

The genus Psephellus Cass. (Compositae, Cardueae) revisited with a broadened concept

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The genus *Psephellus Cass. (Compositae, Cardueae)* revisited with a broadened concept

Abstract

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A new concept of the genus *Psephellus* is presented on the basis of morphological, anatomical, palynological and caryological evidence. The few molecular data seem to confirm the monophyly of the genus. The following former sections of *Centaurea* are included: *C. sect. Psephelloideae*, *Psephellus, Hyalinella, Aetheopappus, Amblyopogon, Heterolophus, Czerniakovskya, Odontolophoideae, Odontolophus, Xanthopsis, Uralepis* and *Sosnovskya*. New combinations under *Psephellus* are provided for these sections and for 35 species, especially from Turkey and Iran. *Psephellus* in this broadened sense has 75-80 species and a distribution with a centre in E Anatolia, Caucasia and NW Iran; only few species occur outside this area. Close relationships exist between different sections despite considerable differences especially in the characters of the pappus.

Introduction

In the *Centaureinae* the concept of genera varies enormously. This is clearly shown by the following list with the number of genera discerned by various authors:

Hoffmann (1894): 9 genera

Bobrov & Čerepanov (1963): 26 genera (only 'Flora SSSR area', but most genera occur there)

 Dostál (1973):
 51 genera

 Dittrich (1977):
 7 genera

 Bremer (1994):
 31 genera

Our aim is to establish moderately large genera which are monophyletic (see Wagenitz & Hellwig 1996). This is possible if morphological and molecular data are combined. One of these genera is presented here. It first emerged from the study of the pollen morphology (Wagenitz 1955). It could be shown that there is one group of sections of *Centaurea* s.l. (the *Psephellus* group of Wagenitz & Hellwig 1996) with a very conspicuous pollen type named *Centaurea dealbata* type. *C. dealbata* Willd. is the type of the genus *Psephellus* Cass. *Psephellus* has been accepted as a genus by Boissier (1875), Sosnovsky (1948), Dostál (1973), Gabrieljan (1995), but has been sunk into *Centaurea* in the 'Flora SSSR' (Bobrov & Čerepanov 1963). The same pollen type is found in several

sections of *Centaurea* centering in the area of E Turkey, Caucasia and NW Iran (with few representatives in the Carpathians and Russia). This group of taxa has some macromorphological features in common and is further united by micromorphological and karyological traits. The few molecular data seem to confirm the monophyly of the genus. Petit (1997) does not include any of the taxa concerning us here in his cladistic analysis of morphological data of the *Cardueae*. Besides the features common to the genus, it is held together by the geographical distribution. Remarkable is the absence of annuals or biennials and of spines or spinules on the phyllaries. *Psephellus dealbatus* and some allied species are decorative garden plants. The genus shows no weedy tendencies.

Characters

Macromorphological characters. Herbaceous or suffruticose perennials. Leaves (at least the young ones) always tomentose with an indument of minute woolly hairs or with additional hairs with pedestal. Leaves variously divided, not decurrent. Appendage of phyllaries usually not decurrent, membranous, entire, dentate or ciliate, never with a spine. Receptacle with smooth bristles, persistent at maturity of the achenes. Marginal flowers with staminodes, often strongly radiant. Flowers purple, pink or pale yellow to whitish. Achenes medium-sized to large, laterally flattened to almost rounded in *Psephellus hedgei*. Pappus very variable, rarely lacking, when present always with biseriate glandular hairs at least on the inner pappus elements.

Micromorphological characters of phyllaries and flowers. Phyllaries without crystals. Corolla tube with small prismatic Ca-oxalate crystals or small prismatic crystals and small plates of Ca-oxalate. Cells at the base of the corolla tube strongly elongated with the walls evenly thickened (not thickened in *Psephellus bellus* and *P. marschallianus*). Apical appendages of the anthers obtuse and rather soft (with the exception of most species in *P. sect. Psephelloidei* and sect. *Amblyopogon*). Filaments with papillae or short hairs not exceeding half the width of the filaments. Style branches united, only in the uppermost part diverging.

Anatomical characters of the achenes. Dittrich (1968) investigated species belonging to four sections of *Psephellus* s.l. and united them in his "Aetheopappus-Psephellus branch". Our studies on a much extended basis revealed the following features. Achenes elliptical in cross-section, almost circular in *P. hedgei*, usually with elaiosome (exceptions: see description of the sections), with unicellular hairs except in *P. pulcherrimus* (glabrous), in *P. trinervius* also with biseriate glandular hairs, surface smooth or with horizontal ridges, apically rounded (*P. xanthocephalus*) or crowned by a smooth or pinnacled rim. Area of detachment in a lateral or (species of *P. sect. Psephelloidei*) basal-lateral position, surrounded by a hardened and often brighter zone, except in *P. xanthocephalus*. Cells of the fruit wall parenchyma lignified, except in *P. trinervius*. Outer layers of the pericarp without, inner layer with long prismatic Ca-oxalate crystals and with a dense layer of long prisms outside the testa epidermis. Seeds with hilum lateral.

Pollen morphology. This has first been investigated by Wagenitz (1955) as mentioned above. The "dealbata" type", or more correct "Centaurea dealbata" type" is characterised by a spheroid to subprolate shape, a well developed inner row of bacula, a scarcely visible outer row of bacula and a minutely scabrate surface. It shows some similarity with the pollen types of Centaurea montana and C. cyanus, which, however differ markedly by their subprolate to prolate shape and the more or less triangular cross-section with the colpae on the planes. The "Psephellus type" established by Avetisjan (1964) included these two types and is thus less useful for taxonomic purposes. She gives, however, a list of additional taxa from Psephellus s.l. investigated by her.

Chromosomes. Results of karyological investigations in this group were rare and controversial for some time. Only recently reliable data for several of the sections have been available. From

these it clearly emerges that n = 15 is the base number of the whole group. Deviating numbers have been published by some Russian and Armenian botanists but have not been confirmed by other authors. Polyploidy seems to be very rare, the only record is the count of 2n = 50-60 by Poddubnaja-Arnoldi (1931) for three closely allied species of P. sect. Hyalinella. B-chromosomes have been found in several species. The base number 15 is known from several other taxa (Klasea, Centaurea sect. Centaurea) in the Centaureinae and is probably primitive here.

Molecular data. So far only Psephellus dealbatus (Susanna & al. 1995), P. hedgei, P. bellus and P. trinervius (Hellwig 1996) have been included in phylogenetic analyses using molecular markers. In these studies the ITS regions of the nuclear ribosomal repeat were sequenced. As in Susanna's investigation P. dealbatus was the only representative of the Psepellus group, no conclusion on the monophyly of this group could be made. In Hellwig's study three species were included in the ITS data set and two of them (P. hedgei and P. bellus) were also included in an RFLP analysis of the chloroplast DNA (Hellwig 1996). In both cases Psephellus proved to be monophyletic. The bootstrap support for Psephellus in the ITS data set was moderately high (73 % in 1000 replicates) and comparable to the support for the Cyanus/Protocyanus group in the same analysis. Psephellus bellus and P. hedgei were grouped into a monophyletic clate with 100 % bootstrap support also in the restriction site analysis. Phylogenetic reconstruction in the subtribe Centaureinae (Hellwig 1996) using a data set combined from ITS sequence data and morphological data showed Psephellus as a monophyletic group which was well supported in a bootstrap analysis (94 %). The number of synapomorphies of Psephellus in the ITS sequence analysis was low (4) when compared to the respective values for Plectocephalus (9), Acrocentron (9) and Cyanus/Protocyanus (6). In contrast, there are 11 synapomorphic changes for the Psephellus group in the RFLP analysis of the cpDNA. This is the highest value for a clade within the subtribe Centaureinae and equals the number of synapomorphies for the whole subtribe (Hellwig 1996). The relatively high bootstrap value in the sequence analysis together with a low number of synapomorphies may be explained by the congruence of the changes in these few characters. Within Centaureinae, Psephellus can be qualified as a slowly evolving monophyletic clade when compared to the Jacea group, for example. This statement, however, is based only on the small amount of molecular information available so far. A detailed molecular study of Psephellus is under way.

Affinities and phylogenetic position

There are many features shared by all species of *Psephellus*, admittedly however, several of these are plesiomorphic, such as the lack of crystals in the phyllaries, the staminodes and the chromosome number. The pollen type is clearly an apomorphic feature, probably the obtuse anther appendages are another one, but it is not found in all species. They are otherwise only known from few remote genera such as *Acroptilon*, *Callicephalus* and the *Carthamus* group.

Centaurea sect. Cyanus (better treated as a genus Cyanus Mill.) resembles Psephellus in some important characters. Both genera have similar pollen types differing markedly from all others by the well developed inner row of bacula in combination with a very inconspicuous outer row and loss of the spines (pollen grains only minutely scabrate). It is remarkable too that in both groups the phyllary appendages are never spiny. There are, however, important differences: in Cyanus the appendages are strongly decurrent, crystals are present in the phyllaries, the base chromosome numbers are n = 8, 10, 11, 12 and the style branches are much shorter and completely free. Further features of Cyanus absent in Psephellus are the curved apical anther appendages and the characteristic trichomes at the detachment area of the achenes.

Psephellus has several features in common with Centaurea s.str. and Cheirolophus, e.g. the occurrence of staminodes and the chromosome base number (n = 15 in Centaurea, 15 and 16 in Cheirolophus), but the pollen types and the apical anther appendages are very different.

Extrafloral nectaries, which can be found on the outer face of the phyllaries in *Cyanus* and on the inner surface in *Centaurea*, are lacking in *Psephellus*.

Comparison with previous systems

Two extreme position are possible in the system of the *Centaureinae* with respect to the group we are concerned with. Several authors (Hoffmann 1894, Dittrich 1977, Bremer 1994) include all the sections of *Psephellus*, as treated here, in *Centaurea*, while Dostál (1973) recognizes four genera with pollen of the *Centaurea dealbata* type: *Aetheopappus, Psephellus, Heterolophus* and *Odontolophus*. It is not clear if the other relevant taxa were not known to him or are to be included in these. As Table 1 shows, there are also several authors who have treated some of the taxa as separate genera, others as subgenera of *Centaurea*. Boissier (1875), who relied heavily on the pappus when delimiting *Centaurea* (see Wagenitz 1963), dispersed the species of our group in several genera:

- 1. typical double *Centaurea* pappus: *Centaurea* sect. *Jacea* § *Psephelloideae* Boiss., *C.* sect. *Phalolepis* (later *C.* sect. *Hyalinella* Tzvelev and *C.* sect. *Uralepis* (DC.) Wagenitz)
- 2. pappus simple or double with plumose bristles: *Aetheopappus* (this pappus type seems to vary even within *C. pulcherrima* s.l.)
- 3. pappus very short and deciduous: *Psephellus* Cass.
- 4. pappus short and not distinctly double: *Phaeopappus* Boiss. (species now belonging to *Psephellus* sect. *Odontolophus* and sect. *Sosnovskya*).

His system is certainly unnatural and inacceptable in the view of our present knowledge.

The systems by Bobrov & Čerepanov (1963) and Tahtadžjan (1995) fail, however, likewise in creating a phylogenetically sound system, as they distribute the members of the *Psephellus* group in several subgenera inside and one or two genera outside *Centaurea* (Table 1.).

Table 1. Status of the	ne sections of <i>Psephellus</i> in previou	is systems (C . = $Centaurea$, –	— = taxon not treated).		
P. sect.	Boissier (1875)	Bobrov & Čerepanov Tahtadžjan (1995)			
Psephelloidei	C. sect. Jacea § Psephelloideae & C. sect. Phalolepis p.p.	C. subg. Pseudohyalea p.p.			
Psephellus	Psephellus	C. subg. Psephellus	Psephellus		
Hyalinella	C. sect. Phalolepis p.p.	C. subg. Hyalinella	C. subg. Hyalinella		
Aetheopappus	Aetheopappus	Aetheopappus	Aetheopappus		
Amblyopogon	Psephellus p.p. & C. sect. Jacea § Psephelloideae	C. subg. Amblyopogon	_		
Heterolophus	C. sect. Jacea § Psephelloideae	C. subg. Heterolophus	_		
Czerniakovskya	_	C. subg. Czerniakovskya —			
Odontolophoidei	Psephellus p.p.	C. subg. Odontolophopsis			
Odontolophus	Phaeopappus p.p.	C. subg. Odontolophus			
Xanthopsis	Psephellus p.p.	C. subg. Xanthopsis			
Uralepis	C. sect. Phalolepis p.p.	_	_		
Sosnowskya	Phaeopappus p.p.	C. subg. Sosi	novskya		

Subdivision of the genus

The main differences within Psephellus s.l. concern the habit, the marginal flowers and the characters of the pappus. According to the habit of the plants two groups of sections can be distinguished, but there is no clear-cut division between them (Table 2). In the sections with a "Psephellus habit" the plants are mesomorphic, the stems single or few, erect or ascending to prostrate, they have usually pinnatisect leaves and relatively large heads with showy marginal flowers. With one exception the flowers are pink to purple (in Table 2 "purple" denotes different shades from pink and rose-purple to purple). Several species in this group live in subalpine to alpine habitats. In the second group ("Xanthopsis habit") the plants have numerous stems from a woody base, the leaves are predominantly undivided and linear-lanceolate, the small heads have inconspicuous marginal flowers and the flowers are purple or vellowish. The plants of this second group have a more xeromorphic habit and inhabit mountain steppe habitats or even desert-like places. As can be seen from Table 2, there are intermediate groups which do not fit this pattern: P. sect. Czerniakovskya has the Psephellus habit but yellowish not radiant flowers, while P. sect. Odontolophus with the Xanthopsis habit has radiant flowers. This distribution of characters shows the close phylogenetic connections between all these taxa. It is worth mentioning that some authors have already considered an amplification of the genus Psephellus. This is shown by the names or combinations Psephellus aucherianus (DC.) Boiss., P. erivanensis Lipsky, P. incanescens (DC.) Boiss., P. integrifolius (C. A. Mey.) C. Koch, P. marschallianus (Spreng.) C. Koch and P. xanthocephalus (DC.) Boiss. & Buhse. The similarities in habit are also shown by the names *Psephelloides* or *Psephelloideae* given to two different sections.

	1						
P. sect.	h	leaves	phyllary appendage	marginal flowers	flower colour	pappus	pappus bristles
Psephelloidei	1	tomentose	entire/ dentate	large	purple	double	scabrous
Psephellus	1	bi-coloured	dentate	large	purple	short, deciduous	scabrous
Hyalinella	1	bi-coloured	denticulate	large	purple	double	sabrous
Aetheopappus	1	tomentose	dentate	large	purple/ yellow	double/ simple	plumose
Amblyopogon	1	tomentose	ciliate	not radiant	purple	short or 0	scabrous
Heterolophus	1	bi-coloured	ciliate/ dentate	radiant	purple	double	scabrous
Czerniakovskya	1	tomentose	ciliate	not radiant	yellowish	double	scabrous
Odontolophoidei	2	tomentose	ciliate	not radiant	purple	double, short	scabrous
Odontolophus	2	tomentose	ciliate/ lacerate	radiant	pink	double/ short	scabrous
Xanthopsis	2	tomentose	ciliate	not radiant	yellowish	short or 0	scabrous
Uralepis	2	tomentose/ glabrous	entire/ dentate	not radiant	yellowish	double, long	scabrous
Sosnovskya	2	tomentose/ glabrous	ciliate	slightly radiant	pink or whitish	double/ simple	scabrous

Conspectus of the genus Psephellus s.l.

Psephellus Cass. in Cuvier, Dict. Sci. Nat. 43: 488. 1826.

Type: *Centaurea dealbata* Willd. ≡ *Psephellus dealbatus* (Willd.) C. Koch

Psephellus sect. Psephelloidei (Boiss.) Wagenitz & Hellwig, comb. nova

Type: Centaurea pyrrhoblephara Boiss. ≡ Psephellus pyrrhoblepharus (Boiss.) Wagenitz

- ≡ Centaurea sect. Jacea § Psephelloideae Boiss., Fl. Orient. 3: 616. 1875 ≡ Centaurea sect. Psephelloideae (Boiss.) Sosn. in Věstn. Tiflissk. Bot. Sada, ser. 2, 5: 29. 1931.
- = Centaurea sect. Pseudohyalea Tzvelev in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR 19: 428. 1959 ≡ Centaurea subg. Pseudohyalea (Tzvelev) Tzvelev, in Bobrov & Čerepanov, Fl. SSSR 28: 486. 1963. Type: Centaurea pergamacea DC.

Perennial herbs with woody rootstock. Stems erect or ascending, simple or sparsely branched. Leaves tomentose, rarely glabrescent, undivided, lyrate or pinnatipartite, not decurrent. Involucre 15-30 mm long and 10-30 mm broad, ovoid to subglobose. Phyllaries in several series, appendages membranous, usually large and semicircular to ovate or rhombic, sometimes shortly decurrent, margin entire, denticulate or regularly ciliate, the terminal mucro often shorter than the cilia, rarely slightly longer or totally lacking. Flowers rose-purple, the marginal radiant, often strongly so, with staminodes, the central flowers numerous. Achenes 5-8 mm long, detachment area sublateral. Pappus (2-)5-13 mm, of scabrous bristles, the inner row of short scales.

The section shows considerable variation in the structure of the appendages, which may be entire, denticulate or with long cilia and decurrent or well differentiated. As the plate in Wagenitz (1975: 561) shows, there are many transitions in this character and the separation of *C*. sect. *Pseudohylaea* is scarcely justified. The appendages of the anthers are also variable, usually acute but obtuse in *Psephellus gilanicus* and *P. mucroniferus*.

Species and distribution: 12 species in central, S and E Anatolia and three additional in Iran, one of these also in Transcaucasia.

- Psephellus bornmuelleri (Hausskn. ex Bornm.) Wagenitz, **comb. nova** ≡ Centaurea bornmuelleri Hausskn. ex Bornm. in Mitt. Thüring. Bot. Vereins 20: 21. 1905.
- P. brevifimbriatus (Hub.-Mor.) Wagenitz, comb. nova ≡ Centaurea brevifimbriata Hub.-Mor. in Bauhinia 3: 315. 1967.
- P. gilanicus (Bornm.) Wagenitz, comb. nova ≡ Centaurea gilanica Bornm. in Mitt. Thüring. Bot. Vereins 20: 23. 1905.
- P. gracillimus (Wagenitz) Wagenitz, comb. nova ≡ Centaurea gracillima Wagenitz in Notes Roy. Bot. Gard. Edinburgh 33: 225. 1974.
- P. hadimensis (Wagenitz, Ertugrul & Dural) Wagenitz, comb. nova ≡ Centaurea hadimensis Wagenitz, Ertugrul & Dural in Willdenowia 28: 157. 1998.
- P. holtzii (Wagenitz) Wagenitz, comb. nova ≡ Centaurea holtzii Wagenitz in Notes Roy. Bot. Gard. Edinburgh 33: 226. 1974.
- P. huber-morathii (Wagenitz) Wagenitz, comb. nova ≡ Centaurea huber-morathii Wagenitz in Notes Roy. Bot. Gard. Edinb. 33: 226. 1974.
- P. leuzeoides (Jaub. & Spach) Wagenitz, comb. nova ≡ Hyalea leuzeoides Jaub. & Spach, Ill. Pl. Orient. 3: 21, 216, 1847.
- P. mucroniferus (DC.) Wagenitz, comb. nova = Centaurea mucronifera DC., Prodr. 6: 569. 1838.
- P. oltensis Wagenitz, nom. nov. ≡ Centaurea taochia Sosn. in Věstn. Tiflissk. Bot. Sada, ser. 2, 5: 30. 1931.
- P. pergamaceus (DC.) Wagenitz, comb. nova ≡ Centaurea pergamacea DC., Prodr. 6: 569. 1838.
- P. psephelloides (Freyn & Sint.) Wagenitz, comb. nova ≡ Centaurea psephelloides Freyn & Sint. in Österr. Bot. Z. 42: 237. 1892.
- P. pyrrhoblepharus (Boiss.) Wagenitz, comb. nova ≡ Centaurea pyrrhoblephara Boiss., Diagn.
 Pl. Orient., ser. 2, 3: 66. 1856.

P. schischkinii (Tzvelev) Wagenitz, comb. nova ≡ Centaurea schischkinii Tzvelev in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR 20: 399. 1960.

P. xeranthemoides (Rech. f.) Wagenitz, comb. nova ≡ Centaurea xeranthemoides Rech. f. in Anz. Österr. Akad. Wiss., Math.-Naturwiss. Kl. 88: 264. 1951.

Systematic position: Allied to Psephellus sect. Aetheopappus and sect. Psephellus.

Lit.: Sosnovsky 1931; Wagenitz 1975: 559-564, 1980: 399-402.

Psephellus sect. Psephellus

- ≡ Centaurea sect. Psephellus (Cass.) DC., Prodr. 6: 575. 1838 ≡ Centaurea subg. Psephellus (Cass.) Spach, Hist. Nat. Véget. (Phan.) 6: 11. 1841 ≡ Psephellus sect. Dealbati Sosn. in Zametki Sist. Geogr. Rast. 14: 12. 1948. Type: Centaurea dealbata Willd.
- = Psephellus sect. Hypoleuci Sosn. in Zametki Sist. Geogr. Rast. 14: 6. 1948 ≡ Centaurea sect. Hypoleucae (Sosn.) Sosn. in Bobrov & Čerepanov, Fl. SSSR 28: 424. 1963. − Type: Centaurea hypoleuca DC.
- = Psephellus sect. Leucophylli Sosn. in Zametki Sist. Geogr. Rast. 14: 7. 1948 ≡ Centaurea sect. Leucophyllae (Sosn.) Sosn. in Bobrov & Čerepanov, Fl. SSSR 28: 428. 1963. Type: Centaurea leucophylla M. Bieb.

Perennial herbs, often with ascending or prostrate stems with few branches and a central rosette of leaves. Leaves lyrate to pinnatisect or more rarely undivided, arachnoid on the upper side, densely tomentose on the lower. Involucre c. 14-21 mm long and 12-20 mm broad, cup-shaped. Phyllaries in several series, nearly glabrous; appendages membranous, triangular to ovate, ciliate, without prominent terminal mucro or spinule, not decurrent. Flowers purple or the central whitish, the marginal strongly to moderately radiant, infundibuliform, with 5-6 segments, with staminodes; central flowers numerous. Achenes 5-6 mm long, only slightly laterally compressed, detachment area lateral, with elaiosome. Pappus 1-1.5 mm, of deciduous scabrous bristles, inner row shorter.

Chromosome numbers: 12 counts, all with 2n = 30, have been reported for different species (Matveeva & Tichonova ined. in Fedorov 1969; Žukova 1967, cited from Moore 1973; Čuksanova & al. 1968; Davlianidze 1985; Ghaffari & Chariat-Panahi in Taxon 34: 549. 1985). For *Psephellus somcheticus* 2n = 30 is known too, only Tonjan (1968) gave 2n = 28 for this species.

Species and distribution: 30 species are enumerated by Sosnovsky (1963) for the 'Flora SSSR area', where nearly all species of the section occur. Some have been added later (Galuško & Alieva 1976, Gabrieljan & Tahtadžjan 1992, Gabrieljan 1994), but species delimitation is very critical in this section and several of these may better be looked at as subspecies. The distribution centres in Caucasia, extending to the Crimea, E Anatolia and N Iran.

Systematic position: Allied to *Psephellus* sect. *Psephelloidei*, *Aetheopappus* and others, mainly distinguished by characters of the pappus.

Lit.: Sosnovsky 1948, 1963; Gabrieljan 1995.

Psephellus sect. Hyalinella (Tzvelev) Wagenitz & Hellwig, comb. nova

Type: Centaurea simplicicaulis Boiss. & Huet ≡ Psephellus simplicicaulis (Boiss. & Huet) Wagenitz ≡ Centaurea sect. Hyalinella Tzvelev in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR 19: 426. 1959 ≡ Centaurea subg. Hyalinella (Tzvelev) Tzvelev in Bobrov & Čerepanov, Fl. SSSR 28: 488. 1963.

= Centaurea sect. Albovia Tzvelev in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR 19: 421. 1959. – Type: Centaurea pecho Albov.

Perennial herbs with branched rootstock and erect or ascending stems, simple or with few branches in or below middle. Leaves arachnoid and glabrescent above, densely appressed-tomentose below, the lower pinnatisect to lyrate with elliptic to ovate lateral segments, sometimes undivided, middle leaves similar but with narrower segments or undivided like the few upper leaves. Involucre 12-19 mm long, (6-)8-14 mm broad, ovoid. Phyllaries in several series, nearly glabrous, the appendages nearly circular to broadly ovate, brown in the centre with hyaline or straw-coloured, denticulate or ciliate margin, not or very slightly decurrent. Flowers rose-coloured, the marginal scarcely to distinctly radiant, with staminodes, central flowers numerous. Achenes 4-5 mm long, laterally compressed, with lateral detachment area, without elaiosome. Pappus 5-8(-10) mm long, of scabrous bristles, inner row short, scaly.

Chromosome numbers: Three species belonging to the *Psephellus simplicicaulis* group have been counted with 2n = 50-60 (Poddubnaja-Arnoldi 1931).

Species and distribution: Seven species have been described, but several of these seem to belong to the polymorphous *Psephellus simplicicaulis*. The small species group is distributed in NE Anatolia and Transcaucasia.

Psephellus bellus (Trautv.) Wagenitz, comb. nova ≡ Centaurea bella Trautv. in Bull. Acad. Imp. Sci. Saint-Pétersbourg 10: 394. 1866.

- P. pecho (Albov) Wagenitz, comb. nova ≡ Centaurea pecho Albov in Bull. Herb. Boissier, ser. 1, 2: 640, 1894.
- P. simplicicaulis (Boiss. & Huet) Wagenitz, comb. nova ≡ Centaurea simplicicaulis Boiss. & Huet in Boiss., Diagn. Pl. Orient., ser. 2, 3: 67. 1856.

Systematic position: Allied to Psephellus sect. Psephelloidei and sect. Psephellus.

Lit.: Cvelev 1963; Wagenitz 1975: 565-566.

Psephellus sect. Aetheopappus (Cass.) Wagenitz & Hellwig, comb. nova

Type: *Centaurea pulcherrima* Willd. ≡ *Psephellus pulcherrimus* (Willd.) Wagenitz

= Aetheopappus Cass. in Cuvier, Dict. Sci. Nat. 50: 250. 1827 = Centaurea sect. Aetheopappus (Cass.) DC., Prodr. 6: 574. 1838 = Centaurea ser. Aetheopappus (Cass.) Benth. in Bentham & Hooker, Gen. Pl. 2: 480. 1873.

Perennial herbs with erect stem, usually unbranched or with 1-3 branches. Leaves tomentose on both sides or glabrescent above, very variable, ovate to narrowly lanceolate in outline, the lower entire, denticulate, lyrate or pinnatipartite, the median and upper usually undivided, the upper with an appendage similar to that of the phyllaries. Involucre 18-28 mm long and 15-30 mm broad, subglobose. Phyllaries in several series, the appendages very large, membranous, brownish, triangular to lanceolate or ovate with numerous regular cilia, not decurrent. Flowers rose-purple or pale yellow, the marginal strongly radiant with more than 5 segments, with staminodes, the central numerous. Achenes 6-6.5 mm long, flattened, with small sublateral detachment area without elaiosome. Pappus 11-16 mm, of barbellate to plumose bristles, the inner row short in Psephellus appendicigerus, not distinct in P. pulcherrimus.

Species and distribution: Two main species, *Psephellus appendicigerus* in NE Anatolia, the polymorphous *P. pulcherrimus* in E Anatolia and Transcaucasia. The latter may actually comprise several distinct species.

Psephellus appendicigerus (C. Koch) Wagenitz, comb. nova ≡ Centaurea appendicigera C. Koch in Linnaea 24: 425. 1851.

P. pulcherrimus (Willd.) Wagenitz, **comb. nova** ≡ Centaurea pulcherrima Willd., Sp. Pl. 3(3): 2298. 1803.

Systematic position: Allied to Psephellus sect. Psephelloidei and sect. Psephellus.

Lit.: Sosnovsky 1953, 1963: 353-356; Wagenitz 1975: 567-569.

Psephellus sect. Amblyopogon (DC.) Wagenitz & Hellwig, comb. nova

Type: Amberboa incanescens DC. \equiv Psephellus incanescens (DC.) Boiss.

= Amberboa sect. Amblyopogon Fisch. & C. A. Mey. ex DC., Prodr. 6: 561. 1838 = Amblyopogon (DC.) Jaub. & Spach, Ill. Pl. Orient. 3: 23. 1847 = Centaurea sect. Amblyopogon (DC.) Sosn. in Věstn. Tiflissk. Bot. Sada, ser. 2, 5: 21. 1931 = Centaurea subg. Amblyopogon (DC.) Tzvelev in Bobrov & Čerepanov, Fl. SSSR 28: 472. 1963.

Herbaceous perennials with decumbent or erect and very short stems, simple or sparsely branched, stems (always?) arising from the base of the rosette. Leaves tomentose on both sides, lyrate, pinnatisect or undivided. Involucre 13-30 mm long, 10-20 mm broad, ovoid. Phyllaries in several series, appendages membranous, lanceolate or triangular, not or shortly decurrent, ciliate. Flowers rose-purple, the marginal not or scarcely radiant, with staminodes, the central rather numerous. Achenes 4-8 mm long, detachment area lateral, large (in Psephellus karduchorum), with elaiosome. Pappus usually short, 1-2.5 mm, of scabrous bristles or slender scales, lacking in P. poluninii, 8 mm long in P. congestus, inner row shortest, sometimes indistinctly so.

Chromosome numbers: Unknown.

Species and distribution: Five species are known, two of them only from the type, all with a restricted distribution in E Anatolia, Talysh and W Iran.

Psephellus congestus (Wagenitz) Wagenitz, comb. nova ≡ Centaurea congesta Wagenitz in Rechinger, Fl. Iran. 139b: 405. 1980.

- P. incanescens (DC.) Boiss., Fl. Orient. 3: 610. 1875.
- P. integrifolius C. Koch in Linnaea 24: 438. 1851 ≡ Centaurea integrifolia C. A. Mey., Verz. Pfl. Casp. Meer.: 64. 1831, nom. illeg. [non Tausch 1828] ≡ C. meyeranus Tzvelev in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR 19: 418, 1959.
- P. karduchorum (Boiss.) Wagenitz, comb. nova ≡ Centaurea karduchorum Boiss., Fl. Orient. 3: 633, 1875.
- P. poluninii (Wagenitz) Wagenitz, comb. nova ≡ Centaurea poluninii Wagenitz in Notes Roy.
 Bot. Gard. Edinburgh 33: 228. 1974.

Systematic position: Probably related to *Psephellus* sect. *Psephelloidei*, but with reduced marginal flowers and the "myrmecochory syndrom": short or prostrate stems, large achenes with short pappus and with elaiosome. *P. congesta* is aberrant with its long pappus.

Lit.: Sosnovsky 1931; Cvelev 1963: 472 ff.; Wagenitz 1975: 569-570, 1980: 404-406.

Psephellus sect. Heterolophus (Cass.) Wagenitz & Hellwig, comb. nova

Type: Centaurea sibirica L. \equiv Psephellus sibiricus (L.) Wagenitz

≡ Heterolophus Cass. in Cuvier, Dict. Sci. Nat. 50: 250. 1827 ≡ Centaurea subg. Heterolophus (Cass.) Spach, Hist. Nat. Véget. (Phaner.) 6: 11. 1841 ≡ Centaurea sect. Heterolophus (Cass.) M. Dittrich in Bot. Jahrb. Syst. 88: 156. 1968.

Perennials with woody base and several simple or sparsely branched ascending or prostrate stems, arising from the base of the rosette. Leaves tomentose, especially on the lower side, partly pinnatipartite, partly undivided. Involucre c. 14-22 mm long and 10-20 mm broad, cup-shaped to subglobose. Capitula heterogamous. Phyllaries in several series, slightly woolly, appendages membranous, not decurrent, very variable from suborbicular to lanceolate or triangular or even linear-lanceolate with distinct long cilia or lacerate or dentate. Flowers rose-purple, the marginal distinctly radiant with 4-7 broad segments, with staminodes, central flowers numerous. Achenes 4-7 mm long, laterally compressed, detachment area lateral-basal, with elaiosome. Pappus 1-2.5(-3) mm long, of scabrous bristles, inner row short.

Chromosome numbers: Three counts with 2n = 30 have been reported for *Psephellus sibiricus* (Rostovzeva 1979, Pulkina 1988 [two provenances]). For *P. marschallianus* 2n = 18 has been re-

corded from cultivated material; especially in the case of cultivated plants misidentification may be involved, another count by Kuzmen & Georgieva (in Taxon 32: 665. 1983) revealed 2n = 20. Checking of these numbers is necessary.

Species and distribution: According to Klokov (1963) there are six species distributed from Bulgaria, Ukraine and S Russia to W Siberia and Central Asia. They form evidently a closely knit group as all of them have been assigned either to *Centaurea sibirica* or *C. marschalliana*. The variability of the appendages is very marked in this section.

Psephellus marschallianus (Spreng.) C. Koch in Linnaea 24: 438 ≡ Centaurea marschalliana Spreng., Syst. Veg. 3: 398. 1826.

P. sibiricus (L.) Wagenitz, **comb. nova** \equiv *Centaurea sibirica* L., Sp. Pl. 2: 913. 1753.

Systematic position: Closely related to *Psephellus* sect. *Amblyopogon* and *Czerniakovskya. P.* sect. *Amblyopogon* is distinguished mainly by its inconspicuous, not radiant marginal flowers.

Lit.: Klokov 1963.

Psephellus sect. Czerniakovskya (Czerep.) Wagenitz & Hellwig, comb. nova

Type: Centaurea kopet-daghensis Iljin ≡ Psephellus kopet-daghensis (Iljin) Wagenitz

= Centaurea subg. Czerniakovskya Czerep. in Bobrov & Čerepanov, Fl. SSSR 28: 609. 1963 = Centaurea sect. Czerniakovskya (Czerep.) Wagenitz in Rechinger, Fl. Iran. 139b: 407. 1980.

Perennial with woody rhizome with several ascending to nearly prostrate stems. Stems simple or with few branches. Leaves tomentose, lanceolate. Involucre 15-20 mm long and 8-15 mm broad, cup-shaped. Phyllaries in several series, woolly, appendages triangular, ciliate, the terminal mucro scarcely differing from the cilia, not decurrent (Psephellus kopet-daghensis) or decurrent (P. iljinii). Capitula heterogamous. Flowers pale yellow to rose-coloured, the sterile marginal not or slightly radiant, with staminodes, the central hermaphrodite numerous. Achenes 7-8 mm long, laterally compressed, detachment area lateral, with(?) elaiosome. Pappus 3-8 mm long, of scabrous bristles, the inner row of shorter scales.

Chromosome numbers: Unknown.

Species and distribution: Only two species known from Turkmenia (Kopet-Dagh) and N Iran. The species are similar in habit but differ remarkably in the appendages.

Psephellus iljinii (Czerniak.) Wagenitz, **comb. nova** ≡ Centaurea iljinii Czerniak. in Repert. Spec. Nov. Regni Veg. 27: 285. 1930.

P. kopet-daghensis (Iljin) Wagenitz, comb. nova ≡ Centaurea kopet-daghensis Iljin in Izv. Bot. Sada Akad. Nauk SSSR 30: 359. 1932.

Systematic position: Closely allied to *Psephellus* sect. *Amblyopogon* and perhaps not really distinct, as the length of the pappus is the main distinguishing character.

Lit.: Čerepanov 1963: 418-420; Wagenitz 1980: 407-409.

Psephellus sect. Odontolophoidei (Tzvelev) Wagenitz & Hellwig, comb. nova

Type: Centaurea aucheriana DC. ≡ Psephellus aucherianus (DC.) Boiss. (≡ Phaeopappus microcephalus Jaub. & Spach, nom. illeg.)

≡ Centaurea sect. Odontolophoideae Tzvelev in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR 19: 422. 1959 ≡ Centaurea subg. Odontolophopsis Tzvelev in Bobrov & Čerepanov, Fl. SSSR 28: 485. 1963 ≡ Phaeopappus sect. Psephelloides Jaub. & Spach, Ill. Pl. Orient. 3: 16. 1847, non Centaurea sect. Psephelloideae Boiss. 1875, nec Psephellus sect. Psephelloidei (Boiss.) Wagenitz & Hellwig 2000.

Perennial herbs, woody at base, with several stems branched from near the base or in the lower half. Leaves floccose or appressed tomentose, the lower (and median) petiolate and lyrate,

pinnatifid or pinnatipartite or undivided, the median and upper sessile, lanceolate to nearly linear. *Involucre* 10-20 mm long, 6-22 mm broad, ovoid to nearly globose. *Phyllaries* in several series, appendages membranous, straw-coloured, concealing the basal part of the phyllaries or nearly so, ovate to circular, ciliate, not decurrent. *Capitula* heterogamous. *Flowers* pink, the marginal not or slightly radiant, with 5-6 segments, with staminodes. *Achenes* 4-6 mm long, laterally compressed, smooth, detachment area lateral, relatively large. *Pappus* 1-4.5 mm long, of scabrous bristles, the inner row short.

Chromosome numbers: Only one count, 2n = 30 for *Psephellus phaeopappoides* (Garcia-Jacas & al. 1998), has been reported.

Nomenclature: The oldest name at the rank of a section is *Phaeopappus* sect. *Psephelloides* Jaub. & Spach, but this must be looked at as an orthographic variant of *Centaurea* sect. *Psephelloideae* Boiss. \equiv *Psephellus* sect. *Psephelloidei* (Boiss.) Wagenitz & Hellwig and cannot be used in *Psephellus* at the same time.

Species and distribution: Three species in E Anatolia, Transcaucasia and NW Iran.

Psephellus aucherianus (DC.) Boiss., Fl. Orient. 3: 611. 1875.

- P. eugenii (Sosn.) Wagenitz, comb. nova ≡ Centaurea eugenii Sosn. in Věstn. Tiflissk. Bot. Sada, ser. 2, 5: 32. 1931.
- P. phaeopappoides (Bordzil.) Wagenitz, comb. nova ≡ Centaurea phaeopappoides Bordzil. in Žurn. Inst. Bot. Vseukrajins'k. Akad. Nauk 3: 82. 1935.

Systematic position: Closely allied to *Psephellus* sect. *Xanthopsis*. Leaves similar to those in *P*. sect. *Odontolophus*.

Lit.: Cvelev 1959, 1963: 485-486; Wagenitz 1975: 570.

Psephellus sect. Odontolophus (Cass.) Wagenitz & Hellwig, comb. nova

Type: Centaurea trinervia Willd. ≡ Psephellus trinervius (Willd.) Wagenitz

= Odontolophus Cass. in Cuvier, Dict. Sci. Nat. 50: 252. 1827 = Centaurea sect. Odontolophus (Cass.) DC., Prodr. 6: 579. 1838 = Centaurea subg. Odontolophus (Cass.) Spach, Hist. Nat. Vég. (Phaner.) 6: 11. 1841.

Perennial with woody rhizome, stems strongly branched near the base with numerous long branches with one capitulum. Leaves narrowly lanceolate, thinly tomentose, indumentum of woolly hairs and hairs with pedestal. Involucre 15-17 mm long, c. 10 mm broad, cup-shaped to subcylindric. Phyllaries in several series, glabrous, appendages hyaline, ovate to suborbicular, shortly ciliate or lacerate, decurrent. Capitula heterogamous. Marginal flowers pink, radiant, with 7-8 broad segments; central flowers numerous, whitish to pink, anther tube rose-violet. Achenes 4-6 mm, laterally compressed, with relatively large basal-lateral detachment area, with biseriate glandular hairs, with elaiosome. Pappus 1-2.5 mm long, of scabrous bristles, inner row similar, but shorter.

Chromosome numbers: Only one count is available: 2n = 32 (Guinochet & Foissac 1962). This may be a real deviation from the usual number or due to B-chromosomes.

Species and distribution: The best known species, *Psephellus trinervius*, is distributed from Romania (Carpathian) through S Russia (Ukraine?) and the Crimea to Caucasia. Two other species are from Caucasia.

- Psephellus avaricus (Tzvelev) Wagenitz, comb. nova ≡ Centaurea avarica Tzvelev in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR 20: 27. 1960.
- P. kobstanicus (Tzvelev) Wagenitz, comb. nova ≡ Centaurea kobstanica Tzvelev in Bot. Mater.
 Gerb. Bot. Inst. Komarova Akad. Nauk SSSR 19: 425. 1959.
- P. trinervius (Willd.) Wagenitz, comb. nova ≡ Centaurea trinervia Steph. ex Willd., Sp. Pl. 3(3): 2301. 1803.

Systematic position: Allied to *Psephellus* sect. *Uralepis* and *Sosnovskya*.

Lit.: Janka 1882; Cvelev 1963: 481-485.

Psephellus sect. Xanthopsis (DC.) Wagenitz & Hellwig, comb. nova

Type: Amberboa xanthocephala DC. ≡ Psephellus xanthocephalus (DC.) Boiss. & Buhse

= Amberboa sect. Xanthopsis DC., Prodr. 6: 561. 1838 = Xanthopsis (DC.) C. Koch in Linnaea 24: 422. 1851 = Amblyopogon sect. Xanthopsis (DC.) Grossh. in Trudy Prikl. Bot. Ser.1. Sist. Rast. Obščie Vopr. Rasteniev. 2: 243. 1937 = Centaurea sect. Xanthopsis (DC.) Tzvelev in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR 19: 418. 1959 = Centaurea subg. Xanthopsis (DC.) Tzvelev in Bobrov & Čerepanov, Fl. SSSR 28: 474. 1963.

Perennials with woody base, branched from near the base, the branches with one to several capitula, tomentose especially in the lower part. Leaves appressed-tomentose, more or less glabrescent, the lower petiolate, the upper sessile, all undivided and linear-lanceolate to lanceolate or the lower pinnatipartite to lyrate. Involucre 11-18 mm long, 6-11 mm broad, ovoid. Phyllaries in several series, their glabrous basal part totally concealed by the large appendages. Appendages membranous, whitish to straw-coloured, ovate or hemispherical to nearly circular, not decurrent, denticulate to ciliate. Capitula heterogamous. Flowers whitish to sulphur-yellow, the marginal with staminodes, nearly filiform, not radiant, about as long or slightly shorter than the central ones, with 4-5 segments, the central rather few, hermaphrodite. Achenes 5-7 mm long, laterally compressed, detachment area lateral, small, probably without elaiosome. Pappus 0.5-1 mm (7-8 mm in Psephellus straminicephalus), of scabrous bristles, inner row scarcely different (shorter or equal in P. straminicephalus).

Chromosome numbers: Two counts are available for *Psephellus xanthocephalus*: n = 15 (Bakshi Khaniki 1995) and 2 n = 30 + 0-3 B (Garcia Jacas & al. 1998). Tonjan (1968) gives 2n = 32 for *P. erivanensis*.

Species and distribution: Three or four species in E Anatolia, the Aras valley and NW Iran. *Psephellus straminicephalus* differs by the long pappus.

Psephellus erivanensis Lipsky, Fl. Caucasi, suppl. 1 [= Acta Horti Tiflis 6]: 64. 1902

- P. straminicephalus (Hub.-Mor.) Wagenitz, comb. nova ≡ Centaurea straminicephala Hub.-Mor. in Bauhinia 3: 316. 1967.
- P. xanthocephalus (DC.) Fisch. & C. A. Mey. ex Boiss. & Buhse in Nouv. Mém. Soc. Imp. Naturalistes Moscou 12: 129. 1860 ≡ Amberboa xanthocephala DC., Prodr. 6: 561. 1838.

Systematic position: Close to *Psephellus* sect. *Sosnovskya*. *P.* sect. *Amblyopogon* has some affinities too, but differs in habit.

Lit.: Gabrieljan 1988; Grossgejm 1937; Cvelev 1963: 474-477; Wagenitz 1975: 571-572, 1980: 411-412.

Psephellus sect. Uralepis (DC.) Wagenitz & Hellwig, comb. nova

Type: *Microlonchus persicus* DC. ≡ *Psephellus persicus* (DC.) Wagenitz

= *Microlonchus* sect. *Uralepis* DC., Prodr. 5: 563. 1838 = *Centaurea* sect. *Uralepis* (DC.) Wagenitz in Bot. Jahrb. Syst. 82: 195. 1963.

Perennial with woody base and several erect to ascending stems, branched from the base with long branches with one capitulum. Lower *leaves* tomentose, lanceolate to rhomboid, sometimes lyrate, denticulate with cartilaginous teeth, median and upper nearly glabrous, linear-lanceolate or linear. *Involucre* 13-16 mm long and (5-)8-12 mm broad, cup-shaped. *Phyllaries* in several series, coriaceous, glabrous, appendage crescent-shaped, hyaline, entire or denticulate, decurrent. *Flowers* ochroleucous, the marginal not radiant, sterile, with staminodes and sometimes a rudimentary style, with filiform segments. *Achenes* 6-7 mm long, laterally compressed, detachment

area small, lateral, probably without elaiosome. *Pappus* 7-9 mm long, of scabrous bristles, the inner row of scales 3-4(-5) mm long.

Chromosome numbers: Unknown.

Species and distribution: Only one species, endemic in W and central Iran.

Psephellus persicus (DC.) Wagenitz, **comb. nova** ≡ *Microlonchus persicus* DC., Prodr. 6: 563. 1838 = *Centaurea gaubae* (Bornm.) Wagenitz in Bot. Jahrb. Syst. 82: 195. 1963.

Nomenclature: In *Psephellus* the oldest available epithet must be used again. For details see Wagenitz (1963: 196).

Systematic position: Although superficially similar, *Psephellus persicus* has surely no affinity with *Mantisalca* (*Microlonchus*) as supposed by Candolle. It clearly belongs to the group of sections with pollen of the *Centaurea dealbata* type, but is rather isolated. The habit is similar to *P*. sect. *Odontolophus* and *Sosnovskya*

Lit.: Wagenitz 1963: 195-197, 1980: 410-411.

Psephellus sect. Sosnovskya (Takht.) Wagenitz & Hellwig, comb. nova

Type: Centaurea amblyolepis Ledeb. ≡ Psephellus amblyolepis (Ledeb.) Wagenitz

≡ Sosnovskya Takht. in Sovetsk. Bot. 1936(5): 98. 1936 ≡ Centaurea sect. Sosnovskya (Takht.) Wagenitz in Bot. Jahrb. Syst. 82: 193. 1963 ≡ Centaurea subg. Sosnovskya (Takht.) Czerep. in Bobrov & Čerepanov, Fl. SSSR 28: 477. 1963.

Perennials with woody base, stems branched near the base with numerous long branches with one capitulum, woolly at base. Leaves thinly tomentose, glabrescent, narrowly lanceolate to entire, the lower sometimes with few distant lobes or teeth or lyrate, the upper linear, nearly needle-like. Involucre c. 15-17 mm long, 8-13 mm broad, cup-shaped. Phyllaries in few series, glabrous, the appendages triangular to crescent-shaped, not or slightly decurrent, ciliate. Capitula heterogamous. Flowers whitish or pink, the marginal slightly radiant, with 5-6 narrow segments, with staminodes, the central flowers rather numerous. Achenes 5.5-6 mm long, detachment area small (only 1.5 mm in P. amblyolepis), lateral-basal. Pappus 3-5 mm long, of scabrous bristles, the inner row slightly shorter or not differentiated.

Chromosome numbers: Unknown.

Species and distribution: Four species occur in the Caucasian region (Čerepanov 1963). They are apparently closely related and two of them may be only subspecies of *Psephellus amblyolepis*. A further species, *P. galactochrous* (Rech. f.) Parsa, occurs in N Iran.

- Psephellus amblyolepis (Ledeb.) Wagenitz, comb. nova ≡ Centaurea amblyolepis Ledeb., Fl. Ross. 2: 703. 1845 ≡ Phaeopappus amblyolepis (Ledeb.) Boiss., Fl. Orient. 3: 601. 1875 ≡ Sosnovskya amblyolepis (Ledeb.) Takht. in Sovetsk. Bot. 1936(5): 99. 1936 & in Repert. Spec. Nov. Regni Veg. 41: 191. 1936.
- P. arpensis (Czerep.) Wagenitz, comb. nova ≡ Sosnovskya arpensis Czerep. in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. SSSR 20: 484. 1960 ≡ Centaurea arpensis (Czerep.) Czerep. in Bobrov & Čerepanov, Fl. SSSR 28: 481. 1963.
- P. galactochrous (Rech. f.) Parsa, Fl. Iran 3: 633. 1948 ≡ Centaurea galactochroa Rech. f. in Repert. Spec. Nov. Regni Veg. 48: 153. 1940.

Systematic position: Closely related to *Psephellus* sect. *Odontolophus* and probably better included in it, differing mainly in the less radiant marginal flowers and not or scarcely decurrent appendages.

Lit.: Wagenitz 1963: 193-195; Čerepanov 1963: 477-481.

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