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

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

Abstract


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, Phaeasium, 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, ligu-late 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.
The recent molecular phylogeny of *Crepis* by Enke & Gemeinholzer (2008) based on ITS and matK sequence data proved the genus to be polyphylectic 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*, *Phaeacasium* and *Pterotheca*, parts of which have sometimes been treated as a separate genus *Lagoseris* (Cerepanov 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 Babcock (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).

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* achenes 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
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 2x 24 h. Dehydration was facilitated by a subsequent treatment of ascending ethanol dilutions (70 %, 80 %, 90 %, 96 % and 2x 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 protoplasmic 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...
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.

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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).

<table>
<thead>
<tr>
<th>Species</th>
<th>Clade</th>
<th>Section</th>
<th>Achene cross section type</th>
<th>Ø (µm)</th>
<th>spikes/100 µm</th>
<th>no. of cells in Ø</th>
<th>Pollen type</th>
<th>Ø (µm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Askellia flexuosa</td>
<td>Askellia</td>
<td>Ixeridopsis</td>
<td>Ia</td>
<td>—</td>
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<td>—</td>
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<td>—</td>
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<tr>
<td>A. pygmaea</td>
<td>Askellia</td>
<td>Ixeridopsis</td>
<td>Ia</td>
<td>30–32</td>
<td>1–4</td>
<td>6–7</td>
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<td>—</td>
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<tr>
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<td>Lapsana</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>T¹</td>
<td>—</td>
</tr>
<tr>
<td>Rhagadiolus sp.</td>
<td>Rhagadiolus</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
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<td>—</td>
</tr>
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<td>Lagoseris</td>
<td>Microcephalum</td>
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<td>—</td>
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<td>—</td>
<td>—</td>
<td>—</td>
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<tr>
<td>C. pulchra</td>
<td>Lagoseris</td>
<td>Phaeacium</td>
<td>—</td>
<td>14–15</td>
<td>0–2</td>
<td>2–3</td>
<td>C</td>
<td>28–34</td>
</tr>
<tr>
<td>C. purpurea</td>
<td>Lagoseris</td>
<td>Lagoseris</td>
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<td>—</td>
<td>—</td>
</tr>
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<td>C. praemorsa</td>
<td>Lagoseris</td>
<td>Intybellia</td>
<td>Ia</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>T¹</td>
<td>38–46¹</td>
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<td>C. sancta</td>
<td>Lagoseris</td>
<td>Pteroheca</td>
<td>III</td>
<td>10–11</td>
<td>0–2</td>
<td>2–3</td>
<td>T</td>
<td>28–34</td>
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<tr>
<td>C. lampsanooides</td>
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<td>Mesomeris</td>
<td>Ib</td>
<td>19–20</td>
<td>6–7</td>
<td>4–6</td>
<td>C</td>
<td>31–37</td>
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<tr>
<td>C. mollis</td>
<td>Clade I</td>
<td>Mesomeris</td>
<td>Ic</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>C³</td>
<td>34–38¹</td>
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<td>Brachypodes</td>
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<td>35–37</td>
<td>4–6</td>
<td>6–7</td>
<td>—</td>
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<td>Desiphylion</td>
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<td>—</td>
<td>—</td>
<td>—</td>
<td>C</td>
<td>36–42</td>
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<td>C. tectorum</td>
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<td>Mesophylin</td>
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<td>2–3</td>
<td>3–4</td>
<td>T(C¹)</td>
<td>26–32</td>
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<td>Clade III</td>
<td>Hostia</td>
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<td>—</td>
<td>T</td>
<td>26–32</td>
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<td>Clade III</td>
<td>Zacintha</td>
<td>IV</td>
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<td>3–4</td>
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<td>Psilochaenia</td>
<td>II</td>
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</tr>
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<td>Clade V</td>
<td>Berinia</td>
<td>Ia</td>
<td>—</td>
<td>—</td>
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<td>—</td>
<td>—</td>
</tr>
<tr>
<td>C. dioecridis</td>
<td>—</td>
<td>Brachypodes</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>C</td>
<td>26–32</td>
</tr>
<tr>
<td>C. hypocharidea</td>
<td>Clade V</td>
<td>Anisoramphus</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>T</td>
<td>31–37</td>
</tr>
<tr>
<td>C. neglecta</td>
<td>Clade VI</td>
<td>Phytodesia</td>
<td>Ia</td>
<td>—</td>
<td>—</td>
<td>—</td>
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<tr>
<td>C. biennis</td>
<td>Clade VII</td>
<td>Berinia</td>
<td>Ib</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>T(C¹)</td>
<td>33–39</td>
</tr>
<tr>
<td>C. bungei</td>
<td>Clade VII</td>
<td>Mesophylin</td>
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<td>37–40</td>
<td>3–4</td>
<td>6–7</td>
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<tr>
<td>C. leontodontoides</td>
<td>Clade VIII</td>
<td>Gephyroides</td>
<td>IV</td>
<td>13–14</td>
<td>2–4</td>
<td>2–3</td>
<td>T</td>
<td>25–31</td>
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<tr>
<td>C. albida</td>
<td>Clade IX</td>
<td>Paleya</td>
<td>Ib</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>T</td>
<td>26–32</td>
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<tr>
<td>C. vesicaria</td>
<td>Clade X</td>
<td>Lepidoseris</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>C(T³)</td>
<td>27–33</td>
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<tr>
<td>C. capillaris</td>
<td>Clade XI</td>
<td>Phytodesia</td>
<td>Ib</td>
<td>16–17</td>
<td>3–4</td>
<td>4–5</td>
<td>T¹</td>
<td>34–41¹</td>
</tr>
</tbody>
</table>
The pappus bristles of the sampled species of the Lagoiseris 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 echinolate 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 officinale subgroup (Fig. 5L, C. albida, C. biennis, C. foetida, C. hypothaeidea, 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 Iseris, 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 Cephalidinae, e.g., in Ixeridium (A. Gray) Tzvelev, their karyotypes, however, showing distinct differences (Pak & Kawano 1992; Pak 1993).

Sennikov & Iliarionova (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. tenaxifolia with x = 5 was transferred to Crepidioidium, see Tzvelev 2008).

Iseris 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, Phaeasium, 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 Czerespanov (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 (Czerespanov 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 Taraxacum oficinale 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. multi- 
caulis* and *C. pulchra* (as representatives of the *Lagoseris* 
group) are very similar in the composition of their phy-
tochemical 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 spe-
cies of sections *Intybellia*, *Phaeasium*, *Lagoseras*, *Mi-
crocephalum* 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 *Lagoseras* group. Conclusively, 
no argument could be found to encourage an exclusion 
of the species of the *Lagoseras* group from *Crepis*; nei-
ther 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 *Lagoseras* clade from *Crepis*, it is proposed to pres-
serve the current generic circumscription of *Crepis*, even 
though it would be parahyletic 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 morphologi-
cal distinctness of both genera. Furthermore, the phylo-
geny of *Crepis* s.l. (Enke & Gemeinholzer 2008) might 
reflect a more complex evolutionary history than can be 
drawn from dichotomous branching patterns of phyloge-
netic trees, so further analyses and investigations are still 
needed.

As shown above, *Crepis* sect. *Lagoseras* and *Pterothe-
cra* are also morphologically closely related, corroborat-
ning their clustering in the same subclade.

*Crepis multi-caulis* (as the only representative of *C. 
sect. Microcephalum* sampled in the molecular analysis 
of Enke & Gemeinholzer (2008)) resembles *C. sancta* 
(sect. *Pterotheca*) in some aspects of morphology and 
karyotype (Babcok & Jenkins 1943), but not in the re-
ceptacular palaee as they are lacking in *C. multi-caulis*. *C. 
multi-caulis* 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 *Lagoseras* (see Taxonomic conclu-
sions, below).

*Crepis praemorsa* and *C. incarnata* of *C. sect. Inty-
bellia* are very closely related and sometimes treated as 
subspecies of *C. praemorsa* (e.g., Sell 1976, Siljak-Yako-
vlev & Cartier 1982). The section is closely related to 
*C. sect. Phaeasium*, typified by *C. pulchra*. Babcok & 
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 systemati-
cally discriminating factor. The karyotypic resemblance 
between *C. praemorsa* and *C. pulchra* is likewise sup-
ported, when banding patterns given by Siljak-Yakovlev 
& Cartier (1982) for *C. praemorsa* and Dimitrova & Greilhuber (2001) for *C. pulchra* are compared. Both 
 moluclar markers (ITS, matK) support the close rela-
tionship of these two sections (Enke & Gemeinholzer 
2008). This provides sufficient evidence to merge sec-
tions *Intybellia* and *Phaeasium*. 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 chromosome number of *x* = 6. The 
correct name of this section is *C. sect. Hieracioides*.

Clade II. — The species in clade II belong to five differ-
ent sections: *Crepis nicaeensis* to sect. *Phytodesia*, *C. tec-
torum* to sect. *Mesophylium*, *C. paludosa* and *C. viscidula* 
to sect. *Desiphylion*, *C. jacquini* and *C. kernerii* to sect. 
*Brachypodes* and *C. lacerav to sect. Berinia*. *C. tectorum* is 
sister to *C. nicaeensis* in the ITS phylogeny, whereas *C. 
tectorum* and *C. micrantha* (also sect. *Phytodesia*) clus-
ter together in the chloroplast based phylogeny (Enke & 
Gemeinholzer 2008). These three polymorphic species 
share some similarity, such as annuality, a wide distribu-
tion and some gross morphological congruencies. Thus it 
appears reasonable to transfer *C. tectorum* to sect. *Phytode-
 sia*, which is correctly named *C. sect. Alethocrepis* and 
 typified by *C. nicaeensis*.

To draw taxonomic conclusions for the other spe-
cies 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. tergluoenis*), 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. kernerii* 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 resem-
bance in gross morphology to *C. kernerii* 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. kotschyan*, *C. ru-
bran*, *C. thomsonii*, *C. trichocephala*, *C. tybakiensis*), two
species of sect. Zacintha (C. pusilla, C. zacintha) and two of sect. Berinia (C. heldreichiana, C. triassii). 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 to 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 triassii 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: Corynbiormae, Subcorynbiormae, Divaricateae 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. Psilochaenia.

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. Mesophyilon, (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. jacquinii and C. kerneri both in clade II, C. doriitica 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. jacquinii and C. aurea have $x = 5$. The chromosome numbers of C. rhaetica and C. doriitica are unknown.

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. nigriscens* is very similar to *C. tectorum*, mainly differing in the type of pubescence on the stem and involucrem as well as in a larger and darker corolla (Czercepanov 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. *Mesophylium* 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. *Brachypododes*) 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. *Brachypododes*, 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. *Psammooseris*), *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. *Omaloclione*) 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 Tatra 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. Omaloclone, 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. Nemaunchenes), C. auriculatifolia (sect. Berinia), C. biennis (sect. Berinia), C. darvazica (sect. Berinia) and C. setosa (sect. Nemaunchenes). C. aspera provides the type of sect. Nemaunchenes 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]

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 Bieb. – former C. sect. Phaecasium
*C. gymnopus Koidz.
*C. reuteriana Boiss. – former C. sect. Phaecasium
*C. stojanovi T. Georgiev – former C. sect. Phaecasium

≡ Crepis sect. Microcephalum Bieb. (1947) – Type: C. gmelini (L.) Tausch

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) Bieb.
*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 Bieb.
*C. elbrusensis Boiss
*C. elongata Bieb. (incl. C. tibetica Bieb.) – former C. sect. Microcephalum
*C. gmelini (L.) Tausch

Crepis sect. Hieracioides Froel. (1838)

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

*C. hierosolimitana 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)

Note. — The circumscription Babcock (1947b) gave of this section is generally applicable also on Crepis sect. Phytodesia (sensu Babcock 1947b) and 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. Mesophylyon
*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)

Note. — The nomenclature of the section follows Czerepanov (1964). The section is maintained with reservation as in Babcock (1947b) with reservation as the type species Crepis terglouensis has not been sampled for DNA.
*C. jacquinii Tausch (incl. C. kernerii 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 (Haq.) A. Kern

Crepis sect. Hapalostephium (D. Don) Froel. (1838)

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. paludosus (L.) Moench
*C. viscidula Froel. (incl. C. geracioide Hausskn.)
*C. sibirica 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. heldreichiana (Kuntze) Greuter (= C. taygetica Babc.) – transferred from C. sect. Berinia
*C. kotschyanana (Boiss.) Boiss. – former C. sect. Hostia
*C. pusilla (Sommer) Mérxm. – added to Crepis by Mérxmüller (1968)
*C. rubra L. – former C. sect. Hostia
*C. triasii (Cambess.) Nyman – transferred from C. sect. Berinia
*C. trichocephala (Krasch.) V. V. Nikin (= C. foetida subsp. afghanistanica Babc.) – former C. sect. Hostia
*C. tybakienis 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) Bentham. (1873)
≡ Soyeria Monnier (1829). – Type: C. pontana (L.) Dalla Torre
*C. baldaccii Halácsy – transferred from C. sect. Berinia
*C. pontana (L.) Dalla Torre (≡ C. boccone 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. nevii 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 & Hems.
*C. urundica Babc.

Crepis sect. Phytodesia (Nutt.) Babc. (1947)
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. atrirabba* A. Heller
*C. bakeri* Greene
*C. barbigeria* 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.) Babcock
≡ *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, Sub-corymbiformae, Divaricatae and Stricteae by Babcock (1947b), therefore they are not maintained here.

*C. chondrilloides* Jacq.


*C. guioliana* Babcock.
*C. macropus* Boiss. & Heldr.
*C. merrxmuelleri* 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. athou* Boiss.
*C. ciliata* K. Koch
*C. dens-leonis* K. Koch
*C. incana* Sm.
*C. khorassanica* Boiss.
*C. pannonica* (Jacq.) K. Koch
*C. pantoecekkii* (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 ob lanceolate obtusa ad acuta ad basin angustata, caulina inferioria similis, interdum amplexicaulis, caulina superrioria bracteiformia; capitula parva numerosa; squamis involucri acutis, exterioribus 4–6 parvis, inferioribus 8–14, setosis eglandulosi vel glandulosi; ligulae flavae parte exteriore rubescente; achaenia fusiforma attenuata vel rostrata 10 costata. 2n = 6, 8.

Annuals with 1-many stems up to 50 cm tall. Branched from near to base or middle. Basal leaves ob lanceolate, 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. 2n = 6, 8.

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

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

Crepis sect. *Mesophylion* Babcock (1947)

Type: *C. bungei* Ledeb.
≡ *Crepis* sect. *Macropodes* Babcock (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* Babcock.)
*C. chrysantha* (Lede.) Turcz. – transferred from C. sect. *Sucissocrepis* (formerly C. sect. Brachyptodes)
*C. crocea* (Lamk.) Babcock. – former C. sect. *Macropodes*, placed into clade VII by Enke & al. (subm.)
*C. nigrescens* Pohle
*C. oreades* Schrenk – former C. sect. *Macropodes*
*C. polytricha* (Lede.) Turcz. – transferred from C. sect. *Sucissocrepis* (formerly C. sect. Brachyptodes)
*C. armena* Froel. – former C. sect. *Macropodes*
*C. bithynica* Boiss. – former C. sect. *Macropodes*
*C. demavendi* Bornm. – former C. sect. *Macropodes*
*C. faureliana* Maire – former C. sect. *Macropodes*
*C. heterotricha* Froel. – former C. sect. *Macropodes*
*C. wildenowii* Czerep. (incl. *C. pinnatifida* (Willd.) Froel.) – former C. sect. *Macropodes*
*C. robertioides* Boiss. – former C. sect. *Macropodes*, position within genus unclear as only chloroplast marker data available, provisionally included
*C. schachtii* Babcock. – former C. sect. *Macropodes*
*C. tenerriina* (Schweinf. & Asch.) R. E. Fr. – former C. sect. *Macropodes*
*C. xylorrhiza* Sch. Bip. – former C. sect. *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 caulodial, 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. leontodontoides* All. – transferred from sect. **Gephyroides**

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

Type: **C. tingitana** Ball

*§C. tingitana* Ball

≡ **C. suberosstris** Batt.

**Crepis** sect. **Paleya** (Cass.) Babc. (1947)

Type: **C. albida** Vill.

*§C. albida* Vill.

≡ **C. achyrophonoides** Vatke

≡ **C. elymaitica** Bornm.

**Crepis** sect. **Lepidoseris** (Rchb.) Babc. (1947)

≡ **Barkhausia** [unranked] **Lepidoseris** Rchb. (1831–32). – Type: **C. vescaria** 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** (Jàv.) Babc.) – transferred from **C. sect. Psammoseris**.

≡ **C. bursifolia** L. – transferred from **C. sect. Psammoseris**.

*§C. dianthoseris* N. Kilián & 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. **Mesophylium** (formerly C. sect. **Macropodes**).

**C. inopinata** (Cufod.) N. Kilián & al. – placed here because of the close morphological resemblance to **C. dianthoseris** and its geographic distribution.

*§C. newii* Oliver & Hiern (incl. **C. braccae** Babc., **C. cameroonica** Hutch. & Dalziel, **C. keniensis** (R. E. Fr.) Babc., **C. kilimandscharica** O. Hoffm., **C. mernaensis** Babc., **C. mildbraedii** Babc., **C. suffruticosa** Babc., **C. swynnertonii** S. Moore) – transferred from **C. sect. Anisoramphus**

≡ **C. vescaria** L.

≡ **C. balliana** Babc.

≡ **C. erythia** Pau (= **C. bourgeau 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. marshallii** (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 sect. **Aleurotheprepis** (formerly C. sect. **Phytopedesia**)

*§C. oporinoides** Froel. – transferred from sect. **Berinia**

≡ **C. pygmaea** L.

*§C. pyrenaica** (L.) Greuter (= **C. blattariooides** (L.) Vill.) – transferred from sect. **Soyeria**

**Crepis** sect. **Spaithoides** 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 in 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.

**Crepis** sect. **Nemauchenens** (Cass.) Benth. (1873)

≡ **Nemauchenens** Cass. (1818). – Type: **Nemauchenens ambiguata** 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* (Gord.) Willk.
*C. aspera* L. – molecularly isolated within *Crepis.*
*C. juvenalis* (Delile) F. W. Schultz

*C. setosa*
*C. muhlisii* Babc.
*C. aculeata* (DC.) Boiss.
*C. atheniensis* Babc.,
*C. nigricans* Viv.
*C. filiformis*.
*C. bursifolia* and
*C. sension of Patras.
*C. abyssinica* Willk.
*C. amplexifolia* (Godr.) Willk.
*C. aculeata* (DC.) Boiss.
*C. atheniensis* Babc.
*C. nigricans* Viv.
*C. filiformis*.
*C. bursifolia* and
*C. sension of Patras.
*C. abyssinica* Willk.

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, Pyrenees, N. Enke NE0016 (B); *C. foetida subsp. commutata* (Spreng.) Babc., Greece, Tokmaka, 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. leontodonoides* All., France, Corse, BG Liege (B); *C. mollis* (Jacq.) Asch., Poland, Koziol s.n. (B); *C. multicaulis* Ledeb., Russia, Altay, Raub-Straube 020302 (B); *C. multicaulis* Ledeb., Kirghizia, Tien Shan, Dürbye s.n. (B); *C. neglecta* (Sm.) Vierh., Greece, Etolia, 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 5263 (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. albidula* 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, Tokmaka, J. R. Edmondson & McClintock E 2513 (E); *C. hypochoeridea* (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. albidula* 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, Tokmaka, J. R. Edmondson & McClintock E 2513 (E); *C. hypochoeridea* (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).