

The systematic position of *Centaurea ensiformis* and *Centaurea isaurica* from Turkey and the evolution of some characters in *Centaurea*

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ABSTRACT

The systematic affinities of *Centaurea ensiformis* and *Centaurea isaurica*, two rare Turkish endemics, were difficult to establish on the basis of morphological characters. Their systematic position was recently unraveled by DNA sequence analyses, and they appear to be related to sect. *Cheirolepis*. We have carried out a detailed study of the main morphological characters that are used for the sectional classification of *Centaurea*, the appendages of the bracts and the achenes, in a wide sample of sect. *Cheirolepis*. The main conclusion is that the extremes of diversity in the shape of the appendages can be connected by intermediate forms, and a hypothesis of the evolution of the appendages is offered. This hypothesis, together with some cases of parallel evolution, would explain why there are so many examples of misclassifications based on this character alone. Regarding achenes, our conclusion is that they are important for the species level, but not useful for sectional classification of this group. Finally, the closely related sect. *Plumosipappus*, described mainly on microcharacters of the pappus, must be merged into *Cheirolepis*.

Keywords: compositae, *Centaurea*, Turkey, systematics, evolution

INTRODUCTION

Despite the deep thrust of the studies within the genus *Centaurea* in recent times, some enigmas persist regarding the affinities of a few species whose position is uncertain within the genus on the basis of morphological characters. This paper focuses on *Centaurea ensiformis* P. H. Davis and *C. isaurica* Hub.-Mor., two puzzling and interesting narrow endemics from Turkey that were hitherto considered isolated taxa without close relatives.

Centaurea ensiformis was described from the serpentines of the Sandras Dag in SW Anatolia (Davis, 1956) and even now the plant is only known from the type locality where it thrives, forming a large population of thousands of individuals (Fig. 1). Davis (1956) stressed the difficulties of establishing the affinities of the species, and tentatively placed it in sect. *Phalolepis* (Cass.) DC. on the basis of the scariose-lacerate appendages of the bracts. However, at the same time, he sug-

gested that its closest relative could be *Centaurea lactucifolia* Boiss., curiously, from a different section, *Acrocentron* (Cass.) DC. Later, Wagenitz (1975), unable to ascribe *C. ensiformis* to any section, listed it as *incertae sedis* and pointed out some similarities in the involucre to *C. saligna* (C. Koch) Wagenitz, which has the same pollen type. Wagenitz (1975) revised the morphological resemblances to *C. lactucifolia*, put forward by Davis (1956) and dismissed because *C. lactucifolia* has a different pollen type from *C. ensiformis*. *Centaurea isaurica*, by its side, was described from the Tauros range near Karaman in southern Anatolia. Until recently, it was an imperfectly known species, according to Wagenitz (1975), because the type was an immature individual without flowers or achenes. Wagenitz (1975) pointed out a possible relationship to sect. *Pseudoseridia*

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Fig. 1. Type and unique locality of *Centaurea ensiformis* in the Sandras Dag.

Wagenitz or, alternately, to sect. *Cheirolepis* (Boiss.) O. Hoffm.

Recent analyses of DNA sequences (Susanna, in prep.) confirm a close relationship of *C. ensiformis* and *C. isaurica* to the complex of sections *Cheirolepis-Plumosipappus* (Czerep.) Wagenitz, a group defined on a molecular basis by Garcia-Jacas et al. (2000). We shall shortly revise the morphology of *C. ensiformis* and compare it to some of its close relatives, three out of the seven Turkish species of sect. *Cheirolepis* (*C. deflexa* Bornm., *C. drabifolia* Boiss., and *C. kotschy* Boiss.) and the only species described in sect. *Plumosipappus* (*C. paphlagonica* (Czerep.) Wagenitz). As the sectional classification of *Centaurea* relies heavily on the morphology of the appendages of bracts and of the achenes (Garcia-Jacas et al., 2001), we shall center our study on these two characters.

MATERIAL AND METHODS

We have based our study on our own collections from Turkey (Table 1). Achenes were examined through an Olympus SZX9 binocular microscope, and the bristles of the pappus through an Olympus U-TV1X microscope. In both cases microphotographs were taken with an Olympus Camedia Master C3030 electronic camera. Digital images of whole plants, heads, and bracts were obtained with a Microtek ArtixScan 1100 scanner. All the descriptions of the appendages refer to the middle bracts of the capitulum.

Table 1
Origin of the materials

Species	Voucher
<i>Centaurea deflexa</i> Wagenitz	Turkey, Konya: between Çukuryurt pass and Gevne valley, 25 km from Taşkent, 1700 m, <i>Ertuğrul, Garcia-Jacas, Susanna 2274 & Uysal</i> , 1.8.2002 (BC)
<i>Centaurea drabifolia</i> Boiss.	Turkey, Antalya: near Ovacık, mountain slopes 500 m SW from the village, 2000 m, <i>Ertuğrul, Garcia-Jacas, Susanna 2261 & Uysal</i> , 30.7.2002 (BC)
<i>Centaurea ensiformis</i> P. H. Davis	Turkey, Muğla: Köyceğiz district, Sandras Dag range 13 km from Ağla, 1700 m, serpentine, <i>Ertuğrul, Garcia-Jacas, Susanna 2251 & Uysal</i> , 29.7.2002 (BC)
<i>Centaurea kotschy</i> (Boiss. & Heldr.) Hayek	Turkey, Karaman: Taşkale near Karaman, slopes at the Avdan mountain, 1300 m, <i>Ertuğrul, Garcia-Jacas, Susanna 2289 & Uysal</i> , 2.8.2002 (BC)
<i>Centaurea isaurica</i> Hub.–Mor.	Turkey, Karaman: Ayrançı, northern slopes of Avdan mountain, 1500 m, <i>Ertuğrul 2311</i> , 22.7.2000 (herbarium KNYA)
<i>Centaurea paphlagonica</i> Wagenitz	Turkey, Konya: between Çukuryurt pass and Gevne valley 25 km from Taşkent, 1700 m, <i>Ertuğrul, Garcia-Jacas, Susanna 2274 & Uysal</i> , 1.8.2002 (BC)

RESULTS

Centaurea deflexa Bornm.

(Fig. 2a)

Appendages orbiculate, 10 mm wide including the lateral fimbriae, subglabrous, very scariose, straw-colored with darker center, slightly hooded in the middle, laterally fimbriate with long fimbriae 2.5–4 mm and a longer, faintly prickly apical fimbria 2.5–4 mm (Fig. 4a,d).

Achenes broadly lanceolate, 4 mm long and 2.5–3 mm wide, brown-blackish with lighter stripes, shiny

(Fig. 5a). Pappus of long-barbellate bristles to 10 mm long (Fig. 5g).

Centaurea drabifolia Boiss.

(Fig. 2b)

Appendages up to 7.5 mm wide including the lateral fimbriae, very scariose, subglabrous, straw-colored, with a very narrow lamina 2 mm wide and a robust, vulnerant, terminal spine 6 mm long, laterally fimbriate at the basis with fimbriae 2.5–3.5 mm long (Fig. 4b,e).

Achenes linear-lanceolate, 5 mm long and 2–2.5 mm



Fig. 2. Habit of (a) *Centaurea deflexa*; (b) *C. drabifolia*; (c) *C. ensiformis*. Scale bars: 2 cm.

wide, blackish with lighter stripes, shiny (Fig. 5b). Pappus of barbellate bristles 6.5–8 mm long (Fig. 5h).

Centaurea ensiformis P. H. Davis
(Fig. 2c)

Appendages oval in outline, markedly hooded or spoon-like, 9 mm wide including the lateral fimbriae, subglabrous, very scarioso, straw-colored, laterally lac-

erate-fimbriate with very short fimbriae 0.5–1 mm long and a weakly prickly apical fimbria 1.5–3 mm long, basally prolonged into a faint keel along the upper part of the lamina (Fig. 4c,f).

Achenes lanceolate, 7 mm long and 3–3.5 mm wide, straw-colored, shiny (Fig. 5c). Pappus up to 7 mm long, easily deciduous, with very shortly pinnulate bristles (Fig. 5i).

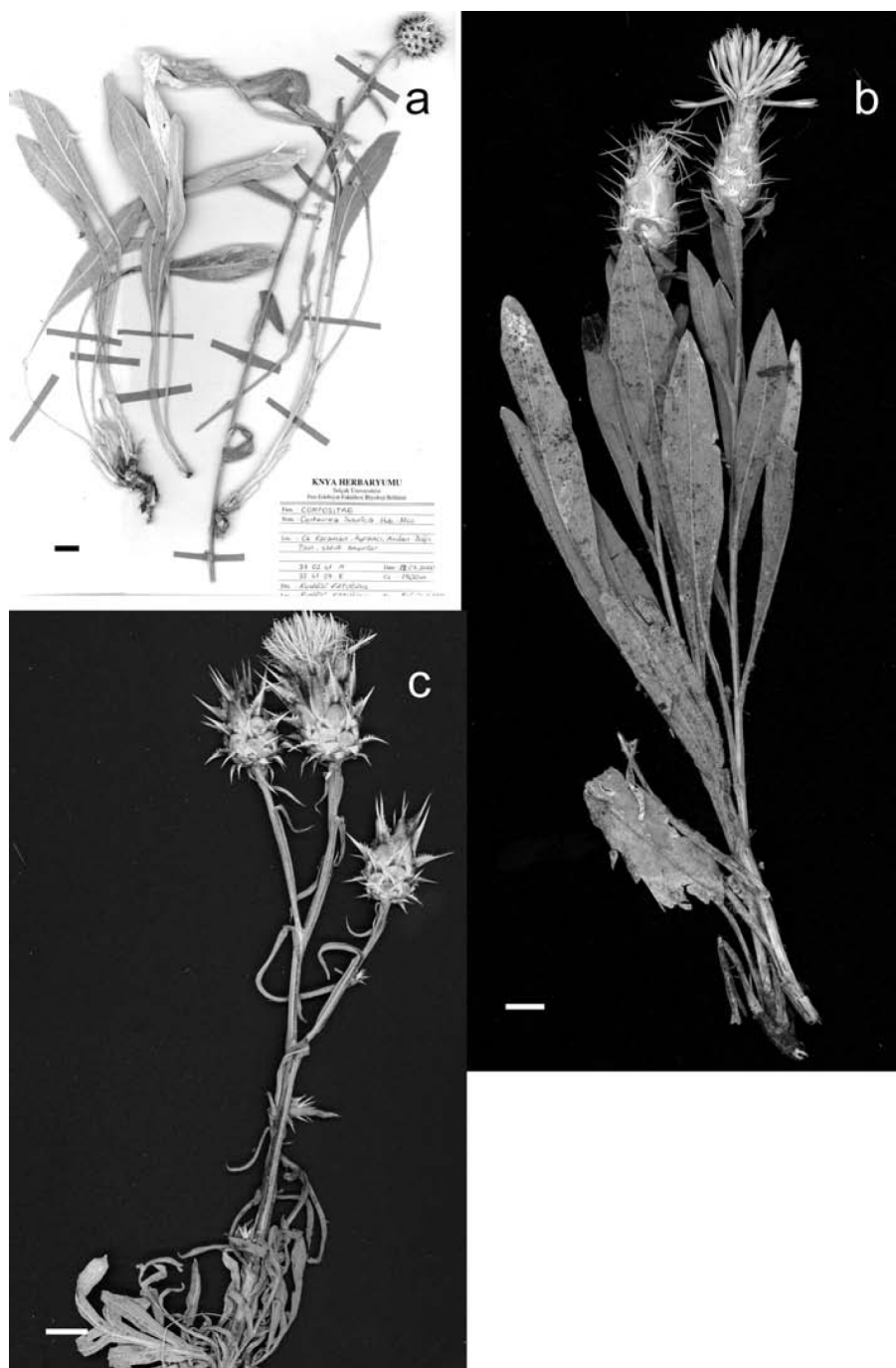


Fig. 3. Habit of (a) *Centaurea isaurica*; (b) *C. kotschyi*; (c) *C. paphlagonica*. Scale bars: 2 cm.

Centaurea isaurica Hub.-Mor.
(Fig. 3a)

Appendages 9 mm wide including the lateral fimbriae, subglabrous, scariose, formed by a small blackish lamina 2–2.5 mm wide with 5–6 palmate straw-colored

spines, the lateral ones 4–4.5 mm long and the terminal one only slightly longer (Fig. 4g,j).

Achenes linear-lanceolate, 4.5–5 mm long and 2 mm wide, straw-colored or brown-striped, with lighter stripes (Fig. 5d). Pappus short, ca. 4 mm long, of short-barbellate bristles.

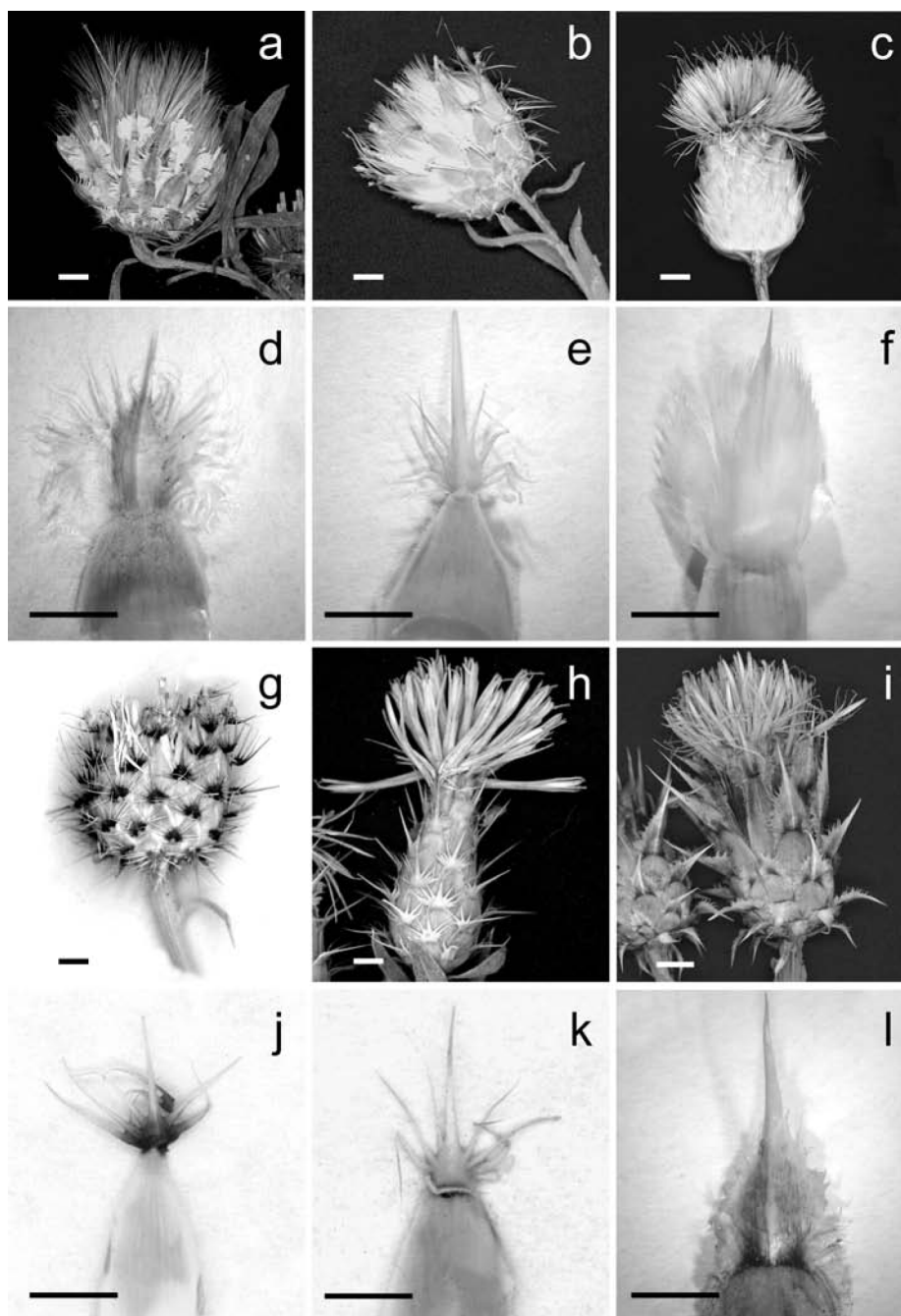


Fig. 4. Detail of the heads and bracts of (a) *Centaurea deflexa*; (b) *C. drabifolia*; (c) *C. ensiformis*; (d) *C. deflexa*; (e) *C. drabifolia*; (f) *C. ensiformis*; (g) *C. isaurica*; (h) *C. kotschyi*; (i) *C. paphlagonica*; (j) *C. isaurica*; (k) *C. kotschyi*; (l) *C. paphlagonica*. Scale bars: 1 cm for the heads, 4 mm for the bracts.

***Centaurea kotschyi* Boiss.**

(Fig. 3b)

Appendages 9 mm wide including the lateral fimbriae, subglabrous, scariose, straw-colored, reduced to a lamina 2–2.5 mm wide, and 6–8 palmate spines 4–5 mm long, the terminal one more robust and markedly longer, up to 7 mm (Fig. 4h,k).

Achenes ovate, 5–5.2 mm long and 3 mm wide, brown-blackish, lighter at the base, not as shiny as the rest of the studied species (Fig. 5e). Pappus of long-barbellate bristles up to 7.5 mm long (Fig. 5j).

***Centaurea paphlagonica* (Bornm.) Wagenitz**

(Fig. 3c)

Appendages lanceolate, 7 mm wide including the lateral fimbriae, subglabrous, very scariose, straw-colored with two darker spots at the base of the lamina, narrowly

hooded or spoon-like, laterally lacerate with very short laciniae 0.5–1.7 mm and a longer, robust, and vulnerant apical spine 7 mm long (Fig. 4i,l).

Achenes narrowly linear-lanceolate, 4.5–5 mm long and 2 mm wide, brown-variegate, shiny (Fig. 5f). Pappus of long-barbellate bristles 8–9 mm long (Fig. 5k).

DISCUSSION AND CONCLUSIONS**(a) The appendages**

All the studied species are narrowly connected, according to molecular evidence. On this basis, the evolution of the shapes of the appendages could be unraveled. The first question could be: Are these appendages really so different? The answer is, actually, that they aren't. We can trace a line from the first model, the appendage of

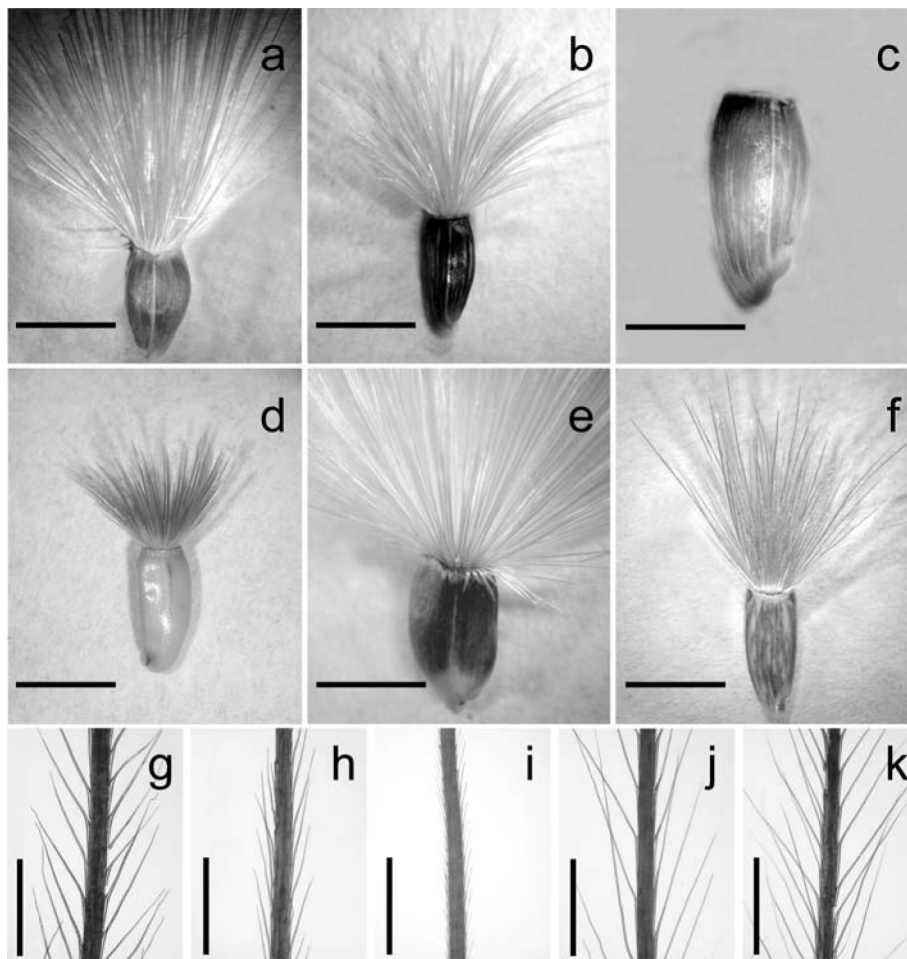


Fig. 5. Microphotographs of the achenes of (a) *Centaurea deflexa*; (b) *C. drabifolia*; (c) *C. ensiformis*; (d) *C. isaurica*; (e) *C. kotschyi*; (f) *C. paphlagonica*. Scale bars = 5 mm. Detail of pappus bristles of (g) *C. deflexa*; (h) *C. drabifolia*; (i) *C. ensiformis*; (j) *C. kotschyi*; (k) *C. paphlagonica*. Scale bars: 0.4 mm.

Centaurea ensiformis, to the last one, the model of the appendage of *C. isaurica* and *C. kotschyi*.

Our hypothesis of evolution is as follows. The appendage of the first type, the *C. ensiformis* model, can be described as having a wide orbicular lamina with the margin lacerate and a single, weak apical spine (Fig. 4f). In the second model, the apical spine is vulnerant and the margins are lacerate-fimbriate, like the appendages of *C. deflexa* and *C. paphlagonica* (Fig. 4d,l). The third model shows a growth of the lateral fimbriae that become spiny, like the appendages of *C. drabifolia* (Fig. 4e). In the final model, the appendix is reduced to a set of palmate spines with the terminal one only slightly longer, like *C. isaurica* and *C. kotschyi* (Fig. 4j,k). The existence of intermediates connecting two a priori very different models, those of *C. ensiformis* and *C. kotschyi*, reduces the taxonomic importance of the shape of the appendages.

Other groups of *Centaurea* also show striking differences in the appendages without taxonomic implications; for example, lacerate, fimbriate, and long-pectinate appendages coexist in sect. *Jacea* (Mill.) DC. Even some species of this section (e.g., *C. pectinata* L.) were unfoundedly segregated from sect. *Jacea* to a new genus, *Leptanthus* Neck. (later combined as section *Leptanthus* (Neck.) DC.), on the basis of the very long, recurved, pectinate appendages. Another example is the complex of sections *Melanoloma* (Cass.) DC. and *Seridia* (Juss.) DC. (Garcia-Jacas et al., 2000), a natural group with extreme differences in the appendages. Maybe the most extreme case is *C. aspera* L., a species usually with palmate-spiny appendages like the rest of the species of sect. *Seridia*; a very common variety of *C. aspera*, var. *subinermis* DC., does not have palmate spines, but an unarmed, very short lacerate appendage.

(b) The achenes

Morphology of the achenes is fairly variable and of little use beyond the species level; all of the achenes fall within the very broad range of the *Centaurea* model, with hilum lateral and double pappus. However, we have examined the character “plumose” of the bristles, which was alleged by Czerepanov (1960) for segregating *C. paphlagonica* to a new genus, *Plumosipappus* Czerep., later combined as section by Wagenitz (1963). Figure 5g–k shows the bristles of sections *Cheirolepis* and *Plumosipappus*; differences are minor, and the “plumose” character of the bristles was overestimated. None of these bristles can be considered plumose in the sense of, for example, the genera of the *Cirsium* group (Susanna and Garcia-Jacas, in press), and *Plumosipappus* should be considered a mere synonym of *Cheirolepis*.

We must conclude that the appendages are very useful and relevant at the species level, but their importance

has been overestimated at the section level. The hypothesis of evolution we have outlined explains the connections revealed by DNA sequence analyses between sections with very different appendage models, and the minor relevance of different models within the same section. On the other hand, parallel evolution in other groups of *Centaurea* has led to extreme similarities that don't reflect common origin, as was reported by Wagenitz (1974). For example, the appendages of the bracts of sect. *Pseudoseridia*, a close relative of sect. *Cheirolepis*, are identical to those of the unrelated sect. *Seridia* from the Western Mediterranean.

As to the achenes, their relevance is similar to that of the bracts. They are very useful for species characterization, but they have often been misleading at the section level.

It is a general rule that classifications based on only one character are misleading, but in *Centaurea* and related genera this is especially true. A careful examination of many characters, including molecular evidence, is the only possible approach for reaching a natural classification of this entangled complex of sections.

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