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Contributions towards a revised infrageneric classification of *Crepis (Cichorieae, Compositae)*

Abstract

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A recent molecular analysis of *Crepis* by Enke & Gemeinholzer based on ITS and *matK* sequences proved the genus to be polyphyletic and split into three statistically well supported clades. The first clade comprises the majority of the sampled species as *Crepis* s.str., the second clade species of five *Crepis* sections *(Intybellia, Lagoseris, Phaecasium, Microcephalum* and *Pterotheca)* as well as the genera *Lapsana* and *Rhagadiolus,* the third clade *C.* sect. *Ixeridopsis* as part of the *Youngia* group. The present paper summarises and discusses the available molecular, morphological (additional micromorphological data of pollen, achenes and pappus presented in the present paper) and karyological findings, makes suggestions towards delimitation and infrageneric classification of *Crepis* and specifies problems to be solved by future studies. It is concluded that (1) the recent resurrection of *Askellia* as a separate genus is well advised, (2) the genera *Lapsana* and *Rhagadiolus* should, for the time being, be maintained in their current generic circumscription and (3) *Crepis,* consequently, be treated as a paraphyletic taxon. A revised infrageneric classification of *Crepis,* maintaining 21 of Babcock's 27 sections, some in a revised circumscription, is provided; in addition, *C.* sect. *Calliopea* is re-established and *C.* sect. *Neglectoides* is described as new to science. For several species or species groups the findings are ambiguous or contradicting and their placement questionable. Approximately 55 % of the species were not included in a molecular analysis yet and their sectional placement based on morphological data only is thus tentative.

Additional key words: *Asteraceae, Askellia, Lagoseris, Lapsana, Rhagadiolus,* taxonomy

Introduction

Since Tournefort (1694) first recognised the *Cichorieae* as systematic entity by the uniform character combination of milky latex and capitula with 5-dentate, ligulate flowers, the circumscription of the *Cichorieae* did not change much until the most recent classification by Kilian & al. (2009). The generic and suprageneric classification of the tribe, in contrast, was subject to strong changes. The subtribe *Crepidinae* gained special attention in the first half of the 20th century through the work of two North American botanists, E. B. Babcock and G. L. Stebbins, who studied the genera of the *Crepidinae* not only morphologically but also cytologically and used the results to establish new classifications and generic circumscriptions (e.g., Babcock & al. 1937; Babcock & Stebbins 1937; Babcock & Jenkins 1943; Babcock 1947a, b). Among the most notable works of this period is Babcock's (1947a, b) monograph of the genus *Crepis*. *Crepis* L. with over 200 species (Bremer 1994) is widely distributed throughout the northern hemisphere and Africa. Babcock (1947a, b) provided a classification of the 196 species recognised in 27 sections, assuming this sectional system to reflect the phylogenetic relations within the genus.

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The recent molecular phylogeny of *Crepis* by Enke & Gemeinholzer (2008) based on ITS and *matK* sequence data proved the genus to be polyphyletic and split into three statistically well supported clades: (1) the *Askellia* clade includes *C.* sect. *Ixeridopsis,* is part of the *Youngia* group and corroborates its recognition as a separate genus *Askellia* W. A. Weber (1984); (2) the *Lagoseris* clade surprisingly comprises the morphologically easily distinguished genera *Lapsana* L. and *Rhagadiolus* Juss. as well as *Crepis* species of the sections *Intybellia, Lagoseris, Microcephalum, Phaecasium* and *Pterotheca,* parts of which have sometimes been treated as a separate genus *Lagoseris* (Czerepanov 1964); (3) the *Crepis* s.str. clade includes the majority (ca. 80 %) of the sampled species (Enke & Gemeinholzer 2008: fig.1–2; see also Fig. 4).

The analysis by Enke & Gemeinholzer (2008), moreover, revealed that the infrageneric classification of Babock (1947b) is in many cases not congruent with molecular clades, indicating that Babcock's sections do not represent natural groups. In fact, many molecular clades comprise members of more than one section, whereas most sections emerge into more than one clade (Enke & Gemeinholzer 2008: fig. 2; see also Fig. 1).

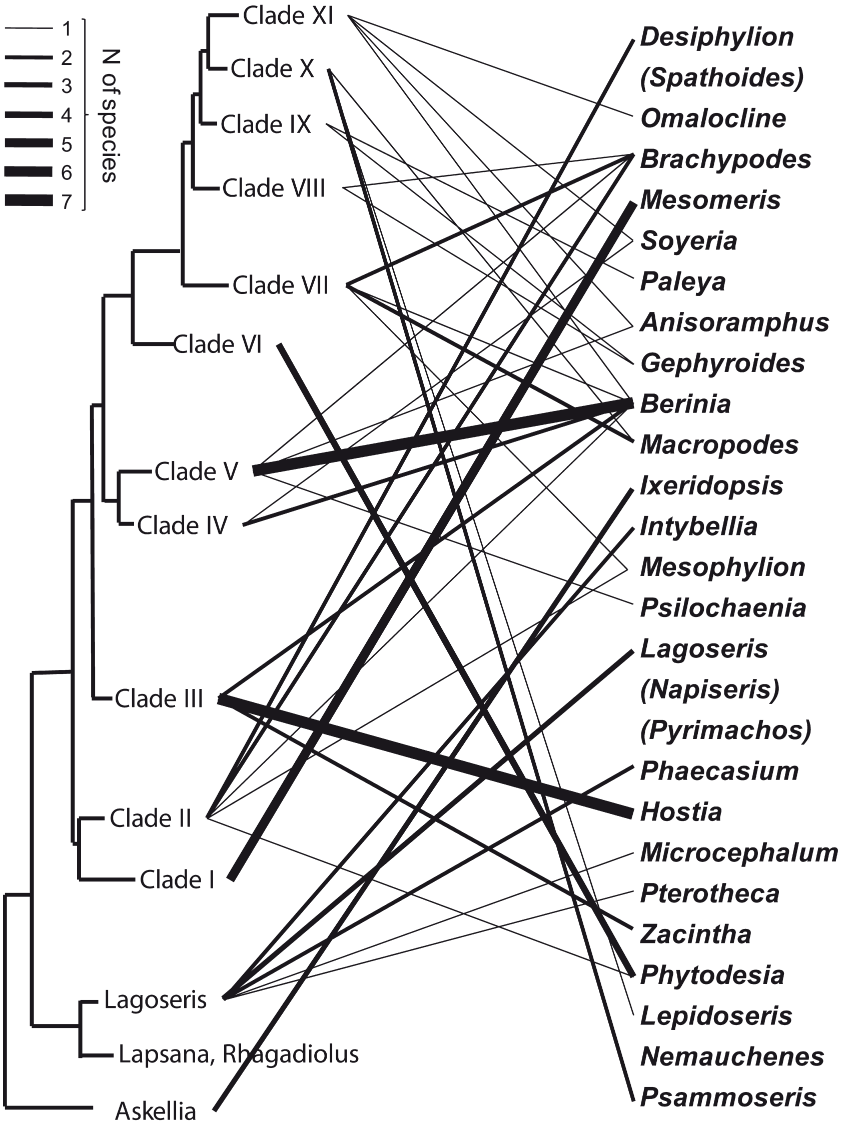

Fig. 1. Distribution of Babcock's (1947b) sections (right) on molecular clades (left) following Enke & Gemeinholzer (2008). – Line width corresponds to number of species. Sections in brackets have not been sampled for molecular data.

The aims of the present paper are twofold: (1) To summarise and critically reassess the available findings relevant for a revised circumscription and infrageneric classification of *Crepis*. (2) To make a suggestion, on the basis of this assessment, towards the delimitation of the genus *Crepis,* to outline the consequences for a revision of the infrageneric classification of *Crepis* and to specify problems to be solved by future studies.

Material and methods

Reassessment of the available findings. **—** The findings used for the revision of the circumscription and infrageneric classification of *Crepis* come from three sources: (a) morphological, karyological and biogeographic data published in the literature, (b) recently presented molecular and cytological data (Enke & Gemeinholzer 2008; Enke & al. subm.), (c) additional micromorphological data presented in this paper.

Micromorphological analyses. — For the assessment of relations within *Crepis* achene cross sections, pollen morphology and pappus ultrastructure were studied in a sample of species across the genus in its wide sense.

Ultra thin sections for light microscopy. — Achenes of 21 species (see Table 1 and Appendix) were taken from herbarium sheets or living plants. Dried achenes were stored in 96 % ethanol; achenes from living material were progressively dehydrated by ascending ethanol solutions (30 %, 50 %, 70 %, 90 %, and 96 %), remaining 24 h in each dilution. For infiltration with resin (Unicryl, BBI International) the objects were first transferred into a mix of 1 : 2 Unicryl and ethanol (96 %), then stepwise

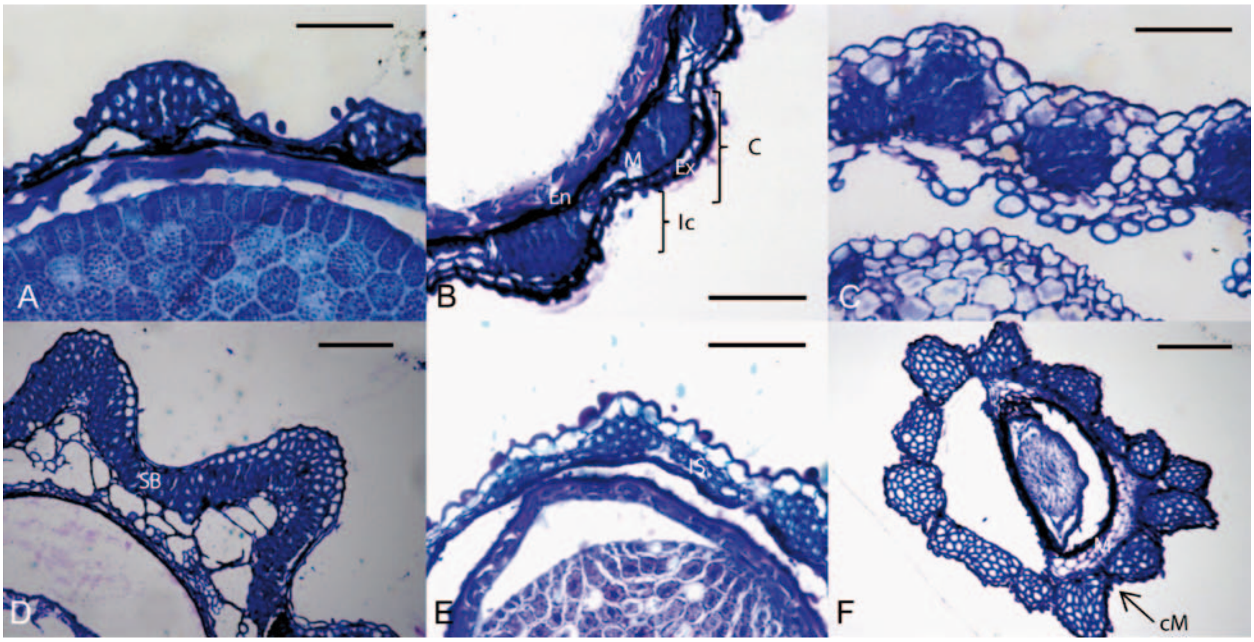

Fig. 2. Achene cross sections stained with toluidine blue – A: type Ia, *Askellia pygmaea;* B: type Ib, *Crepis foetida;* C: type Ic, *C. mollis;* D: type II, *C. acuminata;* E: type III, *C. multicaulis;* F: type IV, *C. zacintha.* – cM = collapsed mesocarp, C = costa, En = endocarp, Ex = exocarp, Ic = intercostae, IS = intercostal sclerenchyma, M = mesocarp, SB = sclerenchymatic band. – Scale bars: A-C, E = 50 µm, D, F = 100 µm.

into 1 : 1, 2 : 1 and last into 100 % Unicryl. The samples remained 3–6 days (depending on size) at each step. The objects were embedded in gelatine capsules filled with resin and dried for 3–5 days in a heating cabinet at 40 °C. The ultra thin transverse sections (3–4 µm thick) through the middle part of the achene were cut at a rotation microtome (Supercut 2065, Reichert/Jung), stained with toluidine blue (Serva, 0.5 %, 20–35 s), mounted in corbit-balm (Kobe) and dried for 2 days at 40 °C. Micrographs were taken using a Zeiss microscope Standard 14 mounted with the digital documentation system Zeiss Axio Cam MRc and Axio Vision software (release 4.4, Zeiss).

Preparation of pollen for SEM. — Pollen samples were taken from 12 species (see Table 1 and Appendix). Prior to coating, pollen grains were treated by acetolysis following Erdtman (1960) to avoid artefacts caused by the protoplast, then suspended in ethanol and cleaned from debris in an ultrasonic bath. The pollen suspension was transferred onto a 14 mm cover slip mounted on an SEM stub and left to dry. The samples were coated with gold and studied with a LEO Supra 55VP.

Preparation of pappus hairs for SEM. — Whole achenes with pappus hairs attached belonging to 10 species (see Table 1 and Appendix) were sampled for SEM and fixed in FAA (5 ml formaldehyde solution (min. 35 %), 15 ml glacial acetic acid, 20 ml ethanol (96 %), and 60 ml aqua dest.) for 2× 24 h. Dehydration was facilitated by a subsequent treatment of ascending ethanol dilutions (70 %, 80 %, 90 %, 96 % and 2× 100 % at each step for at least 1 h). Then the samples were treated with acetone (100 %) twice for 1 h, transferred to the Critical Point Drier K 850 (Emitech) for final desiccation and subsequently mounted on aluminium stubs and coated with gold/palladium (layer thickness 20 nm) in a Low Voltage Cool Sputter Coater K 550 (Emitech). The specimen stubs were studied with a Philips SEM 515.

Results

(1) Micromorphological analyses

The results are summarised in Table 1.

***Achene anatomy.* —** The achenes are normally of rounded outline with (8–)10–12(–20) costae (= ribs) consisting of sclerenchymatous cell bundles. The exocarp is one-layered with a thick outer cell wall, but the cells can be collapsed. Parenchymatic regions may or may not be present in the mesocarp between costae or between costae and testa. The endocarp is two-layered and collapsed (Fig. 2B). Four different achene types were found in *Crepis* s.l. (Fig. 2).

Type Ia: Achenes are of a rounded outline. The cells of the exocarp have thick outer cell walls but are (partly) collapsed. The 10–12 costae are far apart with distinct intercostal areas where parenchyma cells are partly collapsed. No intercostal sclerenchymatous cells are present (Fig. 2A).

Type Ib: Similar to Ia, except that intercostal parenchyma cells are well developed. 3–6 layers of protoplastic parenchyma cells are present in the mesocarp between the testa and the costae (Fig. 2B).

Type Ic: This type has no distinct costae. Sclerenchymatous islands are embedded in the parenchymatous

Table 1. Summary of micromorphological results. Species ordered for affiliation to molecular clades (after Enken & Gemeinholzer 2008) and the sectional classification according to Babcock (1947b) is indicated. Pollen (all of the *Cichorium intybus* type): C = *C. intybus* subgroup, T = *Taraxacum officinale* subgroup, [1] data supplemented from Blackmore (1984).

Species	**Clade**	**Section**	**Achene cross section**		**Pappus**		**Pollen**	
			type	**Ø (µm)**	**spikes/ 100 µm**	**no. of cells in Ø**	**type**	**Ø (µm)**
Askellia flexuosa	*Askellia*	*Ixeridopsis*	Ia	–	–	–	–	–
A. pygmaea	*Askellia*	*Ixeridopsis*	Ia	30–32	1–4	6–7	–	–
Lapsana communis	*Lapsana*	–	–	–	–	–	T[1]	–
Rhagadiolus sp.	*Rhagadiolus*	–	III	–	–	–	–	–
Crepis multicaulis	*Lagoseris*	*Microcephalum*	III	–	–	–	–	–
C. pulchra	*Lagoseris*	*Phaecasium*	–	14–15	0–2	2–3	C	28–34
C. purpurea	*Lagoseris*	*Lagoseris*	IV	–	–	–	–	–
C. praemorsa	*Lagoseris*	*Intybellia*	Ia	–	–	–	T[1]	38–46[1]
C. sancta	*Lagoseris*	*Pterotheca*	III	10–11	0–2	2–3	T	28–34
C. lampsanoides	Clade I	*Mesomeris*	Ib	19–20	6–7	4–6	C	31–37
C. mollis	Clade I	*Mesomeris*	Ic	–	–	–	C[1]	34–38[1]
C. kerneri	Clade II	*Brachypodes*	Ib	35–37	4–6	6–7	–	–
C. paludosa	Clade II	*Desiphylion*	II	–	–	–	C	36–42
C. tectorum	Clade II	*Mesophylion*	Ib	14–15	2–3	3–4	T(C[1])	26–32
C. foetida	Clade III	*Hostia*	Ib	–	–	–	T	26–32
C. zacintha	Clade III	*Zacintha*	IV	16–17	3–4	4–5	–	–
C. acuminata	Clade V	*Psilochaenia*	II	–	–	–	–	–
C. chondrilloides	Clade V	*Berinia*	Ia	–	–	–	–	–
C. dioscoridis	–	*Brachypodes*	–	–	–	–	C	26–32
C. hypochaeridea	Clade V	*Anisoramphus*	–	–	–	–	T	31–37
C. neglecta	Clade VI	*Phytodesia*	Ia	–	–	–	–	–
C. biennis	Clade VII	*Berinia*	Ib	–	–	–	T(C[1])	33–39
C. bungei	Clade VII	*Mesophylion*	–	37–40	3–4	6–7	–	–
C. leontodontoides	Clade VIII	*Gephyroides*	IV	13–14	2–4	2–3	T	25–31
C. albida	Clade IX	*Paleya*	Ib	–	–	–	T	26–32
C. vesicaria	Clade X	*Lepidoseris*	–	–	–	–	C(T[1])	27–33
C. capillaris	Clade XI	*Phytodesia*	Ib	16–17	3–4	4–5	T[1]	34–41[1]

cells of the mesocarp. No intercostal sclerenchyma is found. The outer walls of the one-layered exocarp are only slightly thickened (Fig. 2C).

Type II: The achenes are of round outline, with 8–12 pointed costae. Parenchyma is well developed beneath the sclerenchyma of the costae, but often collapsed in the intercostal regions. The sclerenchyma builds a band in the intercostal areas (Fig. 2D).

Type III: Achenes are ± round in outline. The costae are (weakly) prominent, intercostal regions are mostly made up of 1–6 cell layers. Intercostal sclerenchymatous cells are present (Fig. 2E).

Type IV: The exocarp can be collapsed. Costae are very prominent with deep or no intercostal furrows. Sometimes 3–6 layers of protoplastic parenchymatous cells are found between testa and sclerenchyma but never between the sclerenchymatous islands of the costae. Even though the costae seem to merge in some cases, they are always separated by a layer of collapsed parenchyma cells or intercostal furrows (Fig. 2F).

Pappus bristles. — The pappus bristles vary in diameter, in the number of cells in cross section and in the prominence and frequency of the spikes. The different pappus bristles are shown in Fig. 3.

Askellia pygmaea (Fig. 3A), representing the *Askellia* clade, has pappus bristles of 6–8 cells and 30–32 µm in diameter. The bristles have 1–4 spikes per 100 µm and are thus smooth.

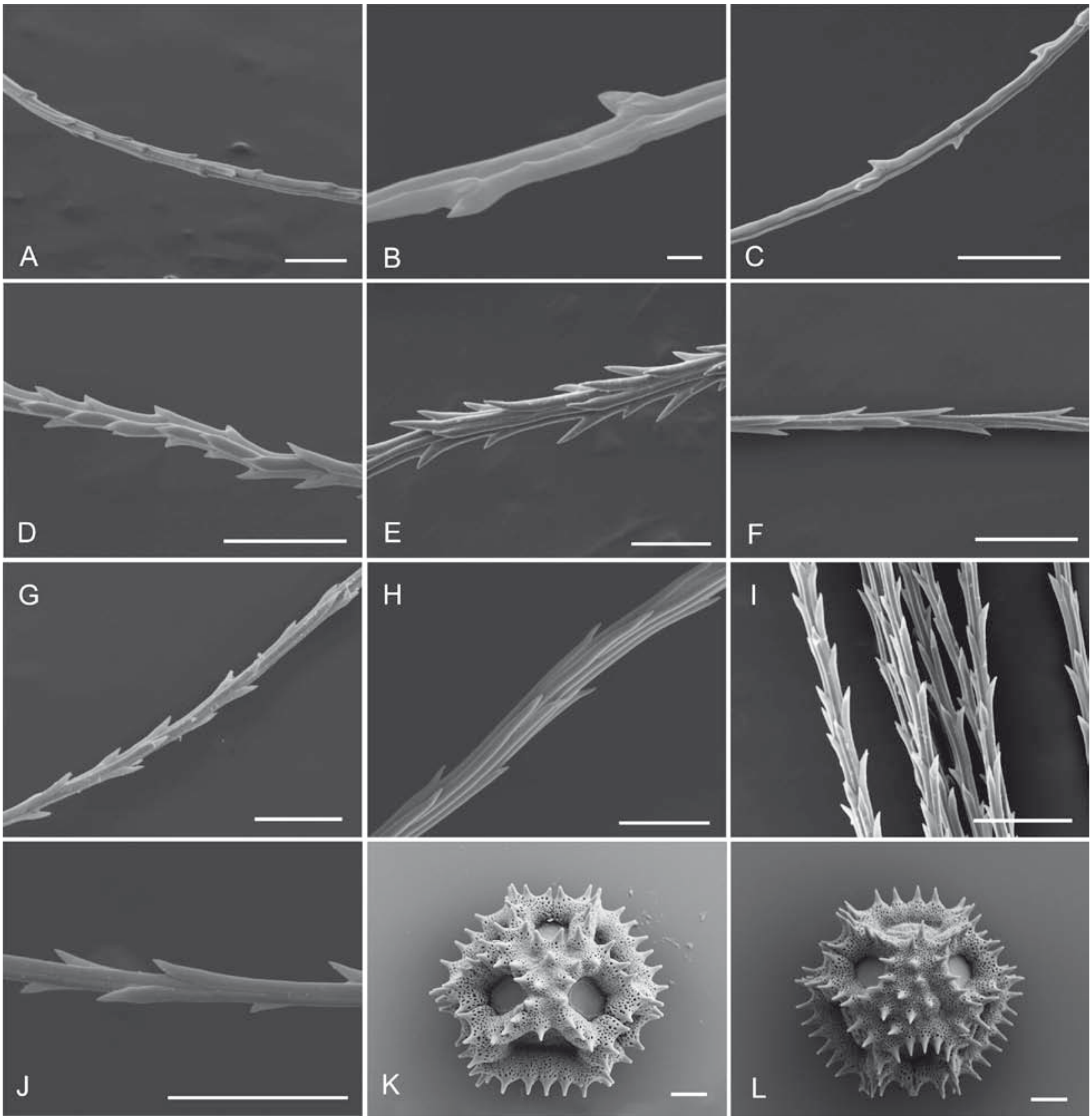

Fig. 3A-J: Scanning electron micrographs of pappus bristles – *Askellia pygmaea* (A); *Crepis sancta* (B); *C. pulchra* (C); *C. lampsanoides* (D); *C. kerneri* (E); *C. tectorum* (F); *C. zacintha* (G); *C. bungei* (H); *C. leontodontoides* (I); *C. capillaris* (J). – K-L: pollen grains in polar view: *C. dioscoridis,* representing the *Cichorium intybus* subgroup pollen type (K), *C. tectorum,* representing the *Taraxacum officinale* subgroup pollen type (L). – Scale bars: A–J = 100 µm, B = 10 µm, K–L = 4 µm.

The pappus bristles of the sampled species of the *Lagoseris* clade are finer than those of the *Askellia* clade (only 10–15 µm and 2–3 cells in diameter). The pappus hairs macroscopically appear soft and bendable. The spikes are very far apart (0–2 per 100 µm) but sticking out prominently (Fig. 3B, C, Table 1).

Within the *Crepis* s.str. clade the pappus bristles vary considerably, even in the limited number of samples studied (Fig. 3D-K, Table 1), but are generally rather stiff (14–37 µm and 2–7 cells in diameter) and have 2–7 prominent spikes per 100 µm. The differences between the clades appear to be rather gradual, the sampling, however, is too limited to draw conclusions.

Pollen morphology. — Terminology is according to Blackmore (1984). All sampled species have echinolophate pollen of the *Cichorium intybus* type (Fig. 5K-L). Five species are of the *Cichorium intybus* subgroup (Fig. 5K, *Crepis dioscoridis, C. lampsanoides, C. paludosa, C. pulchra, C. vesicaria*), seven species of the *Taraxacum officinalis* subgroup (Fig. 5L, *C. albida, C. biennis, C. foetida, C. hypochaeridea, C. leontodontoides, C. sancta,* *C. tectorum*). Grain size ranges from 25–42 µm. In the three widespread species *C. biennis, C. tectorum* and *C. vesicaria* the present results contradict their characterisation by Blackmore (1984), which could hint on intraspecific variance or transitional pollen types.

(2) Reassessment of morphological, karyological and molecular findings for the delimitation and infrageneric classification of *Crepis*

The naming of taxa and their discussion follows the clades shown in Fig. 4, which graphically summarises the findings of the ITS data sets by Enke & Gemeinholzer (2008), Enke & al. (2008) and Enke & al. (subm.). The main focus of the sectional allocation of taxa in the revised infrageneric classification is laid on the ITS phylogeny (Fig. 4); the results of the *matK* analysis are largely congruent with the ITS analysis, but the topology of the chloroplast phylogeny is far less resolved (Enke & Gemeinholzer 2008). However, evidence from the molecular analysis of the *matK* marker as well as karyology, (micro-)morphology and geographic distribution is included and, where relevant, discussed. The revised sectional classification of the *Crepis* species is summarised in the part “Taxonomic conclusion”, below.

(2.1) *Askellia.* — The statistically well supported *Askellia* clade, even though in close vicinity to *Crepis* s.str., is not a sister group in the ITS phylogeny (Enke & Gemeinholzer 2008: fig. 1). In the *matK* phylogeny it falls into one group with *Ixeris, Youngia* and *Garhadiolus* (Enke & Gemeinholzer 2008: fig. 2). Therefore, the molecular results strongly support the exclusion of *C.* sect. *Ixeridopsis* from the genus *Crepis* and its recognition as a separate genus *Askellia* (Weber 1984). A morphometrical analysis by Pak & Bremer (1995) showed a similar result. In fact, species of this clade are easily distinguishable from all other members of *Crepis* s.l. in their typical growth in low tussocks, the cylindrical involucrum, the general absence of hairs, the nearly always entire leaves, the smaller number of florets (5–15, in *Crepis* s.str. generally between 20–200) and the chromosome number of $x = 7$. The number is otherwise not known in *Crepis* (Babcock 1947b) but present in the *Crepidinae,* e.g., in *Ixeridium* (A. Gray) Tzvelev, their karyotypes, however, showing distinct differences (Pak & Kawano 1992; Pak 1993).

Sennikov & Illarionova (2008) and Tzvelev (2008) followed Weber’s (1984) treatment of *Crepis* sect. *Ixeridopsis* as a separate genus *Askellia,* because they considered the terete and finely ribbed achenes with a very thin pericarp (Fig. 2A, see also Pak 1993) as a unique feature of *Askellia*. My own investigations, however, revealed that this achene type (type Ia) is also present in species of the other two main clades.

Adylov & Zuckerwanik (1993), reassigned the Central Asian species of *Askellia* to *Youngia,* but *Askellia* differs from *Youngia* clearly in the chromosome number and in achene morphology: *Youngia* exhibits compressed and angular achenes and has a basic chromosome number of $x = 8$ (Babcock & Jenkins 1937; *Y. tenuifolia* with $x = 5$ was transferred to *Crepidifolium,* see Tzvelev 2008).

Ixeris differs from *Askellia* in its higher basic chromosome number and higher florets numbers as well as by its fusiform, flattened and winged achenes achenes (Pak 1993; Pak & Kawano 1990).

(2.2) *Lagoseris* clade, *Lapsana* and *Rhagadiolus.* — The close relation of *Crepis* sections *Intybellia, Phaecasium, Lagoseris, Microcephalum* and *Pterotheca* of the *Lagoseris* clade with *Lapsana* and *Rhagadiolus* is statistically well supported by both the nuclear and chloroplast phylogenies (Enke & Gemeinholzer 2008). All sampled species of the five *Crepis* sections appear in the *Lagoseris* clade, no sectional overlap with *Crepis* s.str. could be observed (Fig. 4 and Enke & Gemeinholzer 2008).

Two of the five *Crepis* sections within the *Lagoseris* clade, namely *Lagoseris* and *Pterotheca,* are treated as a separate genus *Lagoseris* by Czerepanov (1964). The exclusion of both sections from *Crepis* is mainly based on the presence of conspicuously long, bristle-like paleae on the receptacle, which sometimes exceed the achenes (Czerepanov 1964). These are, however, lacking in the other three sections of the *Lagoseris* clade. Moreover, Babcock (1947a) reported the natural occurrence of individuals of *C. sancta* (*C.* sect. *Pterotheca*) lacking paleae and already Collins (1924) discovered that the presence and absence of receptacular paleae is due to a very simple genetic mechanism. Furthermore, receptacular paleae are not restricted to sections *Lagoseris* and *Pterotheca,* they are also present in *C. commutata* (*Crepis* s.str., sect. *Hostia,* syn. *C. foetida* subsp. *commutata;* Babcock & Cave 1938), there being awned linear bracts. These findings led Babcock (1947a) to the inclusion of *Pterotheca* and *Lagoseris* into *Crepis*.

The *Crepis* species of the *Lagoseris* clade show only minor differences in pappus ultrastructure from *Crepis* s.str. (Table 1, Fig. 3), which are not conclusive because of the limited sampling, but no significant discontinuity. Achene anatomy shows considerable variation within the *Crepis* species of the *Lagoseris* clade, with three types (Ia, III and IV) represented by the five species sampled. Two of them are also present among the species of the *Crepis* s.str. clade sampled, only type III is so far restricted to the *Lagoseris* clade and also present in *Rhagadiolus*. The pollen of *Lapsana* is similar to the pollen of *Crepis* (*Cichorium intybus* type, subtype *Taraxcum officinale* subgroup, Table 1), but according to Osman (2006) *Rhagadiolus* has a distinct pollen type with 21 lacunae compared to only 15 in *Crepis* and *Lapsana.*

The here discussed data are ambiguous with respect to the question whether to exclude the five sections clustering within the *Lagoseris* clade from *Crepis,* or to treat *Crepis* as paraphyletic genus. The variation of characters within *Crepis* species of the *Lagoseris* clade

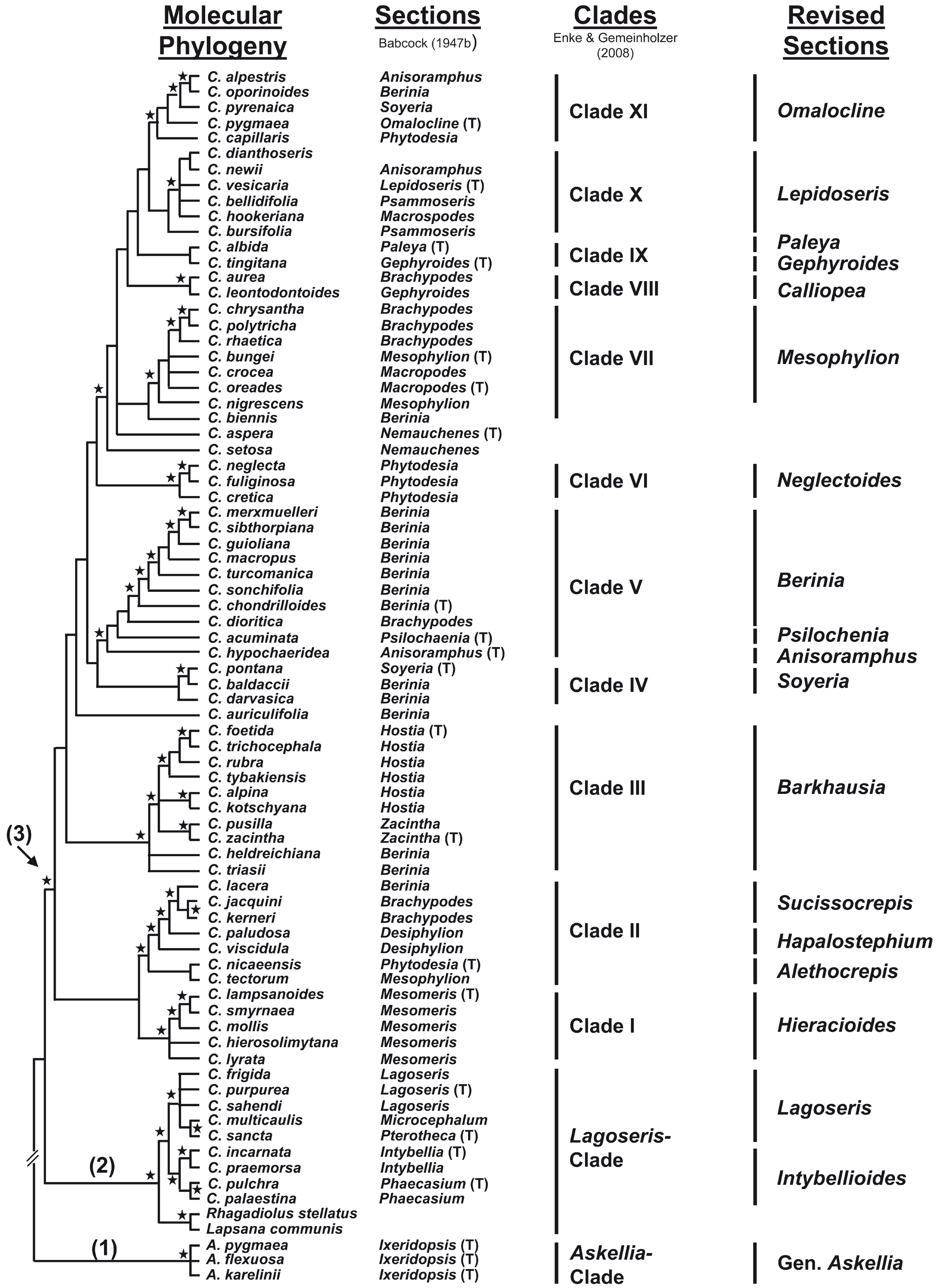

Fig. 4. Graphic summary of the ITS phylogenies published by Enke & Gemeinholzer (2008), Enke & al. (2008) and Enke & al. (subm.). Also shown are the sectional affiliation according to Babcock (1947b), the molecular clades following Enke & Gemeinholzer (2008) and the revised sections. Asterisks mark nodes that are supported with more than 80 % bootstrap and/or posterior probability of 0.8. – (1) *Askellia* clade, (2) *Lagoseris* clade, (3) *Crepis* s.str. clade; (T) following Babcock's section name indicates the corresponding species as the type of that name.

is mostly within the range known for species of *Crepis* s.str. Chemosystematical evidence shows that *C. multicaulis* and *C. pulchra* (as representatives of the *Lagoseris* group) are very similar in the composition of their phytochemical compounds to the other 21 sampled *Crepis* species (all belonging to *Crepis* s.str.), whereas *Lapsana* differs (Zidorn 2008). For all features shared by the species of sections *Intybellia, Phaecasium, Lagoseris, Microcephalum* and *Pterotheca* equivalent features could be found within *Crepis* s.str. *Lapsana* and *Rhagadiolus* differ from all *Crepis* species in achene features and the latter distinctly in pollen type. As has been shown by Tegel (2002), the cell wall structure of the testa epidermis in the achenes is fenestrate in *Lapsana* and *Rhagadiolus;* whereas it is unstructured in all sampled *Crepis* species except for *C. biennis* (Tegel (2002) sampled *C. sancta* and *C. pulchra* of the *Lagoseris* group). Conclusively, no argument could be found to encourage an exclusion of the species of the *Lagoseris* group from *Crepis;* neither could any convincing argument be found to merge *Lapsana* and *Rhagadiolus* into *Crepis.* As the discussed characters allow no palpable decision whether to exclude the *Lagoseris* clade from *Crepis*, it is proposed to preserve the current generic circumscription of *Crepis*, even though it would be paraphyletic from a molecular point of view, until further evidence emerges. To expand the generic description of *Crepis* to include *Lapsana* and *Rhagadiolus* seems inappropriate given the morphological distinctness of both genera. Furthermore, the phylogeny of *Crepis* s.l. (Enke & Gemeinholzer 2008) might reflect a more complex evolutionary history than can be drawn from dichotomous branching patterns of phylogenetic trees, so further analyses and investigations are still needed.

As shown above, *Crepis* sect. *Lagoseris* and *Pterotheca* are also morphologically closely related, corroborating their clustering in the same subclade.

Crepis multicaulis (as the only representative of *C.* sect. *Microcephalum* sampled in the molecular analysis of Enke & Gemeinholzer (2008)) resembles *C. sancta* (sect. *Pteroctheca*) in some aspects of morphology and karyotype (Babcock & Jenkins 1943), but not in the receptacular paleae as they are lacking in *C. multicaulis*. *C. multicaulis* and *C. sancta* also show a close relation in the molecular phylogeny (Enke & Gemeinholzer 2008). Following the molecular results and the above discussed morphological and karyological similarities, the sections *Lagoseris, Pterotheca* and *Microcephalum* are merged into a single section *Lagoseris* (see Taxonomic conclusions, below).

Crepis praemorsa and *C. incarnata* of *C.* sect. *Intybellia* are very closely related and sometimes treated as subspecies of *C. praemorsa* (e.g., Sell 1976, Siljak-Yakovlev & Cartier 1982). The section is closely related to *C.* sect. *Phaecasium,* typified by *C. pulchra*. Babcock & Jenkins (1943) found identical karyotype features in the two sections but did not merge them into one because of differences in root morphology. *C. praemorsa* features a rhizome, whereas *C. pulchra* and *C. incarnata* possess a taproot. As root morphology is influenced by ecological factors (Verboom & al. 2004), it is inapt as systematically discriminating factor. The karyotypic resemblance between *C. praemorsa* and *C. pulchra* is likewise supported, when banding patterns given by Siljak-Yakovlev & Cartier (1982) for *C. praemorsa* and Dimitrova & Greilhuber (2001) for *C. pulchra* are compared. Both molecular markers (ITS, *matK*) support the close relationship of these two sections (Enke & Gemeinholzer 2008). This provides sufficient evidence to merge sections *Intybellia* and *Phaecasium*. The correct name of the united section is *C.* sect. *Intybellioides* (see Taxonomic conclusions, below).

(2.3) *Crepis* s.str.

Clade I. — Clade I corresponds to Babcock's *Crepis* sect. *Mesomeris* and is well supported by both ITS and *matK* (Enke & Gemeinholzer 2008). The species in this section all have a basic chromsome number of $x = 6$. The correct name of this section is *C.* sect. *Hieracioides.*

Clade II. — The species in clade II belong to five different sections: *Crepis nicaeensis* to sect. *Phytodesia, C. tectorum* to sect. *Mesophylion, C. paludosa* and *C. viscidula* to sect. *Desiphylion, C. jacquini* and *C. kerneri* to sect. *Brachypodes* and *C. lacera* to sect. *Berinia*. *C. tectorum* is sister to *C. nicaeensis* in the ITS phylogeny, whereas *C. tectorum* and *C. micrantha* (also sect. *Phytodesia*) cluster together in the chloroplast based phylogeny (Enke & Gemeinholzer 2008). These three polymorphic species share some similarity, such as annuality, a wide distribution and some gross morphological congruencies. Thus it appears reasonable to transfer *C. tectorum* to sect. *Phytodesia,* which is correctly named *C.* sect. *Alethocrepis* and typified by *C. nicaeensis*.

To draw taxonomic conclusions for the other species within this clade poses a problem, as neither of the type species of Babcock's sections *Desiphylion (Crepis sibirica),* correctly to be named *C.* sect. *Hapalostephium,* and *Brachypodes (C. tergluoensis),* correctly to be named *C.* sect. *Sucissocrepis,* has been included into a molecular analysis. Statistically well supported by both ITS and *matK* is only the close relation between *C. kerneri* and *C. jacquini,* both in Babcock's sect. *Brachypodes* (Enke & Gemeinholzer 2008). So it is proposed to maintain both sections until the type species have been included in a molecular analysis.

As *Crepis lacera* of sect. *Berinia* shows some resemblance in gross morphology to *C. kerneri* and *C. jacquini,* it should be included in *C.* sect. *Sucissocrepis* (≡ *C.* sect. *Brachypodes.*

Clade III. — Clade III comprises seven species of sect. *Hostia (Crepis alpina, C. foetida, C. kotschyana, C. rubra, C. thomsonii, C. trichocephala, C. tybakiensis),* two species of sect. *Zacintha (C. pusilla, C. zacintha)* and two of sect. *Berinia (C. heldreichiana, C. triasii)*. In the ITS phylogeny *C. thomsonii* falls within the subspecies of *C. foetida* (Enke & Gemeinholzer 2008) and therefore confirms its inclusion in *C. foetida* by Jeffrey (1966).

Both sections *Hostia* and *Zacintha* have their distributional centre in the E Mediterranean and spread to the W Mediterranean and eastwards into Central Asia. It has been shown for the species of sect. *Hostia* that the inner involucral bract enclose the marginal achenes in maturity, the same is known for the species of sect. *Zacintha* in a more poignant form (Babcock 1947b). So it is proposed to unite both sections. The correct name for the united section is *C.* sect. *Barkhausia*. In the chloroplast phylogeny *Crepis pusilla* and *C. zacintha* fall within the *C. neglecta* group (clade VI); this association, however, is only weakly supported and could be an indication of reticulate evolution (Enke & Gemeinholzer 2008).

Crepis heldreichiana should also be included in sect. *Barkhausia* as it shows morphological resemblances and fits into the E Mediterranean centre of distribution as it is occurring in Greece on the Peloponnesus.

Crepis triasii shows considerable difference in morphology to the other species of clade III (Babcock 1947b) but this could be a result of the species' endemic occurrence on the Balearic Islands. The ITS phylogeny, however, well supports its inclusion into clade III, so it is treated as a member of sect. *Barkhausia*.

Clade IV. — Clade IV includes *Crepis baldaccii* and *C. darvazica* of sect. *Berinia* as well as the type species of sect. *Soyeria, C. pontana. C. baldaccii* and *C. pontana* have a similar karyotype (Babcock 1947b), justifying the transfer of *C. baldaccii* to sect. *Soyeria*. The relation to *C. darvazica,* however, is only weakly supported by ITS data and not at all by *matK* data (Enke & Gemeinholzer 2008). *C. darvazica* will remain without sectional assignment until presumed close relatives (e.g., *C. straussii* (Babcock 1947b)) will be molecularly analysed.

Clade V. — Most species of sect. *Berinia* sampled for DNA sequence data cluster in clade V (Fig. 1; Enke & Gemeinholzer 2008). Sect. *Berinia,* the biggest section in Babcock's (1947b) infrageneric classification, is divided into four subsections: *Corymbiformae, Subcorymbiformae, Divaricatae* and *Strictae,* which are however, not supported by molecular data (Enke & Gemeinholzer 2008). The type species of sect. *Berinia* is *C. chondrilloides,* which clusters within clade V, so the section name applies to the species of clade V, excluding two species: *C. acuminata* (sect. *Psilochaenia*) and *C. hypochaeridea* (type species of sect. *Anisoramphus*).

Crepis acuminata differs from all other species of clade V in morphology, karyology and geographic distribution. As all members of sect. *Psilochaenia* it occurs exclusively in North America, is polyploid and has a basic chromosome number of $x = 11$. The singularity of these features within *Crepis* s.str. support the maintenance of sect. *Psilochenia*.

Crepis hypochaeridea (sect. *Anisoramphus*) differs from the rest of the species of clade V mainly in its South African distribution. Most of the African species are found in the large section *Anisoramphus,* of which only two further species have been sampled: *C. alpestris* (clade XI) and *C. newii* (clade X). Both species are to be excluded from *Anisoramphus* (see discussion under the respective clades). Due to lack of data on the relation within African *Crepis* species, *C. hypochaeridea* has to represent sect. *Anisoramphus*. A discussion of some N and E African species as included in the analysis by Enke & al. (2008) is given under clade X.

Clade VI. — Clade VI partly reflects the relations Babcock (1947b) assumed for sect. *Phytodesia*. The *Crepis neglecta* complex comprises in addition to *C. neglecta* (including subspecies) also *C. fuliginosa* and *C. cretica*. The closer relation within these species than to the others of the same section is also reflected in their karyotypes (Babcock & Jenkins 1943). Cytological studies by Tobgy (1943) and Kamari (1976) demonstrated the close relation within this complex. Clade VI can be considered to be equivalent to the *C. neglecta* complex. The type species of *Phytodesia*, however, is *C. nicaeensis* of clade II, so a new section for this group is necessary.

Clade VII. — The species of clade VII belong to three different sections: (1) *Crepis chrysantha, C. polytricha* and *C. rhaetica* belong to sect. *Brachypodes,* (2) *C. bungei* and *C. nigrescens* to sect. *Mesophylion,* (3) *C. oreades* and *C. crocea* to sect. *Macropodes*. *C. bungei* and *C. oreades* are the type species for their sections. The sister taxon to the above mentioned is the polyploid *C. biennis* (sect. *Berinia*), the split is, however, not statistically supported in the ITS phylogeny (Enke & Gemeinholzer 2008). As there is considerable doubt about the exact position of *C. biennis* within *Crepis* (unpublished molecular data) a sectional designation of this species is postponed until its genetic variability is further investigated.

Sect. *Brachypodes* is strongly polyphyletic according to the molecular data. Seven out of ten species in this section have been sampled for DNA sequence data; three species (namely *Crepis chrysantha, C. polytricha* and *C. rhaetica*) cluster in clade VII, whereas the four others cluster in three different clades: *C. jacquini* and *C. kerneri* both in clade II, *C. dioritica* in clade V and *C. aurea* in clade VIII (Enke & Gemeinholzer 2008). *C. chrysantha* and *C. polytricha* have a basic chromosome number of $x = 4$, *C. jacquini* and *C. aurea* have $x = 5$. The chromosome numbers of *C. rhaetica* and *C. dioritica* are unknown.

Sect. *Mesophylion* includes four species, *Crepis bungei, C. ircutensis, C. nigrescens* and *C. tectorum*. Czerepanov (1964) treated *C. ircutensis* as conspecific with *C. bungei*. *C. bungei* and *C. tectorum* show a distant relation in the *matK* analysis but cluster in completely different clades in the nuclear phylogeny: *C. bungei* in clade VII and *C. tectorum* in clade II (Fig. 4, Enke & Gemeinholzer 2008). Morphologically *C. nigrescens* is very similar to *C. tectorum,* mainly differing in the type of pubescence on the stem and involucrum as well as in a larger and darker corolla (Czerepanov 1964). In the molecular phylogeny it is, however, sister to *C. bungei* (Enke & Gemeinholzer 2008). *C. bungei* and *C. tectorum* share a similar karyotype (Babcock 1947b).

Crepis oreades and *C. crocea* from sect. *Macropodes* are the only species in the section with a Central Asian distribution, whereas all other species are of Mediterranean or African distribution. The only other member of sect. *Macropodes* sampled for DNA sequence data is *C. hookeriana*, a NW African species, found in clade X (Enke & Gemeinholzer 2008) and shows alliances to species centred in N Africa/SE Spain, e.g., *C. dianthoseris, C. albida, C. tingitana* and *C. oporinoides* and beyond in the Mediterranean and S Europe to species such as *C. vesicaria* and *C. alpestris* (Enke & al. 2008).

The Central Asian species of clade VII *(Crepis bungei, C. chrysantha, C. crocea* and *C. polytricha)* are obviously related as the species are similar in morphological, karyological and molecular features (Fig. 4, Table 2; Enke & Gemeinholzer 2008; Enke & al. subm.). Two additional species in clade VII that share morphological and molecular similarities are *C. oreades* and *C. rhaetica* (Enke & Gemeinholzer 2008). *C. bungei* and *C. oreades* are considered to be the putative diploid parents of the tetraploid *C. crocea,* whereas *C. chrysantha* is suspected to be one of the parents of the tetraploid *C. polytricha* (Babcock 1947b). As far as known, all of the above mentioned species have a basic chromosome number of $x = 4$ (Babcock 1947b).

For the species of clade VII it is proposed to fuse sect. *Macropodes* and sect. *Mesophylion* into one section and to transfer *Crepis chrysantha, C. polytricha* and *C. rhaetica* into a new section.

Clade VIII. — Clade VIII includes only *Crepis aurea* (sect. *Brachypodes*) and *C. leontodontoides* (sect. *Gephyroides*). Both species have similar and fairly small karyotypes (Babcock & Jenkins 1943). The two species have been considered to be closely related before, but have been placed into different sections due to different root morphology (Babcock & Jenkins 1943; Babcock 1947b). Avery (1930) reported viable hybrids between these two species. Their close relation is likewise well supported by nuclear and chloroplast data (Enke & Gemeinholzer 2008). *C. aurea* and *C. leontodontoides* should be placed into one section, but not necessarily in sect. *Brachypodes,* as both species show considerable differences in the karyotype to other species of this section (Babcock & Jenkins 1943). Sect. *Gephyroides,* however, is not suited to include *C. aurea* and *C. leontodontoides,* as *C. tingitana,* whose sister taxon in the molecular phylogeny is *C. albida* (sect. *Paleya*), is the type species of sect. *Gephyroides* and differs morphologically as well as karyologically from both *C. aurea* and *C. leontodontoides*. Therefore, *C.* sect. *Calliopea* is re-established to accommodate the two species.

Clade IX. — Clade IX includes *Crepis albida* (type species of *C.* sect. *Paleya*) and *C. tingitana* (type species of sect. *Gephyroides*). The species of sect. *Paleya* have very broad outer involucral bracts and conspicuously long corolla tubes, features that are absent in *C. tingitana*. Furthermore, there is no statistical support for the split between the two species in the ITS phylogeny and no relation in the *matK* analysis (Enke & Gemeinholzer 2008). Therefore, both sections are, for the time being, maintained.

Clade X. — Clade X includes *Crepis bellidifolia* and *C. bursifolia* (both sect. *Psammoseris*), *C. hookeriana* (sect. *Macropodes*), *C. newii* (sect. *Anisoramphus*), *C. vesicaria* (type species of sect. *Lepidoseris*) and *C. dianthoseris* (former *Dianthoseris schimperi*). These species are distributed from W Europe through the Mediterranean to E Africa and share a basic chromosome number of $x = 4$. Except for *C. dianthoseris,* where there is no information available, the involucral bracts of species of this clade get spongy thickened in maturity, most distinctive in *C. vesicaria* (Babcock 1947b). It is proposed to include all species of this clade in sect. *Lepidoseris,* of which *C. vesicaria* is the type species. *C. inopiniata* (former *Nannoseris inopiniata,* Enke & al. 2008) can safely be included in sect. *Lepidoseris* because of the strong morphological similarity to *C. dianthoseris*.

Clade XI. — Clade XI comprises five species of five different sections: *Crepis alpestris* (sect. *Anisoramphus*), *C. oporinoides* (sect. *Berinia*), *C. pyrenaica* (sect. *Soyeria*), *C. pygmaea* (type species of monotypic sect. *Omalocline*) and *C. capillaris* (sect. *Phytodesia*). The clade is well supported by ITS data, the chloroplast phylogeny, however, shows *C. capillaris* to be isolated from the rest of the species of clade XI (Enke & Gemeinholzer 2008), but the split is not well supported.

Crepis alpestris and *C. pyrenaica* form natural hybrids (Babcock 1947b), indicating close relation, which is mirrored by the molecular results (Enke & Gemeinholzer 2008). *C. oporinoides* also clusters closely with these two species.

The species of clade XI show overlapping distribution patterns: *Crepis pyrenaica* and *C. pygmaea* occur mainly in the Pyrenees and the Alps, the latter being an alpine species, whereas *C. pyrenaica* is montane to subalpine. *C. alpestris,* another montane and subalpine species, is distributed in the E Alps and eastward into the Balkan and Tatry Mountains. *C. oporinoides* is an alpine species of the mountains of S Spain. *C. capillaris* is the most widespread species in this clade, occurring in S and Central Europe from the lowland to the subalpine zone.

Even though the species of clade XI are morphologically distinct, which could partly be a reflection of their specialised habitats (e.g., alpine species), their molecular relation is very close, so they are all placed into sect. _Omalocline,_ of which _Crepis pygmaea_ provides the type.

Species of unclear affinity. — Five species included in the molecular analysis did not cluster within a clade or remained with unresolved relationship. These are _Crepis aspera_ (sect. _Nemauchenes_), _C. auriculifolia_ (sect. _Berinia_), _C. biennis_ (sect. _Berina),_ _C. darvazica_ (sect. _Berinia_) and _C. setosa_ (sect. _Nemauchenes_). _C. aspera_ provides the type of sect. _Nemanchenes_ and _C. setosa_ is maintained in this section because the split between these two species is not well supported by ITS (Enke & Gemeinholzer 2008) and unpublished molecular data indicate a close relation between them. The other three species remain without sectional assignment until further molecular analyses clarify their relation to other species within the genus. As _C. biennis_ provides the type of the name _Crepis,_ it is a consequence of its uncertain affinity that it cannot be decided at present which section has to be named as the typical section of the genus.

Taxonomic conclusions for the infrageneric classification of _Crepis_

A comparison of all species sampled for DNA sequence data (Enke & Gemeinholzer 2008) in regard to Babcock's (1947b) sectional classification, the clades inferred by a molecular phylogenetic approach (Enke & Gemeinholzer 2008) and the proposed revised sectional system is shown in Fig. 4.

Based on the discussion above, a revised infrageneric classification of _Crepis_ is outlined. Species marked with an asterisk were included in the molecular analyses of Enke & Gemeinholzer (2008), Enke & al. (2008) and Enke & al. (subm.). Species in bold are reassigned to new sections. For species without asterisk no molecular data are available. Species preceded by a question mark need further consideration and their placement is provisional; usually their sectional placement by Babcock (1947a, b) has been maintained for the time being.

Taxonomy and nomenclature of the species follows the _Cichorieae_ Portal (ICN 2009+).

Crepis L.
Type: _Crepis biennis_ L.

Crepis sect. **_Intybellioides_** Froel. (1838)
≡ _Crepis_ sect. _Intybellia_ Benth. (1873) ≡ _Intybellia_ Monnier (1829), non Cass. (1821). – Type: _Intybellia incarnata_ (Jacq.) Monnier, nom. illeg. [= _C. incarnata_ Tausch]
= _Crepis_ sect. _Phaecasium_ (Cass.) Babc. (1947) ≡ _Phaecasium_ Cass. (1826). – Type: _C. pulchra_ L.

Note. — _Crepis_ sect. _Intybellioides_ is based on the illegitimate genus _Intybellia_ Monn., whereas _Intybellia_ Cass. falls into the synonymy of _C._ sect. _Lagoseris_ (= _C._ sect. _Pterotheca_). Already Monnier (1929) included _C. pulchra_ into his _Intybellia_ along with _C. praemorsa_ and _C. incarnata_. In its revised circumscription the section unites the species of Babcock's sections _Intybellia_ and _Phaecasium._ The diagnosis of either section by Babcock (1947b) remains generally unchanged except that the united sections now includes both rhizomatous and taprooted species.

*_C. incarnata_ Tausch
*__*C. palaestina*__ (Boiss.) Bornm. – former _C._ sect. _Phaecasium_
*_C. praemorsa_ (L.) Walther
*__*C. pterothecoides*__ Boiss. – included by _matK_ data
*__*C. pulchra*__ L. – former _C._ sect. _Phaecasium_
?__*C. amanica*__ Babc. – former _C._ sect. _Phaecasium_
?_C. gymnopus_ Koidz.
?__*C. reuteriana*__ Boiss. – former _C._ sect. _Phaecasium_
?__*C. stojanovi*__ T. Georgiev – former _C._ sect. _Phaecasium_

Crepis sect. **_Lagoseris_** (M. Bieb.) Benth. (1873) ≡ _Lagoseris_ M. Bieb. (1810). – Type: _Lagoseris crepoides_ M. Bieb. [≡ _C. purpurea_ (Willd.) M. Bieb.]
= _Crepis_ sect. _Microcephalum_ Babc. (1947) – Type: _C. gmelini_ (L.) Tausch
= _Crepis_ sect. _Pterotheca_ (Cass.) Babc. (1947) – Type: _C. sancta_ (L.) Bornm.

Note. — The description for this section given by Babcock (1947b) is generally applicable, but has to be emended to include rhizomatous plants and plants with small heads and as few as 30 florets per head. In the case of _Crepis sancta_ triformic achenes are found. _C._ sect. _Lagoseris_ and _C._ sect. _Pterotheca_ are treated as genus _Lagoseris_ by Czerepanov (1964).

*_C. frigida_ (Boiss.& Balansa) Babc.
*__C. multicaulis__ Ledeb. – former _C._ sect. _Microcephalum_
*_C. purpurea_ (Willd.) M. Bieb.
*_C. sahendi_ Boiss. & Buhse
*__C. sancta__ (L.) Bornm. – former _C._ sect. _Pterotheca_
?_C. connexa_ Babc.
?_C. elbrusensis_ Boiss
?__*C. elongata*__ Babc. (incl. _C. tibetica_ Babc.) – former _C._ sect. _Microcephalum_
?_C. gmelini_ (L.) Tausch

Crepis sect. **_Hieracioides_** Froel. (1838)
≡ _Crepis_ sect. _Mesomeris_ Babc. (1947) – Lectotype (designated by Czerepanov 1964: 623): _C. lampsanoides_ (Gouan) Tausch

Note. — This section is preserved in the same delimitation as in Babcock (1947b); nomenclature follows Czerepanov (1964: 623).

*_C. hierosolimytana_ Boiss.
*_C. lampsanoides_ (Gouan) Tausch
*_C. lyrata_ (L.) Froel.
*_C. mollis_ (Jacq.) Asch.
*_C. smyrnaea_ Froel.

?_C. fraasii_ Sch. Bip. (= _C. montana_ d'Urv.; incl. _C. mungieri_ Boiss. & Heldr.)
?_C. willemetioides_ Boiss.

Crepis sect. _Alethocrepis_ Bisch. (1851)
≡ _Crepis_ sect. _Phytodesia_ Babc. (1947). – Lectotype (designated by Czerepanov 1964: 673): _Crepis nicaeënsis_ Pers.

Note. — The circumscription Babcock (1947b) gave of this section is generally applicable also on _Crepis tectorum,_ even though it has slightly larger heads than the rest of the species.
*_C. nicaeensis_ Pers.
*_C. micrantha_ Czerep. (= _C. parviflora_ Desf). – only _matK_ data available
***_C. tectorum_** L. – transfer from _C._ sect. _Mesophylion_
?_C. apula_ (Fiori) Babc. – of unclear relation within former _C._ sect. _Phytodesia_ (sensu Babcock 1947b)
?_C. insignis_ Babc.
?_C. suffreniana_ (DC.) J. Lloyd – of unclear relation within former _C._ sect. _Phytodesia_ (sensu Babcock 1947b)

Crepis sect. _Sucissocrepis_ Sch. Bip. ex Bisch. (1851)
≡ _Crepis_ sect. _Brachypodes_ Babc. (1947) – Lectotype (Czerepanov 1964: 615): _C. tergluoensis_ (Hacq.) A. Kern.

Note. — The nomenclature of the section follows Czerepanov (1964). The section is maintained with reservation, as the type species _Crepis tergluoensis_ has not been sampled for DNA.
*_C. jacquinii_ Tausch (incl. _C. kerneri_ Rech. f.)
***_C. lacera_** Ten. (= _C. latialis_ Sebast.) – transferred from _C._ sect. _Berinia_
C. bertiscea Jav. – transferred from _C._ sect. _Berinia,_ because morphologically very close to _C. lacera_
?_C. hokkaidoensis_ Babc.
?_C. terglouensis_ (Hacq.) A. Kern

Crepis sect. _Hapalostephium_ (D. Don) Froel. (1838)
≡ _Hapalostephium_ D. Don (1829) ≡ _Crepis_ sect. _Desiphylion_ Babc. (1947) – Lectotype (Czerepanov 1964: 608): _C. sibirica_ L.

Note. — This section is maintained in the same delimitation as in Babcock (1947b) with reservation as the type species _Crepis sibirica_ has not been sampled of DNA.
*_C. paludosa_ (L.) Moench
*_C. viscidula_ Froel. (incl. _C. geracioides_ Hausskn.)
?_C. sibirica_ L.

Crepis sect. **_Barkhausia_** (Moench) Gaudin (1829) ≡ _Barkhausia_ Moench (1794). – Type: _C. alpina_ L.
= _Crepis_ sect. _Zacintha_ (Mill.) Babc. (1947) ≡ _Zacintha_ Mill. (1754). – Type: _C. zacintha_ (L.) Loisel.
= _Crepis_ sect. _Hostia_ (Moench) Babc. (1947) ≡ _Hostia_ Moench (1802) ≡ _Crepis_ sect. _Anisoderis_ (Cass.) Benth. (1873) ≡ _Anisoderis_ Cass. (1827). – Type: _C. foetida_ L.

Note. — The description given by Babcock (1947b) for _Crepis_ sect. _Zacintha_ is generally applicable for this section uniting his sections _Zacintha_ and _Hostia,_ but has to be emended towards a larger size of flower heads, achenes and pappus.
***_C. alpina_** L. – former _C._ sect. _Hostia_
***_C. foetida_** L. (incl. _C. thomsonii_ Babc., _C. schimperi_ (A. Rich.) Schweinf., _C. eritreensis_ Babc.) – former _C._ sect. _Hostia_
***_C. heldreichiana_** (Kuntze) Greuter (= _C. taygetica_ Babc.) – transferred from _C._ sect. _Berinia_
***_C. kotschyana_** (Boiss.) Boiss. – former _C._ sect. _Hostia_
***_C. pusilla_** (Sommier) Merxm. – added to _Crepis_ by Merxmüller (1968)
***_C. rubra_** L. – former _C._ sect. _Hostia_
***_C. triasii_** (Cambess.) Nyman – transferred from _C._ sect. _Berinia_
***_C. trichocephala_** (Krasch.) V. V. Nitkin (= _C. foetida_ subsp. _afghanistanica_ Babc.) – former _C._ sect. _Hostia_
***_C. tybakiensis_** Vierh. – former _C._ sect. _Hostia_
*_C. zacintha_ (L.) Loisel.
?_C. dioscoridis_ L.
?_C. multiflora_ Sm.
?_C. patula_ Poir.
?**_C. syriaca_** (Bornm.) Babc. & Navashin – former _C._ sect. _Hostia_

Crepis sect. _Soyeria_ (Monnier) Benth. (1873)
≡ _Soyeria_ Monnier (1829). – Type: _C. pontana_ (L.) Dalla Torre
***_C. baldaccii_** Halácsy – transferred from _C._ sect. _Berinia_
*_C. pontana_ (L.) Dalla Torre (≡ _C. bocconei_ P. D. Sell, nom. illeg.)
?_C. conyzifolia_ (Gouan) A. Kern

Crepis sect. _Anisoramphus_ (DC.) Babc. (1947)
≡ _Anisoramphus_ DC. (1838) – Type: _C. hypochaeridea_ (DC.) Thell.

Note. — This section needs careful reconsideration not only because the molecular sampling is very poor. Of the three species sampled (_Crepis hypochaeridea_, _C. newii_ and the sole non African species of _C._ sect. _Anisoramphus_ sensu Babcock (1947) _C. alpestris_) only _C. hypochaeridea_ remains in the present section.
*_C. hypochaeridea_ (DC.) Thell (incl. _C. caudicaulis_ Babc., _C. chirindica_ S. Moore, _C. congoensis_ Babc., _C. simulans_ S. Moore)
?_C. carbonaria_ Sch. Bip. (incl. _C. ellenbeckii_ R. E. Fr., _C. glandulosissima_ R.E.Fr.)
?_C. gossweileri_ S. Moore
?_C. iringensis_ Babc.
?_C. schultzii_ (Hochst.) Vatke
?_C. subscaposa_ Collett & Hemsl.
?_C. urundica_ Babc.

Crepis sect. _Psilochenia_ (Nutt.) Babc. (1947)
≡ _Psilochenia_ Nutt. (1841). – Type: _C. occidentalis_ Nutt.

Note. — The North American species of *Crepis* sect. *Psilochaenia* are polyploid and their placement within the genus remains unclear at present.

**C. acuminata* Nutt.
?*C. atribarba* A. Heller
?*C. bakeri* Greene
?*C. barbigera* Coville
?*C. intermedia* A. Gray
?*C. modocensis* Greene
?*C. monticola* Coville
?*C. occidentalis* Nutt.
?*C. pleurocarpa* A. Gray
?*C. runcinata* (E. James) Torr. & A. Gray.

Crepis **sect.** ***Berinia*** (Brign.) Babc.

≡ *Berinia* Brign. – Type: *Berinia andryaloides* Brign. [≡ *C. chondrilloides* Jacq.]

Note. — Molecular investigations (Enke & Gemeinholzer 2008) could not find support for the infrasectional subdivision into four subsections *Corymbiformae, Subcorymbiformae, Divaricatae* and *Strictae* by Babcock (1947b), therefore they are not maintained here.

**C. chondrilloides* Jacq.
****C. dioritica*** Boiss. (incl. *C. albiflora* Babc.) – transferred from *C.* sect. *Sucissocrepis* (formerly *C.* sect. *Brachypodes*)
**C. guioliana* Babc.
**C. macropus* Boiss. & Heldr.
**C. merxmuelleri* Kamari & Hartvig
**C. sibthorpiana* Boiss. & Heldr.
**C. sonchifolia* (M. Bieb.) C.A. Mey
**C. turcica* Degen & Bald. – inclusion into *C.* sect. *Berinia* supported by chloroplast marker
**C. turcomanica* Krasch.
?*C. athoa* Boiss.
?*C. ciliata* K. Koch
?*C. dens-leonis* K. Koch
?*C. incana* Sm.
?*C. khorassanica* Boiss.
?*C. pannonica* (Jacq.) K. Koch
?*C. pantocseckii* (Vis.) Latzel
?*C. straussii* Bornm.

Crepis **sect.** ***Neglectoides*** Enke, **sect. nov.**

Type: *C. neglecta* L.

Herbae annuae; *caules* singuli vel plures, max. 50 cm alti, in parte basali vel mediano ramosi; *folia* setosa eglandulosa, basalia oblanceolata obtusa ad acuta ad basin angustata, caulina inferioria similia, interdum amplexicaulia, caulina superioria bracteiformia; *capitula* parva numerosa; *squamis* involucri acutis, exterioribus 4–6 parvis, interioribus 8–14, setosis eglandulosis vel glandulosis; *ligulae* flavae parte exteriore rubescente; *achaenia* fusiforma attenuata vel rostrata 10 costata. 2*n* = 6, 8.

Annuals with 1-many stems up to 50 cm tall. *Branched* from near to base or middle. *Basal* leaves oblanceolate, obtuse to acute, narrowed at base; lower cauline leaves like basals but sometimes amplexicaul; upper cauline leaves bractlike. *Leaves* with short eglandular hairs. *Capitula* small and many. *Involucral* bracts acute, outer very small (4–6). *Inner* phyllaries 8–14, eglandular setose or with glandular hairs. *Ligules* yellow and usually reddish on outside. *Achenes* fusiform, attenuate or distinctly beaked, 10 ribbed. 2*n* = 6, 8.

Note. — The name *Neglectoides* refers to the *Crepis neglecta*-like phenotype of the plants within this section.

****C. neglecta*** L. (incl. *C. corymbosa* Ten.) – excluded from *C.* sect. *Phytodesia* sensu Babcock (1947b)
****C. fuliginosa*** Sibth. & Sm. – excluded from *C.* sect. *Phytodesia* sensu Babcock (1947b)
****C. cretica*** Boiss. – excluded from *C.* sect. *Phytodesia* sensu Babcock (1947b)
C. hellenica Kamari – excluded from *C.* sect. *Phytodesia* sensu Babcock (1947b); included into *C. neglecta* group by Kamari (1976)

Crepis **sect.** ***Mesophylion*** Babc. (1947)

Type: *C. bungei* Ledeb.

= *Crepis* sect. *Macropodes* Babc. (1947) – Type: *C. oreades* Schrenk

Note. — Babcock's (1947b) description for *Crepis* sect. *Mesophylion* has to be emended in some points: the section now also includes species with a rhizome, more than one stem, 10–75 florets per head, larger flower heads (up to 2.5 cm) and shortly beaked achenes. The name *C.* sect. *Mesophylion* was chosen over *C.* sect. *Macropodes* as the latter refers to strongly developed taproots (Babcock 1947b) which is not present in all species now included into the present section.

**C. bungei* Froel. (incl. *C. ircutensis* Babc.)
****C. chrysantha*** (Ledeb.) Turcz. – transferred from *C.* sect. *Sucissocrepis* (formerly *C.* sect. *Brachypodes*)
****C. crocea*** (Lamk.) Babc. – former *C.* section *Macropodes*, placed into clade VII by Enke & al. (subm.)
**C. nigrescens* Pohle
****C. oreades*** Schrenk – former *C.* section *Macropodes*
****C. polytricha*** (Ledeb.) Turcz. – transferred from *C.* sect. *Sucissocrepis* (formerly *C.* sect. *Brachypodes*)
****C. rhaetica*** Hegetschw. – transferred from *C.* sect. *Sucissocrepis* (formerly *C.* sect. *Brachypodes*)
?***C. armena*** Froel. – former *C.* section *Macropodes*
?***C. bithynica*** Boiss. – former *C.* section *Macropodes*
?***C. demavendi*** Bornm. – former *C.* section *Macropodes*
?***C. faureliana*** Maire – former *C.* section *Macropodes*
?***C. heterotricha*** Froel. – former *C.* section *Macropodes*
?***C. willdenowii*** Czerep. (incl. *C. pinnatifida* (Willd.) Froel.) **–** former *C.* section *Macropodes*
?****C. robertioides*** Boiss. – former *C.* section *Macropodes,* position within genus unclear as only chloroplast marker data available, provisionally included
?***C. schachtii*** Babc. – former *C.* section *Macropodes*
?***C. tenerrima*** (Schweinf. & Asch.) R. E. Fr. – former *C.* section *Macropodes*
?***C. xylorrhiza*** Sch. Bip. – former *C.* section *Macropodes*

Crepis sect. ___Calliopea___ (D. Don) Rouy (1905)

≡ _Calliopea_ D. Don (1829). – Type: _C. aurea_ (L.) Cass.

Note. — Don (1829) based his genus _Calliopea_ on _Crepis aurea_ as its sole member, which consequently provides the type of the name. The section includes rosette perennials with 1–8 not or remotely branched stems. Between 2 and 40 cm tall. All leaves caudical, mostly glabrous or sparsely hairy. If cauline leaves present, bractlike. Basal leaves 1–25 × 0.5–5.5 cm, obovate to oblanceolate, dentate to pinnatifid. Involucrum campanulate and tomentulose. Involucral bracts linear-lanceolate, obtuse. Ligules yellow or orange with a reddish or reddish-purple outer face. Achenes 3.5–6 mm, fusiform and strongly attenuated into slightly expanded disc. 10–16 ± spiculate ribs. $2n = 10$.

*___C. aurea___ (L.) Cass. – transferred from _C._ sect. _Sucissocrepis_ (formerly _C._ sect. _Brachypodes_)
*___C. leontodontoides___ All. – transferred from sect. _Gephyroides_

Crepis sect. ___Gephyroides___ Babc. (1947)

Type: _C. tingitana_ Ball
*_C. tingitana_ Ball
?_C. suberostris_ Batt.

Crepis sect. ___Paleya___ (Cass.) Babc. (1947)

Type: _C. albida_ Vill.
*_C. albida_ Vill.
?_C. achyrophoroides_ Vatke
?_C. elymaitica_ Bornm.

Crepis sect. ___Lepidoseris___ (Rchb.) Babc. (1947)

≡ _Barkhausia_ [unranked] _Lepidoseris_ Rchb. (1831–32). – Type: _C. vesicaria_ L.

Note. — The description for this section as given by Babcock (1947b) can be maintained. The genus now, however, includes with _Crepis hookeriana_ and _C. dianthoseris_ species without beaked achenes and _C. newii_ lacks the otherwise typical ciliate receptacle.

*___C. bellidifolia___ Loisel. (incl. _C. albanica_ (Jáv.) Babc.) – transferred from _C._ sect. _Psammoseris._
*___C. bursifolia___ L. – transferred from _C._ sect. _Psammoseris._
*___C. dianthoseris___ N. Kilian & al. – The outer involucral bracts, which are nearly as long as the inner in _C. dianthoseris_ are untypical for _Crepis_, but can be interpreted as consequence of the acaulescent habitus (Enke & al. 2008). Close relation to and similar geographic distribution as _C. newii._
*___C. hookeriana___ Ball. – transferred from sect. _Mesophylion_ (formerly _C._ sect. _Macropodes_).
___C. inopinata___ (Cufod.) N. Kilian & al. – placed here because of the close morphological resemblance to _C. dianthoseris_ and its geographic distribution.
*___C. newii___ Oliver & Hiern (incl. _C. bruceae_ Babc., _C. cameroonica_ Hutch. & Dalziel, _C. keniensis_ (R. E. Fr.) Babc., _C. kilimandscharica_ O. Hoffm., _C. meruensis_ Babc., _C. mildbraedii_ Babc., _C. suffruticosa_ Babc., _C. swynnertonii_ S. Moore) – transferred from _C._ sect. _Anisoramphus_
*_C. vesicaria_ L.
?_C. balliana_ Babc.
?_C. erythia_ Pau (= _C. bourgeaui_ Maire, incl. _C. fontiana_ Maire)
?_C. canariensis_ (Sch. Bip.) Babc.
?_C. claryi_ Batt.
?_C. clausonis_ (Pomel) Pomel
?_C. divaricata_ (Lowe) F. W. Schultz.
?_C. libyca_ (Pamp.) Babc.
?_C. marschallii_ (C. A. Mey.) F. W. Schultz
?_C. noronhaea_ Babc.
?_C. salzmannii_ Babc.
?_C. sprengelii_ Nicotra (= _C. spathulata_ Guss.)

Crepis sect. ___Omalocline___ (Cass.) Benth. (1873)

≡ _Omalocline_ Cass. (1827) – Type: _Omalocline prunellifolium_ (Guan) Cass. [≡ _C. pygmaea_ L.]

*___C. alpestris___ (Jacq.) Tausch – transferred from _C._ sect. _Anisoramphus_
*___C. capillaris___ (L.) Wallr. – transferred from _C._ sect. _Alethocrepis_ (formerly _C._ sect. _Phytodesia_)
*___C. oporinoides___ Froel. – transferred from _C._ sect. _Berinia_
*_C. pygmaea_ L.
*___C. pyrenaica___ (L.) Greuter (= _C. blattarioides_ (L.) Vill.) – transferred from _C._ sect. _Soyeria_

Crepis sect. ___Spathoides___ Babc. (1947)

Type: _C. kashmirica_ Babc.

Note. — The single species of this section has not been included in the molecular analyses. The section is maintained in the same circumscription as in Babcock (1947b).

Crepis sect. ___Napiseris___ Babc. (1947)

Type: _C. napifera_ (Franch.) Babc.

Note. — This monotypic section is maintained in the same circumscription as by Babcock (1947b). The section has not been included into the molecular analysis.

Crepis sect. ___Pyrimachos___ Babc. (1947)

Type: _C. phoenix_ Dunn

Note. — This section of SE Asian species is maintained in the same circumscription as by Babcock (1947b). The section has not been included into the molecular analysis.

C. bodinieri H. Lѐv.
C. chloroclada Collett & Hemsl.
C. lignea (Vaniot) Babc.
C. phoenix Dunn
C. rigescens Diels

Crepis sect. ___Nemauchenes___ (Cass.) Benth. (1873)

≡ _Nemauchenes_ Cass. (1818). – Type: _Nemauchenes ambigua_ Cass. [= _C. aspera_ L.]

Note. — This section is maintained in the same delimitation as in Babcock (1947b).
C. atheniensis Babc.
C. aculeata (DC.) Boiss.
C. amplexifolia (Godr.) Willk.
**C. aspera* L. – molecularily isolated within *Crepis*.
C. juvenalis (Delile) F. W. Schultz
C. muhlisii Babc.
**C. setosa* Haller f. – molecularily isolated within *Crepis*

Crepis sect. ***Psammoseris*** (Boiss.) Babc. (1947)
≡ *Psammoseris* Boiss. & Reut. (1849). – Type: *C. senecioides* Delile

Note. — This section is nearly preserved in the same delimitation as in Babcock (1947b), except for the exclusion of *Crepis bellidifolia* and *C. bursifolia*.
C. filiformis Viv.
C. nigricans Viv.
C. ruepellii Sch. Bip. (incl. *C. friesii* Babc., *C. ugandesis* Babc., *C. abyssinica* Sch. Bip., *C. forskalii* Babc.)
C. senecioides Delile

Species of unclear affinity
**Crepis auriculifolia* Spreng (incl. *C. raulini* Boiss.) – excluded from *C.* sect. *Berinia*
**C. biennis* L. – excluded from *C.* sect. *Berinia*
**C. darvazica* Krasch (incl. *C. songorica* (Kar. & Kir.) Babc.) – excluded from *C.* sect. *Berinia*

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Appendix

Samples for achene ultra thin sections

Askellia: *A. flexuosa* (Ledeb.) W. A. Weber, China, Gansu, *Kürschner & Sonnentag 01-203* (B); *A. pygmaea* (Ledeb.) Sennikov, Canada, Fairy Lake, *J. A. Calder s.n.* (B).

Crepis: *C. acuminata* Nutt., USA, California, *L. S. Rose s.n.* (B); *C. albida* Vill., Spain, Almeria, *R. Valdes s.n.* (B); *C. aurea* Rchb., Austria, *N. Enke NE0142* (B); *C. biennis* L., Austria, *N. Enke NE0143* (B); *C. capillaris* (L.) Wallr., Spain, Pyrenees, *N. Enke NE0043* (B); *C. chondrilloides* Jacq., *Bornmüller s.n.* (B); *C. foetida* L., Greece, Cyprus, *R. Hand 5263* (B); *C. kerneri* Rech. f., Italy, Dolomites, *N. Enke NE104* (B); *C. lampsanoides* (Gouan) Tausch, France, Pyrenees, *N. Enke NE0020* (B); *C. leontodontoides* All., Italy, Sicily, *Greuter & Agababian 24457* (B); *C. mollis* (Jacq.) Asch., Poland, *Koziol s.n.* (B); *C. multicaulis* Ledeb., Russia, Altay, *Raab-Straube 020302* (B); *C. multicaulis* Ledeb., Kirghizia, Tien Shan, *Dürbye s.n.* (B); *C. neglecta* (Sm.) Vierh., Greece, Etolias, *Nielssen s.n.* (B); *C. paludosa* Moench, France, Pyrenees, *N. Enke NE0019* (B); *C. praemorsa* (L.) Tausch, Italy, Bolzano, *van Bouggenhout s.n.* (B); *C. purpurea* (Willd.) M. Bieb., Russia, *Steven s.n.* (B); *C. rubra* L., Greece, Etolia, *E. Willing 13378* (B); *C. sancta* (L.) Babc., Persia, *K. H. Rechinger s.n.* (B); *C. sancta* (L.) Babc., France, Gard, *J. Lambinon s.n.* (B); *C. tectorum* L., Switzerland, Vallis, *N. Enke NE0076* (B); *C. zacintha* (L.) Babc., Greece, Cyprus, *R. Hand 5323* (B).

Rhagadiolus: *R. stellatus* (L.) Gaertn., *R. Hand 2265* (B), Cyprus; *R. stellatus.*(L.) Gaertn., *W. Lang s.n.* (B) Cyprus, Salamis.

Sampled for SEM of pollen

Crepis: *C. albida* Vill., Spain, Almeria, *Cannon & al. 1023* (E); *C. biennis* L., Austria, *N. Enke NE0146* (B); *C. dioscorides* L., Greece, Peloponnesus, *Raus & al. s.n.* (B); *C. foetida* subsp. *commutata* (Spreng.) Babc., Greece, Tokmakia, *J. R. Edmondson & McClintock E 2513* (E); *C. hypochaeridea* (DC.) Thell., South Africa, *N. J. Devenish 1657* (E); *C. lampsanoides* (Gouan.) Tausch, Spain, Oviedo, *D. W. Dresser 1256a* (E); *C. leontodontoides* All., France, Corse, *BG Liege* (B); *C. paludosa* (L.) Moench, Germany, M. F. Gardner, *S. G. Gardner s.n.* (E); *C. pulchra* L., BG Konstanz *137-02-06-70* (B); *C. sancta* (L.) Babc., Italy, Siena, *Romi s.n.* (B); *C. tectorum* L. Finland, Nylandia, *Aune Haakana s.n.* (E); *C. vesicaria* L., Frankreich, Pyrenees, *N. Enke NE0016* (B).

Sampled for SEM of pappus bristles

Crepis: *C. albida* Vill., Spain, Almeria, *Cannon & al. 1023* (E); *C. biennis* L., Austria, *N. Enke NE0146* (B); *C. dioscorides* L., Greece, Peloponnesus, *Raus & al. s.n.* (B); *C. foetida* subsp. *commutata* (Spreng.) Babc., Greece, Tokmakia, *J. R. Edmondson & McClintock E 2513* (E); *C. hypochaeridea* (DC.) Thell., South Africa, *N. J. Devenish 1657* (E); *C. lampsanoides* (Gouan.) Tausch., Spain, Oviedo *D. W. Dresser 1256a* (E); *C. leontodontoides* All., France, Corse, *BG Liege* (B); *C. paludosa* (L.) Moench, Germany, *M. F. Gardner & S. G. Gardner s.n.* (E); *C. pulchra* L., BG Konstanz *137-02-06-70* (B); *C. sancta* (L.) Babc., Italy, Siena, *Romi s.n.* (B); *C. tectorum* L., Finland, Nylandia, *Aune Haakana s.n.* (E); *C. vesicaria* L., Frankreich, Pyrenees, *N. Enke NE0016* (B).