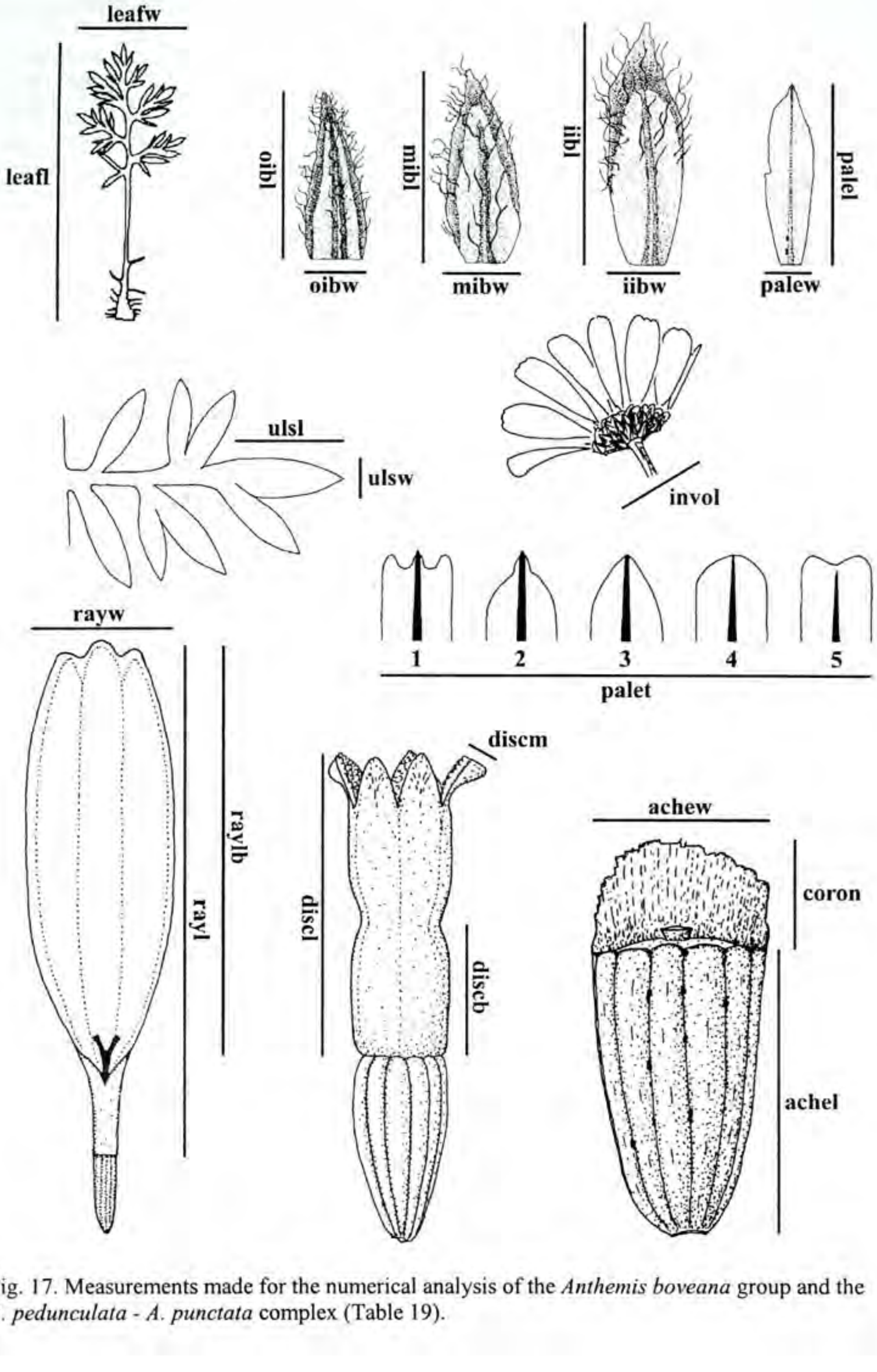

Fig. 17. Measurements made for the numerical analysis of the *Anthemis boveana* group and the *A. pedunculata* - *A. punctata* complex (Table 19).

Table 20. Data for the multivariate analysis of the *Anthemis boveana* group (character symbols are explained in Table 19 and Fig. 17).

OTU	leafl	ulsl	ulsi	invol	rayno	oibl	oibi	oibs	mibl	mibi	mibs	iibl	iibi
1	1.80	1.90	2.80	9.17	13.00	3.17	2.50	1.17	4.13	2.70	2.50	4.10	2.68
2	1.70	2.00	2.80	10.33	13.33	3.70	3.00	1.50	4.80	2.47	2.67	4.70	2.59
3	2.10	2.20	3.50	9.67	12.33	2.90	2.67	1.00	4.67	3.21	2.33	4.27	3.43
4	1.70	2.50	3.80	10.67	13.33	3.00	2.41	1.00	4.00	3.20	1.67	4.10	2.93
5	1.90	3.10	4.30	10.00	14.00	3.27	2.80	1.00	3.97	2.70	1.83	4.20	2.99
6	1.70	2.40	2.70	10.83	11.67	3.27	2.65	1.17	4.27	2.77	2.17	3.93	2.89
7	1.70	1.90	2.60	10.33	10.00	2.73	2.16	1.17	3.77	2.06	2.00	3.90	2.29
8	2.40	2.30	2.40	11.67	12.33	3.47	2.45	1.17	4.47	2.51	2.17	4.93	2.25
9	2.20	1.60	3.10	9.10	?	2.57	3.69	1.17	3.17	2.78	1.83	3.83	2.68
10	1.60	2.00	2.60	8.33	9.00	2.20	3.16	1.17	2.93	3.04	2.17	2.80	3.11
11	2.20	1.80	3.00	8.00	7.00	1.50	2.14	1.00	2.60	2.17	2.00	2.80	2.80
12	1.60	2.10	2.80	11.00	13.67	3.30	3.53	1.50	4.60	3.39	2.33	4.30	3.61
13	1.90	2.50	4.80	10.33	13.00	2.90	3.33	1.33	3.43	3.55	2.17	3.37	3.63
14	2.30	1.90	3.20	9.83	13.00	2.03	2.19	1.00	3.80	2.95	2.00	3.97	2.79
15	1.90	1.70	3.40	10.83	13.00	2.97	3.41	1.17	3.83	3.30	1.67	4.20	3.25
16	2.50	1.60	3.10	8.77	12.33	2.67	3.41	1.50	3.07	3.44	1.83	3.50	3.83
17	2.50	2.10	3.60	8.50	12.67	2.13	3.32	1.33	2.87	3.22	1.67	3.13	3.37
18	3.20	1.80	3.20	8.93	12.33	2.27	3.70	1.17	2.87	3.19	1.50	3.23	4.10
19	2.90	2.10	3.30	9.00	13.00	2.60	3.30	1.75	3.90	3.55	2.00	3.65	3.85
20	2.40	2.20	3.80	9.23	12.00	2.63	3.45	1.33	3.27	3.40	1.83	3.13	3.78
21	2.40	2.10	3.20	9.67	13.67	3.07	4.29	1.17	3.57	4.19	1.50	3.80	4.40
22	2.30	1.90	2.90	9.33	12.00	2.80	3.48	1.17	3.47	3.26	2.50	3.17	3.97
23	2.10	2.50	3.80	11.00	13.50	3.00	3.75	1.25	3.40	3.57	2.00	3.80	3.15
24	1.70	2.00	3.10	9.00	13.00	2.25	2.65	1.25	3.25	2.72	2.25	3.35	3.71
25	1.60	1.80	3.80	7.07	12.33	2.33	3.07	1.33	3.20	3.51	2.00	2.73	4.04
26	1.60	1.60	3.20	6.50	8.00	1.75	1.86	1.75	2.40	2.21	2.00	2.60	2.91
27	1.40	2.60	4.30	8.67	7.33	2.43	2.97	1.33	2.77	2.87	2.00	2.97	3.31
28	1.50	2.70	4.20	7.00	7.33	1.73	2.54	1.17	2.37	3.10	2.17	2.20	2.75
29	1.30	1.90	2.60	6.50	5.67	2.73	2.85	1.83	3.07	2.97	2.00	2.90	3.48
30	1.90	1.80	2.40	6.40	7.00	2.03	2.46	1.17	2.67	2.50	2.00	2.63	2.76
31	1.30	2.50	3.70	7.37	7.33	2.93	3.28	1.33	3.17	3.19	2.17	3.23	3.52
32	1.70	1.80	2.80	9.17	10.00	2.27	2.92	1.50	2.83	3.18	1.83	3.27	4.12
33	1.30	2.20	4.70	6.50	7.00	2.37	2.99	1.33	2.93	3.04	2.00	2.93	3.40

The resulting arrangement of OTUs in the two-dimensional factor space of PC 1 : PC 2 and PC 1 : PC 3 is shown in Fig. 18-19. It shows a good correlation of morphological variation and geographical origin. With the exception of *Anthemis boveana* var. *jahandiezii* (OTUs 24-25), variation is found to be much smaller within groups of specimens from the same area than between these groups. This supports the assumed morphological distinctness of the taxa as here circumscribed.

In terms of PC 1, major differences were found between the Algerian populations of *Anthemis boveana* (OTUs 1-8) on the one hand and the W and N Moroccan populations of *A. gharbensis* (OTUs 16-23), *A. tenuisecta* (OTUs 26-33), *A. boveana* var. *aguilarii*

Table 20 (continued).

iibs	palel	palei	pales	palet	rayl	rayw	rayi	discl	disci	discm	achel	achew	OTU
2.83	3.33	3.42	3.00	2.00	9.37	4.07	1.91	2.87	1.73	0.24	1.27	0.78	1
2.83	3.33	3.63	2.17	2.17	11.80	3.77	2.68	3.33	1.89	0.28	1.27	0.76	2
2.67	3.20	3.70	2.67	2.00	9.67	4.07	2.02	2.93	2.17	0.29	1.13	0.72	3
2.83	3.83	2.95	2.83	2.33	9.93	3.87	2.06	3.27	1.75	0.19	1.33	0.78	4
2.50	3.47	3.74	2.50	2.00	9.23	3.53	2.15	3.10	1.94	0.18	1.31	0.61	5
2.50	3.80	3.64	2.00	2.00	9.27	3.53	2.10	3.27	1.69	0.26	1.18	0.87	6
2.83	3.53	2.49	2.33	2.00	13.57	5.17	2.14	3.60	1.72	0.21	1.25	0.69	7
2.67	3.77	2.83	2.67	2.83	15.17	6.70	1.91	3.50	1.78	0.24	1.33	0.85	8
2.17	3.20	4.06	2.50	2.83	7.43	3.77	1.59	3.10	2.27	0.19	1.80	1.00	9
2.33	3.50	4.81	2.33	2.50	5.10	2.77	1.42	3.17	2.07	0.13	1.85	1.03	10
2.00	3.60	4.00	2.50	3.00	6.70	3.70	1.49	3.50	2.33	0.25	1.85	1.05	11
2.50	3.57	4.80	2.17	3.00	8.17	4.30	1.52	3.27	2.01	0.21	1.57	0.87	12
2.33	3.50	5.00	2.00	3.00	10.37	4.07	2.00	3.47	1.96	0.23	1.58	0.82	13
2.67	3.40	5.40	2.50	2.17	8.03	3.50	1.81	3.03	2.17	0.25	1.80	0.78	14
2.50	3.70	5.64	2.00	2.50	6.80	3.07	1.78	2.87	2.15	0.23	1.52	0.83	15
2.00	3.07	6.33	2.17	3.83	7.87	3.00	2.10	2.30	2.88	0.12	1.17	0.55	16
2.33	3.17	5.04	2.17	3.83	8.70	3.43	2.05	2.83	1.98	0.13	1.35	0.51	17
2.33	3.30	5.25	2.50	3.50	9.27	3.90	1.89	2.67	2.06	0.15	1.20	0.58	18
2.25	3.45	4.93	2.50	4.00	12.35	3.95	2.72	2.75	2.12	0.14	?	?	19
2.00	3.73	5.33	2.17	3.33	8.57	3.50	2.02	2.90	2.03	0.14	?	?	20
2.17	3.57	7.07	2.00	4.50	9.73	4.07	1.95	3.23	1.87	0.17	1.23	0.57	21
3.00	3.03	5.37	2.33	4.67	9.83	3.63	2.24	2.70	2.29	0.13	1.40	0.65	22
3.00	3.65	4.89	2.00	3.75	10.25	4.05	2.19	2.60	2.38	0.16	?	?	23
2.50	2.95	4.52	2.25	3.25	10.25	4.40	1.96	2.60	2.00	0.19	1.38	0.75	24
2.17	2.47	5.77	2.00	3.17	6.40	2.57	1.99	2.17	2.17	0.15	?	?	25
3.00	2.80	2.96	3.00	3.50	5.45	3.35	1.27	2.60	2.08	0.20	1.02	0.68	26
2.50	2.77	4.15	2.00	3.67	6.83	3.80	1.46	2.57	1.84	0.18	1.27	0.71	27
2.50	2.13	3.39	2.50	3.00	5.37	3.27	1.28	2.17	1.91	0.20	1.05	0.65	28
2.67	3.10	3.96	2.33	3.67	6.10	3.23	1.52	2.60	2.11	0.13	1.21	0.67	29
2.67	2.93	4.06	2.17	3.17	6.43	3.47	1.53	2.57	1.93	0.15	1.13	0.66	30
2.33	3.43	4.13	2.50	3.00	7.23	3.37	1.80	2.70	1.80	0.13	1.22	0.69	31
2.17	3.33	4.79	2.00	3.00	7.87	4.90	1.28	2.87	1.88	0.14	1.18	0.71	32
2.33	2.97	4.71	2.17	3.00	7.30	3.80	1.60	2.03	1.98	0.15	1.27	0.65	33

(OTUs 9-11), and var. *jahandiezii* (OTUs 24-25) on the other hand, specimens from C Morocco assigned to *A. maroccana* (OTUs 12-15) forming a transitional cluster between the two groups. Variable loadings on PC 1 indicate that this pattern mainly results from differences in size of involucres, ray and disc florets, and shape of tips of pales. PC 2 mainly contributes to the dismembering of the W & N Moroccan taxa, resulting in a marked polarity between the NW Moroccan *A. gharbensis* and the SW Moroccan *A. tenuisecta. A. boveana* var. *jahandiezii* forms a transitional cluster between the two taxa. *A. boveana* var. *aguilarii* falls within the range of *A. tenuisecta* on PC 1 and PC 2, but is conspicuously set off from the latter in terms of PC 3, due to differences in achene

Table 21. Variable loadings on PC 1 to PC 3 of principal component analysis (PCA) of the *Anthemis boveana* group (character symbols are explained in Table 19 and Fig. 17). Dominating loadings on each principal component are shown in bold-face type.

Character	PC 1	PC 2	PC 3
leafi	−.003	**.560**	.418
ulsl	.244	.117	**−.549**
ulsi	−.294	.146	**−.452**
invol	**.747**	.519	.157
rayno	.354	**.640**	−.176
oibl	**.649**	.494	−.184
oibi	−.331	**.749**	.180
oibs	−.365	.076	−.243
mibl	**.817**	.388	−.122
mibi	−.392	**.762**	−.033
mibs	.377	−.242	−.356
iibl	**.840**	.391	.102
iibi	−.592	**.600**	.070
iibs	.476	−.254	−.397
palel	.593	.417	.342
palei	−.555	**.661**	.315
pales	.302	−.443	−.051
palet	**−.654**	.378	.058
rayl	**.699**	.461	−.093
rayw	**.613**	.080	.088
rayi	.383	**.666**	−.266
discl	**.751**	.077	.402
disci	−.464	.228	.274
discm	**.733**	−.229	.048
achel	.290	−.498	**.573**
achew	.338	−.564	**.509**

dimensions and length and form of ultimate leaf segments.

An even clearer picture of the relations between the taxa in the *Anthemis boveana* group emerges when qualitative characters are taken into consideration. A conspicuous difference between the Algerian and Moroccan representatives of this group concerns the tip of the pales. *A. boveana* from Algeria has pales with cuspidate tips formed by the protruding midrib; plants from the Moroccan populations, even the somewhat intermediate *A. maroccana,* have pales with acute to blunt or even emarginate, translucent, yellow tinged, and somewhat hooded tips which are never formed by the midrib of the pales. Since the sister taxon of the *A. boveana* group, *A. chrysantha,* possesses pales with cuspidate tips, there is good reason to assume the yellow and hooded tips to be the derived character state and, hence, the Moroccan taxa to form a monophyletic group.

A further dismembering of that monophyletic group is achieved by using morphological and anatomical characters of the achenes. As discussed earlier (Oberprieler 1994), the NW Moroccan populations of the *Anthemis boveana* group are characterised by disc achenes that are unique not only within the species group but among all N African representatives of the genus. The 10 acute-angled ribs are smooth, devoid of tubercles, and bear characteristically formed mucilage cells which are strongly elongated and form continuous slime ribbons on the narrow ridges (Fig. 3B, 70). Smooth achenes are also found in *A. boveana* var. *jahandiezii* and in the N populations of *A. tenuisecta,* but there the mucilage cells are short, isodiametric or but slightly elongate, and the ribs are more rounded and less prominent than in the NW Moroccan populations. These were newly described as *A. gharbensis* (Oberprieler 1994).

A further distinct entity among the Moroccan populations of the *Anthemis boveana* group is *A. maroccana* (from the C Moroccan highlands around Fès, the adjacent foothills of the Middle Atlas, and the Rif mountains) plus *A. boveana* var. *aguilarii* (from higher altitudes in the Rif mountains). Both taxa tend to have very large achenes (*A. maroccana:*

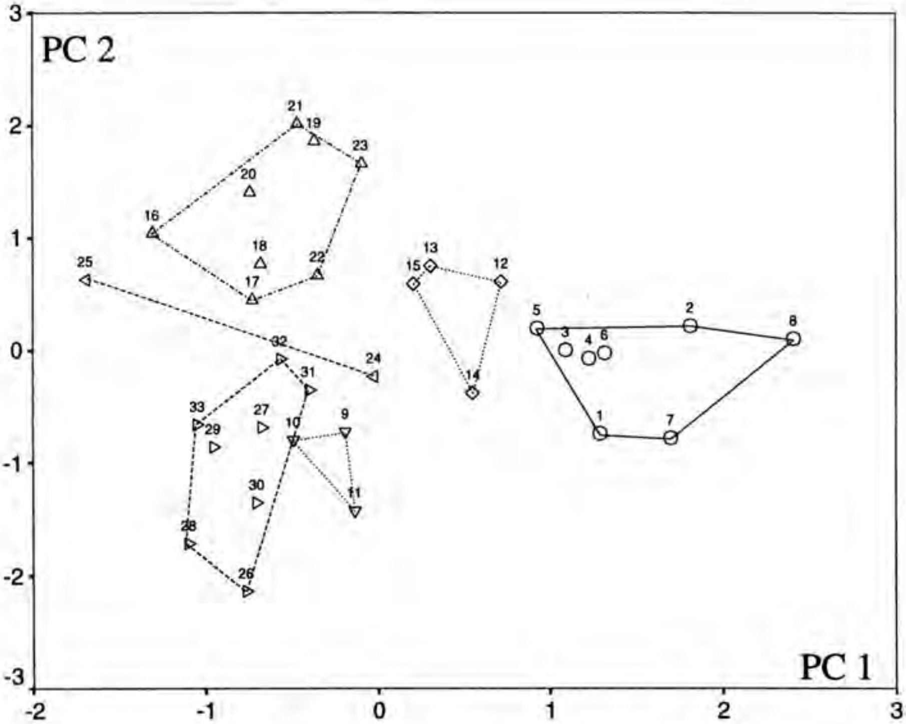

Fig. 18. *Anthemis boveana* group. Ordination of OTUs (○ = *A. boveana,* ◇ = *A. maroccana* subsp. *maroccana;* ▽ = *A. maroccana* subsp. *aguilarii;* △ = *A. gharbensis;* ▷ = *A. tenuisecta* subsp. *tenuisecta;* ◁ = *A. tenuisecta* subsp. *jahandiezii*) in two-dimensional factor space formed by principal components PC 1 (28.6 %) and PC 2 (21.1 %) of a principal component analysis of morphological data given in Table 20.

1.5-1.8 mm; *A. boveana* var. *aguilarii:* 1.8-1.9 mm), when achenes are less than 1.6 mm long in all other taxa of the species group as well as in *A. chrysantha.* The large achenes are therefore a synapomorphic character state of the two taxa which are treated as subspecies of *A. maroccana* here (subsp. *maroccana* and subsp. *aguilarii*), differing in achene size, corona length, and number of ray florets per head, and being geographically and altitudinally separated.

A third clear cut entity is *Anthemis tenuisecta* from the coastal plains around Cap Ghir and Agadir in SW Morocco, with some inland populations around Marrakech. As confirmed by PCA, this species is characterized by rather small capitula, very short ray florets with nearly circular limbs, relatively broad leaves with very low index values, and achenes usually not exceeding 1.3 mm in length. Additional qualitative characters further emphasise the distinctness of this taxon. In contrast to all other members of the *A. boveana* group and *A. chrysantha,* the disc achenes of *A. tenuisecta* usually have a very thin pericarp lacking sclerenchymatic tissue (Fig. 84). Moreover, *A. tenuisecta* has a characteristic procumbent habit, with stems which branch repeatedly and bear a relatively high number of

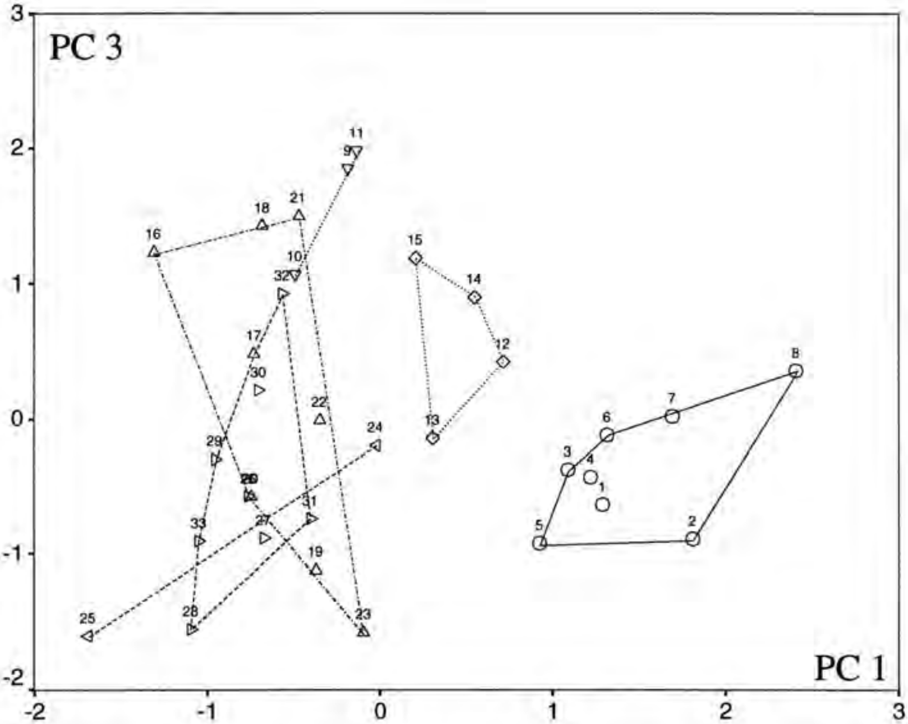

Fig. 19. *Anthemis boveana* group. Ordination of OTUs (○ = *A. boveana,* ◇ = *A. maroccana* subsp. *maroccana;* ▽ = *A. maroccana* subsp. *aguilarii;* △ = *A. gharbensis;* ▷ = *A. tenuisecta* subsp. *tenuisecta;* ◁ = *A. tenuisecta* subsp. *jahandiezii*) in two-dimensional factor space formed by principal components PC 1 (28.6 %) and PC 3 (9.0 %) of a principal component analysis of morphological data given in Table 20.

heads. The leaves are usually sessile, i.e. their bases bear entire or dissected teeth which grade into primary leaf lobes along the main axis, while the other species usually lack basal teeth and their leaves are distinctly petiolate. Plants of *A. tenuisecta* from around Cap Ghir, in the N part of the species range, have smooth achenes with very rounded and low ribs (Fig. 84, bottom), whereas in the southern populations, around Agadir and Safi, and inland around Marrakech, the sculpturing of achenes is more pronounced and even strongly tuberculate achenes are found (Fig. 84, top).

Anthemis boveana var. *jahandiezii*, which grows in a small area of the coastal plain around Safi, is geographically and morphologically transitional between *A. tenuisecta* and *A. gharbensis*. With the latter it shares the erect, sparsely branched habit and the relatively long ray florets, but it lacks the uniquely sculptured achenes of *A. gharbensis* with their extremely elongate mucilage cells. From *A. tenuisecta* it differs in habit and in the sclerenchymatic tissue of its achenes (Fig. 88), but it shares the rather sessile leaves and the small heads of the latter. Additionally, achenes with rounded and rather low ribs as in *A. boveana* var. *jahandiezii* are also found in populations of *A. tenuisecta* around Cap Ghir. It is mainly the latter feature that suggests inclusion of *A. boveana* var. *jahandiezii* in *A. tenuisecta*, as an independent subspecies.

13. Species delimitation in the *Anthemis pedunculata* – *A. punctata* complex

The *Anthemis pedunculata* - *A. punctata* complex comprises all short- to long-lived perennial representatives of the genus in N Africa except *A. maritima* and *A. cretica*, which also belong to the section *A.* sect. *Hiorthia* but hold a relatively remote taxonomic position. Members of the complex are widely distributed throughout the mountainous areas of Spain, Morocco, Algeria, and Tunisia, and show considerable variation throughout that range, which has led to the description of a multitude of taxa of specific or infraspecific rank.

The first to be described was *Anthemis punctata*, a species with very large flower heads from the mountains around Tunis, diagnosed and figured by Vahl (1791). Soon after, Desfontaines (1799) described *A. pedunculata*, with comparatively smaller heads, based on plant material presumably collected in W Algeria. Boissier (1838) added *A. tuberculata*, a small-headed plant with tuberculate achenes from the Sierra Nevada in S Spain. Mainly based on characters concerning leaf dissection (*A. tenuisecta* Pomel [non Ball]), colour of the membranous margins of involucral bracts *(A. clausonis)*, shape of involucral bracts *(A. atlantica)*, and sculpturing of achenes *(A. granulata)*, Pomel (1874-1875) named further Algerian taxa of the group at species rank. Battandier (in Battandier & Trabut 1892) recognised one more Algerian species similar to *A. punctata*, *A. kabylica*, raising in rank a variety of *A. montana* described a few years before (Battandier in Battandier & Trabut 1888-1890) from the Djurdjura mountains. In Morocco, Humbert & Maire (in Maire 1927) described *A. laeviuscula* as a segregate of *A. pedunculata*, but soon later Maire (in Jahandiez & Maire 1934) sunk it to a variety under the latter species. The last two species added to the group were the Spanish *A. turolensis* and *A. guardielae*, described by Caballero (1942a, b).

heads. The leaves are usually sessile, i.e. their bases bear entire or dissected teeth which grade into primary leaf lobes along the main axis, while the other species usually lack basal teeth and their leaves are distinctly petiolate. Plants of *A. tenuisecta* from around Cap Ghir, in the N part of the species range, have smooth achenes with very rounded and low ribs (Fig. 84, bottom), whereas in the southern populations, around Agadir and Safi, and inland around Marrakech, the sculpturing of achenes is more pronounced and even strongly tuberculate achenes are found (Fig. 84, top).

Anthemis boveana var. *jahandiezii*, which grows in a small area of the coastal plain around Safi, is geographically and morphologically transitional between *A. tenuisecta* and *A. gharbensis*. With the latter it shares the erect, sparsely branched habit and the relatively long ray florets, but it lacks the uniquely sculptured achenes of *A. gharbensis* with their extremely elongate mucilage cells. From *A. tenuisecta* it differs in habit and in the sclerenchymatic tissue of its achenes (Fig. 88), but it shares the rather sessile leaves and the small heads of the latter. Additionally, achenes with rounded and rather low ribs as in *A. boveana* var. *jahandiezii* are also found in populations of *A. tenuisecta* around Cap Ghir. It is mainly the latter feature that suggests inclusion of *A. boveana* var. *jahandiezii* in *A. tenuisecta*, as an independent subspecies.

13. Species delimitation in the *Anthemis pedunculata* – *A. punctata* complex

The *Anthemis pedunculata* - *A. punctata* complex comprises all short- to long-lived perennial representatives of the genus in N Africa except *A. maritima* and *A. cretica*, which also belong to the section *A.* sect. *Hiorthia* but hold a relatively remote taxonomic position. Members of the complex are widely distributed throughout the mountainous areas of Spain, Morocco, Algeria, and Tunisia, and show considerable variation throughout that range, which has led to the description of a multitude of taxa of specific or infraspecific rank.

The first to be described was *Anthemis punctata*, a species with very large flower heads from the mountains around Tunis, diagnosed and figured by Vahl (1791). Soon after, Desfontaines (1799) described *A. pedunculata*, with comparatively smaller heads, based on plant material presumably collected in W Algeria. Boissier (1838) added *A. tuberculata*, a small-headed plant with tuberculate achenes from the Sierra Nevada in S Spain. Mainly based on characters concerning leaf dissection (*A. tenuisecta* Pomel [non Ball]), colour of the membranous margins of involucral bracts *(A. clausonis)*, shape of involucral bracts *(A. atlantica)*, and sculpturing of achenes *(A. granulata)*, Pomel (1874-1875) named further Algerian taxa of the group at species rank. Battandier (in Battandier & Trabut 1892) recognised one more Algerian species similar to *A. punctata*, *A. kabylica*, raising in rank a variety of *A. montana* described a few years before (Battandier in Battandier & Trabut 1888-1890) from the Djurdjura mountains. In Morocco, Humbert & Maire (in Maire 1927) described *A. laeviuscula* as a segregate of *A. pedunculata*, but soon later Maire (in Jahandiez & Maire 1934) sunk it to a variety under the latter species. The last two species added to the group were the Spanish *A. turolensis* and *A. guardielae*, described by Caballero (1942a, b).

The species complex around *Anthemis pedunculata* and *A. punctata* has never been comprehensively revised. Only geographically restricted treatments in Floras are available. Battandier (in Battandier & Trabut 1888-1890) treated *A. kabylica* and *A. punctata* as varieties of the polymorphic and wide spread *A. montana,* known today as *A. cretica,* while *A. pedunculata* (including Pomel's illegitimate *A. tenuisecta*) and *A. tuberculata* (with Pomel's *A. atlantica* in synonymy) were separated at species level, the latter to differ by its strongly tuberculate achenes and its abruptly acuminate pales. *A. granulata* was recognised as a variety of *A. tuberculata,* differing from the typical variety by its achenes having a short adaxial corona. *A. clausonis,* characterised by its pale membranous margins of involucral bracts, was kept as an independent species, its resemblance to *A. pedunculata* being however stated.

The treatment of the *Anthemis pedunculata - A. punctata* group in Battandier & Trabut (1905) differs markedly from Battandier's previous account: *A. kabylica* and *A. punctata* were considered independent species, while *A. montana* was left with only one variety endemic to the Babors mountains of Algeria, formally described as *A. numidica* (Battandier & Trabut 1888-1890). *A. pedunculata* was expanded to include two varieties: one was based on the Algerian *A. clausonis;* the other, the annual var. *decumbens,* had been described in the meantime by Bonnet & Barratte (1896) from Tunisia and included *A. stiparum,* described by Pomel (1874-1875) from Algeria. *A. tuberculata,* which like *A. pedunculata* was said to comprise annual, biennial and perennial plants, was treated again as a independent species with not further subdivision.

A further deviating assessment of the species group was proposed by Battandier (1910), who treated *Anthemis kabylica* as a variety of *A. punctata* and added a new variety *(A. punctata var. baborensis). A. clausonis* and *A. granulata* (the latter in contrast to the treatment in Battandier & Trabut 1888-1890, where it is placed near *A. tuberculata*) are considered to be independent microspecies ("petites espèces") related to *A. pedunculata. A. tuberculata,* was again is kept separate, but *A. stiparum, A. sabulicola,* and *A. decumbens* were placed in its vicinity as "types secondaires".

Maire (in Jahandiez & Maire 1934) provided a taxonomic treatment of the group for Morocco, in which *Anthemis tuberculata* was treated as a second subspecies of *A. pedunculata,* both subspecies being represented by numerous varieties, e.g. *A. laeviuscula* as variety of *A. pedunculata* subsp. *pedunculata* and *A. granulata* as variety of *A. pedunculata* subsp. *tuberculata. A. punctata,* was said to have two varieties in Morocco: var. *maroccana* in the W High Atlas and var. *abylaea* in the W Rif mountains.

Mainly based on Battandier's and Maire's works, the treatment of the *Anthemis pedunculata - A. punctata* complex by Quézel & Santa (1963) contributed little to the understanding of its taxonomy: *A. kabylica* was omitted; *A. punctata* var. *punctata* and var. *baborensis* were kept separate from *A. pedunculata,* which was considered to comprise subsp. *pedunculata* (with a var. *clausonis*), subsp. *tuberculata* and subsp. *granulata.*

Pottier-Alapetite (1981) adopted Battandier & Trabut's (1905) broad concept of *Anthemis pedunculata.* While *A. punctata* was kept as an independent species, her *A. pedunculata* comprises not only the usually perennial taxa var. *clausonis* and subsp. *tuberculata* but also the annual var. *decumbens* and subsp. *glareosa* from S Tunisia.

The taxonomy of the European representatives of the *Anthemis pedunculata - A. punctata* complex is far less complicated than that of its N African members. After the description of *A. tuberculata* and its two varieties var. *microcephala* and var. *discoidea* by

Boissier (1838, 1840) and a presumably erroneous indication of *A. punctata* by Willkomm (1893), no further taxa were noted for the Iberian peninsula until Caballero (1942a, b) described two new species, *A. turolensis* and *A. guadielae*. Fernandes (1976) sank the latter into the synonymy of *A. tuberculata* and treated the former as a subspecies of the same. Later (Fernandes 1983), she confirmed this concept and further discussed the differences between *A. tuberculata* and *A. pedunculata:* she considered *A. tuberculata* to have larger achenes with marked and strongly tuberculate ribs, narrow pales which gradually taper into dark tips, hemispherical receptacles, and disc florets with only inconspicuously spongy basal parts; *A. pedunculata* to have smaller and less conspicuously tuberculate achenes, broad pales with abruptly acuminate tips, subconical receptacles, and disc florets with strongly inflated, spongy basal parts. Since she did not use the type material of *A. pedunculata* for her comparison but a specimen from E Algeria (which I consider to belong to *A. pedunculata* subsp. *atlantica*), these differences are not however appropriate to distinguish the two entities. In contrast to Fernandes (1976, 1983), Benedí i González (1987) considered *A. guadielae* to be a synonym of *A. tuberculata* subsp. *turolensis,* said to differ from subsp. *tuberculata* by broader pales with tips usually not tinged with black or brown, smaller leaves, and smaller achenes. He did not further discuss the differences between *A. tuberculata* and *A. pedunculata* or the variation within the latter species. The treatment of *A. tuberculata* in modern Spanish Floras is variable: Valdés & al. (1987) listed it as an independent species, Bolòs & Vigo (1995) gave it the status of a subspecies of *A. pedunculata*.

As mentioned above, Willkomm (1893) definitively indicated *Anthemis punctata,* which Willkomm & Lange (1865) had listed among their "species inqirendae", for Spain. However, the specimen he cited was found by Benedí i González (1987) to fall within the morphological range of *A. tuberculata*. The latter author, however, considers one specimen from Sevilla province in S Spain to belong to *A. punctata*. Plants from Sicily with rather large flower heads, similar to plants from Tunisia, were considered to represent *A. punctata* by Gussone (1843) and Fiori & Béguinot (1903), or were treated as an independent species, *A. cupaniana* (e.g. by Nyman 1878-1882, Pignatti 1982). Fernandes (1975a, 1976) placed the Sicilian taxon as a subspecies under *A. punctata,* differing from the Tunisian subsp. *punctata* by its relatively more stout, smooth and indistinctly ribbed achenes.

The different taxonomic concepts briefly summarised above, make it obvious that variation within the N African representatives of the group is still poorly understood, but that the group's centre of diversity lies there, so that any conclusion solely or predominantly based on plant material from outside Africa is at the very best a crude approximation.

The present study is based on more than 500 specimens from the N African area of the group. In addition, plant material from the Iberian peninsula and from Sicily was studied. Besides morphology, cytological aspects were duly considered, since Vogt & Oberprieler (1993) had found that polyploidy played a role in the evolution of the group, plants of *Anthemis pedunculata* s.l., at least in Morocco, showing two different ploidy levels ($2x$, $4x$). As for the *A. boveana* group, a multivariate approach was made to assess morphological variation within the *A. pedunculata* - *A. punctata* complex. Further information for the interpretation of morphological and cytological findings was drawn from the application of the molecular technique of DNA amplification from arbitrary primers (RAPD). It soon

Table 22. List of OTUs used in the numerical (PCA) and/or molecular (RAPD) analysis of the *Anthemis punctata – A. pedunculata* complex. Indication of ploidy is reported from Table 18.

No.	ploidy	Location	Specimen	Analysis
A. abylaea				
1	4*x*	Ma: Djebel Fahies.	*Vogt 12045* (B)	PCA + RAPD
2	[4*x*]	Ma: Beni-Hosmar.	29 Jun 1930, *Maire* (MPU) [Type]	PCA
A. pedunculata var. *pedunculata*				
3	[2*x*]	[N Africa]	(G) [Type]	PCA
4	[2*x*]	Hs: Sa. de los Filabres.	*Rico* (SALA 59886)	PCA + RAPD
5	[4*x*]	Hs: Sierra Nevada.	*Boissier* (G)	PCA
6	2*x*	Ma: Djebel Tizirene.	*Vogt 9628 & Oberprieler 4064* (B)	PCA + RAPD
7	2*x*	Ma: Djebel Foughal.	*Vogt 15264 & Oberprieler 9573* (B)	PCA + RAPD
8	2*x*	Ma: Foum Kheneg.	*Vogt 9440 & Oberprieler 3878* (B)	PCA + RAPD
9	2*x*	Ma: Aïn Leuh - Azrou.	*Vogt 9414 & Oberprieler 3852* (B)	PCA
10	4*x*	Ma: Djebel Tazzeka.	*Vogt 9487 & Oberprieler 3923* (B)	PCA + RAPD
11	4*x*	Ma: Djebel Tassaot.	*Vogt 9647 & Oberprieler 4083* (B)	PCA + RAPD
12	4*x*	Ma: Djebel Foughal.	*Vogt 15280 & Oberprieler 9589* (B)	PCA + RAPD
13	4*x*	Ma: Foum Kheneg.	*Vogt 9440 & Oberprieler 3878* (B)	PCA + RAPD
14	4*x*	Ma: Djebel Lekst.	*Vogt 11829 & Oberprieler 6277* (B)	PCA
15	4*x*	Ma: Tahout-ou-Fillali.	*Oberprieler 3478* (Herb. Oberprieler)	PCA
16	[?]	Ma: Djebel Tazzeka.	18 Jun 1925, *Maire* (P) [Type of *A. laeviscula*]	PCA
17	[?]	Ma: Djebel Ouensa.	22 Jun 1875, *Ibrahim* (MPU) [Type of *A. punctata* var. *maroccana*]	PCA
18	[2*x*]	Ag: Tiaret.	*Pomel* (P) [Type of *A. granulata*]	PCA
19	[2*x*]	Ag: Yakouren.	*Podlech 39294* (MSB)	PCA
20	[2*x*]	Ag: Col Telmet.	*Podlech 38937* (MSB)	PCA + RAPD
21	[2*x*]	Ag: Takerbouzt.	*Podlech 38994* (MSB)	PCA + RAPD
22	[2*x*]	Ag: Djebel Babor.	*Dubuis* (MSB)	PCA
23	[2*x*]	Ag: Miliana.	Jun 1856, *Pomel* (MPU) [Type of *A. tenuisecta*]	PCA
24	[?]	Ag: Tizi N´Kouilal.	*Podlech 39137* (MSB)	PCA
25	[?]	Ag: Bossuet	6 Jun 1927, *Faure* (MPU) [Type of *A. punctata* var. *microcephala*]	PCA
A. pedunculata var. *discoidea*				
26	2*x*	Ma: Djebel Tidirhine.	*Vogt 9576 & Oberprieler 4012* (B)	PCA + RAPD
A. pedunculata subsp. *atlantica*				
27	[?]	Ag: Khenchala.	Jun 1874, *Pomel* (P) [Type]	PCA
28	[2*x*]	Ag: Djebel Babor.	*Podlech 39380* (MSB)	PCA + RAPD
29	[?]	Ag: Djebel Tougour.	*Balansa 967* (MPU)	PCA
30	[4*x*]	Ag: Djebel Cheliah.	11 Jun 1853, *Perraudière* (P)	PCA
31	4*x*	Tn: Forêt de Kesra.	*Vogt 13510 & Oberprieler 7815* (B)	PCA + RAPD
32	2*x*	Tn: Djebel Chambi.	*Vogt 12606 & Oberprieler 6911* (B)	PCA + RAPD
A. pedunculata subsp. *turolensis*				
33	2*x*	Hs: Beteta - Mazegoza.	*Vogt 15350 & Oberprieler 9659* (B)	PCA + RAPD

Table 22 (continued).

No.	ploidy	Location	Specimen	Analysis
A. punctata subsp. *punctata*				
34	[?]	Ag: Tamesguida.	*Battandier* (P) [Type of *A. punctata* var. *baborensis*]	PCA
35	4*x*	Tn: Djebel Zaghouan.	*Vogt 13823 & Oberprieler 8128* (B)	PCA + RAPD
36	4*x*	Tn: Djebel Dyr.	*Vogt 12353 & Oberprieler 6658* (B)	PCA + RAPD
A. punctata subsp. *kabylica*				
37	[?]	Ag: Tirourda.	Jun 1882, *Battandier* (P) [Type]	PCA
38	[?]	Ag: Tala Guilef.	*Davies 53190* (RNG)	PCA
A. cupaniana				
39	-	Si: Palermo, S. Martino.	*Todaro 1102* (P) [Type]	PCA
A. ubensis				
40	2*x*	Tn: Forêt de Kesra.	*Vogt 13524 & Oberprieler 7829* (B)	PCA + RAPD
41	2*x*	Tn: Djebel Dyr.	*Vogt 12352 & Oberprieler 6657* (B)	PCA + RAPD
42	2*x*	Tn: Djebel Goraa.	*Vogt 12216 & Oberprieler 6521* (B)	PCA
43	2*x*	Tn: Table de Jugurtha.	*Vogt 12467 & Oberprieler 6772* (B)	PCA
A. confusa Pomel				
44	2*x*	Tn: Tataouine - Chenini.	*Vogt 13093 & Oberprieler 7398* (B)	RAPD
45	2*x*	Tn: Redeyef - Tamerza.	*Vogt 12747 & Oberprieler 7052* (B)	RAPD
46	2*x*	Tn: Jelma.	*Vogt 13333 & Oberprieler 7638* (B)	RAPD
A. stiparum subsp. *stiparum*				
47	2*x*	Ag: Aflou - El Bayadh.	*Podlech 34022* (MSB)	RAPD
A. stiparum subsp. *sabulicola*				
48	2*x*	Ag: El Golea - Ghardaia.	*Podlech 35456* (MSB)	RAPD
A. zaianica				
49	2*x*	Ma: Dj. Tougroulmès.	*Vogt 14840 & Oberprieler 9149* (B)	RAPD

became obvious that there are not only problems of taxon delimitation within the *A. pedunculata* - *A. punctata* complex but also with the delimitation of this complex against other morphologically and/or genetically related species and species groups. In particular, the role of the Tunisian annuals (*A. ubensis* and *A. confusa* of the present study) often treated as *A. pedunculata* var. *decumbens* was difficult to interpret and these taxa were therefore included in our morphological and/or molecular analysis, together with a Moroccan population of annuals *(A. zaianica)* found to be morphologically intermediate between *A. pedunculata* s.l. and the annuals of *A.* ser. *Bourgaeinianae*, and with another species of that series, *A. stiparum*.

Material and methods

Numerical analysis of morphological characters. – 43 specimens (OTUs) representative of the entire morphological and geographical range of the *Anthemis pedunculata* - *A. punctata* complex, plus the N Tunisian *A. ubensis*, were measured or scored for 26 morphological characters (Table 19, Fig. 17). The OTUs (Table 22) were either single herbarium specimens or sets of duplicates from the same gathering. Type material of most of the relevant names was included in this study. On each specimen 3-5 measurements were made for each character, the results averaged, and the mean values used in the multivariate analysis (Table 23). Principal component analysis (PCA) was performed using the SPSS FOR WINDOWS software package. Missing values (marked by a question mark in Table 23), were replaced by the mean value of all other OTUs for the corresponding character.

Plant material for RAPD analysis. – 26 OTUs were selected for use in the RAPD analysis (see Table 22). 20 were representatives of the *Anthemis pedunculata* - *A. punctata* complex, plus *A. ubensis*, also used in the morphological analysis. To these, specimens of *A. confusa*, *A. stiparum*, and *A. zaianica* (OTUs 44-49) were added to address the questions of the relations of these species with the *A. pedunculata* - *A. punctata* complex. Single plants of the selected specimens were used as source for DNA extraction.

DNA extraction. – DNA was extracted from dried and crushed leaf material according to a method devised by Hellwig & al. (unpubl.). 30-40 mg dry plant tissue was used. Lysis was performed in 0.8 ml 2 % CTAB-buffer at 60°C for 20 min. A first centrifugation for 10 min at 15800 g at room temperature cleaned the supernatant from cell debris. The following steps use buffers of Quiagen Inc. 1 Vol. QA-ns buffer (double concentrated Quiagen QBT buffer without NaCl) was added to the supernatant. A second centrifugation (10 min at 15800 g at room temperature) followed. The supernatant was then loaded onto a Quiagen tip 20 column equilibrated previously with buffer QBT and washed 4 times with 1 ml QC buffer. DNA was eluted with 1115 µl QF buffer and precipitated by addition of 0.7 Vol. (805 µl) isopropanol. After mixing, the precipitate was sedimented during 30 min centrifugation at 15800 g at room temperature. Pellets were washed with 0.4 ml ice cold ethanol and sedimented again by a 10 min centrifugation at 15800 g. The supernatant was discarded and the pellets were air-dried. The not too dry pellets were then resuspended in 50 µl TE buffer pH 8.0.

RAPD amplification. – Polymerase chain reactions (PCR) were performed in 50 µl of the buffer supplied by the Taq polymerase manufacturer (Appligene), 0.2 mM dATP, 0.2 mM dGTP, 0.2 mM dCTP, 0.2 mM TTP, 0.25 µM primer, 1 µl template DNA (c. 2-8 ng/µl) and 2.5 units of Taq polymerase (Applygene). Primers A01 to A12 of Primer Kit A from OperonTechnologies Inc. (U.S.A.) were used in the 12 independent PCR reactions; primer sequences are given in Table 24. Amplification was carried out in a thermocycler programmed for 1 min denaturation at 95°C, followed by 35 cycles of 1 min at 93°C, 30 sec annealing at 35°C, 1 min extension at 72°C, and a last additional 2.5 min extension at 72°C. Products of amplification were separated on 3 % TAE-agarose gels by electrophoresis, stained with ethidium bromide, and documented with a Polaroid camera. Lengths of amplification products were calculated using λ/Hind III and pBR/Alu I markers. Since a well-known problem with RAPD analyses is the difficulty to reproduce RAPD patterns exactly (Oxelman 1996), all DNA templates for one primer were run with the same master mix of reaction components in the same termocycler at the same time.

Data analysis. – Following recommendations by Koch (1995), only amplification products having lengths between 300 bp and 1500 bp were scored and used for the calculations. Shorter or longer amplification products are often of artificial nature, and their amplification is highly random. Co-migrating bands shared by at least two of the OTUs were considered informative and used to build up the present/absent data matrix given in Table 25. Question marks denote cases of faint band patterns due to failed DNA amplification. From the data matrix a distance matrix ($D_{AB} = 1 - S_{AB}$) was computed using Jaccard's association index ($S_{AB} = N_{AB} / (N_A + N_B)$; where N_{AB} = number of joint amplification bands; N_A = number of bands in OTU A; N_B = number of bands in OTU B) as the measure of similarity (Sneath & Sokal 1973: 131). For this operation the computer package SYN-TAX III (Podani 1988) was used. Dendrogram construction was performed by using the neighbor-joining method (Saitou & Nei 1987) provided in the computer package PHYLIP Version 3.5c (Felsenstein 1994). Since this method produces an unrooted tree, the tree was rooted using the midpoint-rooting option (program RETREE of PHYLIP) which places the root of the tree to the longest interior branch. For bootstrap analysis, 100 replicates of the original data set were obtained running the bootstrap option of PHYLIP (program SEQBOOT). For each replicate a distance matrix was computed with SYN-TAX III, and a dendrogram constructed as above. The resulting 100 dendrograms were summarised in a majority-rule consensus tree with PHYLIP (program CONSENSE) and midpoint-rooted (program RETREE).

Numerical analysis of morphological characters

Principal component analysis (PCA) of morphological data yielded seven components with eigenvalues higher than 1, accounting for 78.8 % of the total variance of the data set. Character loadings on the first three components of PCA are listed in Table 26. The first principal component (PC 1; 30.9 % of the total variance) is dominated by variables describing dimensions of leaves (leafl, ulsl), involucres (invol, oibl, mibl, iibl), pales (palel), ray and disc florets (rayl, discl), and the number of ray florets per capitulum (rayno). PC 2 (16.0 % of the total variance) falls back markedly behind PC 1. The only characters with high loadings are those describing the shape of inner involucral bracts (iibs), the shape of pales (palei, pales), and the shape of the tips of pales (palet). PC 3, accounting for 10.4 % of the total variance, is dominated by variables describing the shape of the outer involucral bracts (oibi, oibs) and length of achenes (achel).

As seen on plots of the first three principal components of the PCA (Fig. 20-21), PC 1, which is dominated by size features, separates fairly well *Anthemis pedunculata* and *A. ubensis* on the left from *A. punctata, A. cupaniana, A. punctata* subsp. *kabylica,* and *A. abylaea,* characterized by long basal leaves, large involucres, long pales, and long ray and disc florets, and placed further right. However, the differences are not too clear cut; the type specimen of *A. punctata* subsp. *kabylica* (OTU 37), in particular, is very close to representatives of *A. pedunculata* s.l.

The two subgroups resulting from ordination on PC 1 are further subdivided on PC 2 (Fig. 20). Within the *Anthemis punctata* group of taxa we find a clear discontinuity between *A. punctata* subsp. *punctata* (OTUs 34-36) and *A. cupaniana* (OTU 39) on the one hand, and *A. punctata* subsp. *kabylica* (OTUs 37-38) and *A. abylaea* (Otus 1-2) on the other. This is mainly due to the shape of the inner involucral bracts and pales which are found to be elliptical in outline in *A. punctata* subsp. *kabylica* and *A. abylaea* but obovate in *A. punctata* subsp. *punctata* and *A. cupaniana*. The type of *A. punctata* var. *baborensis* (OTU 34) is definitively closer to *A. punctata* subsp. *punctata* than to subsp. *kabylica*.

Table 23. Data for the multivariate analysis of the *Anthemis punctata – A. pedunculata* complex (character symbols are explained in Table 19 and Fig. 17).

OTU	leafl	leafi	ulsl	ulsi	invol	rayno	oibl	oibi	oibs	mibl	mibi	mibs	iibl
1	49.00	2.04	2.88	3.21	16.83	18.00	4.57	2.77	1.17	6.33	3.77	1.67	6.77
2	51.50	3.32	3.14	2.97	13.80	22.00	4.00	2.98	1.00	5.35	3.37	1.25	6.90
3	33.33	3.36	2.36	3.13	9.80	16.50	2.75	2.82	1.00	3.85	4.17	1.75	4.10
4	18.50	3.38	1.60	3.18	8.20	10.67	2.13	2.13	1.00	3.03	2.85	1.17	3.03
5	25.33	3.62	1.74	2.98	10.33	?	2.47	1.85	1.00	3.53	2.61	1.67	4.23
6	28.25	2.20	2.14	2.40	10.33	12.33	3.07	2.87	1.33	4.00	3.24	1.67	3.87
7	45.75	2.36	2.20	2.85	12.40	12.60	3.97	2.67	1.00	4.97	3.24	1.50	5.23
8	15.00	2.50	1.40	2.38	8.67	10.33	2.70	2.38	1.00	3.37	3.16	1.67	3.63
9	23.40	3.27	1.63	2.59	10.00	13.00	2.90	2.95	1.00	3.37	3.26	1.50	3.73
10	29.25	2.43	1.96	2.47	10.33	13.67	3.63	3.35	1.00	4.70	3.70	1.50	4.63
11	35.40	3.01	2.34	2.61	10.67	11.33	2.83	1.78	1.00	4.20	2.70	1.83	4.47
12	37.67	3.73	2.26	2.76	11.67	13.60	3.57	3.06	1.00	4.40	2.82	1.33	5.03
13	36.75	2.86	2.90	2.69	9.33	13.50	3.33	2.96	1.00	3.97	3.25	1.50	4.63
14	27.00	3.25	1.83	2.28	11.67	13.17	3.23	2.86	1.00	3.60	3.18	1.67	4.33
15	38.00	2.93	2.22	2.22	10.83	12.25	2.53	2.85	1.00	3.00	3.34	1.50	3.83
16	35.67	3.39	2.14	2.58	9.50	13.00	2.80	2.49	1.00	3.38	2.81	1.50	4.15
17	40.50	4.05	1.78	2.12	12.83	16.67	3.30	2.76	1.00	3.95	2.63	1.00	5.15
18	24.00	3.52	1.40	2.17	10.40	13.50	2.80	2.91	1.00	4.10	3.05	1.75	3.98
19	43.60	2.77	2.07	3.51	11.50	13.25	2.83	2.87	1.50	3.13	2.50	2.17	3.43
20	33.67	3.16	2.36	2.56	10.60	12.67	3.53	3.12	1.00	4.37	3.22	1.67	5.43
21	22.00	3.00	1.68	2.42	10.00	15.80	3.07	2.84	1.50	3.67	3.54	2.00	3.70
22	27.00	3.00	2.13	2.77	10.83	14.80	3.13	2.55	1.00	4.07	3.00	1.67	4.43
23	48.67	2.98	2.93	5.56	11.17	?	2.53	2.73	1.00	3.00	2.80	1.50	4.10
24	31.17	2.99	2.22	2.41	11.33	18.20	3.97	3.01	1.50	4.73	3.31	2.00	5.17
25	27.00	3.00	1.70	2.04	9.75	?	3.00	2.40	1.00	4.05	2.82	1.75	3.70
26	22.75	2.14	2.20	2.52	8.00	0.00	2.03	1.76	1.00	3.07	2.31	1.33	3.10
27	20.50	3.12	1.64	2.32	10.00	?	2.65	2.52	1.00	3.35	2.35	1.50	3.45
28	30.00	3.33	1.42	2.48	9.80	14.00	2.57	1.93	1.17	3.50	2.04	2.33	4.03
29	25.50	2.81	2.05	2.67	10.83	13.00	3.07	2.48	1.00	4.07	2.64	2.00	4.63
30	26.50	4.10	1.68	2.52	10.67	12.00	3.10	2.50	1.00	4.43	3.70	1.83	4.40
31	43.80	2.83	2.42	2.83	13.17	16.33	3.90	2.93	1.17	4.70	2.93	1.83	5.40
32	29.80	3.74	1.77	2.74	12.50	14.50	3.93	2.93	1.00	4.70	2.63	1.33	4.87
33	20.83	3.40	1.28	2.49	9.63	14.80	3.13	2.55	1.17	3.73	2.74	1.83	3.83
34	37.00	2.83	4.22	3.87	11.80	13.00	3.75	2.42	1.00	4.25	2.43	1.25	5.05
35	51.80	3.16	2.76	2.97	12.83	14.00	3.47	2.68	1.00	5.00	2.94	1.83	5.60
36	46.50	3.61	2.98	2.65	14.83	17.17	3.70	2.12	1.00	4.87	2.72	1.67	6.60
37	28.60	2.42	1.94	2.12	11.00	23.00	3.30	2.81	1.00	4.28	2.82	1.67	5.47
38	59.75	2.91	3.16	2.48	17.20	19.33	4.95	3.19	1.25	5.60	3.61	1.75	6.45
39	65.00	2.29	4.20	3.46	15.33	21.00	3.60	2.40	1.00	4.70	2.61	1.50	5.30
40	28.00	2.65	1.53	2.44	11.50	14.83	3.90	3.39	1.17	5.00	3.31	2.00	5.93
41	28.83	3.57	1.50	2.54	10.83	13.17	3.70	2.68	1.17	4.37	2.70	1.83	5.23
42	21.00	2.78	1.57	2.97	11.00	10.50	3.40	2.60	1.00	4.33	2.92	1.83	4.30
43	26.33	3.10	1.32	2.17	11.00	13.17	3.27	2.91	1.17	4.10	2.37	2.17	4.68

Table 23 (continued).

iibi	iibs	palel	palei	pales	palet	rayl	rayi	discl	disci	achel	achew	coron	OTU
4.06	2.00	4.82	5.97	2.00	2.00	17.47	2.76	3.73	2.25	2.68	1.27	005	1
4.20	2.50	5.23	7.60	2.00	2.00	15.65	2.69	3.23	2.26	2.16	1.23	0.00	2
3.92	2.25	2.76	5.06	2.00	2.00	9.70	2.86	2.60	2.36	1.60	0.70	0.15	3
2.97	2.00	2.77	5.29	2.00	2.00	9.17	2.14	2.63	2.34	1.67	1.03	0.20	4
2.96	2.17	3.28	5.22	2.00	1.85	7.15	1.54	2.60	2.60	2.19	1.15	0.30	5
3.07	2.00	3.44	6.50	2.00	2.00	7.50	2.06	2.78	2.32	1.95	0.98	0.05	6
3.83	1.83	4.06	6.70	2.00	2.00	14.53	2.54	3.07	2.31	?	?	?	7
3.48	2.33	2.86	6.65	2.00	2.00	8.00	1.67	2.25	2.40	1.83	0.98	0.23	8
3.68	1.67	2.52	7.70	2.00	2.00	9.27	2.39	2.63	2.29	1.73	0.87	0.06	9
3.78	2.00	3.78	6.88	2.00	2.00	9.60	2.05	3.00	2.37	2.42	1.16	0.15	10
3.15	2.17	3.70	6.01	2.00	2.00	10.03	1.91	3.30	2.36	1.83	0.92	0.10	11
3.44	2.00	3.68	5.05	2.00	2.00	10.73	2.04	2.88	2.76	1.93	0.97	0.08	12
3.67	2.00	3.76	6.17	2.00	2.00	13.43	2.78	2.93	2.39	1.85	0.93	0.14	13
3.64	2.00	3.58	7.90	2.00	2.00	8.88	1.88	3.05	2.90	2.22	1.08	0.24	14
4.26	1.83	3.06	5.15	2.00	1.70	9.50	2.32	2.90	2.18	1.90	0.99	0.21	15
3.81	1.75	4.22	7.56	2.00	2.00	8.30	1.64	2.93	2.61	2.23	1.10	0.23	16
4.17	2.00	3.80	7.71	2.00	2.00	16.10	2.91	2.97	2.37	2.20	1.07	0.15	17
2.37	2.50	3.15	4.79	2.25	2.00	11.90	2.06	2.83	2.90	1.80	1.00	0.30	18
2.97	2.17	3.22	5.11	2.00	1.80	11.50	2.63	3.25	2.65	1.62	0.93	0.02	19
3.47	2.67	4.22	4.97	2.00	1.90	13.80	2.20	3.22	2.49	1.73	0.93	0.00	20
3.02	2.67	3.25	6.39	2.00	2.00	11.20	2.50	3.40	2.54	1.77	0.92	0.08	21
3.05	2.83	3.46	5.12	2.50	1.50	12.83	2.76	2.90	2.46	1.57	0.92	0.00	22
3.29	2.25	3.73	6.60	2.10	2.00	10.80	3.00	2.93	2.58	2.05	0.94	0.21	23
4.04	2.00	3.90	7.71	2.00	2.00	12.13	2.68	2.93	2.75	1.53	0.83	0.16	24
2.31	3.00	2.98	4.11	2.30	1.60	8.43	2.21	2.63	2.26	1.61	0.96	0.27	25
2.38	2.00	2.76	4.92	1.80	2.00	?	?	2.83	2.52	2.18	1.00	0.28	26
2.11	2.50	3.90	4.30	2.40	1.30	12.30	2.62	3.00	2.50	1.75	0.75	0.06	27
1.87	3.00	3.34	3.45	2.70	1.00	9.60	2.32	2.63	2.24	1.79	0.80	0.00	28
2.90	3.00	4.08	4.68	2.30	1.70	10.95	2.26	2.98	2.90	2.00	1.03	0.20	29
3.27	2.67	3.28	4.55	2.50	1.50	8.55	2.40	2.83	2.23	2.08	0.94	0.11	30
2.66	2.83	4.36	3.92	2.20	1.60	13.95	2.58	3.35	2.39	1.96	0.99	0.10	31
2.61	2.50	3.63	3.37	3.00	1.13	10.76	2.05	3.17	2.19	1.98	0.85	0.38	32
2.81	2.00	2.86	5.16	2.00	1.90	9.60	2.18	2.73	2.46	?	?	?	33
2.28	2.75	4.21	5.53	2.10	1.50	14.00	2.55	3.17	3.17	1.85	0.95	0.10	34
2.62	2.67	4.92	5.15	2.00	1.40	12.27	2.77	3.35	2.95	2.20	1.08	0.73	35
2.96	2.67	4.32	4.35	2.50	1.10	13.93	2.61	3.45	2.43	2.25	0.94	0.35	36
3.87	2.00	4.88	9.56	2.00	2.00	11.40	2.91	3.23	2.55	2.15	0.95	0.30	37
4.78	2.25	4.90	8.17	2.00	2.00	19.60	2.47	3.80	2.86	?	?	0.50	38
2.65	2.00	4.70	5.11	2.38	1.13	13.05	2.13	3.27	2.55	2.03	1.02	0.47	39
3.62	2.33	4.20	3.95	2.10	1.20	8.77	2.26	2.95	2.41	1.55	0.76	0.02	40
2.91	2.17	4.22	3.29	2.70	1.10	10.20	2.17	3.15	2.49	1.39	0.77	0.04	41
2.69	2.33	4.03	3.09	2.75	1.13	8.80	1.82	3.03	2.12	1.90	0.90	0.82	42
2.25	3.00	3.38	3.21	2.90	1.00	7.80	2.10	2.75	2.48	?	?	?	43

On the left side of the plot (Fig. 20), taxa belonging to *Anthemis pedunculata* s.l. are also scattered along PC 2 and form a transitional series, ranging from plants with extremely low scores (indicating narrow inner involucral bracts and narrow pales that gradually taper to the tip) to those with very high scores (indicating broad inner involucral bracts and broad pales with tricuspidate or abruptly acuminate tips). This morphological variation shows a clear correlation with geographical origin: Plants from the W part of the distributional area of the group (Spain and Morocco) are placed at the negative end of PC 2, while the positive end is formed by populations of *A. ubensis* (OTUs 40-43) from Tunisia and populations from E Algeria ascribed to *A. pedunculata* subsp. *atlantica* (OTUs 27-32), the extremes being connected by a cluster of specimens from W and C Algeria (OTUs 18-25) that hold a intermediate position and include the types of *A. granulata* (OTU 18) and *A. punctata* var. *microcephala* (OTU 25). The types of *A. tenuisecta* Pomel, nom. illeg. (OTU 23), and *A. pedunculata* (OTU 3) are nested within the Moroccan and Spanish representatives, along with *A. tuberculata* var. *discoidea* (OTU 26), *A. turolensis* (OTU 33), *A. laeviuscula* (OTU 16), and *A. punctata* var. *maroccana* (OTU 17).

PC 3 (Fig. 21) contributes little to a further understanding of taxon relations within the *Anthemis punctata* and the *A. pedunculata* groups. The geographical cline within *A. pedunculata,* as revealed by PC 2, is lost in PC 3.

For the Moroccan representatives of *Anthemis pedunculata* s.l. there seems to exist a week correlation between morphology and chromosome number: diploid representatives (OTUs 6, 8, 9) are mainly found to have rather low scores on PC 1, the tetraploids (OTUs 10-15) tend to have higher scores on that axis, mainly due to size differences between the two cytotypes. However, the position of OTU 7, a diploid specimen from NE Morocco, shows that exceptions to this pattern occur.

Table 24. Base sequences of primers used in the RAPD analysis of the *Anthemis pedunculata – A. punctata* complex.

Primer	Base sequence	Primer	Base sequence
A-01	5´-CAGGCCCTTC-3´	A-07	5´-GAAACGGGTG-3´
A-02	5´-TGCCGAGCTG-3´	A-08	5´-GTGACGTAGG-3´
A-03	5´-AGTCAGCCAC-3´	A-09	5´-GGGTAACGCC-3´
A-04	5´-AATCGGGCTG-3´	A-10	5´-GTGATCGCAG-3´
A-05	5´-AGGGGTCTTG-3´	A-11	5´-CAATCGCCGT-3´
A-06	5´-GGTCCCTGAC-3´	A-12	5´-TCGGCGATAG-3´

RAPD analysis

Polymerase chain reactions (PCR) using 26 OTUs and 12 different primers resulted in 106 informative amplification bands which are listed in Table 25. The number of informative bands per primer ranged from 1 (primer A-06) to 18 (primer A-11). The dendrogram constructed using the Jaccard index as a distance measure and the neighbor-joining method for the agglomeration of OTUs resulted in the dendrogram shown in Fig. 22. A majority-rule consensus tree based on 100 replicates is presented in Fig. 23. Bootstrap values appear to be rather low throughout the consensus tree, indicating that the data set contains a considerable amount of random noise. The same conclusion is valid for the

Table 25: Distribution of variable amplification bands found in the RAPD analysis of representatives of the *Anthemis pedunculata – A. punctata* complex.

Primer	fragment length (bp)	OTU
		30014201010144443333444222
		34109661728345601026187018
A-01	1425	01000000110010011110000100
	1360	00000000000001110100000100
	1149	01000000000001000001000000
	1101	00000000100000000010000000
	1055	01010001000000000000000000
	1012	00001000000000000000100001
	895	00001000000000000000100000
	844	00000000110000000000000000
	750	11110111111100001111011111
	669	00000000000000000001000001
	644	00000000000000000001100000
	632	00000000000000001010000000
	482	10111000000000010111100111
	435	00100010000100011011000000
A-02	1187	0010000111111001111110?101
	1005	01001110111100000000000000
	985	00100000101100000111100010
	779	00100001010000000111110011
	765	00100001010000000111110011
	751	00100001010010001111110011
	737	00100001010000000111111111
	601	00100000000011111101111000
	579	00001000000001000000010000
	558	00000000010000000000100000
	533	00000000000001000000010000
	509	10100101011110011011110111
	482	11110111111111111111110111
	432	00000100000000000000000001
	355	00100001011100011111110011
	338	00100001111100011111111111
A-03	645	01001000000100000000011001
	565	00010000000001100000001000
	451	1111011111?11100100011011
	428	0111011110 1?10000100111111
A-04	1144	1111010111111101111110?111
	1073	1111010111111101111110?111
	1040	00001000000000100000010000
	761	00000000010100001000100?111
	592	000000000000010000100010000
	470	0010000100000000010000000100
	443	11111111111110000000000000
	426	11111111111110000000000101
	410	11100000010000000000010000
A-05	1127	00000000000000000000010001
	1093	000000000100000000100000000
	1038	0000000101000000100000 1??11
	997	00110000000000000000000000
	667	1000000110100000011111 11?111
	631	1001001001000001?11111?111
	517	000000000000000010000001111
A-06	1034	00001000000000011111000000
A-07	881	000000000000010011111100111
	826	00000000000000000011100000
	696	00000000000000011010000000
	671	00000000000100011110000000
A-08	954	1111111111110??111010??011
	908	000010000000 1??000000??000
	814	0000000000001??101110??000
	713	000000010000 0??000000??001
	642	1111101111110??000001??110
	619	0100000011000??001000??101
	577	0000100100000??001000??011
	467	1000001100000??001000??010
	405	0010000000000??000001??000
A-09	854	0101010111110 0?01001101010
	635	0000001100000 1?00100000001
	614	1111110111010 0?11111100111
	545	1111010011111 0?11110010100
	509	0100010000000 0?00000000000
	436	1010111100010 1?01111011000
A-10	1056	01000100000001000000000000
	1021	00000000100000000000000100
	957	10111011001100000100000000
	870	00000100000001000110000001
	826	11000001000000011000000000
	784	11000001000000011000001111
	668	11111111111111011111111111
	612	11110101010110011111011111
	499	000000000000010000010001000
	485	00110100000000000000000111
A-11	1117	00100000111100010000000000
	1096	00000000010000000100000110
	1034	00100000010000000000000000
	1015	01000000000100010000000000
	959	10001000000000000000000011
	860	00000001000000000000011011
	747	00010010010000010100000000
	698	00001000000001000011010001
	686	11100101010100100000000100
	652	00010110101000011011100010
	620	00000100100000000010001100
	590	00000010100000000100000100
	585	00000000000000000000000011
	562	01000111000000000011010000
	544	00001000100000000000100000
	501	00000010000110000100010000
	379	00000000001111000001010000
	316	00000000000000010001111000
A-12	1218	00000000000000001010000000
	1067	10010000000000000000000000
	655	00000000010000000000000011
	612	00000000000010010010100000
	572	00011000000010000000000111
	561	10100101100000001111100111
	427	00100100000000000000000000
	321	00111011010100001100000000

Table 26. Variable loadings on PC 1 to PC 3 of principal component analysis (PCA) of the *Anthemis punctata* – *Anthemis pedunculata* complex (character symbols are explained in Table 19 and Fig. 17). Dominating loadings on each principal component are shown in bold-face type.

Variable	PC 1	PC 2	PC 3
leafl	**.815**	.090	−.234
leafi	−.214	.172	.028
ulsl	**.689**	.005	−.408
ulsi	.201	−.003	−.403
invol	**.886**	.276	−.068
rayno	**.667**	.129	.265
oibl	**.831**	.264	.277
oibi	.427	−.118	**.612**
oibs	.085	.081	**.609**
mibl	**.802**	.301	.157
mibi	.367	−.430	.501
mibs	−.181	.469	.483
iibl	**.876**	.264	.058
iibi	.539	−.626	.331
iibs	−.105	**.726**	.024
palel	**.835**	.267	−.127
palei	.406	**−.755**	.069
pales	−.207	**.841**	−.011
palet	.122	**−.910**	.076
rayl	**.807**	.047	−.045
rayi	.452	.006	.173
discl	**.804**	.234	−.022
disci	.190	−.013	−.185
achel	.433	−.229	**−.533**
achew	.385	−.374	−.476
coron	.125	.192	−.430

dendrogram in Fig. 22, where most of the interior branches connecting nodes are considerably shorter than the branches between nodes and OTUs, indicating that a high amount of parallelism exists in the data set and that only few amplification bands are significant for the tree topology. However, there is a good correlation of groupings in dendrogram and consensus tree, and only few discrepancies are found, which indicate that the essential structures of the dendrogram are trustworthy despite the low bootstrap values.

The arrangement of OTUs according to their genetic similarity as assessed by RAPD analysis shows some interesting groupings. Four major clusters were found to exist in both the original dendrogram and the consensus tree of the bootstrap analysis. The first group is formed by the annuals of *Anthemis confusa* (OTUs 44-46), *A. stiparum* subsp. *stiparum*

(OTU 47) and subsp. *sabulicola* (OTU 48). This cluster is conspicuously set apart from the rest of the OTUs, which cluster with the comparatively high bootstrap value of 61 %. A second cluster is formed by Tunisian representatives: the annual, diploid *A. ubensis* (OTUs 40, 41), the perennial, tetraploid *A. punctata* (OTUs 35, 36), and a diploid (OTU 32) and tetraploid (OTU 31) of *A. pedunculata* subsp. *atlantica*. The arrangement of OTUs within this cluster differs markedly between the dendrogram and the consensus tree, so that groupings within this cluster are very unstable. Only the position of OTU 32 as an outlayer of this cluster proves to be fairly reproducible.

A third cluster comprises the diploid and tetraploid Moroccan and Spanish representatives of *Anthemis pedunculata* s.l (OTUs 4-13) and, nested among them, *A. abylaea* (OTU 1) and *A. zaianica* (OTU 49). The internal structure of the cluster is faithfully maintained in the consensus tree. A first subcluster is formed by the tetraploid *A. abylaea* (OTU 1) and two tetraploid Moroccan representatives of *A. pedunculata* (OTUs 11-12), while the other tetraploids are nested within the cluster comprising Moroccan diploids (OTUs 6-8), along with representatives of *A. turolensis* (OTU 33) and *A. tuberculata* (OTU 4) from Spain, and *A. tuberculata* var. *discoidea* (OTU 26) and *A. zaianica* (OTU 49).

The fourth cluster is formed by three Algerian representatives of *Anthemis pedunculata* s.l. (OTUs 20, 21, 28). It is linked with the Tunisian cluster in Fig. 22, but in the consensus tree (Fig. 23) it is associated with the cluster of Moroccan OTUs. In view of the very low bootstrap value for the latter grouping (17 %), the position of this cluster is uncertain.

Discussion

The morphological analysis shows a main discontinuity within the data set that is caused by correlated characters describing sizes of leaves, involucres, ray and disc florets. That combination of characters permits to discriminate between *Anthemis punctata* s.l. on the one hand and *A. pedunculata* s.l. on the other hand. The *A. punctata* group, thus defined, comprises taxa that were all treated at infraspecific level within that species in the past: *A. punctata* var. *abylaea* (OTUs 1-2), *A. punctata* var. *kabylica* (OTUs 37-38), *A. punctata* var. *baborensis* (OTU 34), and *A. punctata* subsp. *cupaniana* (OTU 39).

Two taxa assigned to *Anthemis punctata* in the past, however, are found nested within *A. pedunculata* s.l., the first of these is *A. punctata* var. *microcephala,* for which Faure & Maire (in Maire 1931b) stated that it has the habit of *A. tuberculata,* differing in its adaxially coronated achenes, a character which they considered typical of *A. puncata.* Maire (1933) later included *A. punctata* var. *microcephala* in the synonymy of *A. granulata,* which he treated as a variety of *A. pedunculata* subsp. *tuberculata* in Jahandiez & Maire (1934). The inclusion of *A. punctata* var. *microcephala* in *A. pedunculata* s.l. is backed by the morphological analysis presented here, its type (OTU 25) being very similar to that of *A. granulata* (OTU 18). Both types, collected in W Algeria, belong to the group of OTUs intermediate between the Moroccan/Spanish representatives of *A. pedunculata* s.l. and the E Algerian ones.

Anthemis punctata var. *maroccana* (OTU 17) is the other taxon once assigned to *A. punctata* but showing a closer overall similarity with representatives of *A. pedunculata* s.l. in the PCA. It was said by Maire (1931a) to differ from the typical variety of *A. punctata* by its smooth achenes lacking a corona, from *A. punctata* var. *baborensis* by its pubescent leaves and conspicuously mucronate ultimate leaf segments, and from

A. tuberculata by its twice as large capitula. However, Maire (1931b) adds: "Habitus *A. tuberculatae* Boiss." Indeed, specimens from the W High Atlas mountains ascribable to *A. punctata* var. *maroccana* tend to combine characters typical for *A. pedunculata* s.l. (e.g. small leaves, ecoronate achenes) with large flower heads typical of *A. punctata* s.l. However, capitulum size still falls within the variation range of *A. pedunculata* s.l., its tetraploid but also some diploid (OTU 7!) representatives in Morocco. Therefore, *A. punctata* var. *maroccana* is better considered a member of *A. pedunculata* s.l. whose rather large capitula were acquired independently from those of the E Algerian and N Tunisian *A. punctata*. Pending further cytological and genetic studies of these populations in the W High Atlas mountains, they are here treated as belonging to the tetraploid representatives of *A. pedunculata*.

The N Moroccan populations described as *A. punctata* var. *abylaea*, however, appear to be well separated from *A. pedunculata* s.l. in our morphological analysis. The two studied

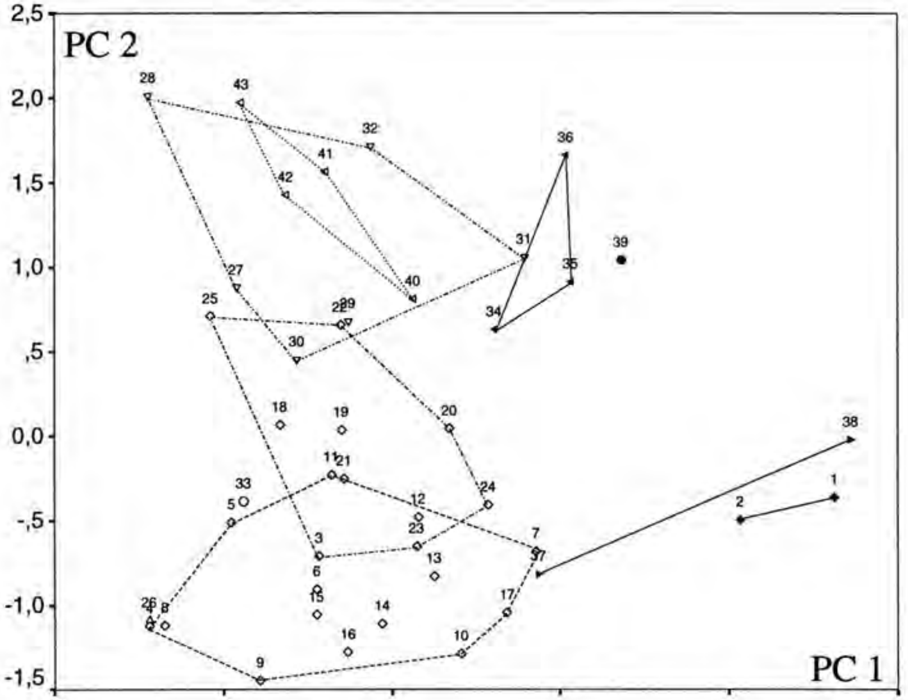

Fig. 20. *Anthemis pedunculata* complex. Ordination of OTUs (◇ = *A. pedunculata* var. *pedunculata;* Δ = var. *discoidea;* ∇ = subsp. atlantica*;* ○ = subsp. *turolensis;* ◀ = *A. punctata* subsp. *punctata;* ▶ = subsp. *kabylica;* ● = *A. cupaniana;* ◆ = *A. abylaea;* ◁ = *A. ubensis)* in two-dimensional factor space formed by principal components PC 1 (30.9 %) and PC 2 (16.0 %) of a principal component analysis (PCA) of morphological data given in Table 23. The Moroccan and Spanish representatives of *A. pedunculata* var. *pedunculata* (OTUs 4-17) are marked with a broken line, the Algerian ones (OTUs 3, 18-25) with a semi-dotted line.

representatives of this taxon (OTUs 1-2) are quite similar to representatives of *A. punctata* var. *kabylica* (OTUs 36-37) from the Djurdjura mountains in C Algeria. That resemblance even induced Font Quer & Pau to identify a collection of Font Quer from the W Rif mountains (Iter Maroccanum 1930: n° 665) as *A. cupaniana* var. *kabylica*. However, there are some differences between the two taxa. Whereas in *A. punctata* var. *kabylica* the involucral bracts are completely glabrous and the disc achenes usually have an adaxial corona, the involucral bracts are conspicuously hairy in *A. punctata* var. *abylaea*, where achenes lack a corona. The results of the RAPD analysis point in a different direction. OTU 1, representing *A. abylaea* in the molecular analysis, is found in a cluster with two tetraploid representatives of *A. pedunculata* s.l., one from a nearby population in the W Rif mountains (OTU 11), the other from the NE Moroccan Beni Snassen mountains (OTU 12). Other tetraploid Moroccan representatives of *A. pedunculata* s.l. (OTUs 10, 13), however, are nested among the Moroccan and Spanish diploids (OTUs 4, 6, 7, 8, 26, 33).

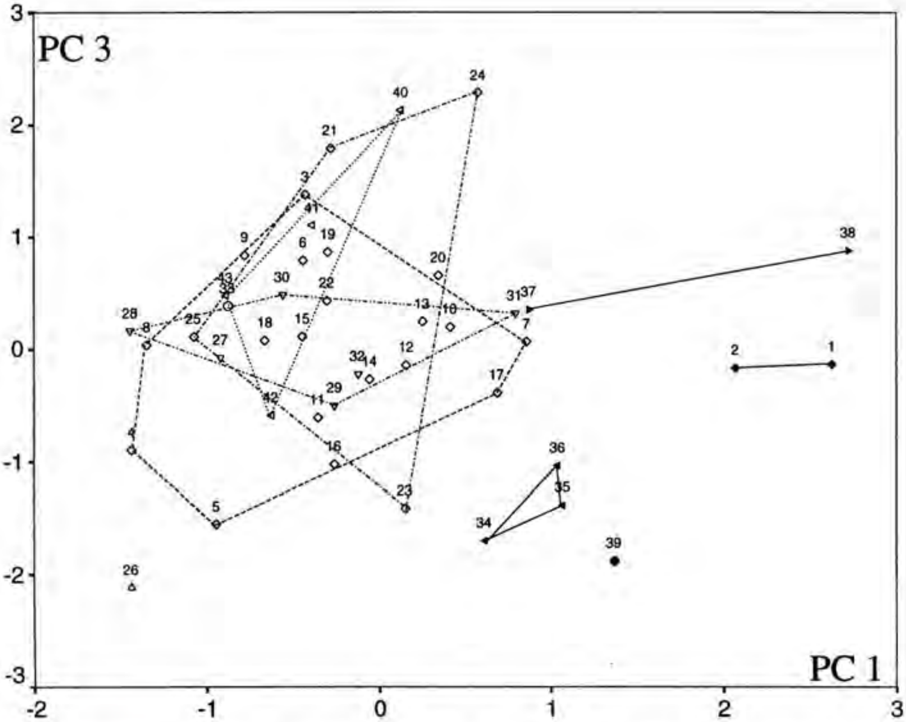

Fig. 21. *Anthemis pedunculata* complex. Ordination of OTUs (◇ = *A. pedunculata* var. *pedunculata;* Δ = var. *discoidea;* ∇ = subsp. atlantica*;* O = subsp. *turolensis;* ◀ = *A. punctata* subsp. *punctata;* ▶ = subsp. *kabylica;* ● = *A. cupaniana;* ◆ = *A. abylaea;* ◁ = *A. ubensis)* in two-dimensional factor space formed by principal components PC 1 (30.9 %) and PC 3 (10.4 %) of a principal component analysis (PCA) of morphological data given in Table 23. The Moroccan and Spanish representatives of *A. pedunculata* var. *pedunculata* (OTUs 4-17) are marked with a broken line, the Algerian ones (OTUs 3, 18-25) with a semi-dotted line.

The two tetraploid groups differ markedly in the number of amplification bands found in the RAPD analysis: OTUs 10 and 13 have 27 and 29 informative bands, respectively, which falls within the range found in the diploids (OTU 4: 28, OTU 6: 23, OTU 7: 29, OTU 8: 27, OTU 26: 28, OTU 33: 27); the tetraploids clustering with *A. abylaea* have higher numbers of informative bands (OTU 1: 39, OTU 11: 39, OTU 12: 38), which may indicate their likely allotetraploid origin – the other tetraploids then being considered autotetraploids. However, most of the bands found in the presumed allotetraploids also occur in the local diploids, and since in the present study no assumption of variation of amplification bands within and between plant populations was made, this "allopolyploidisation" may also result from the combination of two different local genotypes of the same species (when the plants would still be autotetraploids) rather than from the combination of two substantially different genomes of two independent species (as in true allotetraploids). The occurrence of four amplification bands (primer A-02: 779 bp, 765 bp, 751 bp, 737 bp) that are shared by the three presumed allotetraploids, Algerian representatives of *A. pedunculata* s.l., and Tunisian diploids *(A. ubensis)* and tetraploids *(A. punctata)* supports the allotetraploid hypothesis, but further evidence is required.

Only diploid chromosome numbers were so far reported for Moroccan representatives of *Anthemis pedunculata* s.l. (Galland 1985, 1991), but tetraploids proved to be common throughout Morocco (Vogt & Oberprieler 1993 and present study), from the Rif mountains in the N to the Anti-Atlas mountains in the S. They mostly grow in the same area as diploids, often in mixed stands. Since morphological and genetic differences between diploids and tetraploids were found to be small, it is reasonable to assume the tetraploids to be autotetraploids derived directly from the local diploids. Treating diploids and autotetraploids as a different species on the grounds of reproductive isolation is undesirable as long as no new morphological characters evolve within and spread through some or all tetraploid populations. As no such characters were found, diploids and tetraploids are treated as cytotypes of a single species, *A. abylaea* being the single exception to that rule: plants of this tetraploid segregate differ morphologically from all other diploid and tetraploid representatives of *A. pedunculata* s.l. and are therefore treated as members of an independent species.

The patterns observed in Moroccan populations of the *Anthemis pedunculata* - *A. punctata* complex are paralleled to some extent in E Algerian and N Tunisian populations, where the occurrence of diploid annuals (OTUs 40-43) that fall within the morphological range of perennial *A. pedunculata* s.l. (OTUs 27-32) adds to the complexity. Due to their annual habit, these plants were often considered to be closely related to annuals from S Tunisia, and united with them in *A. pedunculata* var. *decumbens*. However, RAPD analysis shows that the N Tunisian annuals are more closely related to the N Tunisian perennials of *A. pedunculata* s.l. and *A. punctata*, while the S Tunisian annuals, treated in the present study as *A. confusa* (OTUs 44-46), are clustered with *A. stiparum* subsp. *stiparum* (OTU 47) and subsp. *sabulicola* (OTU 48) of *A.* sect. *Anthemis*. Morphological evidence shows that the N Tunisian annuals hold an intermediate position between *A. pedunculata* s.l. and *A. secundiramea*, an annual species growing along the E Algerian and N and E Tunisian coasts of the Mediterranean Sea. The N Tunisian annuals share with *A. pedunculata* s.l. the erect habit, dark tipped pales (found at least in some populations), and the occurrence in mountainous inland habitats, while characters typical for *A. secundiramea* are the annual habit, the much-branched capitulescence (stems in

A. pedunculata s.l. usually bear up to three capitula), the peduncles which become inflated at maturity (they remain slender in *A. pedunculata* s.l.), the conical receptacles (hemispherical in *A. pedunculata* s.l.), and the comparatively small achenes with a relatively long corona (*A. pedunculata* s.l. usually has longer achenes with very short coronas). A majority of these characters thus favour a relationship with *A. secundiramea.* The occurrence of a segregate inland taxon of the coastal *A. secundiramea* has a parallel in the case of *A. muricata,* a discoid relative of *A. secundiramea* that occurs only inland in C Sicily. The intermediate annuals of N Tunisia (OTUs 40-43) are thus better placed in the

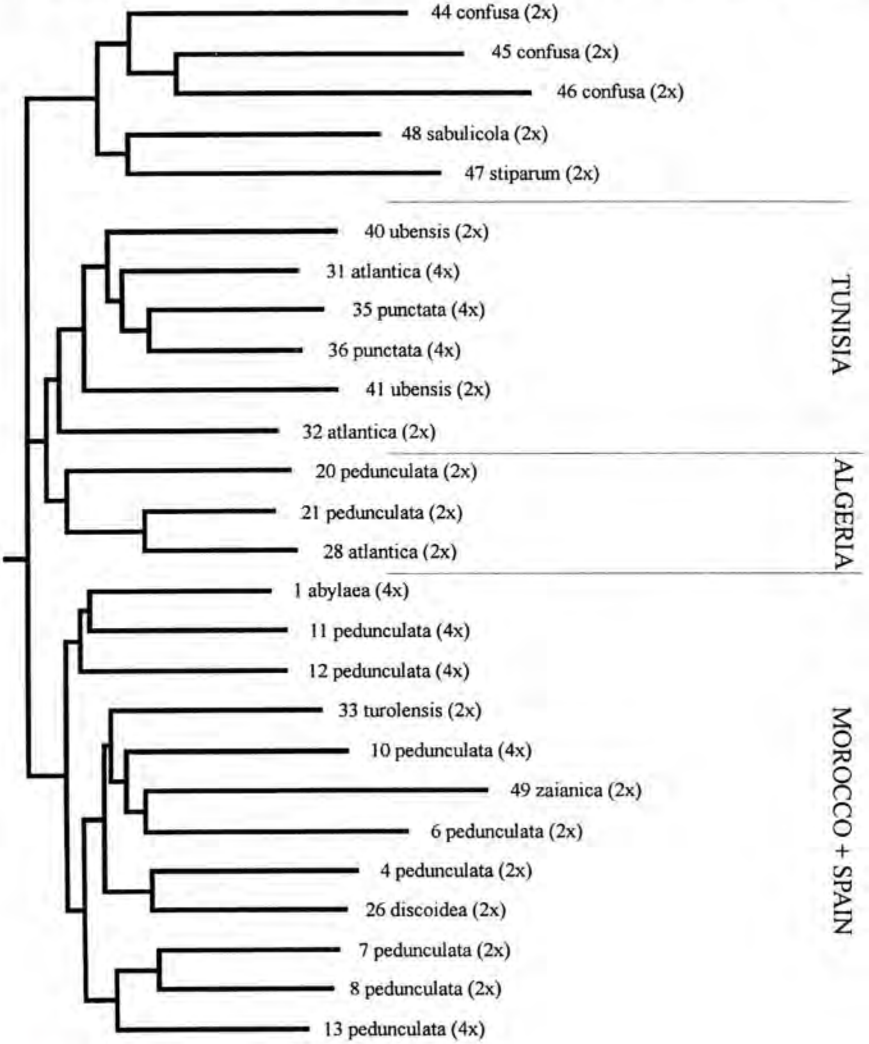

Fig. 22. *Anthemis pedunculata - A. punctata* complex: neighbour-joining distance analysis of Jaccard distances from RAPD patterns given in Table 25.

vicinity of *A. secundiramea* than near *A. pedunculata* s.l., even though the RAPD analysis, where they cluster with representatives of *A. pedunculata* s.l. and *A. punctata* from N Tunisia, suggests intermediacy between *A.* sect. *Anthemis* and sect. *Hiorthia*. The occurrence of aneuploid chromosome numbers in two populations, indicating genomic imbalance, may also point to a possible hybrid origin. Inclusion of the N Tunisian annuals in *A. secundiramea* or *A. pedunculata* would harm the taxonomic integrity of either, and

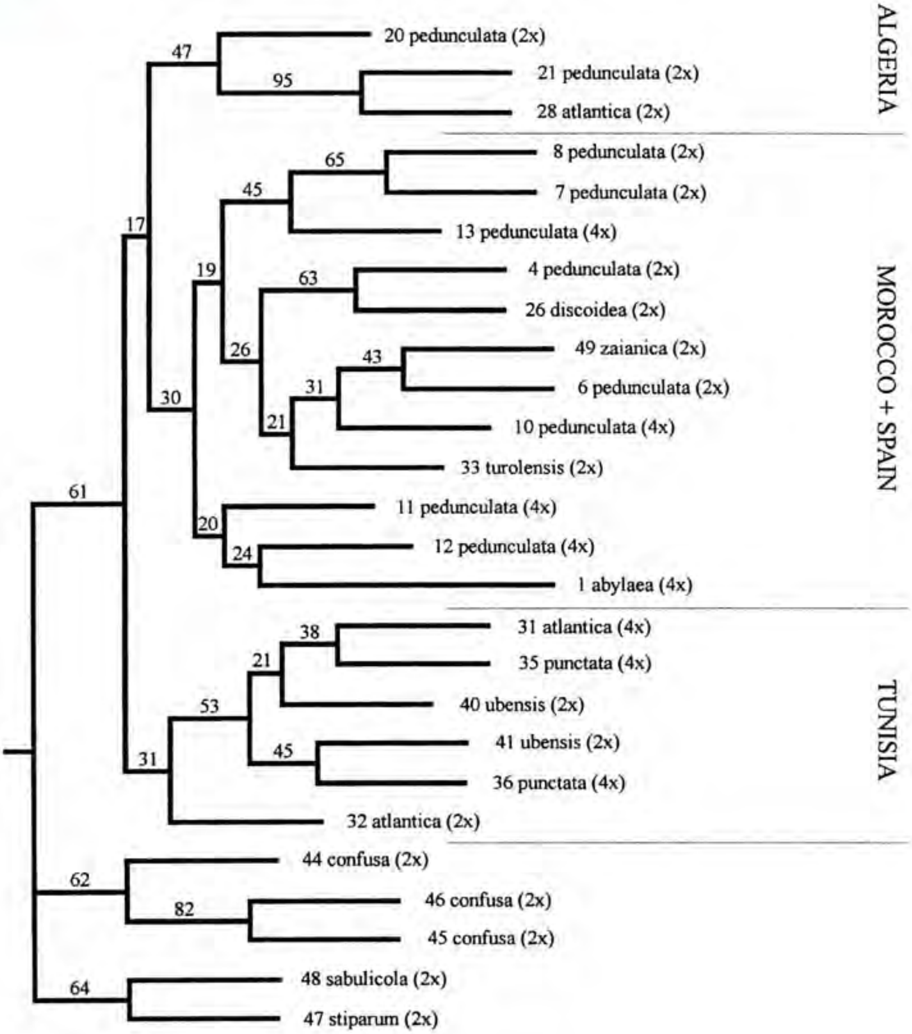

Fig. 23. *Anthemis pedunculata* - *A. punctata* complex: majority-rule consensus dendrogram summarising 100 dendrograms from a bootstrap analysis of RAPD patterns given in Table 25. – Single dendrograms were constructed by neighbour-joining distance analyses of Jaccard distances. Bootstrap values denote the number of trees with a particular grouping of OTUs.

recognition of a separate species, *A. ubensis* (described from E Algeria), is therefore proposed. However, additional field and experimental work is needed to fully understand the complex relationships of that species.

In parallel to the case of *Anthemis abylaea* in Morocco, some of the Tunisian tetraploids (OTUs 34-36) are morphologically distinct enough (see Fig. 21) to warrant their recognition as an independent species, *A. punctata*. Same as *A. abylaea, A. punctata* shows a marked tendency to large flower heads and long basal leafs. It shows a striking overall similarity with a tetraploid from Sicily, described as *A. cupaniana* (OTU 39), that is often treated as a subspecies of *A. punctata*. In the multivarite analysis of morphological characters these two tetraploids are indeed very similar, but there are considerable differences in the shape of the membranous margin of involucral bracts, which in *A. punctata* is broad and bicoloured (darker brown inwardly), but in *A. cupaniana* is narrow and uniformly light to dark brown.

After the segregation of the E Algerian and N Tunisian annuals *(Anthemis ubensis)* and the large-headed *A. punctata,* what remains of *A. pedunculata* s.l. is rather homogenous, consisting of small-headed perennials with a continuous range from Morocco and Spain to N Tunisia. Within this range clinal variation exists in the shape of inner involucral bracts and pales, as shown by PC 2 of the PCA (Fig. 20) and already discussed. The two extremes are connected by a series of intermediate plants throughout W and C Algeria, but may nonetheless deserve recognition as subspecies. The type of *A. pedunculata* (OTU 3) falls within the western group; the deviating populations in E Algeria and N Tunisia are named *A. pedunculata* subsp. *atlantica,* based on *A. atlantica* (OTU 27), described from the Aurès mountains near the Algerian-Tunisian border. Quantitatively, as seen in the PCA plot (Fig. 20), *A. pedunculata* subsp. *atlantica* is very similar to *A. ubensis,* which however differs in its annual growth, much-branched capitulescence, peduncles somewhat inflated at maturity, conical receptacles, and smaller achenes with usually longer coronas.

Anthemis pedunculata subsp. *pedunculata*, comprising diploids and tetraploids and found growing throughout S Spain, Morocco, E and C Algeria, shows little quantitative variation that might call for taxonomic recognition. The sculpturing of achenes has been used to delimit *A. granulata* (with extremely tuberculate achenes) and *A. laeviuscula* (with quite smooth achenes), and also in some floras (e.g. Quézel & Santa 1963) to separate *A. pedunculata* subsp. *pedunculata* and subsp. *tuberculata,* but appears to be quite variable even within populations, and highly dependent on the degree of maturity (the type specimen of *A. laeviuscula* has unripe achenes, plants with ripe achenes collected later at the locus classicus have normally tuberculate achene surfaces), providing scant support to a further subdivision of *A. pedunculata* subsp. *pedunculata.* Only discoid plants, found within the range of *A. pedunculata* subsp. *pedunculata* in S Spain and in the Rif and High Atlas mountains, may deserve formal recognition, as a variety (var. *discoidea*), although they are not geographically separated and may have originated in parallel in the different regions.

Anthemis turolensis (OTU 33), both in morphological and RAPD analysis, is well nested among the OTUs representing *A. pedunculata* subsp. *pedunculata*. According to Benedí i González & Molero i Briones (1985) and Benedí i González (1987), who studied Spanish populations of *"A. tuberculata* subsp. *tuberculata"* (= *A. pedunculata* subsp. *pedunculata)* and subsp. *turolensis*, the two taxa differ in achene length, shape of pales, and the colour and length of leaves. Fernandes (1976) also used achene length to discriminate between "*A. tuberculata* subsp. *tuberculata*" and subsp. *turolensis*. However, the respective ranges of achene length overlap, being 1.3-2.1 mm in *A. tuberculata* subsp. *turolensis* and 1.8-2.5 mm in *A. tuberculata* subsp. *tuberculata*. Benedí i González (1987) describes the pales of *A. tuberculata* subsp. *tuberculata* as linear-subulate and usually tinged with black at the apex, those of *A. tuberculata* subsp. *turolensis* as oblanceolate with concolourous tips. Leaves of *A. tuberculata* subsp. *tuberculata* were found to be dark green and 2-3.5(-6.0) cm long, those of *A. tuberculata* subsp. *turolensis*, light green and only 1.2-2 cm long. As "*A. tuberculata* subsp. *tuberculata*" grows in the S Spanish mountain ranges and subsp. *turolensis* is restricted to mountains in C Spain (Sistema Ibérico), the treatment of *A. turolensis* as a subspecies of *A. pedunculata* (= *A. tuberculata*) is logical.

Anthemis clausonis, restricted to the coasts W of Algiers, also belongs to the *A. pedunculata* group of taxa and is treated here as its subspecies, *A. pedunculata* subsp. *clausonis*. Due to lack of fresh plant material this taxon was omitted from the morphological and molecular analyses. With its narrowly elliptical to subulate pales it clearly falls within the range of *A. pedunculata* subsp. *pedunculata* but differs by its pale membranous margins of the involucral bracts, when in all other taxa of the *A. pedunculata* group they use to be light to dark brown or even black. As *A. ubensis* from E Algeria and N Tunisia, and unlike other members of the *A. pedunculata* group, *A. clausonis* has a fairly branched capitulescence, but it differs from *A. ubensis* by its perennial growth and the shape of involucral bracts and pales. By the pale membranous margins of involucral bracts and the much-branched habit, *A. clausonis* resembles the NE Moroccan *A. mauritiana* and the S Spanish *A. bourgaei* of *A.* ser. *Bourgaeinianae* which, however, are annuals with readily caducous pales.

Anthemis zaianica is here described as new to accommodate a population in the Zaïan area in Morocco that also holds a somewhat intermediate position between the *A. pedunculata* group and *A.* ser. *Bourgaeinianae*. It was not included in the numerical analysis, but morphologically it fits in *A.* ser. *Bourgaeinianae* due to its annual habit and its readily caducous pales. In contrast, results of RAPD analysis place a representative of *A. zaianica* among Moroccan and Spanish populations of *A. pedunculata*, well apart from the two specimens of *A. stiparum*. The dendrogram in Fig. 22 also indicates, however, that *A. zaianica* deviates genetically from its nearest neighbour, OTU 6, since the branch length between *A. zaianica* (OTU 49) and the internal node with OTU 6 is much longer than is the rule for representatives of *A. pedunculata*, i.e. genetic deviation of *A. zaianica* from a joint "common ancestor" conspicuously exceeds that of OTU 6. One may hypothesise that *A. zaianica* is rather an annual segregate of *A. pedunculata* than a member of *A.* ser. *Bourgaeinianae*, and that annual growth and caducous pales have evolved in parallel in *A. zaianica* and in the mentioned series. That hypothesis may be extended to question the monophyly of *A.* ser. *Bourgaeinianae* altogether by assuming that its members all derive from *A. pedunculata*, having become annuals independently in different areas in habitats that favour annual life forms: the dry high plateaus of Algeria *(A. stiparum* subsp. *stiparum* and subsp. *intermedia*, *A. monilicostata)*, the border lands of the Sahara desert *(A. stiparum subsp. sabulicola)*, or the rather arid coastal areas of NE Morocco *(A. mauritiana)* and SW Spain *(A. bourgaei)*. For the latter species a relation to *A. tuberculata* (= *A. pedunculata)* was already suggested by Talavera, cited by Benedí i González (1987: 216). Since *A. pedunculata* is a rather short-lived perennial herb that may often flower already in the first year, the switch to annual life form is easy, and indeed took place in some diploid populations of *A. pedunculata* in Morocco growing as weeds in arable fields, while plants growing on adjacent limestone cliffs were tetraploid and distinctly perennial (e.g. at Foum Kheneg, Middle Atlas, OTUs 8 and 13). Our morphological and molecular studies are not sufficient to prove or disprove the monophyly of *A.* ser. *Bourgaeinianae* (and consequently of both *A.* sect. *Anthemis* and sect. *Hiorthia*). The answer must await a comprehensive study on the phylogeny of the genus. Pending this, I consider the annual habit and the readily caducous pales of *A. zaianica* to be sufficient grounds for its inclusion in *A.* ser. *Bourgaeinianae*.

Variation within *Anthemis pedunculata* in C and E Algeria and N Tunisia is paralleled in *A. punctata* in the same area. In the E Algerian and N Tunisian mountains (where *A. pedunculata* is represented by subsp. *atlantica*) *A. punctata* is characterized by obovate inner involucral bracts and tricuspidate pales *(A. punctata* subsp. *punctata).* The large-headed plants from the Djurdjura mountains (where *A. pedunculata* is represented by subsp. *pedunculata*) differ by having elliptical inner involucral bracts and gradually tapering pales *(A. punctata* subsp. *kabylica).* Perhaps the local small-headed plants did participate in the evolution of the large-headed plants in their area. The large-headed plants being supposedly tetraploid, this participation may consist in the involvement of small-headed diploids in the formation of these tetraploids. As cytological and morphological results demonstrate for Moroccan populations of *A. pedunculata* s.l., the increase of flower heads is not necessarily caused by autotetraploidisation. Thus, the large-headed Algerian plants may well have an allotetraploid origin, with the local *A. pedunculata* only contributing for one half, which would still explain the observed pattern of parallel morphological variation. Since neither cytological nor experimental or molecular investigations were feasible with Algerian plants due to the present inaccessibility of this country, we are unable to test this hypothesis.

A diagrammatic summary of the taxonomic relationships within the *Anthemis pedunculata - A. punctata* complex, as inferred from morphology, chromosome numbers and

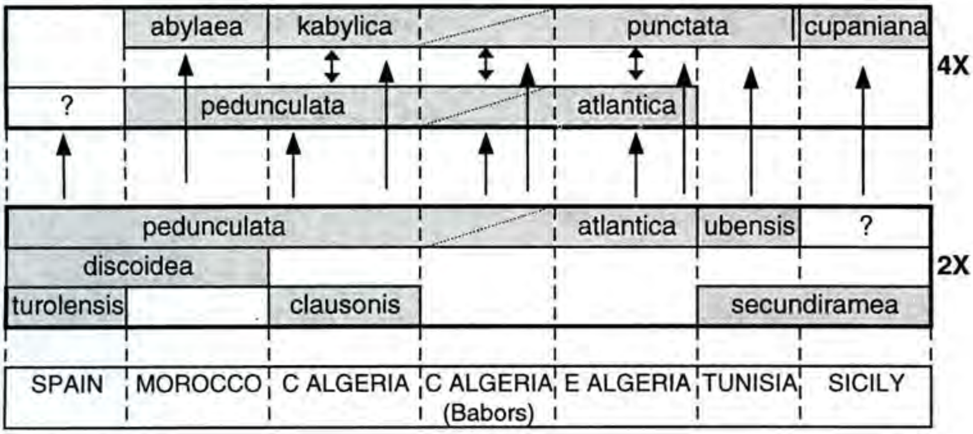

Fig. 24. Diagram summarising the hypothesised taxonomic relationships in the *Anthemis pedunculata - A. punctata* complex.

molecular data is given in Fig. 24. On the diploid level one observes a strong morphological differentiation within *A. pedunculata,* expressed by the recognition of four allopatric subspecies: *A. pedunculata* subsp. *pedunculata* (Betic mountain range of S Spain, all Moroccan mountains from the Rif to the Anti-Atlas, W and C Algeria). In the Algerian Babors mountains (Petite Kabylie), parts of the Aurès range, on the Monts de Constantine and in N Tunisia it is replaced by *A. pedunculata* subsp. *atlantica,* in the Sistema Iberico in C Spain by *A. pedunculata* subsp. *turolensis,* and in a small coastal area W of Algiers by *A. pedunculata* subsp. *clausonis.* In E Algeria and N Tunisia, *A. ubensis,* an annual, presumably hybrid species mediating between *A. pedunculata* and *A. secundiramea,* replaces *A. pedunculata*. Variation observed on the diploid level is to a large extent paralleled on the tetraploid level. Presumed autoploidisation has led and still leads to the formation of tetraploids throughout the range of *A. pedunculata* subsp. *pedunculata* and subsp. *atlantica* that morphologically strongly resemble their diploid progenitors. An allotetraploid origin is suggested for the morphologically deviating taxa of the *A. punctata* group, involving the local diploids of *A. pedunculata* and resulting in *A. punctata* subsp. *punctata* in E Algeria and Tunisia, in *A. punctata* subsp. *kabylica* in the Djurdjura mountains of C Algeria, and in *A. abylaea* in the W Rif mountains in N Morocco. The second species involved in this assumed alloploidisation is not yet known, perhaps some diploid with large flower heads, like the Sicilian endemic *A. ismelia,* may have played this role. Alternatively, one may speculate that *A. punctata* results from the hybridisation of a large-headed tetraploid species, like *A. cupaniana* or *A. cretica* subsp. *columnae,* with local autotetraploids of *A. pedunculata* s.l. At present it is impossible to decide between the two scenarios, further molecular and cytogenetic work, especially in Algeria, being needed.