

Comparative Morphology of Achenes of the Tribe *Anthemideae* CASS. (Family *Asteraceae*) and Its Taxonomic Significance

Srovnávací morfologie nážek
z tribus *Anthemideae* CASS. (čeleď *Asteraceae*) a její taxonomický význam

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Abstract — All the Czechoslovakian species of genera *Anthemis* L., *Matricaria* L., *Tripleurospermum* SCH. BIP., *Chrysanthemum* L. and *Tanacetum* L. belonging to the tribe *Anthemideae* CASS. were studied from the viewpoint of morphological and anatomical features of their achenes. It was found that the characters examined have a taxonomic applicability, on the basis of which a key to species and genera was designed. It remains to process the genera *Achillea* L. and *Artemisia* L. of the tribe *Anthemideae* in the same way.

An orientation survey of material confirmed the previous assumption that the characteristic differentiation features of the morphology and anatomy of achenes of selected genera of the tribe *Anthemideae* CASS. of the family *Asteraceae* might make it possible to distinguish between these taxa simply on the basis of achene structure or even that it will be possible to design a key to the species and genera according to the differences of morphology and anatomy of their achenes.

For the study itself we selected the tribe *Anthemideae* as conceived by CRONQUIST (1955). The original division of the family *Asteraceae* was carried out by CASSINI (1826—1834). BENTHAM (1873) then divided the family *Asteraceae* into 13 tribes. CRONQUIST (l.c.) proceeds in his work from BENTHAM's division (l.c.) but does not recognize the tribe *Helenieae* and hence divides the *Asteraceae* into only 12 groups. In the present study I characterize the tribe *Anthemideae* according to CRONQUIST (l.c.) but I omit the genera *Artemisia* L. and *Achillea* L., partly because of the considerable demands of their technical processing (first of all in the field of the anatomy of the achenes). The two genera are intended to be studied in the future.

The work concerns the following species and genera (the order of the treated taxa and their nomenclature follow DOSTÁL, 1958):

- Anthemis* L. — *A. tinctoria* L.
 A. austriaca JACQ.
 A. arvensis L.
 A. ruthenica M. BIEB.
 A. cotula L.
- Matricaria* L. — *M. chamomilla* L.
 M. discoidea DC.
- Tripleurospermum* SCH. BIP. — *T. maritimum* (L.) SCH. BIP.
- Chrysanthemum* L. — *Ch. alpinum* L.
 Ch. leucanthemum L. s.l.
 Ch. rotundifolium W. et K.
 Ch. corymbosum L. — subsp. *corymbosum*
 — subsp. *clusii* (FISCH.) HAND.-MAZZ.
 Ch. zawadzkkii HERB.
 Ch. serotinum L.
- Tanacetum* L. — *T. vulgare* L.

The species *Anthemis orientalis* (L.) DEG. reported in Czechoslovakia from two localities (village Zlosejn, formerly Zlosyň, with the hill Dřínov near Kralupy on Vlt., and the hill Chotobuš near Dobříš) is not included in the treatment. The author could not locate the species at any of the two above localities. It must have vanished from the localities apparently due to a striking change of their character. The latest report on the species *A. orientalis* (specimens PRC and PR) dates from 1903 (sandhills near Zlosejn, leg. HOMOLKA) and from 1901 (Chotobuš near Dobříš, leg. DOMIN). Herbarium specimens could not be examined since the collected plants were in flower so that no achenes were developed.

Materials and Methods

Significant diacritical characters can be examined only on fully mature and intact achenes. Immature achenes may display only little differentiation of the characteristic structures and different colouring of the various parts which are essential for the classification.

It was found to be preferable to collect achenes at the time when the stems begin to desiccate immediately below the head. The heads, however, may not fully lose their original colour even in the dry state. If they are dry and grey-black or grey-brown (including the ray flowers) one may take it for certain that the achenes, too, will have a different colour than the achenes of intact anthodia. Water (above all rain) is an unfavourable factor which greatly alters the colour and sometimes even the structure of the achene surface. It is thus not recommended to collect wet material. Heavily soaked anthodia usually turn black even if dried quickly and may readily get mouldy.

The collected anthodia were freely spread on a sheet of filter paper. After drying, the achenes of the disk flowers were separated from those of the ray flowers and placed in small test-tubes or cellophane bags provided with data on the collection.

In some cases, particularly with the genus *Chrysanthemum* one may gather anthodia before maturity with fully coloured but still soft achenes which are then left to mature in a dry warm room (whole anthodia). This method is particularly suitable for obtaining perfectly mature achenes of ray flowers, the maturation of which is slower.

By studying a greater number of achenes I selected morphological characters typical of the studied species. These characters were then investigated in the entire collected material. For statistical evaluation I measured the length of achenes (with achenes provided with a border the entire length was determined) and the maximum width of the achenes (if the border was wider than the achene proper, the maximum width was measured at the widest part of the achene and not of its border). The number of ribs on the achenes was determined and with species where the achenes contain a border or a coronet the size of these parts was also determined.¹⁾

To establish the differentiation characters of achene anatomy cross sections through the achenes were prepared. Since the pericarp of most species is heavily sclerenchymatic it must be softened before sectioning. With most species, 2-4 hour soaking in water with a few drops of glycerol is enough. With achenes possessing a particularly developed sclerenchymatic pericarp it was found useful either to boil them in water (*Anthemis cotula*) or in 2N KOH (*A. arvensis* and *A. ruthenica*). The last-named achenes can also be softened with lactophenol. The softening process may then take as long as four weeks.

List of localities where the studied species were collected (the localities are designated according to the map supplement of FUTÁK and DOMIN, 1960):

Anthemis tinctoria L.: Dačice, desolate quarry at Toužín — 26; Lovčovice near Police — 26; Hradová near Tisovec — 70.

A. austriaca JACQ.: Kosmonosy near Ml. Boleslav, camping-site — 30; Zlosejn near Veltrusy, the hill of Dřínov — 43; Jaroměř, fields along the road up to Josefov — 57; Šahy, east of the town, the hill Vysoká — 39; Nové Zámky, fields south-westwards — 50.

A. arvensis L.: Zlosejn near Veltrusy, the field on the hill of Dřínov — 43; Ctiboř near Vlašim,

¹⁾ The measurements were always conducted on 100 achenes from the disk and on 100 achenes from the ray of each sample. An exception was formed here only by the data on the species *Chrysanthemum zawadzki* where 400 achenes from the disk and 400 from the ray were investigated, in spite of the fact that the species is found on a single locality in Czechoslovakia. As I managed to collect a greater amount of material I studied it all to lend the highest possible significance to the results. Similarly, with the species *Ch. serotinum* the same reasons led to measuring 1000 achenes from the disk (no achenes are developed from the ray flowers in this species) on material from two localities. 700 achenes were gathered in a native locality at Latorica-Most, 300 were from the Botanical Garden of the Charles University in Prague.

a field —24; Velká Lhota near Dačice, fieldpath up to Poldovka —26; Šahy, east-southern hillside near the town —39; Javorník near Vlašim, fields —24.

A. ruthenica M. BIEB.: Lysá on Elbe, fields along the road to Nymburk —57; Doksany near Roudnice, bank of the river Ohře —42; Zlosejn near Veltrusy, sandbank south-eastwards of the village —43; Hodonín, Strážnice-Přívov railway station, sandbank —48; Hodonín, Rohatec —48; sandbank near Ratiškovice —48; Nové Zámky, at the railway station —50; Plášťovce, south-western edge of the village —50.

A. cotula L.: Ctiboh near Vlašim —24; Javorník near Vlašim —24; Golčův Jeníkov, along the road to Chotěboř —24; Zlosejn near Veltrusy, in the village —43; Podhořany near Kralupy, in the village —57.

Matricaria chamomilla L.: Dobříš, in front of the castle —44; Vlašim, the field near the Smíkov pond —24; Golčův Jeníkov, along the road to Chotěboř —24; Dačice, at the railway station —26; Český Rudolec near Dačice, in the village —26.

M. discoidea DC.: Podhořany near Kralupy, in the village —57; Kosmonosy near Ml. Boleslav —30; Ctiboh near Vlašim —24; Dolní Radčkov distr. Jindřichův Hradec —26; Blučina near Židlochovice —45.

Tripleurospermum maritimum (L.) SCH. BIP.: Doksany, eastern edge of the village —42; Dobříš, the hill Chotobuř —44; Vlašim, the Kojetice yard —24; Třeboň, the bank of Opatovický pond —29; Vnorovy distr. Hodonín, at the village —48; Nové Zámky, at the railway station —50.

Chrysanthemum alpinum L.: Liptovské Tatry, the ridge of the Smrek mountain cca 1900—2000 m a.s.l. —77a; Lipt. Tatry, Smutné sedlo —77a; Lipt. Tatry, Žiarské sedlo under Plačlivó cca 1850 m —77a; High Tatras, chalet Brnčalova chata —77b; H. Tatras, waterfall under Velické pleso mountainlake —77b; H. Tatras, from Žabie plesa mountain lakes to Váhy saddle-back near Rysy ridge —77b; Botanical garden in Kirovsk — USSR;

Chrysanthemum leucanthemum L. — diploid; the road from Český Rudolec to Markvarec —26; Šahy, meadow under Močiar cca 200 m —39; Belanské Tatry, Predné Medodoly, a meadow in mountain pine cca 1600 m —77c; Bel. Tatry, Zadné Medodoly, north-western meadow cca 1500 m —77c; Bel. Tatry, Dolina siedmich prameňov valley —77c;

tetraploid: Chlum near Vinařice, along the road to Ml. Boleslav —30; Vlašim, Horní Lhota, slope on the edge of the village cca 600 m —24; Vlašim, end of the spruce forest in the valley of Milovanický potok brook —24; Dolní Radčkov near Jindř. Hradec, in the village —26; Dolnice near Cheb, at the railway station —31; Skuteč, between Hněvčice and Perálec —27; High Tatras, Stará Lesná, meadow along the road, southern slope —77b;

hexaploid: Bratislava, hillsides between Devín and Karlova Ves cca 170 m —50; Krupina, rocks about 700 m northwards of Kňazova hora cca 450 m —68; Hradová near Tisovec —69; Hungary — Nagy Szenas hill, southern slope, dolomit; Hungary — Bükk, Szarvaskő.

Ch. rotundifolium W. et K.: High Tatras, Velická dolina valley —77b; High Tatras, path from Kežmarská chata to Biela Voda —77b; H. Tatras, Zelené pleso mountain lake under Brnčalova chata —77b; H. Tatras, Kvetnica —77b; Babia hora, southern slope cca 1000 m —85; Nízke Poloniny, on the frontier ridge between Ďurkovec and Rabia skala —88; Sweden — Botanical garden in Uppsala; USSR — Botanical garden in Kirovsk.

Ch. corymbosum L. subsp. *corymbosum*: Chlum near Ml. Boleslav —30; preserve in Kosmonosy near Ml. Boleslav —30; Karlštejn, southern hillside of Doutnác —43; Dobříš, preserve near the chateau —44; Bielé Karpaty, Radějov, along the road from Murán to Cigánka —63.

Ch. corymbosum subsp. *clusii* (FISCH.) HAND.-MAZZ.: High Tatras, path up to Brnčalova chalet —77b; H. Tatras, the valley of Biela Voda —77b; Bel. Tatry, Holubyho dól —77c; Horne Povážie, Vyšná Boca —80a; Nízke Poloniny, the road between Ďurkovec and Rabia skala —88.

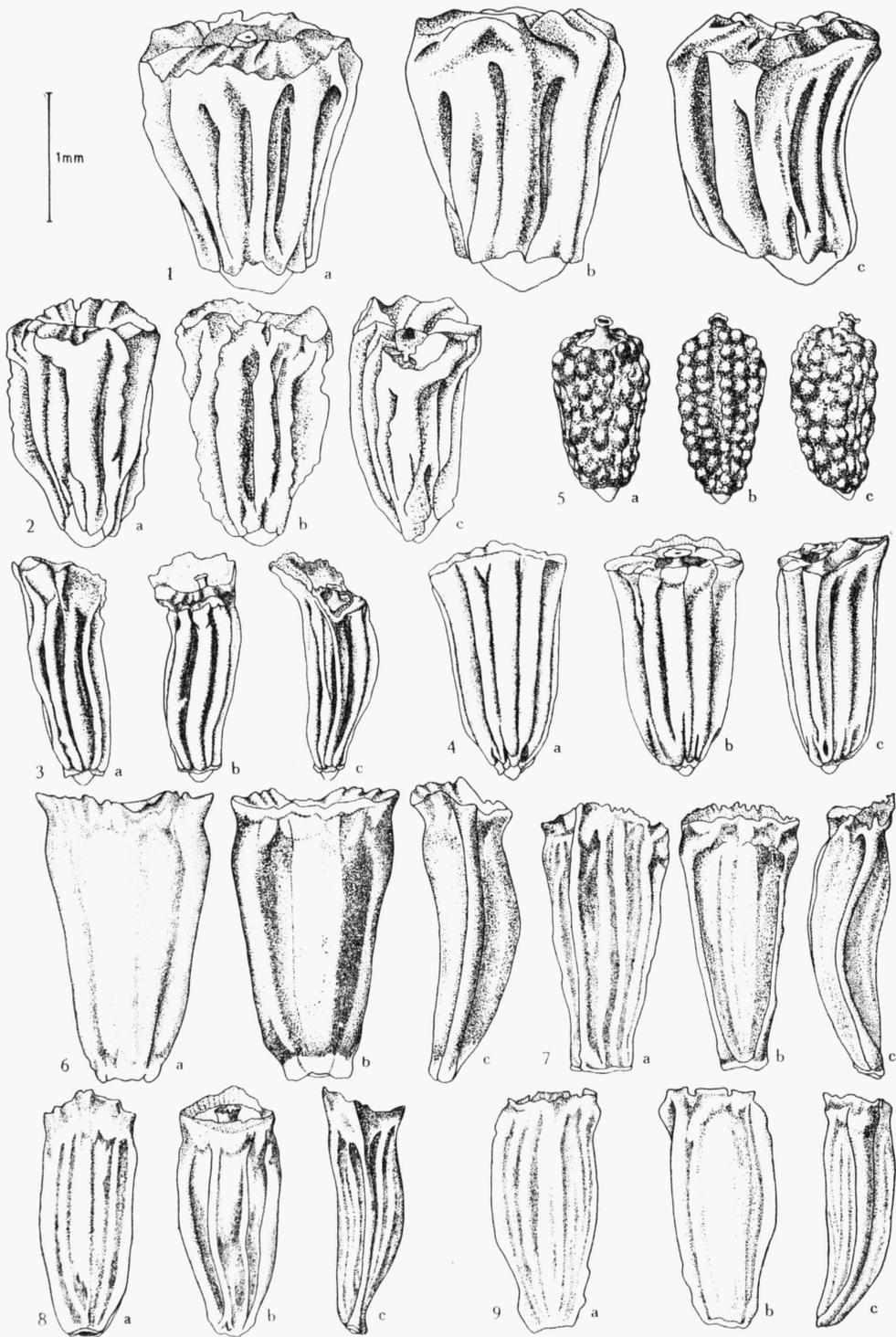
Ch. zawadzki HERB.: Pieniny, on the riverside of Dunajec from Červený Kláštor to Polish frontier —78.

Ch. serotinum L.: Latorica-Most, bottomland forest —52; Botanical garden in Prague.

Tanacetum vulgare L.: Komořany near Prague, on the riverside of Vltava —43; Vlašim, the bank of Smíkov-pond —24; along the road from Dačice to Telč —26; Podlázky near Ml. Boleslav, at weir —30; Veltrusy, around the lock —57; Litomyšl, on the wall of cemetery —27.

Glossary of terms

The achenes of the investigated species possess several characteristic morphological features, readily applicable to differentiating between individual genera and species. These features are not of equal usefulness for the determination of the various taxa and hence are ordered from the more to the less important ones:



Ribs and carinae (shape and number; e.g. Fig. 15–26 and Fig. 13); riblike forms (low and narrow bars of variable number — Fig. 6–9; wide and flat bars in relatively constant number — Fig. 1–4); colouring of the achenes (the same in all parts of achene, Figs 1–9, 17, 18, 25; different on ribs and borders, Fig. 15, 16, 19–24); general shape of the achene; border (absent — Fig. 1, 2, 4, 5, 21; partly present — Fig. 3, 10, 22; along the whole circumference of the achene — Fig. 6–9, 13, 14, 17–20, 23, 24, 26); size of achenes; tip of the achene (flatly obtuse, Fig. 1, 6, 7; obliquely obtuse, Fig. 4, 11, 12); coronet, Fig. 5, 21 (shape, colour); structure of the pericarp surface (macrostructure, Fig. 13, 14, microstructure). The terms used in the key are taken over from DOSTÁL (1948–1950), such as rib, carina, bar, border, but in some cases I was compelled to introduce new designations as no satisfactory terms could be found in publications of a similar nature. Thus the word coronet is used for the residual nectary at the style base, or only for the residual style growing from the centre of the apical plate of the achene (Fig. 3–5, 21). When viewing the achene from the side, the coronet is usually covered with the border (e.g. Fig. 23, 24). CVELEV (1961) does not distinguish between the individual parts at the achene apex (i.e. border and coronet) and uses a summary term coronet for both. The term peduncle is used for the conical structure at the base of the achenes in *Anthemis arvensis* (Fig. 1, 2), *A. ruthenica* (Fig. 3, 4), *A. cotula* (Fig. 5) by means of which the achene is attached to the torus. The structure is characteristic for the above species by its shape. Cross rugosity of the surface refers to the structures difficult to define morphologically located at the achenes of *Tripleurospermum maritimum* (Fig. 13, 14) which is always oriented crosswise, is of different size and corrugated. The surface of the individual wrinkles is finely crenulated. In fully mature achenes the corrugation is very dark-brown or black.

In the anatomy of the achenes of the above species one may distinguish constant diacritical characters concentrated in the pericarp (Fig. 29–41), rarely in the testa (Fig. 34, 38). The seed lobes of all species have a similar structure and they do not appear to possess a taxonomic importance. Along the circumference of the seed lobes (even at the sides adjacent to each other) a cross section will reveal a clearly discrete layer of square cells. At the inner side of both seed lobes there are one or two layers of palisade cells underneath this layer. The remaining tissue of the seed lobes is formed by more or less oval or round cells, which are larger than the square cells of the surface layer. The seed lobes are in close contact with the endosperm (Fig. 27–40) formed in the tangential direction by elongated cells. The walls of these cells are strongly light-refracting and appear white in cross section. The cell content is dark-brown to brown-green, of granular structure. Similarly, the endosperm does not differ much from species to species. The testa is usually multi-layered (Fig. 35–40), in mature achenes the layer(s) nearer the endosperm are compressed while in the layer adjacent to the pericarp the individual cells are clearly seen.² The pericarp is composed of several layers in all cases (Fig. 27–41) as is characteristic for the individual species. Its anatomy is in agreement with the morphology and structure of the achenes.

When investigating the anatomy of the achenes of the studied species the following features were analyzed: distribution and appearance of parenchyma in the pericarp (single-layered — Fig. 40, multi-layered — Fig. 37); distribution and appearance of sclerenchyma in the pericarp (oval braces of the lobes — Fig. 37–39, palisade sclerenchyma — Fig. 30–32, 39, multi-layered sclerenchyma — Fig. 27–29, 41, colouring of cells); number and shape of secretory ducts in the pericarp (Fig. 32b, 33, 35, 36); number of slime cells in the pericarp (always only on the surface, Fig. 29, 34, 35, 38); form of the cross section through the achene (number and shape of the lobes, general appearance); size and shape of epidermal cells; testa (appearance of its cells, shape, colour).

² It would be useful to study the structure of the endosperm and of the testa during ontogenetic development of the achenes as in mature achenes the structure may be unclear and the number of the individual layers cannot be determined accurately (particularly with *Tanacetum vulgare*). I intend to take up the problem using selected species.

Fig. 1–9: *Anthemis arvensis* L. — Fig. 1. Achene from the disk: a — view at the adaxial side of the achene, b — abaxial view, c — lateral view. — Fig. 2. Achene from the ray: a — adaxial view, b — abaxial view, c — lateral view. — *Anthemis ruthenica* M. BIEB. — Fig. 3. The achene from the ray: a — adaxial view, b — abaxial view, c — lateral view. — Fig. 4. Achene from the disk: a — adaxial view, b — abaxial view, c — lateral view. — *Anthemis cotula* L. — Fig. 5. Achene from the disk: a — adaxial view, b — abaxial view, c — lateral view. — *Anthemis austriaca* JACQ. — Fig. 6. Achene from the disk: a — adaxial view, b — abaxial view, c — lateral view. — Fig. 7. Achene from the ray: a — adaxial view, b — abaxial view, c — lateral view. — *Anthemis tinctoria* L. — Fig. 8. Achene from the disk: a — adaxial view, b — abaxial view, c — lateral view. — Fig. 9. Achene from the ray: a — adaxial view, b — abaxial view, c — lateral view.

For designating the individual layers and groups of cells of the pericarp and of other parts of achene, visible in the cross section, I use terms introduced into the literature by NETOLITZKY (1926), KLAN (1947), HORVATIĆ (1963), DOSTÁL and FUTÁK (1966), ČERNOHORSKÝ (1967).

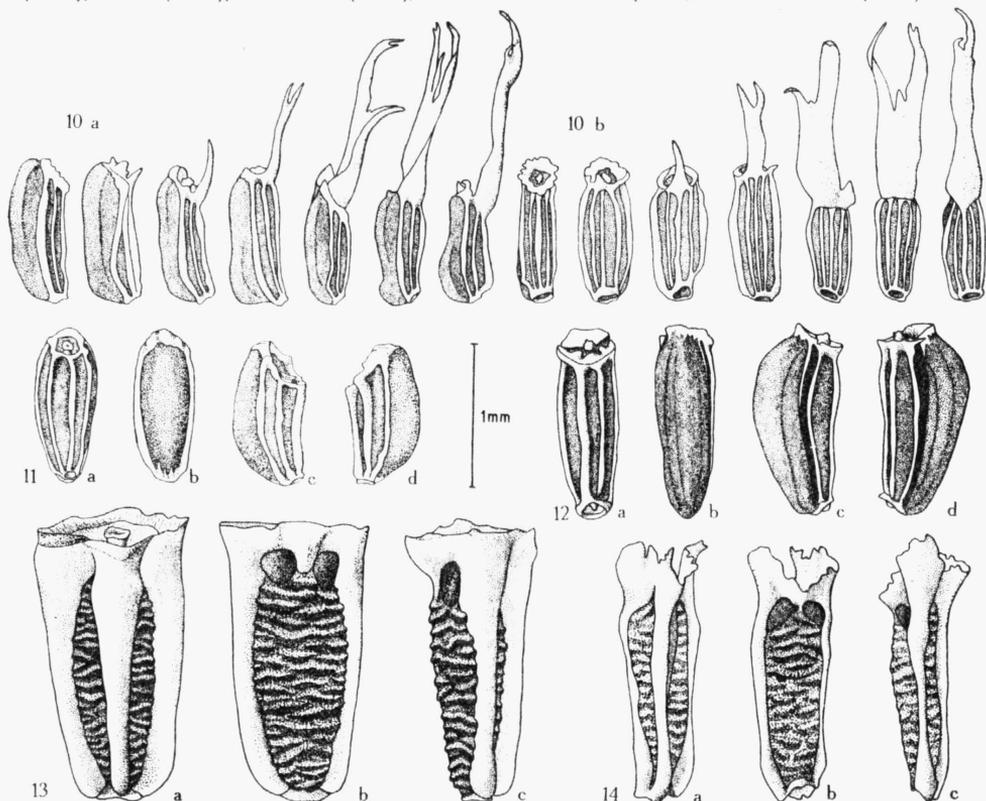


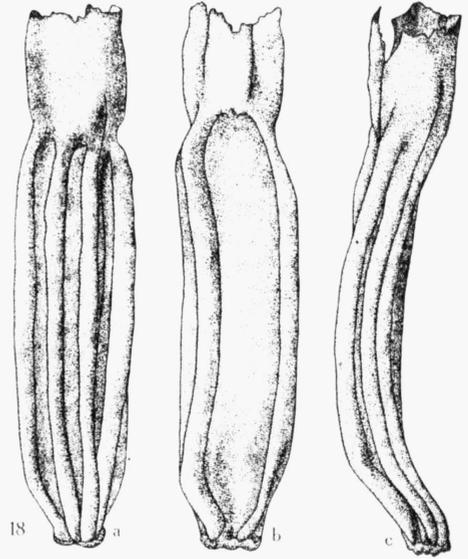
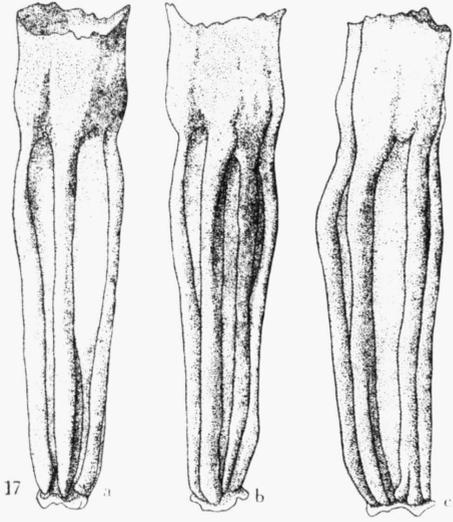
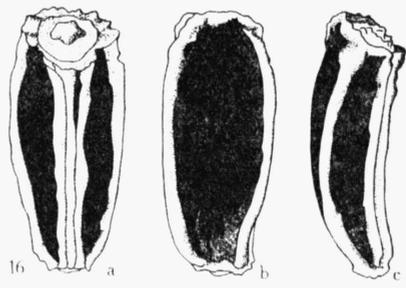
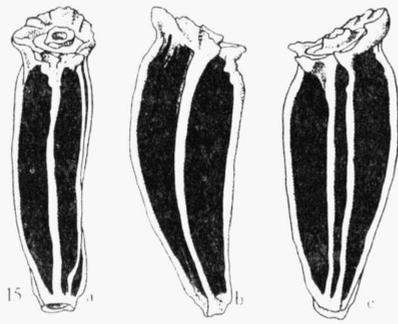
Fig 10—14: *Matricaria chamomilla* L. — Fig. 10. Achenes from the ray, survey of the variability in border forms: a — lateral views, b — adaxial views. — Fig. 11. Achene from the disk: a — adaxial view, b — abaxial view, c, d — lateral views. — *Matricaria discoidea* DC. — Fig. 12. Achene from the disk: a — adaxial view, b — abaxial view, c, d — lateral views. — *Tripleurospermum maritimum* (L.) SCH. Bip. — Fig. 13. Achene from the disk: a — adaxial view, b — abaxial view, c — lateral view. — Fig. 14. Achene from the ray: a — adaxial view, b — abaxial view, c — lateral view.

Statistical evaluation of the species studied

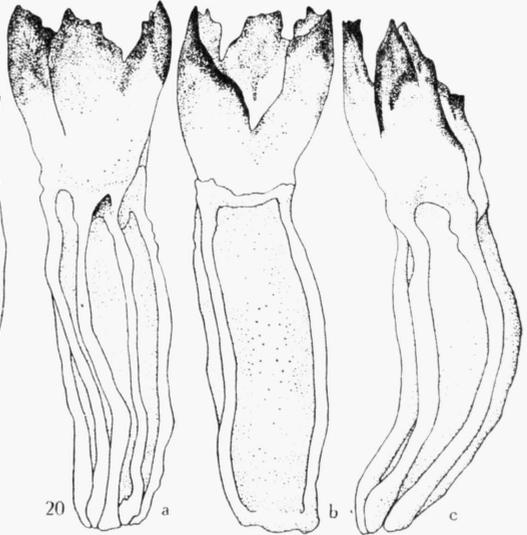
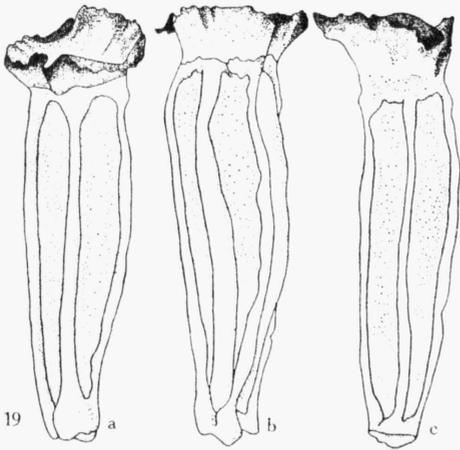
The following list contains values of achene length and width, or of border and coronet length. When processing the measurements I used the statistical mean \bar{x} , the standard error $s_{\bar{x}}$ and standard deviation of the means (HRUBÝ and KONVIČKA, 1954). All values were indicated in mm.

Fig. 15—20: *Chrysanthemum zawadzki* HERB. — Fig. 15. Achene from the disk: a — adaxial view, b, c — lateral views. — Fig. 16. Achene from the ray: a — adaxial view, b — abaxial view, c — lateral view.

Chrysanthemum corymbosum L. s.l. — Fig. 17. Achene from the disk: a — adaxial view, b — abaxial view, c — lateral view. — Fig. 18. Achene from the ray: a — adaxial view, b — abaxial view, c — lateral view. — *Chrysanthemum alpinum* L. — Fig. 19. Achene from the disk: a — adaxial view, b — abaxial view, c — lateral view. — Fig. 20. Achene from the ray: a — adaxial view, b — abaxial view, c — lateral view.



1mm



Anthemis tinctoria (300 achenes of the disk and ray flowers were measured):

achenes from the disk	— length:	$\bar{x} = 1.91$	$s_{\bar{x}} = 0.07$	$s = 1.29$
	width:	$\bar{x} = 0.75$	$s_{\bar{x}} = 0.005$	$s = 0.09$
achenes from the ray	— length:	$\bar{x} = 1.86$	$s_{\bar{x}} = 0.004$	$s = 0.08$
	width:	$\bar{x} = 0.85$	$s_{\bar{x}} = 0.004$	$s = 0.08$

Anthemis austriaca (500 achenes from the disk and ray flowers):

achenes from the disk	— length:	$\bar{x} = 2.43$	$s_{\bar{x}} = 0.01$	$s = 0.24$
	width:	$\bar{x} = 1.06$	$s_{\bar{x}} = 0.006$	$s = 0.14$
	length of border:	$\bar{x} = 0.40$	$s_{\bar{x}} = 0.005$	$s = 0.13$
achenes from the ray	— length:	$\bar{x} = 2.20$	$s_{\bar{x}} = 0.006$	$s = 0.14$
	width:	$\bar{x} = 0.89$	$s_{\bar{x}} = 0.005$	$s = 0.12$
	length of border:	$\bar{x} = 0.20$	$s_{\bar{x}} = 0.003$	$s = 0.07$

Anthemis arvensis (500 achenes from the disk and ray flowers):

achenes from the disk	— length:	$\bar{x} = 2.18$	$s_{\bar{x}} = 0.008$	$s = 0.19$
	width:	$\bar{x} = 1.47$	$s_{\bar{x}} = 0.014$	$s = 0.32$
achenes from the ray	— length:	$\bar{x} = 1.93$	$s_{\bar{x}} = 0.008$	$s = 0.19$
	width:	$\bar{x} = 1.14$	$s_{\bar{x}} = 0.009$	$s = 0.20$

Anthemis ruthenica (800 achenes from the disk and ray flowers):

achenes from the disk	— length:	$\bar{x} = 1.82$	$s_{\bar{x}} = 0.006$	$s = 0.19$
	width:	$\bar{x} = 0.85$	$s_{\bar{x}} = 0.004$	$s = 0.13$
achenes from the ray	— length:	$\bar{x} = 1.74$	$s_{\bar{x}} = 0.005$	$s = 0.15$
	width:	$\bar{x} = 0.66$	$s_{\bar{x}} = 0.003$	$s = 0.10$
	length of border:	$\bar{x} = 0.18$	$s_{\bar{x}} = 0.002$	$s = 0.07$

Anthemis cotula (500 achenes from the disk, no achenes are developed from the ray flowers in this species):

achenes from the disk	— length:	$\bar{x} = 1.53$	$s_{\bar{x}} = 0.005$	$s = 0.12$
	width:	$\bar{x} = 0.60$	$s_{\bar{x}} = 0.003$	$s = 0.06$

Matricaria chamomilla (500 achenes from the disk):³⁾

achenes from the disk	— length:	$\bar{x} = 1.00$	$s_{\bar{x}} = 0.004$	$s = 0.09$
	width:	$\bar{x} = 0.37$	$s_{\bar{x}} = 0.002$	$s = 0.05$

Matricaria discoidea (500 achenes from the disk):

— length:	$\bar{x} = 1.27$	$s_{\bar{x}} = 0.005$	$s = 0.11$
width:	$\bar{x} = 0.47$	$s_{\bar{x}} = 0.003$	$s = 0.06$

Tripleurospermum maritimum (600 achenes from the disk and ray flowers):

achenes from the disk	— length:	$\bar{x} = 1.99$	$s_{\bar{x}} = 0.09$	$s = 0.22$
	width:	$\bar{x} = 0.92$	$s_{\bar{x}} = 0.006$	$s = 0.15$
	length of border:	$\bar{x} = 0.23$	$s_{\bar{x}} = 0.003$	$s = 0.07$
achenes from the ray	— length:	$\bar{x} = 1.86$	$s_{\bar{x}} = 0.009$	$s = 0.23$
	width:	$\bar{x} = 0.87$	$s_{\bar{x}} = 0.009$	$s = 0.22$
	length of border:	$\bar{x} = 0.29$	$s_{\bar{x}} = 0.003$	$s = 0.09$

Chrysanthemum alpinum (700 achenes from the disk and ray flowers):

achenes from the disk	— length:	$\bar{x} = 3.02$	$s_{\bar{x}} = 0.01$	$s = 0.32$
	width:	$\bar{x} = 0.77$	$s_{\bar{x}} = 0.003$	$s = 0.08$
	length of border:	$\bar{x} = 0.60$	$s_{\bar{x}} = 0.006$	$s = 0.17$
achenes from the ray	— length:	$\bar{x} = 3.62$	$s_{\bar{x}} = 0.02$	$s = 0.55$
	width:	$\bar{x} = 0.78$	$s_{\bar{x}} = 0.004$	$s = 0.11$
	length of border:	$\bar{x} = 1.00$	$s_{\bar{x}} = 0.01$	$s = 0.30$

³⁾ Few ray achenes are developed in this species. If they have no border their size is more or less the same as that of disk achenes while the types with a border (Fig. 10a, b) are usually smaller than those from the disk.

Chrysanthemum leucanthemum s.l. (1700 achenes from the disk and ray):⁴⁾

achenes from the disk	length:	$\bar{x} = 2.29$	$s_{\bar{x}}^- = 0.008$	$s = 0.34$
	width:	$\bar{x} = 0.73$	$s_{\bar{x}}^- = 0.002$	$s = 0.09$
	length of coronet:	$\bar{x} = 0.22$	$s_{\bar{x}}^- = 0.001$	$s = 0.06$
achenes from the ray	length:	$\bar{x} = 2.46$	$s_{\bar{x}}^- = 0.015$	$s = 0.63$
	width:	$\bar{x} = 0.78$	$s_{\bar{x}}^- = 0.003$	$s = 0.12$
	length of border:	$\bar{x} = 0.57$	$s_{\bar{x}}^- = 0.008$	$s = 0.36$

Diploid taxon of *Chrysanthemum leucanthemum* (500 achenes from disk and ray flowers):

achenes from the disk	length:	$\bar{x} = 2.11$	$s_{\bar{x}}^- = 0.01$	$s = 0.23$
achenes from the ray	length:	$\bar{x} = 2.09$	$s_{\bar{x}}^- = 0.02$	$s = 0.36$

Tetraploid taxon of *Ch. leucanthemum* (700 achenes from disk and ray):

achenes from the disk	length:	$\bar{x} = 2.18$	$s_{\bar{x}}^- = 0.009$	$s = 0.26$
achenes from the ray	length:	$\bar{x} = 2.13$	$s_{\bar{x}}^- = 0.012$	$s = 0.33$

hexaploid taxon (500 achenes from the disk and ray flowers):

achenes from the disk	length:	$\bar{x} = 2.62$	$s_{\bar{x}}^- = 0.013$	$s = 0.29$
achenes from the ray	length:	$\bar{x} = 3.32$	$s_{\bar{x}}^- = 0.02$	$s = 0.45$

The problems of the mutual relationships between the diploid, tetraploid and hexaploid taxa within *Chrysanthemum leucanthemum* were taken up by ZELEŇ (1969 ms.).

Chrysanthemum rotundifolium (800 achenes from the disk and ray flowers):

achenes from the disk	length:	$\bar{x} = 3.14$	$s_{\bar{x}}^- = 0.01$	$s = 0.39$
	width:	$\bar{x} = 0.70$	$s_{\bar{x}}^- = 0.004$	$s = 0.11$
	length of border:	$\bar{x} = 0.66$	$s_{\bar{x}}^- = 0.008$	$s = 0.25$
achenes from the ray	length:	$\bar{x} = 3.44$	$s_{\bar{x}}^- = 0.01$	$s = 0.36$
	width:	$\bar{x} = 0.71$	$s_{\bar{x}}^- = 0.004$	$s = 0.13$
	length of border:	$\bar{x} = 1.14$	$s_{\bar{x}}^- = 0.009$	$s = 0.28$

Chrysanthemum corymbosum subsp. *corymbosum* (500 achenes):

achenes from the disk	length:	$\bar{x} = 3.40$	$s_{\bar{x}}^- = 0.01$	$s = 0.24$
	width:	$\bar{x} = 0.75$	$s_{\bar{x}}^- = 0.003$	$s = 0.07$
	length of border:	$\bar{x} = 0.66$	$s_{\bar{x}}^- = 0.007$	$s = 0.15$
achenes from the ray	length:	$\bar{x} = 3.56$	$s_{\bar{x}}^- = 0.015$	$s = 0.33$
	width:	$\bar{x} = 0.82$	$s_{\bar{x}}^- = 0.004$	$s = 0.09$
	length of border:	$\bar{x} = 0.68$	$s_{\bar{x}}^- = 0.005$	$s = 0.13$

Ch. corymbosum subsp. *clusii* (500 achenes from the disk and ray):

achenes from the disk	length:	$\bar{x} = 3.68$	$s_{\bar{x}}^- = 0.015$	$s = 0.34$
	width:	$\bar{x} = 0.75$	$s_{\bar{x}}^- = 0.003$	$s = 0.07$
	length of border:	$\bar{x} = 0.77$	$s_{\bar{x}}^- = 0.007$	$s = 0.17$
achenes from the ray	length:	$\bar{x} = 3.67$	$s_{\bar{x}}^- = 0.02$	$s = 0.40$
	width:	$\bar{x} = 0.88$	$s_{\bar{x}}^- = 0.005$	$s = 0.12$
	length of border:	$\bar{x} = 0.87$	$s_{\bar{x}}^- = 0.009$	$s = 0.20$

Chrysanthemum zawadzki (400 achenes from the disk and ray flowers):

achenes from the disk	length:	$\bar{x} = 2.14$	$s_{\bar{x}}^- = 0.008$	$s = 0.17$
	width:	$\bar{x} = 0.67$	$s_{\bar{x}}^- = 0.005$	$s = 0.10$
achenes from the ray	length:	$\bar{x} = 1.85$	$s_{\bar{x}}^- = 0.009$	$s = 0.18$
	width:	$\bar{x} = 0.61$	$s_{\bar{x}}^- = 0.006$	$s = 0.12$

4) The individual taxa within the species *Chrysanthemum leucanthemum* differ from one another in particular in the length of the achenes (differences in the achene width, length of the coronet or border are insignificant). The difference is clearly visible between a diploid and a hexaploid taxon or between a tetra- and hexaploid taxon while between the diploid and tetraploid taxon only an insignificant difference exists. The results of measurement are shown in the following review:

Chrysanthemum serotinum (1000 achenes from the disk, no achenes are developed from the ray flowers in this species):

length:	$\bar{x} = 2.55$	$s_{\bar{x}} = 0.01$	$s = 0.32$
width:	$\bar{x} = 0.85$	$s_{\bar{x}} = 0.003$	$s = 0.09$
length of border:	$\bar{x} = 0.20$	$s_{\bar{x}} = 0.002$	$s = 0.06$
number of ribs on the achenes:	$\bar{x} = 8.04$	$s_{\bar{x}} = 0.02$	$s = 0.73$

Tanacetum vulgare (600 achenes from the disk flowers):

length:	$\bar{x} = 1.78$	$s_{\bar{x}} = 0.005$	$s = 0.14$
width:	$\bar{x} = 0.80$	$s_{\bar{x}} = 0.003$	$s = 0.08$
length of border:	$\bar{x} = 0.22$	$s_{\bar{x}} = 0.001$	$s = 0.04$

Discussion

It was found by a detailed investigation of achenes of the selected species that various features of morphology and anatomy possess different stability and hence are of different taxonomic importance. In view of these facts it was essential to determine for the individual species the truly constant and characteristic features of taxonomic importance.

In the following paragraphs I shall deal in sequence with the significance of the individual characters from the point of view of their stability and importance. The size of achenes of the various species is not a reliable distinguishing character. The range of size variability, in particular of achene length is rather wide for most species so that the limiting values of size of individual species often overlap. The size of achenes can thus serve only as one of the distinguishing features completing the overall character of the achene but it cannot be taken as a principal distinguishing feature. The only exception here is the achene of *Matricaria chamomilla* (Fig. 10, 11) which, by its minute size, permits differentiation from all other species. The achene length can serve partly as one of the characters applicable for differentiating between taxa of *Chrysanthemum leucanthemum* (see the statistical treatment). The ribs and carinae are a more or less diacritical feature of achenes of the species studied, most of all of the disk flowers where the variability of the number of these forms is rather low (up to 10%), like its range (most often ± 1 rib). The number of ribs on achenes from the ray displays a far greater variability than those of the disk even with species containing a constant number of ribs. Likewise, the shape of the ribs and their planar arrangement on achenes does not vary much and can thus serve as a distinguishing feature. The flat wide bars occurring in a relatively constant number (10) on the achenes of *Anthemis arvensis* (Fig. 1, 2) and *A. ruthenica* (Fig. 3, 4) also represent a fine diacritical feature. The bars are separated only by narrow deep grooves which usually do not follow the entire length of the achene. Sometimes, the grooves are branched and form notches in the bars, this complicating their counting. The appearance of ribs and bars is associated with the colour of achenes. The colour changes with the degree of maturity but still it represents a satisfactory diacritical feature for the individual species. A prerequisite here is well developed and ripe material.

A characteristic and stable feature of all species is the conformation of the apical part of the achene, in particular its shape, or the slope of the terminal plane, the shape and size of the coronet and the consistency and height of the border. The height of the border serves for differentiating between achenes of the ray and of the disk flowers, the border of the former being generally much longer (Fig. 19, 20, 23, 24). In *Chrysanthemum leucanthemum*

the border is developed only on the ray achenes (Fig. 22), the achenes of the disk having no border (Fig. 21), as achenes of the disk and ray flowers of *Anthemis arvensis* (Fig. 1, 2) and those of the disk of *A. cotula* (Fig. 5), *A. ruthenica* (Fig. 4) and *Matricaria chamomilla* (Fig. 11).⁵⁾ The border colour

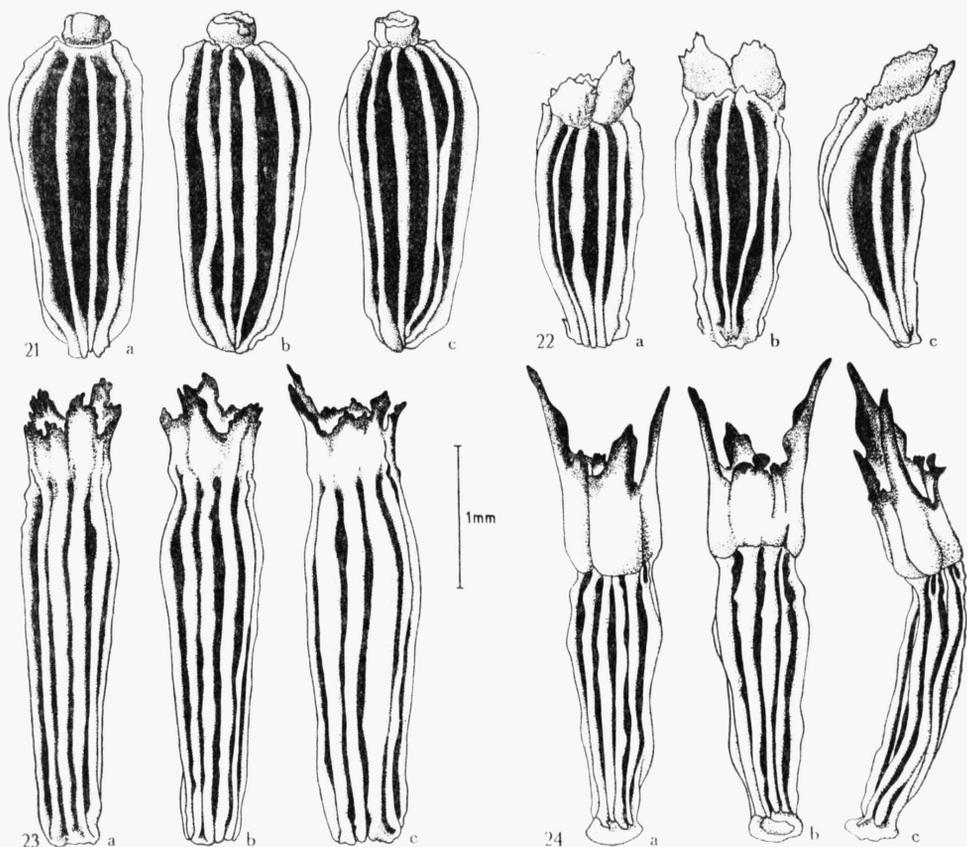


Fig. 21–24: *Chrysanthemum leucanthemum* L. s.l. — Fig. 21. Achene from the disk: a — adaxial view, b — abaxial view, c — lateral view. — Fig. 22. Achene from the ray: a — adaxial view, b — abaxial view, c — lateral view. — *Chrysanthemum rotundifolium* W. et K. — Fig. 23. Achene from the disk: a — adaxial view, b — abaxial view, c — lateral view. — Fig. 24. Achene from the ray: a — adaxial view, b — abaxial view, c — lateral view.

is always the same as that of the ribs. In mature achenes of the disk and of the ray of *Chrysanthemum rotundifolium* (Fig. 23, 24) and *Ch. alpinum* (Fig. 19, 20) the border edge is dark brown (as if scorched). Even this colour can serve in the above species as an auxiliary diacritical feature as it is stable and characteristic for both species.

⁵⁾ Achenes of the ray of *Matricaria chamomilla* display great variability in the conformation of the one-sided, tattered, membranous border (Fig. 10a, b). Most often, however, the border is completely absent in these achenes (Fig. 10a, b — 1st type) or forms only a short narrow end at the adaxial side (2nd type). Occasionally, the border can be longer than the achene itself, very narrow, separated into 2–3 sharp ends at the apex (Fig. 10a, b — 6th and 7th type).

Shape, colour and site of the coronet show low variability but their taxonomic importance is negligible as the coronets of the individual species are shaped very similarly and, when viewed from the side, are usually covered with the border. An exception is formed here by the achenes of the disk of *Chrysanthemum leucanthemum* (Fig. 21) which is strikingly yellow-orange, cylindrical and not covered by the border so that it helps in distinguishing this species.

The surface microstructure of the pericarp, in spite of its relative stability, can be used for species differentiation only in connection with other clearer characters of the achene morphology.

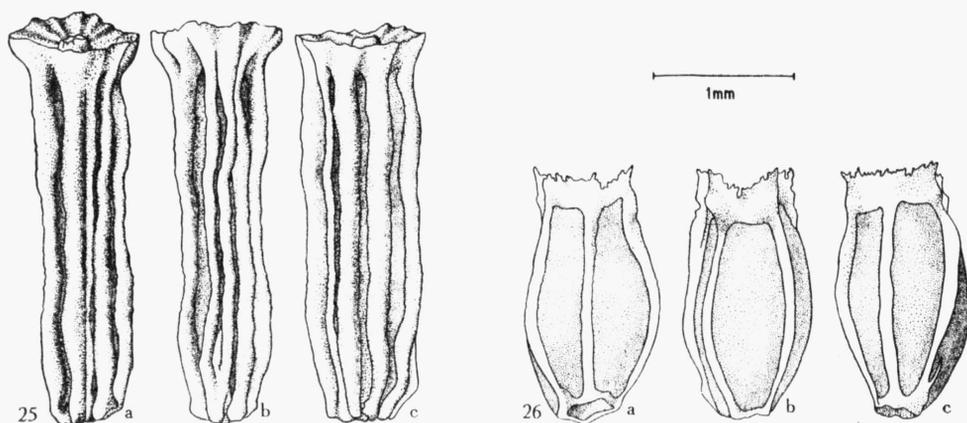


Fig. 25—26: *Chrysanthemum serotinum* L. — Fig. 25. Achene from the disk: a — adaxial view, b — abaxial view, c — lateral view. — *Tanacetum vulgare* L. — Fig. 26. Achene from the disk: a — adaxial view, b — abaxial view, c — lateral view.

The last, even if not negligible, character is the general shape of the achenes. This is a very stable character and characterizes the individual species so that it has a considerable taxonomic importance.

In general it may be said that most of the stable characters mentioned in this chapter have their significance particularly for differentiating between species of a single genus. In spite of this, however, it was possible to apply these characters to assembling a key to genera. E.g., the achenes of *Anthemis* (Fig. 1—9) are markedly differentiated from other genera by the absence of ribs (compare with the explanation of the morphological terms used here). Likewise, the achenes of other genera differ from one another.

A second pronounced group of characters with taxonomic significance is the group of stable diacritical characters of internal morphology of the achene pericarp. Perhaps the most striking and very stable character of this type occurring in some species is the presence of large secretory ducts in the pericarp (Fig. 32b, 33, 35, 36). The taxonomic value of the ducts is given by their shape and number. The shape is a stable quantity, the number more or less stable but sometimes it exhibits slight variation, in common with the number of ribs with which it is directly associated. The same taxonomic value as the secretory ducts is possessed by the slime cells (cellulae mucilaginosae, HORVATIĆ, l.c.; Fig. 29, 34, 35, 38). On a cross section of the achene the cells are placed either at the apices of the pericarp lobes (formed

by ribs, Fig. 35) or along the whole section circumference (Fig. 29, 33). Their shape and localization are stable for a given species.⁶⁾

Another important character of taxonomic significance is the appearance, amount and distribution of the sclerenchyma and parenchyma in the achene pericarp. The distribution of the individual layers is very stable and characteristic for the species. Somewhat more variable is the thickness of the individual layers. In achenes, the lobes of which are formed in cross section by sclerenchyma at their circumference and by parenchyma inside (Fig. 35, 36), the ratio of the two tissue types changing in favour of sclerenchyma with age. However, the lobes never become completely sclerenchymatic.

The size and shape of epidermal cells is a character which is more or less stable for various species but its taxonomic significance is minimal. The differences between species are too small to be of practical importance. An exception is formed by the striking epidermis of *Chrysanthemum leucanthemum* (Fig. 35), the cells of which are largest in the grooves between lobes and decrease gradually toward the pericarp apices terminated with a slime cell.

A stable and typical character observable in cross sections through achenes is also their outline, or the shape of its individual lobes in section with a lobular margin. This character is of taxonomic importance for all the studied species, with the exception of *Anthemis arvensis* (Fig. 27) and *A. ruthenica* (Fig. 28) where the general shape of the section is the same in both species and the depth of pericarp lobularity as well as the shape of the lobes vary. For differentiating between the two species one may use the size of the cross section through their achenes (sections through the achenes of *A. arvensis* are much larger).

All the heretofore named characters of achene anatomy concerned the pericarp. It is thus necessary to characterize the features of the testa, the endosperm and the seed lobes. The seed lobes do not appear to have any taxonomic importance for any of the species studied. They have a characteristic structure (see above) but the structure does not practically differ from species to species. Likewise, the diacritical significance of the endosperm is not great for similar reasons. The taxonomical significance of the testa is also not outstanding.⁷⁾

In follows from the above review of the stability and significance of the diacritical characters of achene morphology and anatomy that the taxonomic importance of the individual characters consist in their confrontation with other characters. The species cannot be determined on the basis of a single character viewed out of context with the whole.

⁶⁾ The number of slime cells is constant only in *Chrysanthemum leucanthemum* (Fig. 35) where it forms the apical cell of each lobe (section through the rib) and is hence equal to the number of ribs (10). In the other three species, the pericarp of which contains slime cells, the number is variable. In *Ch. zawadzki* it is 10–20 (Fig. 38), in *Anthemis cotula* most often 10 (Fig. 29) and in *Matricaria chamomilla* (Fig. 34) there are 5 on the lobe apices at the adaxial and 5 (or more) on the abaxial side. BRIQUET (1916) mentions slime cells in the epidermis of *Anthemis arvensis* (Fig. 27) but I could not confirm their existence in this species.

⁷⁾ In the genus *Chrysanthemum* (Fig. 35–40) the testa is always composed of several layers even at complete maturity of the achenes. The cells of the outer layer are clearly marked, the internal layers are usually compressed and the individual cells are not distinguishable. In *Ch. serotinum* (Fig. 37) and *Ch. zawadzki* (Fig. 38) the cellular layer of the testa is always dark brown, probably filled with a secretion and apparently accounts for the brown-red colour of the achenes of *Ch. zawadzki* (Fig. 15, 16). The testa of the other genera usually shows a simpler structure and is insignificant from the taxonomic point of view.

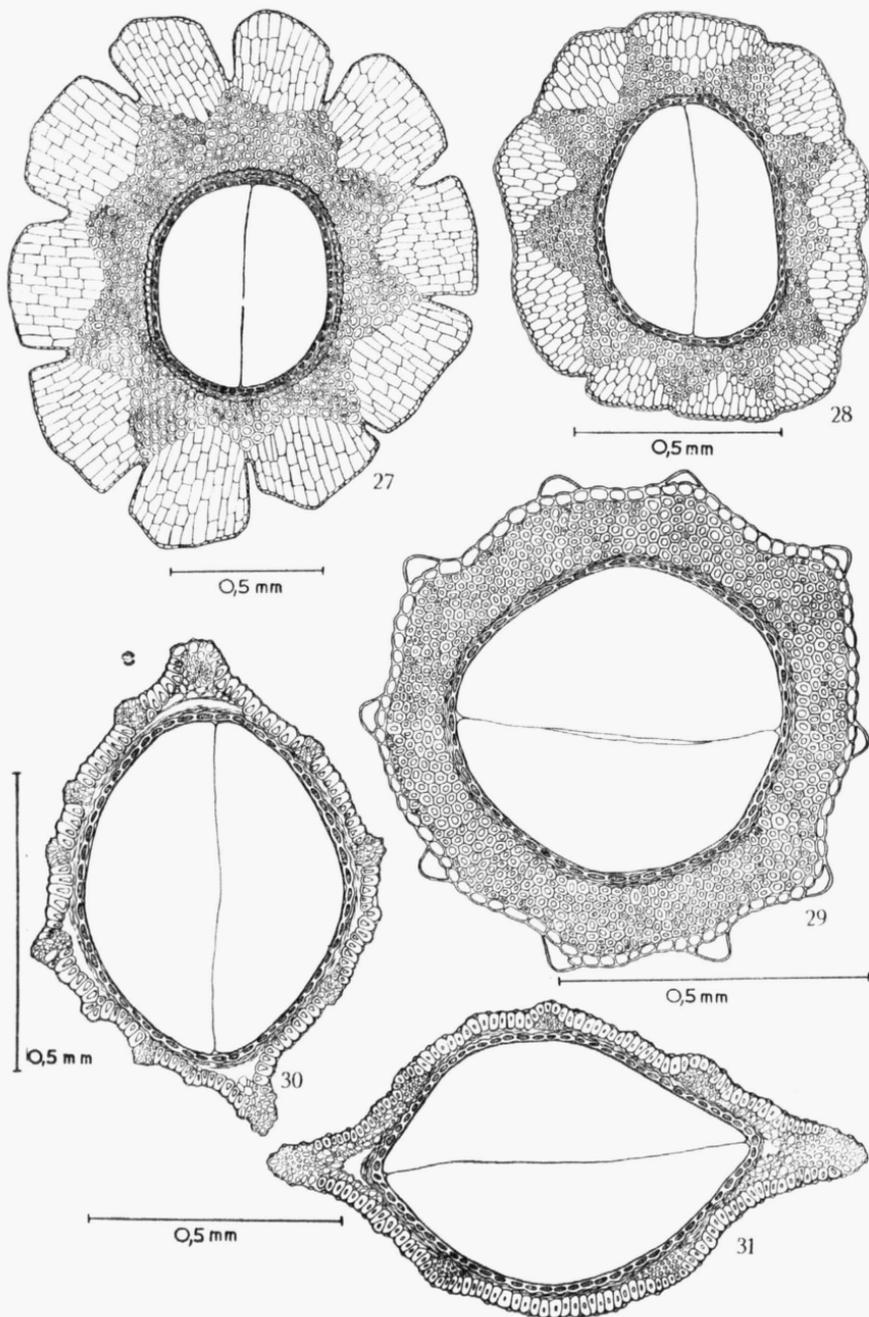


Fig. 27—31: Cross sections in the middle part of the achene. — Fig. 27. *Anthemis arvensis* L. — Fig. 28. *A. ruthenica* M. BIER. — Fig. 29. *A. cotula* L. — Fig. 30. *A. tinctoria* L. — Fig. 31. *A. austriaca* JACQ.

Carpological studies concerning at least some of the species of the tribe *Anthemideae* are rather infrequent. I should perhaps mention the work of BRIQUET (l.c.) and BERTSCH (1941), the first of which deals with the anatomy of achenes of *Anthemis*, *Ormenis* and *Santolina* while the second concerns the morphology of achenes of some genera of the tribe *Anthemideae*. In the paper of BERTSCH (l.c.) a key is presented to the genera and to the species according to achenes. The work contains data on representatives of most monocotyledonous and dicotyledonous plants occurring

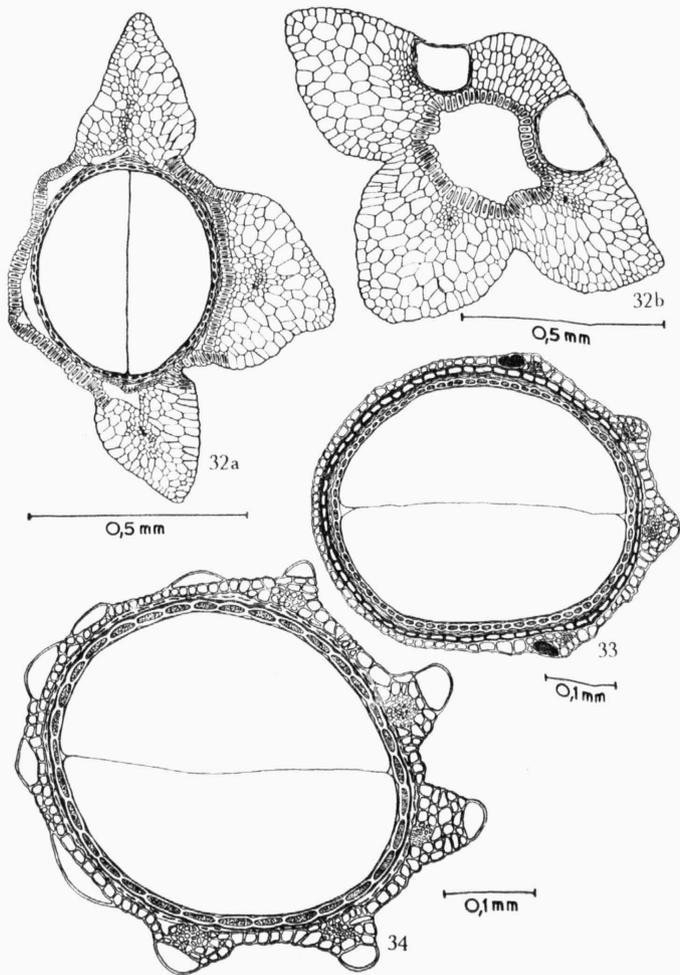


Fig. 32—34: *Tripleurospermum maritimum* (L.) SCH. BIP. — Fig. 32a. Cross section in the middle part of the achene. — Fig. 32b. Cross section in the upper third of the achene (in the spot of the secretory reservoirs). — Fig. 33. *Matricaria discoidea* DC. — cross section in the middle part of the achene. — Fig. 34. *Matricaria chamomilla* L. — cross section in the middle part of the achene.

in this country. The principal diaeretical character used is the size of fruits and their hairs, particularly the first of these being not suitable for the present tribe. Recently, another paper of a similar nature by SCHERMANN (1967) appeared, it being more detailed than the work of BERTSCH (l.c.). The work contains a key to plants according to the structure of their fruits, each of the species having a short description of the fruit and its picture. Some pictures and descriptions (e.g.

Tanacetum vulgare, *Chrysanthemum serotinum*, *Matricaria discoidea*) are at variance with my own observations and with data in the literature. HORVATIĆ (l.c.) studied the anatomy of achenes of *Chrysanthemum leucanthemum* and *Ch. rotundifolium*. He pointed to the substantial differences in their structure. On the basis of this work I decided to study systematically the anatomy of the

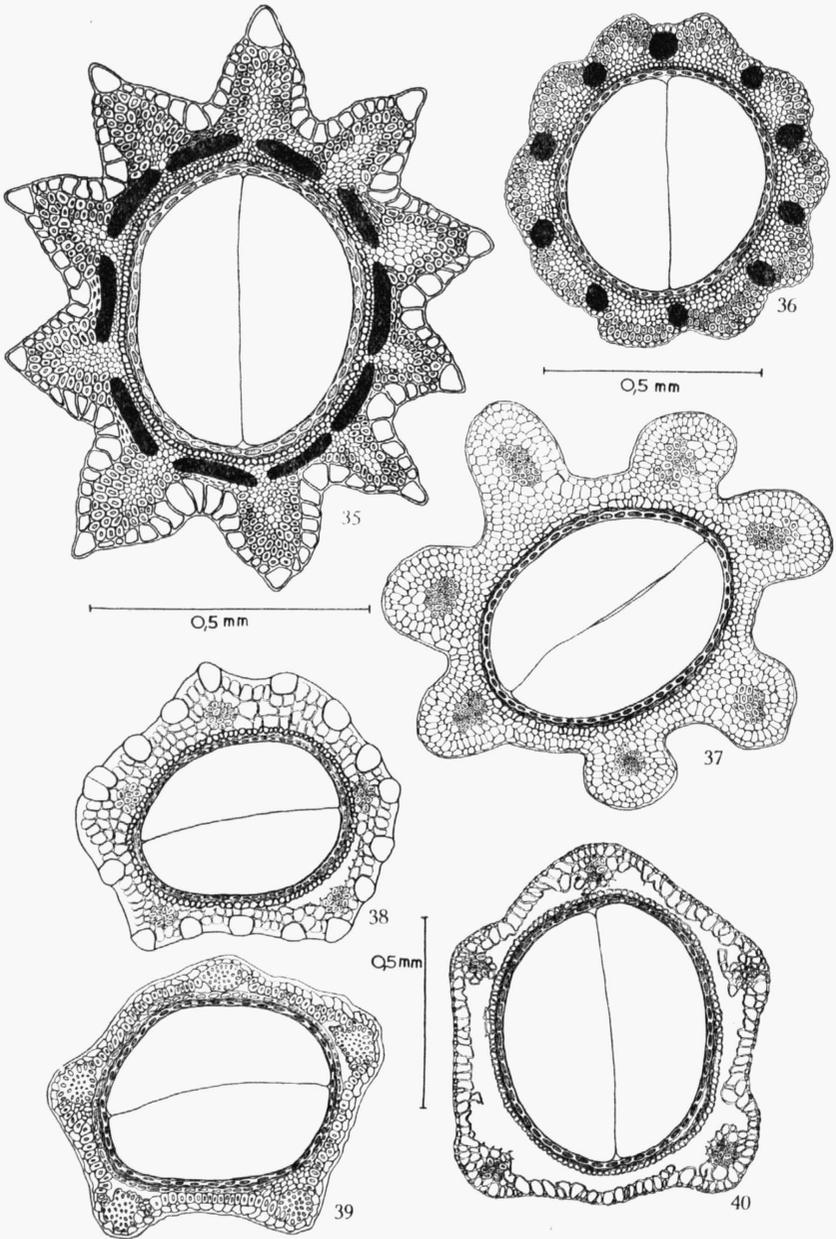


Fig. 35–40: Cross sections in the middle part of the achenes. — Fig. 35. *Chrysanthemum leucanthemum* L. s.l. — Fig. 36. *Ch. rotundifolium* W. et K. — Fig. 37. *Ch. serotinum* L. — Fig. 38. *Ch. zawadzki* HERB. — Fig. 39. *Ch. corymbosum* L. s.l. — Fig. 40. *Ch. alpinum* L.

achenes of the tribe *Anthemideae*. I succeeded in finding stable diacritical characters in the individual species that can be used for their determination. It is of interest that VOŘIŠEK (1951) in his carpological study of Czechoslovak species of the genus *Centaurea* does not mention any differences in the anatomy of their achenes. Some aspects of the anatomy and morphology of achenes of some species of the tribe *Anthemideae* were taken up by ČERNÁ (1957) in her thesis. The thesis centers on the ecology of the plants studied. The part devoted to carpology contains inaccuracies (e. g. erroneous designation of the individual layers on the cross section through the achene, wrong numbers of ribs in the achenes of some species).

In most of the papers having to do with the achenes of the tribe *Anthemideae*, the authors do not differentiate between the ray flower and the disk flower achenes; e.g. BRIQUET and CAVILLIER (1916), HEGI (1918, 1929), DEYL (1956), CVELEV (1961), DOBROCHOTOV (1961), PAVLOV (1966). One can thus easily incur an error during the determination as the achenes of the two types of flowers differ usually quite markedly. A common error found in these papers is also the incorrect number of ribs at the achenes of *Matricaria chamomilla* (mostly 3 instead of 5) and of *M. discoidea* (3 instead of 4). In the last-named species no notice is made of the two secretory ducts running along the entire length of the achene. The ducts are covered only with the epidermis and are filled with a red-brown secretion. The colour of the secretion shines through the single-layered epidermis so that the ducts appear as two distinct bands bordering the outer edge of both end ribs. Hence they are a first-class diacritical character for this species.

HEGI (1918) published schematic representations of cross sections through achenes of *Anthemis arvensis*, *A. tinctoria* and *A. cotula*. The schemes of the first two species are correct, that of the cross section through the achene of *A. cotula* is erroneous both in the overall shape of the section and in the representation of the individual tissues. The outline of the cross section through the achene of *A. cotula* (Fig. 29) is roughly circular rather than rhomboid as mentioned in the paper. I should like at this place to mention the specific structure of parenchymatic cells in the achenes of *A. arvensis*. The walls of these cells are clearly thickened in bordered pits (colon appearance). This peculiarity was observed in the same species by BRIQUET (l.c.). HIRÈCHE (1937) found an analogous structure of cell walls in some north African species of the genus *Leontodon*.

Within the genus *Chrysanthemum* L. a special position is occupied by *Ch. serotinum*. It is typical by its unusual number of ribs and by their shape (the ribs are prominent, do not pass into a membrane border at the apex of the achene). In the other studied species of the genus *Chrysanthemum* the usual considerably constant number of ribs is 5 or 10. In *Ch. serotinum* the most common number is 8 and 7 (in wild-growing flowers as well as in those from the Botanical garden). The specific anatomy of the achenes of this species (and finally also the other characters of the whole plant) sets it apart from the other representatives of the genus *Chrysanthemum* s.l. in the Czechoslovak flora.

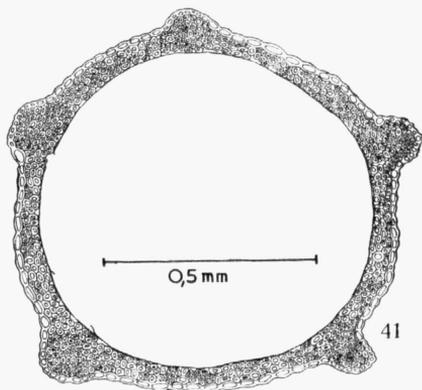


Fig. 41: *Tanacetum vulgare* L. — cross section in the middle part of the achene.

In spite of a detailed study of the structure of achenes of *Chrysanthemum corymbosum* subsp. *corymbosum* as well as *Ch. corymbosum* ssp. *clusii*, the two subspecies are included in the key under one heading as the differences observed in the size of the individual parts of the achene (if they exist at all) are insignificant (see statistical evaluation) and those in the anatomy of achenes are nonexistent. The same view is taken by БИЖОК (1955). The subspecies (considered as species by some authors) differ in the characters mentioned in the keys, in particular in the number of chromosomes (*Ch. corymbosum* subsp. *corymbosum* has $n = 18$, subsp. *clusii* has $n = 9$). Likewise, all the three taxa (diploid, tetraploid, hexaploid) of *Ch. leucanthemum* are included under *Ch. leucanthemum* L. s.l. since no differences in the anatomy or morphology of the achenes of the individual taxa have been found. Differences in size are mentioned in the section of statistical evaluation.

Key to the Genera Based on Achene Morphology

- 1a Achenes without ribs, with at most 9 narrow longitudinal grooves or with 2 lateral carinae and several bars of the same colour and structure as the other parts of the achene *Anthemis* L. (Fig. 1—9)
- 1b Achenes clearly ribbed 2
- 2a On the adaxial side of achenes, 3 powerful ribs (carinae), on the abaxial side cross wrinkles and, beneath the border, 2 small oval planes *Tripleurospermum* SCH. BIP. (Fig. 13, 14)
- 2b Number of ribs greater than 3 3
- 3a Achenes compressed laterally, with 4—5 ribs only on the adaxial side *Matricaria* L. (Fig. 10—12)
- 3b Achenes with ribs along the entire circumference; if they are adaxioabaxially compressed the ribs are only on the adaxial side of the achene (= achenes from the ray). 4
- 4a Length of achenes is at least three times their width *Chrysanthemum* L. (Fig. 15—25)
- 4b Length of achenes is at most twice their width *Tanacetum* L. (F. 26)

Key to Species Based on Achene Morphology

Anthemis L. (Fig. 1—9)

- 1a Achenes with ± 10 not too clearly marked, flat bars, separated by 9 narrow grooves 2
- 1b Achenes without wide bars and grooves, or with two lateral carinae and several low narrow bars 3
- 2a Width of achenes from disk and ray at the widest point is $2/3$ — $4/5$ of length, border is absent, upper edge of achenes flatly obtuse, peduncle as a wide cone, achenes from the ray the same but generally smaller *A. arvensis* L. (Fig. 1, 2)
- 2b Width of achenes from the disk at most $1/2$ of length; of achenes from ray at most $1/3$ of length; achenes from disk without border, upper edge oblique, higher at the adaxial side of achene, peduncle narrowly conical *A. ruthenica* M. BIEB. (Fig. 3, 4)
- 3a Achenes from disk turbinate, tuberculate at the surface, with indistinct bars, without border, coronet distinct, achenes from ray not developed *A. cotula* L. (Fig. 5)
- 3b Achenes from disk and from ray without tubercles, smooth, or with several little prominent bars of the same colour and structure as the whole achene, adaxio-abaxially compressed, coronet covered with border 4
- 4a Achenes from disk and from ray heavily compressed, with wedge-shaped attenuation, achenes from disk \pm rhombic in cross section with 2 sharp lateral carinae over which the border protrudes into pointed ends; achenes from ray flatter, border more clearly developed on the adaxial side *A. austriaca* JACQ. (Fig. 6, 7)
- 4b Achenes less compressed than above, less narrowed toward the base, the border in disk achenes highest in the median of the adaxial side, not pointed in two ends; achenes from ray flatter, border indistinct *A. tinctoria* L. (Fig. 8, 9)

Matricaria L. (Fig. 10—12)

- 1a Achenes from disk with ± 4 ribs on the adaxial side, ribs lighter than the principal achene colour, both marginal ribs bordered externally with a narrow red-brown stripe corresponding to the secretory ducts; no flowers on the ray *M. discoidea* DC. (Fig. 12)

- 1b Achenes from disk and ray with 5 ribs on the adaxial side, without red-brown stripes, achenes from the disk without border, achenes from the ray sometimes with a long membranous border on the adaxial side *M. chamomilla* L. (Fig. 10, 11)

Tripleurospermum SCH. BIP. (Fig. 13, 14)

Achenes with 3 massive carinae (2 lateral, one in the axis of the adaxial side), border collar-like, on the abaxial side, 2 small oval brown-red planes underneath the border; achene surface (except for carinae) cross-rugose, darker than the carinae; achenes from the ray often smaller, cross wrinkling less dense, lighter and flatter *T. maritimum* (L.) SCH. BIP. (Fig. 13, 14)

Chrysanthemum L. (Fig. 15—25)

- 1a 5 ribs on achene 2
 1b More than five ribs on achene 4
 2a Border very small or absent; if present, somewhat higher on the abaxial side of the achene, basic colour of achenes red-brown, border and ribs very light (almost white), achenes from disk laterally compressed, ribs along the whole circumference; achenes from ray adaxio-abaxially compressed, all 5 ribs shifted to adaxial side . . . *Ch. zawadzki* HERB. (Fig. 15, 16)
 2b Border well developed 3
 3a Achenes brown, border and ribs without colour distinction, achenes from disk with ribs along the whole circumference, ribs of achenes from ray shifted to the adaxial side which is concave when viewed from the side *Ch. corymbosum* L. s.l. (Fig. 17, 18)
 3b Achenes silvery gray, ribs lighter than underlying surface, upper edge of border dark brownish, achenes from ray larger than those from disk, their border amounting to as much as 1/2 total achene length *Ch. alpinum* L. (Fig. 19, 20)
 4a Most often 8 (6—9) ribs, achenes \pm cylindrical, border low, achenes light, ribs of the same colour, achenes from ray rudimentary or undeveloped *Ch. serotinum* L. (Fig. 25)
 4b 10 ribs 5
 5a Achenes \pm 3 times longer than wide, elongately obovoid, achenes from ray adaxio-abaxially compressed, both achenes with surface containing narrow, heavily prominent, glossy yellowish or white ribs, separated by wider red-brown or brown-black grooves, achenes strikingly longitudinally striped; achenes from disk without border with a bright—yellow coronet, achenes from ray with irregular tattered border, most outstanding at the adaxial side *Ch. leucanthemum* L. s.l. (Fig. 21, 22)
 5b Achenes 4—5 times longer than wide, \pm cylindrical, narrowed toward the base, the surface with wide, little prominent glossy, straw-coloured ribs, separated by narrow red-brown grooves, achenes less markedly longitudinally striped; achenes from disk and ray with irregular tattered and at the edge browned border along the whole achene circumference, coronet not distinct, achenes from ray adaxio-abaxially compressed, bent *Ch. rotundifolium* W. et K. (Fig. 23, 24)

Tanacetum L. (Fig. 26)

light achenes, \pm obovoid, with 5 ribs lighter than basic colour of achenes, border finely crenated at the edge *T. vulgare* L. (Fig. 26)

Key to Species Based on Achene Anatomy

Anthemis L. (Fig. 27—31)

- 1a Cross section oval to round, part of pericarp formed by multilayered sclerenchymatic ring uninterrupted by multicellular sclerenchymatic braces 2
 1b Cross section ellipsoid, with apices elongated into triangular lobes with a rounded tip, part of pericarp formed by singlelayered palisade sclerenchyma, interrupted by multicellular sclerenchymatic braces 3
 2a Cross section \pm circular, pericarp undivided, formed only by the epidermis with several slime cells and by a multilayered continuous sclerenchymatic ring *A. cotula* L. (Fig. 29)
 2b Cross section oval to circular, pericarp lobular, underneath the epidermis a multilayered parenchymatic tissue, the rectangular cells of which are radially oriented; under the parenchyma there is a thick sclerenchymatic ring with 10 triangular ends, the tips of which point to the notches between pericarp lobes *A. arvensis* L. (Fig. 27)
 *A. ruthenica* M. BIEB. (Fig. 28)
 3a Under the epidermis, a single-layered white palisade sclerenchyma, cell lumina minute, \pm oval, located near cell centre *A. austriaca* JACQ. (Fig. 31)
 3b Under the epidermis, a single-layered yellow palisade sclerenchyma, cell lumina \pm triangular, placed at the adaxial side of cell *A. tinctoria* L. (Fig. 30)

Matricaria L. (Fig. 33, 34)

- 1a Cross section \pm oval, pericarp along the whole circumference single — layered, on the adaxial side generally with 4 little prominent lobes formed by parenchyma with sclerenchymatic brace in the lobe center; 2 red-brown secretory ducts adjacent to the marginal lobes *M. discoidea* DC. (Fig. 33)
- 1b Cross section widely ellipsoid, pericarp formed by epidermis with several slime cells at the circumference, on the adaxial side usually 5 lobes of parenchymatic tissue with sclerenchymatic brace and a slime cell at the top, no secretory ducts . . . *M. chamomilla* L. (Fig. 34)

Tripleurospermum SCH. BIP. (Fig. 32a, b)

Cross section distinctly three-ended, lobes (ends) formed by parenchyma, connected by a layer of radially oriented yellow sclerenchymatic cells; in section through the upper part of the achene the abaxial side shows two \pm semicircular secretory reservoirs, pressed by their flat side to the epidermis *T. maritimum* (L.) SCH. BIP. (Fig. 32a, b)

Chrysanthemum L. (Fig. 35—40)

- 1a Achenes with 10 large secretory ducts 2
- 1b Achenes without secretory ducts 3
- 2a Secretory ducts round in cross section, pericarp with shallow lobes, lobes broadly semicircular, epidermal cells minute *Ch. rotundifolium* W. et K. (Fig. 36)
- 2b Secretory ducts narrowly oval, elongated, pericarp with deep lobes, lobes \pm triangular, epidermal cells between lobes are large, decreasing in size toward the apices *Ch. leucanthemum* L. s.l. (Fig. 35)
- 3a On the section periphery 10—20 slime cells *Ch. zawadzki* HERB. (Fig. 38)
- 3b Achenes without slime cells at periphery 4
- 4a Pericarp sclerenchymatic; shallow lobular, usually with 5 lobes, under epidermis single-layered palisade sclerenchyma, in each lobe a round sclerenchymatic brace *Ch. corymbosum* L. s.l. (Fig. 39)
- 4b Pericarp parenchymatic 5
- 5a Cross section \pm pentagonal, pericarp under epidermis with 1 layer of large parenchymatic cells, along the periphery 5 wide little prominent lobes with a small multilayered sclerenchymatic brace in the centre, pericarp secondarily separated from the testa *Ch. alpinum* L. (Fig. 40)
- 5b Cross section \pm broadly ellipsoid, pericarp with 8 (6—9) \pm semicircular lobes, braced in the centre with sclerenchyma, the parenchyma of the pericarp multilayered even between lobes, pericarp adhering to the wall *Ch. serotinum* L. (Fig. 37)

Tanacetum L. (Fig. 41)

Cross section \pm circular, with 5 small lobes at the periphery, pericarp under epidermis sclerenchymatic, multi-layered; testa, endosperm and seed lobes reaching usually to the achene base and are absent in the section *T. vulgare* L. (Fig. 41)

Summary

It was found that the achenes of all the studied Czechoslovakian species of the tribe *Anthemideae* CASS. possess diacritical features. The features are so stable and characteristic for the individual species (or even genera) that a key to the determination of the taxons could be designed on their basis.

The present study contains a key to the genera based on the achene morphology. No key could be assembled on the basis of their anatomy, there being no diacritical specific features between the various genera.

This is followed by a key to the determination of species based on their morphology and one based on their anatomy. Both keys are intentionally not combined. The resulting effect of both keys is the same but, from a practical point of view, the key based on morphology is preferable.

Souhrn

Zjistila jsem, že na nažkách všech studovaných československých druhů tribus *Anthemideae* CASS. existují rozlišovací znaky. Jsou to znaky natolik stálé a pro jednotlivé druhy (popř. rody) charakteristické, že se mi podařilo na jejich základě sestavit klíč k určení studovaných taxonů.

Ve studii je na prvním místě uveden klíč k určení studovaných rodů, sestavený pouze na

základě znaků vnější morfologie nážek. Nepodařilo se mi sestavit klíč podle znaků vnitřní morfologické stavby nážek, protože jsem nenalezla specifické diakritické znaky mezi jednotlivými rody.

Dále následuje klíč k určení druhů podle vnějších morfologických znaků nážek. Posledním oddílem je klíč k určení těchže taxonů, sestavený na základě vnitřních morfologických znaků, patrných na nážkách. Oba klíče záměrně nejsou spojeny v jeden celek. Výsledný efekt při použití obou klíčů je sice stejný, avšak z hlediska praktického použití je klíč k určení podle vnější morfologie nážek výhodnější.

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