CHARACTER ANALYSIS IN *ACHILLEA* SECT. *SANTOLINOIDEA (COMPOSITAE–ANTHEMIDEAE)*: PART I. LEAF AND FLORAL MORPHOLOGY

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Twenty-two species of *Achillea* sect. *Santolinoidea* (DC.) O. Hoffm., as currently understood, were analysed morphologically. Emphasis was put on clear definitions of characters and their states as were deduced from detailed graphical analysis. Major character sets include details of leaf structure and differentiation of leaflet lobes as well as of floral characters (form of flower heads, ligules, phyllaries, bracts). Character descriptions were compared with floristic literature and original diagnoses, but little consistency was observed in the applied terminology. There is little indication of unifying character states for sect. *Santolinoidea*, as a result of low frequencies of occurrence, although the section appears to be uniform on the basis of the general leaf structure. However, species-specificity of some character states (leaves, bracts, phyllaries) was observed that might prove useful for species delimitation.

Keywords. Character definition, frequency of occurrence, graphical analysis, sectional characterization, species-specificity.

INTRODUCTION

The 24 species of *Achillea* sect. *Santolinoidea* (DC.) O. Hoffm. (*Anthemideae*), as presently understood, are characterized by vermiform leaf shapes, with primary leaflets positioned transverse to the rachis, and with all but one exception (i.e. *A. santolina* L.), more or less imbricate. The characteristic leaf shape is shared with species of sect. *Arthrolepis* (Boiss.) Boiss., and with the closely related monotypic genus *Leucocyclus* Boiss. (Humphries, 1977; Bremer & Humphries, 1993), which are, however, well separated by some major floral characters (Boissier, 1874; Huber-Morath, 1975). Geographically, *Achillea* sect. *Santolinoidea* is centred in the Irano-Turanic region, with only a few taxa extending into the W Mediterranean region and N Africa (Huber-Morath, 1975, 1986).

Dealing with morphological characters in some plant groups can be challenging, particularly in the case of the vermiform leaf structures observed in taxa of *Achillea* sect. *Santolinoidea*. Here the leaves are small, closely appressed, and densely packed due to imbricate leaflet position, so that it is difficult to distinguish useful characters and states particularly of leaflet forms and structures. This problem has been insufficiently addressed in existing floristic literature as well as in original diagnoses. For effective systematic work in *Achillea* sect. *Santolinoidea*, therefore, the initial priority is to find means for adequately and consistently assessing and describing the patterns of variation in morphological features within the group. In our opinion,

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the most successful method to achieve these desired results is through careful graphic analysis, which should also include floral characters frequently used for species characterization (Huber-Morath, 1975, 1986). The present study therefore presents a comparative analysis of both leaf and floral characters, based on clearly defined character traits. For this purpose, a concept of precise definitions of characters and their expressed states was developed, derived through careful graphical analysis. Practically all descriptive characters from leaves and flower heads were analysed in this way. This type of approach is similar to that completed on *Carlina* of the *Compositae* (Meusel & Kästner, 1990, 1994), which yielded good results in species characterization and infrageneric taxonomy. It may be assumed, therefore, that character analysis in *Achillea* sect. *Santolinoidea* might yield similar positive results, both with respect to species-specificity of characters and characterization of this apparently uniform section. In addition, it is hoped to reduce the chance of further misalignments and misdeterminations of species currently found in many herbarium collections. As part of our current studies, the data presented now will be related to growth forms, geographical and ecological characters, to form the focus of a subsequent publication (Valant-Vetschera & Kästner, in prep.).

MATERIAL AND METHODS

Cultivated and herbarium material was used for microscopic and graphical morphological analysis, originating from B, G, JE, BM, W, WU, LI, and personal collections deposited in WU. Material to be analysed was selected at the same stage of development to exclude ontogenetic variation, and it was taken from the same comparable region within the plant (e.g. median cauline leaf). Several populations of each species were compared, and in case of constant character states, one population was selected for illustration. Graphical morphological analysis, following earlier publications (Meusel & Kästner, 1990, 1994) comprised all possible forms of analysing a character prior to illustration in a certain scale. The illustrations resulted from careful observations and measurements of relations, aiming at a naturalistic and not abstracted reproduction of morphological features. Whenever possible, forms were reduced to geometrically defined forms, as based upon the publications from Stearn (1983) and Hickey (1973; see Fig. 3). Characters which could not be based upon geometrical forms, were classified using logically defined states (compare Table 2). In total, 17 characters were established, each with several states. Of these, 10 relate to leaves and their structures, whereas seven relate to the floral region (see Table 2).

RESULTS AND DISCUSSION

Achillea sect. *Santolinoidea* as currently understood comprises 24 species (Huber-Morath, 1975, 1986) of which 22 were morphologically analysed (for taxa and diagnoses see Table 1). No material was available from *A. gypsicola* Hub.-Mor., nor from *A. monocephala* Boiss. & Bal., of which only the type specimen is known. The

TABLE 1. Taxa of *Achillea* sect. *Santolinoidea* analysed graphically

A. aleppica DC. in Prodr. 7: 296 (1838)
  subsp. *aleppica*
  subsp. *zederbaueri* (Hayek) Hub.-Mor. in Ber. Schweiz. Bot. Ges. 84: 147 (1974)
A. armenorum Boiss. & Hausskn. in Boissier, Fl. Or. 3: 269 (1874)
A. aucheri Boiss. in Diagn. Pl. Or. Nov. Sér. 1(6): 87 (1845)
A. conferta DC. in Prodr. VI: 32 (1837)
A. cretica L. in Spec. Pl. 899 (1753)
A. cucullata Hausskn. ex Bornmüller in Feddes Repert. Beih. 89: 327 (1944)
A. eriophora DC. in Prodr. 6: 31 (1838)
A. falcata L. in Spec. Pl. 897 (1753)
A. goniocephala Boiss. & Bal. in Diagn. Pl. Nov. sér. 2(6): 98 (1859)
A. lycaonica Boiss. & Heldr. in Diagn. Pl. Or. sér. 1(11): 17 (1849)
A. magnifica (Heimerl) ex Hub.-Mor. in Notes Roy. Bot. Gard. Edinb. 33: 208 (1974)
A. phrygia Boiss. & Bal. in Diagn. Pl. Nov. sér. 2(6): 99 (1859)
A. pseudoaleppica (Hausskn.) ex Hub.-Mor. in Notes Roy. Bot. Gard. Edinb. 33(2): 209 (1974)
A. santolina L. Sp. Pl. 896 (1753)
A. schischkinii Sosnowsky in Zurn. Russk. Bot. Obsc. Akad. Nauk. 6: 146 (1921)
A. sintenisii Hub.-Mor. in Notes Roy. Bot. Gard. Edinb. 33(2): 210 (1974)
A. spinulifolia Fenzl ex Boissier in Fl. Or. 3: 268 (1874)
A. talagonica Boiss. in Diagn. Pl. Or. sér. 1(11): 17 (1849)
  var. *talagonica*
  var. *oxylepis* (Boiss. & Hausskn.) Hub.-Mor. in Fl. Iranica Lfg 158: 59 (1986)
A. teretifolia Willd., in Sp. Pl. 3: 2198 (1803)
A. vermicularis Trin., in Mém. Acad. Sci. Pétersbg. 6: 494 (1818)
A. wilhelmsii C. Koch in Linnaea 24: 328 (1851)
  subsp. *wilhelmsii*
  subsp. *santolinoides* (Lag.) Vetschera & Kästner in Feddes Repert. 109: 504 (1998)

specific status of *A. monocephala* is doubtful as was shown to be the case with *A. boissieri* (Hausskn.) Boiss., which proved to be synonymous with *A. teretifolia* Willd. (Valant-Vetschera & Kästner, 1998b). Data from this study also proved to be useful for a revision of the concept of *A. wilhelmsii* (Valant-Vetschera & Kästner, 1998a,b). Apart from these single cases, all the other taxa of this section are considered to be reasonably well defined and therefore do not warrant taxonomic revision.

All characters and their states, illustrated in the respective figures, represent constant and stable characters. Characters or features which proved to vary largely among populations were excluded from comparison. The coding and definition of all characters and their states is given in Table 2; for distribution of morphological data as states of 17 characters see Table 3. Characters 1–10 refer to the leaves, their general appearance, as well as the minute structures that can be observed on primary leaflets when viewed under the binocular microscope. Characters 11–17 relate to flower heads, ligule characters, bracts and phyllaries. Divergent forms of species were included as separate units (*A. santolina, A. teretifolia* in Table 3). In both cases, the

TABLE 2. Survey of character states in *Achillea* sect. *Santolinoidea*

Character	Character definition	Character state	Frequency of occurrence
1	LEAF SHAPE STRUCTURES		
	Lax	0	7
	Compact	1	12
	Imbricate	2	7
2	RACHIS		
	Free	0	9
	Partly covered	1	7
	Covered	2	10
3	PARTITION OF LEAFLETS		
	Entire	0	5
	Tripartite – pinnatifid, up to ⅔	1	2
	Tripartite – pinnatipartite, min. ⅔	2	5
	Tripartite – pinnatisect 3/3	3	11
	Pentapartite – pinnatisect 3/3	4	3
4	LEAFLETS: FORM OF MAIN LOBE		
	Oblong	0	2
	Cuneate	1	4
	Obovate	2	14
	Broadly obovate	3	4
	Broadly obovate to cuneate	4	2
5	LEAFLETS: FORM OF LATERAL LOBES		
	Oblong	0	2
	Elliptic	1	7
	Obovate	2	6
	Obovate to cuneate	3	3
	Broadly obovate	4	7
	No form	5	2
6	MAIN LOBE: POSITION TO RACHIS		
	±transverse 90–70°	0	4
	±diagonal 70–40°	1	13
	Diagonal upright 40–10°	2	7
	Upright, appressed <10	3	2
7	LATERAL LOBE: POSITION TO RACHIS		
	±transverse 90–70°	0	2
	±diagonal 70–40°	1	3
	Diagonal upright 40–10°	2	2
	Upright, appressed <10	3	13
	No position	4	5
8	LEAFLET MARGINS: DIFFERENTIATION		
	Edentate	0	2
	Laxely denticulate	1	3
	Distantly crenulate dentate	2	2
	Regularly shortly spiniform dentate	3	3
	Shortly spiniform dentate	4	10
	Spiniform dentate with one distinctly elongated main tooth	5	6

TABLE 2. (*Cont'd*)

Character	Character definition	Character state	Frequency of occurrence
9	LEAFLET MARGINS: SCARIOUS MARGINS		
	Not margined + cartilaginous tips	0	8
	Narrowly margined, p.p. + cartilaginous tips	1	7
	Narrowly margined + cartilaginous tips	2	4
	Distinctly margined + cartilaginous tips	3	6
	Narrowly margined without tips	4	1
10	INDUMENTUM		
	Hardly tomentose	0	12
	Little tomentose	1	7
	Tomentose	2	3
	Very tomentose	3	4
11	FORM OF FLOWER HEADS		
	Patellate	0	3
	Campanulate	1	1
	Narrowly campanulate	2	8
	Broadly semi-ovate	3	2
	Semi-ovate	4	3
	Narrowly semi-ovate	5	4
	Cupulate	6	3
	Obconical	7	2
	Cylindrical, terete	8	2
12	FORM OF LIGULES		
	Reniform	0	1
	Semicircular	1	2
	Semi-elliptic	2	4
	Rectangular	3	3
	Rectangular or broadly obtrapeziform	4	3
	Obtrapeziform	5	8
	Broadly obtrapeziform	6	3
13	MARGIN OF LIGULES		
	Slightly 3-crenate	0	8
	3-crenate	1	9
	Slightly 3-lobate	2	2
	3-lobate	3	3
	Deeply 3-lobate	4	2
14	BASAL INVOLUCRAL BRACTS		
	Angulate-ovate, rounded at base	0	3
	Broadly angulate-ovate, rounded at base	1	5
	Ovate	2	8
	Narrowly ovate	3	6
	Ovate, acute at apex	4	2
	Obovate	5	2

TABLE 2. (*Cont'd*)

Character	Character definition	Character state	Frequency of occurrence
15	UPPER INVOLUCRAL BRACTS		
	Angulate-ovate, rounded at base	0	2
	Spathulate	1	2
	Lanceolate, rounded at base	2	2
	Narrowly ovate	3	11
	Ovate, acute at apex	4	2
	Narrowly ovate, acute at apex	5	1
	Obovate	6	2
	Narrowly obovate	7	4
16	PHYLLARIES (ALL TRUNCATE AT BASE)		
	Narrowly obovate	0	6
	Obovate	1	3
	Narrowly subangulate-obovate	2	2
	Subangulate-obovate	3	2
	Subelliptic	4	8
	Narrowly ovate	5	3
	Subangulate-ovate	6	1
	Lanceolate	7	1
17	COLOUR OF LIGULES		
	Yellow	0	18
	White	1	6
	Ivory	2	4

differences were not considered to be sufficient for establishment of subtaxa (Valant-Vetschera, 1996; Valant-Vetschera & Kästner, 1998b). Apart from the superficial uniformity of leaf structures of this section, it was difficult to find predominating character states that could be used as unifying features (see Table 2, frequencies). The relevance of frequencies will be discussed separately.

1. Leaf characters

All species of this section exhibit vermiform and compound leaves, consisting of a rachis and primary leaflets of varying forms. In a fully developed leaf, leaflets are positioned transverse to the rachis, with a strong tendency to a compact or imbricate position (character nos. 1, 2 in Table 2). In relation to a preference for xeric habitats, this leaf structure has apparently proven successful for the species of sect. *Santolinoidea*. The nature of the transverse insertion of primary leaflets has been subject to an ontogenetic study of leaf development *inter alia* in *A. wilhelmsii* and *A. spinulifolia* (Eberwein, 1995). Thus, the development of primary leaflets is basipetal, and further segmentation follows the mode of polyternation. It is assumed that meristematic incorporation leads to transverse insertions of leaflets, and theories leading to this concept are discussed at length by Eberwein (1995).

TABLE 3. Character states and their distribution in *Achillea* sect. *Santolinoidea*

Character no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
No. of character states	0–2	0–2	0–4	0–4	0–5	0–2	0–4	0–5	0–4	0–3	0–8	0–6	0–4	0–5	0–7	0–7	0–2
Achillea																	
aleppica subsp. *aleppica*	1	1	2	2	2	1	3	4	1	0	5	6	4	3	7	2	0
aleppica subsp. *zederbaueri*	2	2	3	3	4	2	3	4	0	0	5	6	4	3	7	2	2
armenorum	1	0	1	2	4	2	3	4	3	3	0	2	0	4	4	0	1
aucheri	1	1	3	1	2	1	3	5	1	1	2	3	0	0	5	7	2
conferta	1	0	3	4	2	2	3	4	3	1	2	1	1	3	7	0	0
cretica	0	1	2	2	1	1	3	2	0	0	3	3	0	3	3	4	1
cucullata	1	2	3	2	1	2	3	4	1	2	4	3	1	2	3	5	0
eriophora	2	2	3	4	4	0	0	5	2	3	8	1	3	2	1	0	0
falcata	1	1	2	2	2	1	3	4	2	2	6	5	1	1	0	0	0
goniocephala	2	0	3	1	3	3	3	3	1	3	2	2	1	0	7	3	1
lycaonica	1	2	4	2	1	1	1	5	3	1	6	5	3	2	3	5	0
magnifica	0	0	3	2	1	1	1	4	3	1	1	2	3	0	2	5	0
phrygia	2	2	4	2	2	1	3	3	2	3	7	0	0	2	3	6	0
pseudoaleppica	2	2	3	2	4	0	0	5	3	0	8	5	1	1	1	3	0
santolina a	0	0	0	0	0	0	4	0	4	0	2	5	1	5	6	4	0
santolina b	0	0	3	0	0	1	4	0	1	0	2	5	1	5	6	4	0
schischkinii	1	2	2	1	3	1	2	3	0	0	6	1	2	4	4	4	0
sintenisii	2	1	0	3	5	3	4	2	1	1	0	2	2	1	0	4	1
spinulifolia	1	1	1	3	2	2	1	5	2	1	2	2	1	1	3	4	2
talagonica	2	2	2	1	3	2	3	4	3	1	2	6	0	1	2	1	0
teretifolia a	1	0	0	3	5	2	4	1	0	0	0	4	0	2	3	1	1
teretifolia b	1	0	0	3	5	2	4	1	0	0	4	4	0	2	3	1	1
teretifolia c	1	0	0	3	5	2	4	1	0	0	5	4	0	2	3	0	1
vermicularis	0	1	4	2	1	0	2	5	1	2	2	5	1	2	3	4	0
wilhelmsii subsp. *wilhelmsii*	1	2	3	2	1	1	3	4	0	0	7	5	3	3	3	4	0
wilhelmsii subsp. *santolinoides*	1	2	3	2	1	1	3	4	0	0	3	5	3	3	3	1	0

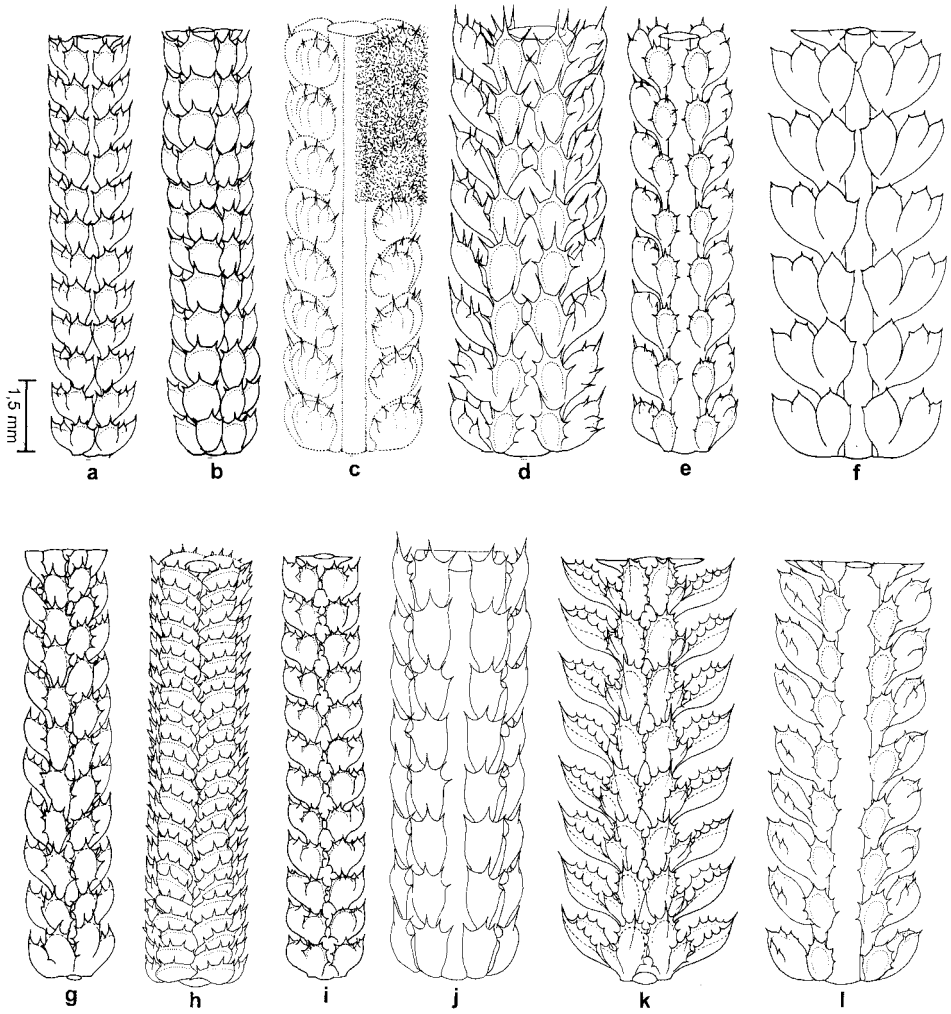

FIG. 1. *Achillea* sect. *Santolinoidea*. Part of median cauline leaves; general shape and leaf structures (variables 1–3, 8, 9, 10): a, *A. aleppica* subsp. *aleppica*; b, *A. aleppica* subsp. *zederbaueri*; c, *A. armenorum*; d, *A. aucheri*; e, *A. conferta*; f, *A. cretica*; g, *A. cucullata*; h, *A. eriophora*; i, *A. falcata*; j, *A. goniocephala*; k, *A. lycaonica*; l, *A. magnifica*.

Some of the characters presented here had not been described before, e.g. the position of lobes to the rachis (character nos. 7, 8 in Table 2) . Also, classification of leaf partition was not used conceptually to characterize the species of this section (character no. 3 in Table 2). Mostly, the form of the leaflet lobes has been described, but could be imagined only with difficulty due to lack of explanatory illustrations. Morphological and graphical analyses of median cauline leaves led to a clearer opinion on the forms of main and lateral lobes of primary leaflets (Fig. 1). This detailed analysis indicates that a combination of forms may be species-specific. Variation was quite low at the infraspecific level when material of the same

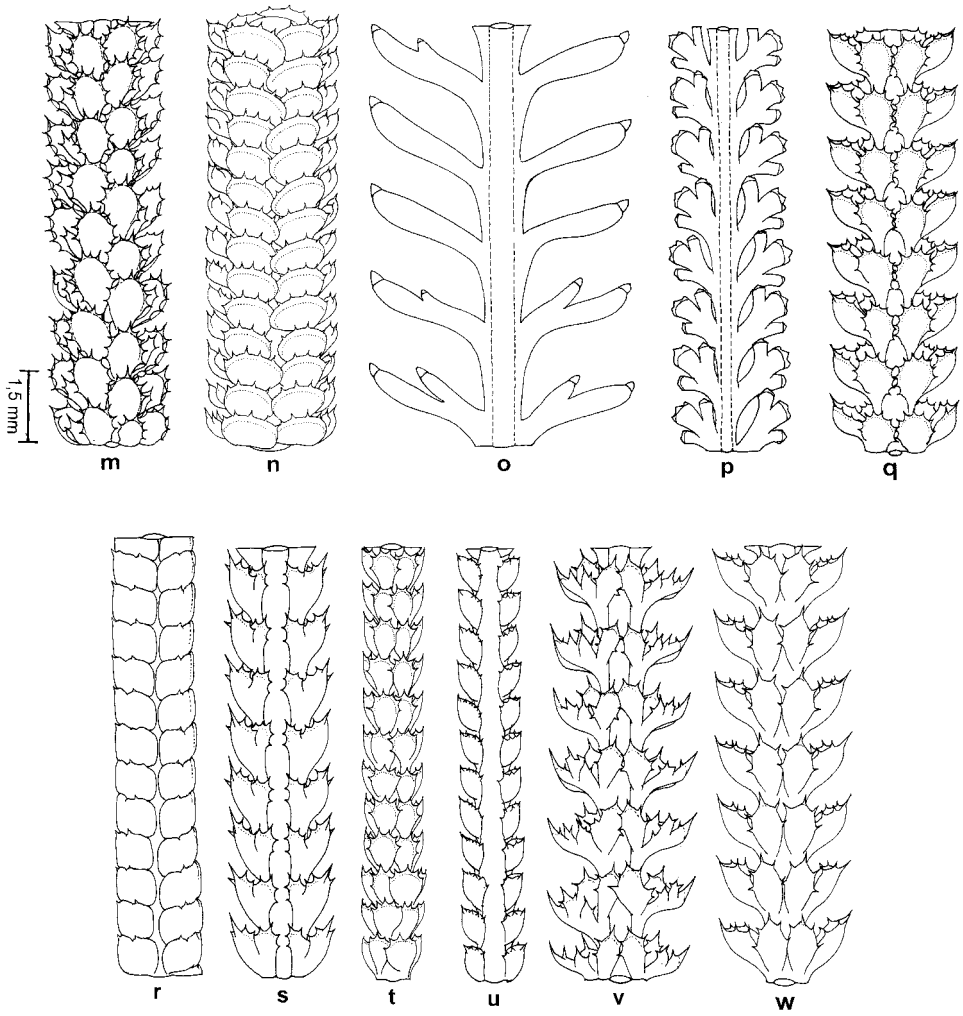

FIG. 1. *(Cont'd)*. *Achillea* sect. *Santolinoidea*. Part of median cauline leaves; general shape and leaf structures (variables 1–3, 8, 9, 10): m, *A. phrygia*; n, *A. pseudoaleppica*; o, *A. santolina* a; p, *A. santolina* b; q, *A. schischkinii*; r, *A. sintenisii;* s, *A. spinulifolia*; t, *A. talagonica*; u, *A. teretifolia* a, b, c; v, *A. vermicularis*; w, *A. wilhelmsii* subsp. *santolinoides* and subsp. *wilhelmsii.*

developmental stage was compared. To get a better view of the form of main and lateral lobes, separate graphic analysis was carried out (Fig. 2), relating to characters 4 and 5 of Tables 2 and 3.

Differences may be observed in forms and the structures of margins. With the latter, two characters appear to be of importance: the differentiations of leaflet margins, with a tendency to spiniform dentate appearance (character no. 8 in Table 2; compare Fig. 4), and the presence of scarious margins and/or cartilaginous tips (character no. 9 in Table 2). Finally, the indumentum, being frequently used as a descriptive character, is listed as character 10 (Table 2). However, it appears that

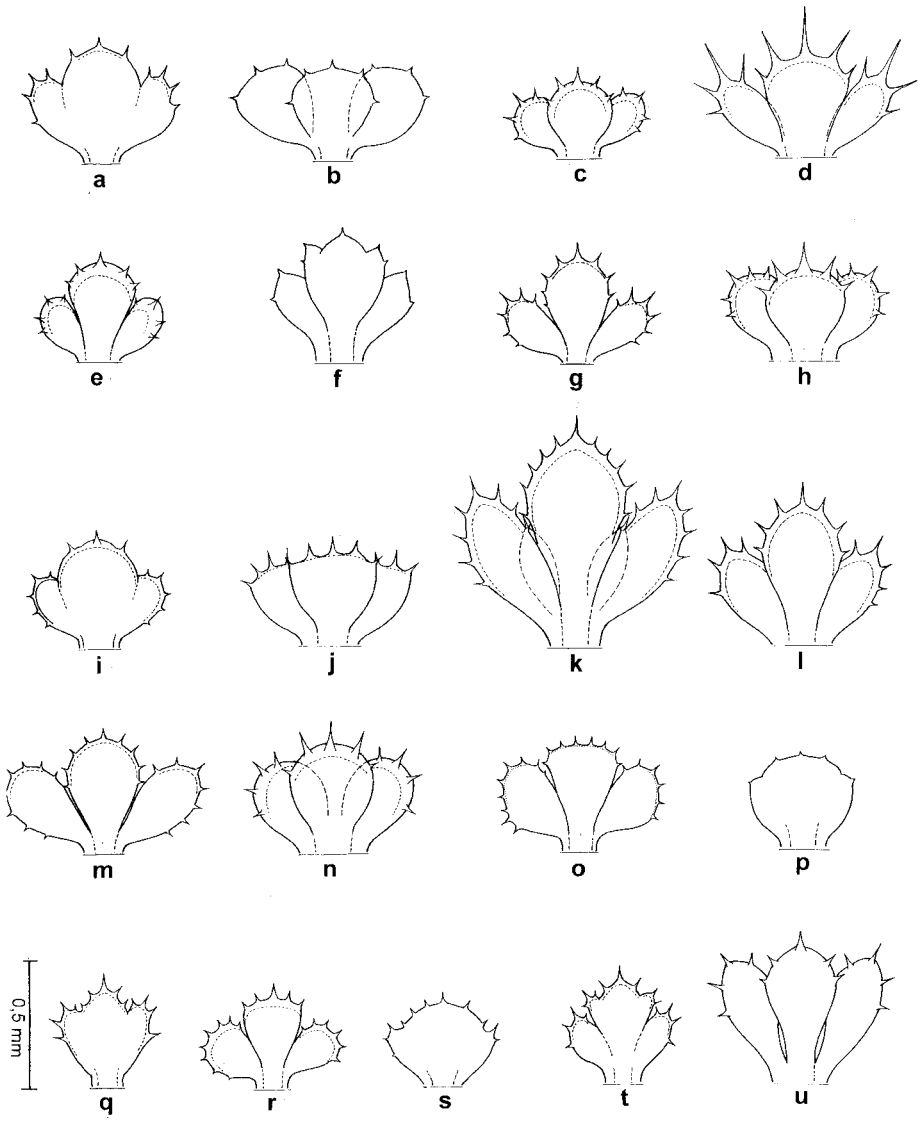

FIG. 2. *Achillea* sect. *Santolinoidea*. Shapes of main and lateral lobes in median cauline leaves (variables 4, 5, 8, 9): a, *A. aleppica* subsp. *aleppica*; b, *A. aleppica* subsp. *zederbaueri*; c, *A. armenorum*; d, *A. aucheri*; e, *A. conferta*; f, *A. cretica*; g, *A. cucullata*; h, *A. eriophora*; i, *A. falcata*; j, *A. goniocephala*; k, *A. lycaonica*; l, *A. magnifica*; m, *A. phrygia*; n, *A. pseudoaleppica*; o, *A. schischkinii*; p, *A. sintenisii;* q, *A. spinulifolia*; r, *A. talagonica*; s, *A. teretifolia* a, b, c; t, *A. vermicularis*; u, *A. wilhelmsii* subsp. *santolinoides* and subsp. *wilhelmsii.*

its use may not have much significance for taxon delimitation. Interestingly, the indumentum most frequently is hardly or scarcely visible, with a few exceptions such as in *A. armenorum* (compare Fig. 1). Apparently, the either compact or imbricate

positioning of lateral leaflets provides a reasonable strategy for surviving in xeric environments. Additionally, flavonoid and terpenoid compounds, which are excreted on the leaf surface, may add significantly to this strategy (Valant-Vetschera & Wollenweber, 1994).

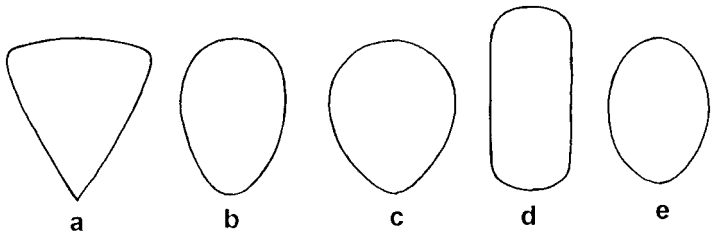

FIG. 3. *Achillea* sect. *Santolinoidea*. Geometric forms relating to all form variables: a, cuneate; b, obovate; c, broadly obovate; d, oblong; e, elliptic.

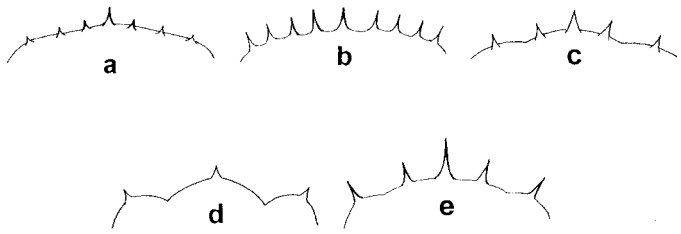

FIG. 4. *Achillea* sect. *Santolinoidea*. Leaflet margins of median cauline leaves (variable 8): a, denticulate; b, regulary shortly spiniform dentate; c, shortly spiniform dentate; d, crenulate dentate; e, shortly spiniform dentate with one elongated main tooth.

Leaf differentiation in seedlings and reduced forms. Some of the species were cultivated from collections from natural habitats. Young seedlings were analysed, comparing shapes of cotyledons and primary leaves (Fig. 5). The primary leaves showed an unexpectedly high degree of differentiation. The transverse position of primary leaflet insertion was already visible, and the second pair of leaves exhibited structures corresponding to fully developed cauline leaves. Such phenomena could not be observed with *Achillea* species from other sections.

Reduced structures may appear in the upper region of the plant (Fig. 6), providing a good indication for possible ontogenetic changes during plant development. This has to be taken into consideration when using such characters for species characterization and for taxonomic purposes.

2. Floral characters

Generally, flower heads of the genus *Achillea* are mostly ligulate, rather small in size and numerous. Large and solitary capitula are rare. Pappus is always absent, and cypselas are flattened and thin-walled with two lateral ribs (Bremer & Humphries,

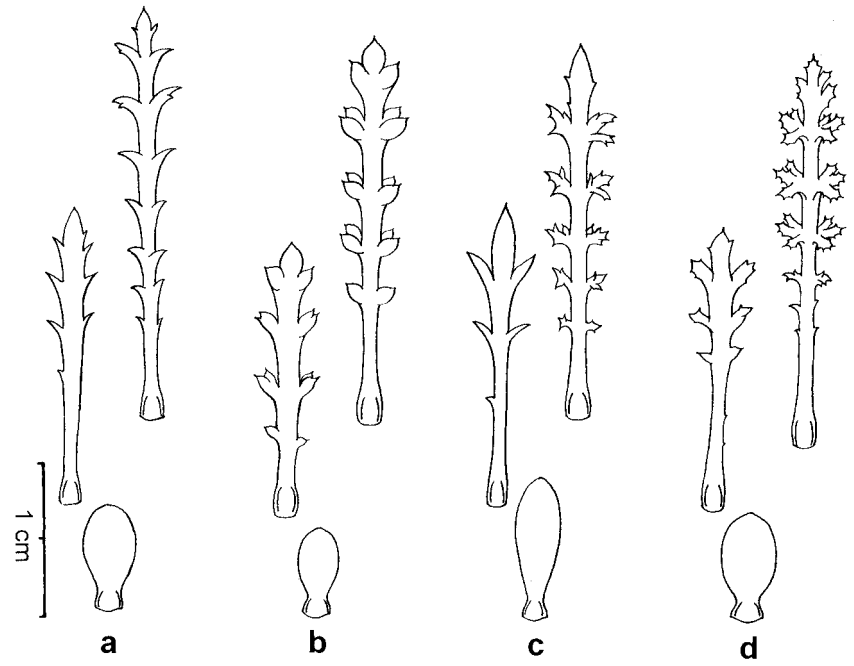

FIG. 5. *Achillea* sect. *Santolinoidea*. Leaf differentiation in seedlings. Bottom to top – cotyledons to primary and secondary leaves: a, *A. lycaonica*; b, *A. aleppica* subsp. *zederbaueri*; c, *A. falcata*; d, *A. spinulifolia.*

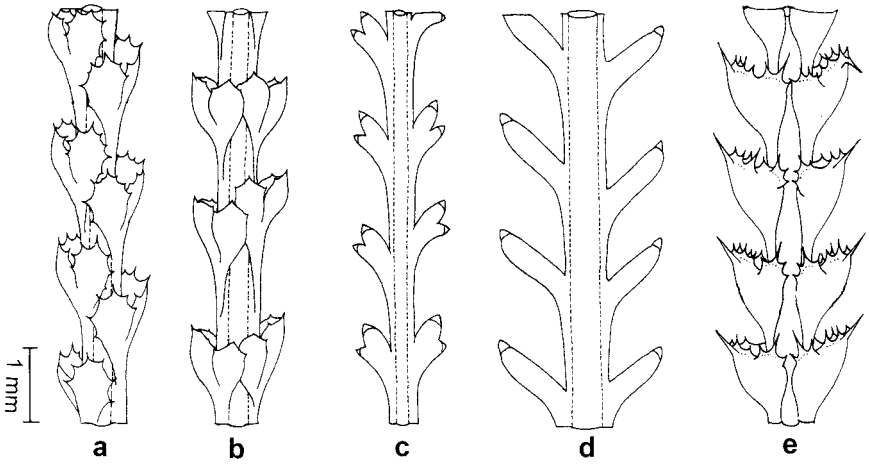

FIG. 6. *Achillea* sect. *Santolinoidea*. Leaf reduction phenomena as observed in upper stem region: a, *A. schischkinii*; b, *A. wilhelmsii* subsp. *wilhelmsii*; c, d, *A. santolina*; e, *A. spinulifolia.*

1993). The colour of ligules varies from white to ivory and yellow with pink rarely observed. With exception of pink colour and single large capitula, all features are also found within sect. *Santolinoidea*. In sect. *Santolinoidea*, bracts are arranged in

about 3–4 imbricate rows. Phyllaries mostly differ in their shape from that of the bracts, and there is no morphological sequence from basal bracts to phyllaries in terms of shape, indumentum and margin. It appears that features related to bracts and phyllaries are shared with species of other sections of *Achillea*.

Analysis of the form of flower heads revealed considerable variation, with 8 character states (character no. 11 in Table 2). A broad range of forms exists (Fig. 7), not only characterizing single species, but exhibiting also infraspecific variation. This was particularly evident with collections of *A. teretifolia* with observed variation within one plant (Valant-Vetschera & Kästner, 1998b). Therefore, it may be concluded that forms of flower heads do not represent very stable character states. Less variation was noted in the form of ligules (six character states, character no. 12 in Table 2) and their margin differentiations (character no. 13 in Table 2; Fig. 8).

Bracts and phyllaries were similarly analysed (Figs 9, 10) with the main emphasis on definition of geometric shapes. In addition, they frequently exhibit an indumentum and a dissection of varying depth of the mostly broad membranaceous margin. Because some variability was noted within these features, a somewhat typical example

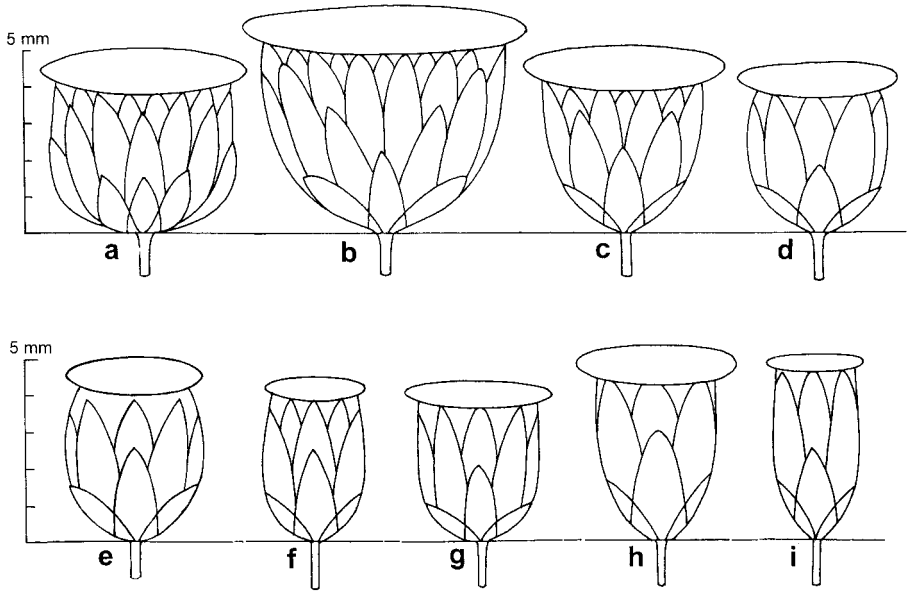

FIG. 7. *Achillea* sect. *Santolinoidea*. Form of flower heads (variable 11): a, patellate: *A. armenorum, A. sintenisii, A. teretifolia* p.p.; b, campanulate: *A. magnifica*; c, narrowly campanulate: *A. aucheri, A. conferta, A. goniocephala, A. santolina, A. spinulifolia, A. talagonica, A. vermicularis*; d, broadly semi-ovate: *A. cretica, A. wilhelmsii* subsp. *santolinoides*; e, semi-ovate: *A. cucullata, A. teretifolia* p.p.; f, narrowly semi-ovate: *A. aleppica* subsp. *aleppica* and subsp. *zederbaueri*, *A. teretifolia* p.p.; g, cupulate: *A. falcata, A. lycaonica, A. schischkinii*; h, obconical: *A. phrygia, A. wilhelmsii* subsp. *wilhelmsii*; i, cylindrical, terete: *A. eriophora, A. pseudoaleppica.*

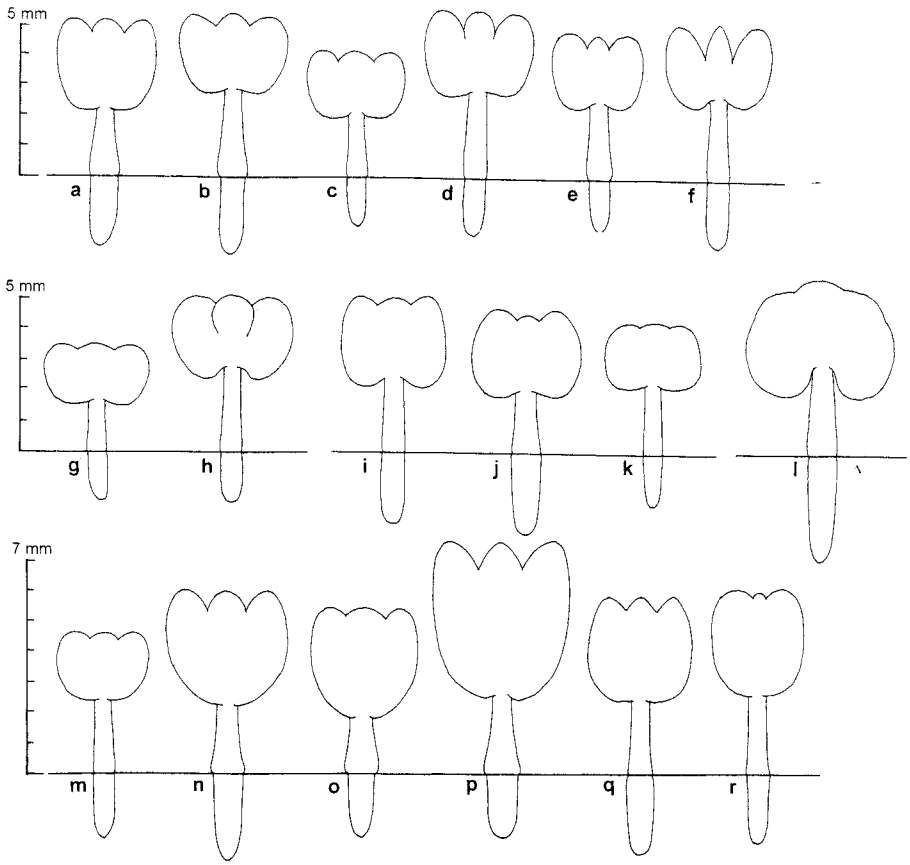

FIG. 8. *Achillea* sect. *Santolinoidea*. Form of ligules (variables 12, 13). Obtrapeziform: a, *A. vermicularis*; b, *A. santolina*; *A. wilhelmsii* subsp. *wilhelmsii*; c, *A. pseudoaleppica*; d, *A. wilhelmsii*; subsp. *santolinoides*; e, *A. falcata*; *A. teretifolia* p.p.; f, *A. lycaonica*, broadly obtrapeziform: g, *A. talagonica*; h, *A. aleppica* subsp. *aleppica* and subsp. *zederbaueri*, ± rectangular; i, *A. cucullata*; j, *A. cretica*; k, *A. aucheri*; *A. teretifolia* p.p., reniform; l, *A. phrygia*, semicircular; m, *A. conferta*; n, *A. schischkinii*, semielliptic: o, *A. goniocephala*; p, *A. sintenisii*; q, *A. spinulifolia*; r, *A. armenorum.*

was selected for the respective illustrations. This particular variation was also the reason for exclusion of these features as expressed states of characters.

The shape of the basal and upper involucral bracts (character nos. 14, 15 in Table 2) appears to be related to the form of the flower heads. Basal bracts are understood as the lower bracts, while upper bracts were dissected from the third row of bracts counted from the insertion of the flower head on the stem. A comparison of shapes from bracts of these regions revealed quite frequently a change in geometric forms and margin structures (see Fig. 9). This observation is considered to be of relevance for describing such characters as taxon-specific.

The phyllaries appeared to be rather uniform within one flower head (character no. 16 in Table 2; Fig. 10). They may be described by their geometric forms, but

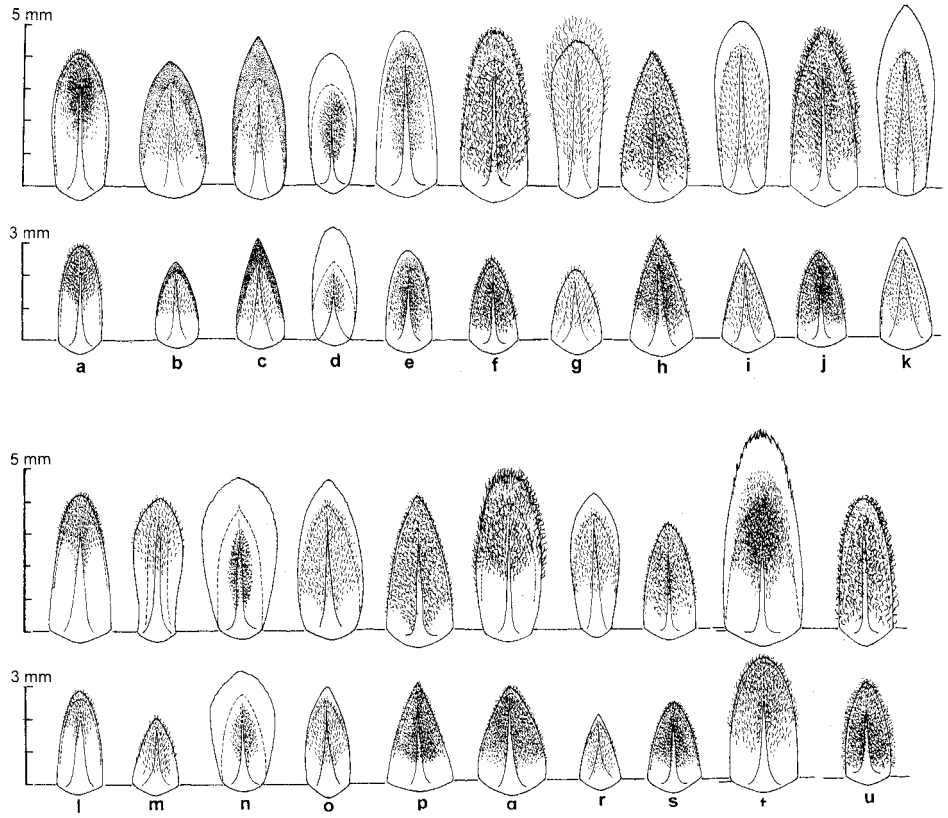

FIG. 9. *Achillea* sect. *Santolinoidea*. Involucral bracts (variables 14, 15): a, *A. aleppica* subsp. *aleppica* and subsp. *zederbaueri*; b, *A. armenorum*; c, *A. aucheri*; d, *A-conferta*; e, *A. cretica*; f, *A. cucullata*; g, *A. eriophora*; h, *A. falcata*; i, *A. goniocephala*; j, *A. lycaonica*; k, *A. magnifica*; l, *A. phrygia*; m, *A. pseudoaleppica*; n, *A. santolina* a,b; o, *A. schischkinii*; p, *A. sintenisii*; q, *A. spinulifolia*; r, *A. talagonica*; s, *A. teretifolia* a, b, c; t, *A. vermicularis*; u, *A. wilhelmsii* subsp. *santolinoides* and subsp. *wilhelmsii*.

restricted by a truncate base which is typical for all taxa studied. It was found hard to group the phyllaries by their shape, preventing their use as group characters. However, they proved helpful for species characterization. The lack of morphological sequences between bracts and phyllaries indicates their separate use as descriptive characters.

As for the colour of ligules, it was decided to separate ivory-coloured from both yellow and white states (character no. 17 in Table 2). It is, however, strongly felt that this character is only of minor importance in this section, contrary to taxonomic implications leading to the segregation of sect. *Filipendulinae* from sect. *Millefolium* (Afanas'ev & Bochantsev, 1961). However, the concept of separating these two units at the section's level was considered to be problematic due to overlapping major characters (Wagenitz 1979).

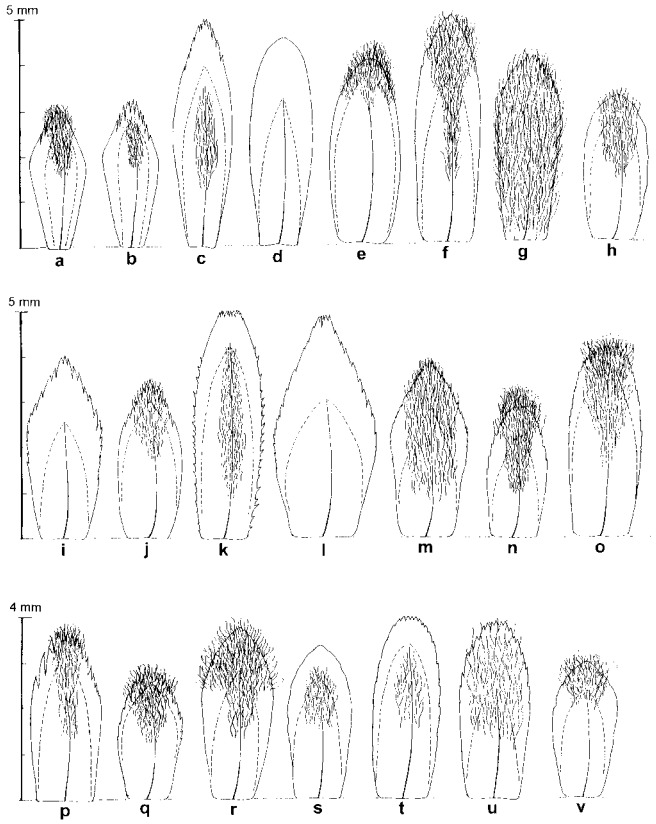

FIG. 10. *Achillea* sect. *Santolinoidea*. Phyllaries (variables 16): a, *A. aleppica* subsp. *aleppica* and subsp. *zederbaueri*; b, *A. armenorum*; c, *A. aucheri*; d, *A. conferta*; e, *A. cretica*; f, *A. cucullata*; g, *A. eriophora*; h, *A. falcata*; I, *A. goniocephala*; j, *A. lycaonica*; k, *A. magnifica*; l, *A. phrygia*; m, *A. pseudoaleppica*; n, *A. santolina* a,b; o, *A. schischkinii*; p, *A. sintenisii*; q, *A. spinulifolia*; r, *A. talagonica*; s, *A. teretifolia* a, b, c; t, *A. vermicularis*; u, *A. wilhelmsii* subsp. *wilhelmsii*; v, *A. wilhelmsii* subsp. *santolinoides.*

3. Comparison of character states with literature data

The analysed character states were compared with species descriptions from Huber-Morath (1975, 1986), which cover all taxa of this section most concisely, although at the floristic level. It was anticipated that these descriptions would use a consistent terminology, in contrast to individual specific diagnoses covering a period of more than 200 years. Some of the leaf characters are described here for the first time (character nos. 6, 7: position of main and lateral lobes to the rachis; character nos. 4, 5: forms of main versus lateral lobes). Similarly, little attention was attributed in these descriptions to parts of the floral characters (character no. 12, form of ligules; character no. 13: margin of ligules; character nos. 14, 15: changes of forms from lower to upper bracts).

The overall degree of terminological correlation proved to be quite low between our data, floristic literature and diagnoses. Ontogenetic variation (see Fig. 5), being apparently reflected by floristic descriptions, the less so by original diagnoses often based on fewer material, may account for inconsistent usage. This may be avoided by analysing comparable parts of the plant and by the use of well-defined terms.

An example of contradictory terminology is found in combinations such as 'lax and imbricate' which were used to describe the leaflet position in various *Achillea* spp. (Huber-Morath, 1975, 1986), but they do not reflect the real appearance of the leaf (see character nos. 1, 2 in Table 2). Diagnoses, on the most part, neglect this character completely and do rarely even indicate the visibility of the rachis (exceptions: *A. aucheri, A. cucullata, A. schischkinii, A. spinulifolia*). The segmentation of primary leaflets provides another example of inconsistent use of terminology. The application of e.g., 'pinnatipartite' versus 'pinnatisect' or 'trilobed' does not correlate at all with our defined character states. Practically no terminological correlation could be achieved between our data and published descriptions for the forms of main and lateral lobes. We based our form descriptions on geometric elements as earlier defined by Stearn (1983), but their use differs markedly from published descriptions (e.g. ovate in literature versus obovate observed now). Discontinuity may also be observed in terminology relating to leaflet margins such as dentation. Whereas some correlations to our defined character states exist, the combination of cartilaginous tips and scarious margins appeared to be rather a new character (character no. 9). Only diagnoses of *A. lycaonica* and *A. vermicularis* mention this fact explicitely. However, Hoffmann (in Engler, 1894) indicates a 'callous margin' as further leaf character of *Achillea* sect. *Santolinoidea,* which we consider to correspond to our term 'cartilaginous margin'. All these observed inconsistencies may account for the frequent misdeterminations found in herbaria.

4. Significance of character state frequencies for sect. Santolinoidea

In search of unifying characters of this section, frequencies of occurrence of the respective character states were calculated (compare Table 2). There is a tendency towards compact leaves (character no. 1), but imbricate positions do not dominate contrary to the section's defining character (Boissier, 1874; Huber-Morath, 1975). In leaf partition (character no. 3), the tripartite-pinnatisect feature is most frequent, but it accounts only for about half of the section's species. Similarly, the diagonal position of the main lobe to the rachis reaches near 50% occurrence (character no. 6), whereas side lobes tend to be upright to the rachis (character no. 7). Shortly spiniform dentate leaflet margins dominate over other forms (character no. 8) also in the near 50% range. The same is true for the hardly tomentose indumentum (character no. 10). The presence of cartilaginous tips may be correlated with the presence of a scarious margin of varying thickness, which was found to dominate in comparison to the lack of such a margin (character no. 9). Forms of flower heads are more diversified (character no. 11), with a slight dominance of the (narrowly) campanulate

form. Similarly, the form of ligules tends to be (broadly) obtrapeziform in nearly 50% of taxa (character no. 12). More significant is the tendency towards (slightly) 3-crenate margins of ligules (character no. 13). Obovate forms seem to occur more frequently in involucral bracts (character nos. 14, 15) and phyllaries (character no. 16). Finally, yellow is the dominating colour of ligules (character no. 17).

From this perspective, it is difficult to recognise unifying character states for circumscribing sect. *Santolinoidea*. Common features are rather represented by characters as such and not by their states. Thus, macromorphological similarities exist as is expressed by characters such as general leaf structure with the formation of transversal leaflets and a tendency towards formation of scarious margins. These characters, however, are shared with species of *Achillea* sect. *Arthrolepis* and the closely related genus *Leucocyclus*. Similarly, species of *Santolina* L. of the *Anthemideae* are at least characterized by lateral leaflet formation, but with a somewhat different leaflet morphology. This similarity has recently proved to be based on common ontogenetic development in species of sect. *Santolinoidea* and of *Santolina chamaecyparissus* L. and *S. pinnata* Vis., respectively (Eberwein, 1995). Within the *Anthemideae*, the genus *Santolina* has been provisionally placed in *Achilleinae* although chemical and other botanical characters do not favour such a grouping (Bremer & Humphries, 1993). From this aspect, the similar ontogeny of leaf formation might be significant and should be further analysed in related *Anthemideae* genera.

CONCLUSIONS

The present study reveals that many of the analysed morphological character states are useful for species characterization. This is particularly true for many structures of leaves and for some of the bracts and phyllaries, respectively. Additional characters such as growth forms and also the geographic distribution may further add significantly to species characterization. Their analysis, along with a key to species, will form the focus of a subsequent paper (Valant-Vetschera & Kästner, in prep.). These data will then also be discussed in relation to earlier studies on flavonoid diversification (Valant-Vetschera, 1981; Valant-Vetschera & Wollenweber, 1994). By including these data we expect further information to either verify or reject the idea of a polyphyletic origin of *Achillea* sect. *Santolinoidea*, as may be interpreted from the distribution pattern of character states.

Sectional characters may be found in the general leaf structure and possibly also in growth forms and habit. However, the taxonomy of sect. *Santolinoideae* cannot be viewed separately from that of the possibly related sect. *Arthrolepis* and the monotypic genus *Leucocyclus*. It is assumed that a detailed phylogenetic study could clarify the status and the position of these sections within *Achillea* in a similar way as was examplified for the genus *Carlina* of the Compositae (Meusel & Kästner, 1990, 1994, 1996; Meusel *et al.*, 1996).

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