Phytotaxa 201 (1): 027–049
www.mapress.com/phytotaxa/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

http://dx.doi.org/10.11646/phytotaxa.201.1.2

Carpology of the genus *Tragopogon* L. (Asteraceae)

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Abstract

67 species of *Tragopogon* were investigated with regard to fruit anatomy. The outer achenes, especially the beak and the central part of the seed-containing body, provide the most valuable features (diameter and outlines of the body and the beak, and arrangement of the mechanical elements in the body parenchyma). Some specimens of widely distributed taxa (e.g. *T. capitatus*, *T. dubius*, *T. pratensis*, *T. pseudomajor*) show variation in the character set and require more investigation prior to further taxonomic treatment. The species studied are classified into informal groups to demonstrate the diversity of carpological traits within the genus, and a comparison is made with the existing molecular phylogeny. The separation of the genus *Geropogon* from *Tragopogon* is supported by the achene anatomy.

Key words: *Geropogon*, *Scorzonerinae*, *Cichorieae*, taxonomy, molecular phylogeny

Introduction

The genus *Tragopogon* L. (Asteraceae: *Cichorieae*, *Scorzonerinae*) comprises about 150 species distributed mostly in semiarid and mountainous regions of Eurasia (Bell *et al.* 2012). As a rule they are easily recognized by the grass-like, long, undifferentiated, basally broadened, semi-amplexicaul leaves; well-developed, sometimes apically inflated peduncules; cylindrical involucres consisting of (5–6)7–12 phyllaries arranged usually in a single row, rarely in 2 rows; large capitula with yellow, reddish yellow or mauve flowers, and large (1 cm and above) tuberculate fruits (achenes) with a plumose pappus. Among the diagnostic characters of infrageneric rank, flower or fruit morphology features are widely used. However, the identification of many species on the basis of herbarium material is problematic because of wide separation between flowering and fruiting phenophases and the inability to observe some characters seen only on living plants, e.g. details of the coloration of the flowers (Figs. 1–3) or stigmas. Occurrence of interspecific hybridization reported in the literature (Ownbey 1950, Ownbey & McCollum 1953, Pires *et al.* 2004, Buggs *et al.* 2008, Mavrodiev *et al.* 2008) or facultative apomixis recently found in *T. dubius* (Kashin *et al*. 2007) may affect the character set of individuals.

In most species of the genus the achenes are differentiated into a wider (seed-containing) body and a thinner beak. The length of the achenes (without pappus) varies from 1 to 5.5 cm, with varying ratio between body and beak. Some species are characterized by a very short beak in comparison with the body (*T. dasyrhynchus*, *T. gaudanicus*, *T. podolicus*, *T. pusillus*, *T. scoparius*, *T. tanaiticus*), and rarely the beak is absent (*T. dubjanskyi*, some individuals of *T. scoparius*); however, most species have developed an elongated beak that may exceed the length of the body. At its apex, below the flat structure from which the pappus bristles arise, termed the pappus disk or annulus (e.g. Nikitin 1933, Kuthatheladze 1957, Borisova 1964, Tzvelev 1989, Li 1993; Soltis 2006; Zhu *et al.* 2011), the beak is scarcely or significantly inflated. The pappus is 0.6–4 cm long, with slightly unequal rows of softly fimbriate plumose bristles.

As in some other Asteraceae (Becker 1913, Grimbach 1914, Mandák 1996), profound heterocarpy is typical of *Tragopogon*. Both extreme (outermost and innermost) fruit types drastically differ in their shape, length, colour, weight, ultrasculpture, or details of anatomy (Voytenko 1981), as well as abscission pattern (Green & Quesada 2011), although the achenes in an intermediate position on the receptacle are characterized by morphological and anatomical structure transitional between that of the outer and inner achenes (Voytenko 1981, Maxwell *et al.* 1994). The lower weight of the central achenes in *Tragopogon* correlates with a greater long-range dispersal in comparison to the outer achenes which have mostly atelechoric dissemination (Voytenko 1981).

Accepted by Alexander Sennikov: 9 Jan. 2015; published: 25 Feb. 2015

FIGURE 1. Image of *Tragopogon gracilis*. Yellow coloured adaxial and mauve abaxial flower surfaces. Central Nepal, Mustang Province, Larjung village. 04.2009. Photographer A.Sukhorukov.

FIGURE 2. Image of *T. coelesyriacus*. Flowers mauve. Israel, Jerusalem. 04.2012. Photographer A.Sukhorukov.

FIGURE 3. Image of *T. dubius*. Flowers yellow. Central Russia, Tambov Province, Umyot distr. 05.2012. Photographer A. Sukhorukov.

The only dispersal unit in *Tragopogon* is a fruit. In contrast to previous data (Fahn & Werker 1972), the capitulum itself does not play a role in dissemination, and there is no special cohesion mechanism at the base of the capitulum.

The outermost achenes are considered to be the most appropriate for diagnosis and are distinguished by clearly expressed characters that are diagnostic at the species level (Voytenko & Oparina 1990). The following morphological characters are used in the identification of species in *Tragopogon*: achene/pappus or body/beak ratios, presence of thickening at the beak apex, or hairs at the base of the annulus, as well as the fine ultrasculpture of the achene surface that usually has tuberculate outgrowths (Blanca & Diaz de la Guardia 1994).

The anatomy of the achenes of *Tragopogon* and related genera has so far been only fragmentarily studied. Besides carpological investigation of *T. dubius* (Voytenko 1981), a comparative study of some *Scorzonera* and *Tragopogon* growing in the Russian Far East was undertaken by Boyko (2000), demonstrating similar topology of the pericarp in both genera. A global investigation of the latter genus has not so far been published. This is also true of the monotypic genus *Gerogopon* L., which is similar to *Tragopogon* in its overall appearance but differs significantly from the latter genus since its outermost achenes have stout awns instead of a hairy pappus.

The aims of the present study are:

(1) to undertake a comparative carpological investigation of *Tragopogon* to reveal all possible structural variants in its outer achenes and describe the correspondence of fruit characters to the recent classification of the genus;

(2) to compare the carpology of the closely related genera *Tragopogon* and *Geropogon*.

Material and Methods

Altogether 67 species of *Tragopogon* and the single species of *Geropogon* were studied carpologically. Cross-sections of the outer achenes were made by hand in three topographical zones: at the base of the achene body, in its central (widest) part, and in the beak. For purposes of comparison the inner achenes of many species were included in the analysis. Some material was collected during field trips (A. Sukhorukov), and those herbarium specimens are preserved at MW. Other samples were carefully removed (with permission) from the herbaria H, HUJ, LE, MW and W (herbarium abbreviations according to Thiers 2008+). The list of the specimens studied is given in the Appendix.

Prior to sectioning, the material was soaked in a mixture of ethyl alcohol, water and glycerine (in equal proportions) for a few days at 30–40°C. Free-hand longitudinal and transverse sections were stained with a 1% aqueous solutions of Safranin and 1% Light Green in concentrated picric acid. The ultrasculpture of the achene surface was investigated using an SEM (JSM-6380 LA) at the Electron Microscopy Laboratory of Moscow M.V. Lomonosov State University. Carpological terminology is according to Werker (1997).

Results

Morphologically and anatomically the outermost achenes provide the most valuable information regarding the carpological diversity in the genus. The inner achenes of all species are similar in their characters, and the carpological description is therefore based on the outermost achenes only.

Shape and thickness of the outer achenes in cross-section

The basal part of the achene is distinctly 5-ribbed in cross-section. Towards its apex, the ribbing pattern of the body and the beak can take different shapes. The body, especially in its middle portion, can be rounded, 5-angled (mostly with 5 additional, less prominent ribs) or (as an intermediate type) indistinctly ribbed, or rarely sharply ribbed with almost equal (*T. bornmuelleri*) or unequal prominent (*T. albinervis*) ribs looking like wings. The shape of the achene beak shows a considerable variation between species. Even achenes with a rounded body often have markedly different shapes of beak, which may have sharply or obtusely angled outlines. Thin beaks of 0.25–0.5 mm in diameter mostly possess 5 or 10 acute ribs in contrast to thicker ones having 10 obtuse ribs. The apex of club-shaped beaks has obtuse ribs. The achenes of *T. samaritani* as well as some forms of *T. dubjanskyi* are rounded irrespective of the topographic zones.

The thickness of the achenes in their widest part (near the middle of the body or in its lower half) varies from (1.0–1.1) 1.2 to 2.9 mm in the majority of species. Larger diameters are rare and restricted to species with a 'winged' body (*T. albinervis*, *T. bornmuelleri*). The bodies of rounded or indistinctly ribbed shapes are always characterized by a smaller (1–1.5 mm) diameter. Thicker bodies appear to be angled or ribbed in cross-section with the exception of some specimens of *T. dubjanskyi*. Towards the beak, the achene thickness decreases abruptly or continuously, including also the species with an indistinct beak, and it usually varies from 0.3 to 1.5 mm.

Anatomical zones of the pericarp

Four anatomical zones can be distinguished in the achenes of *Tragopogon* species. Their shape and thickness depend on the topographic zone of the achene (Fig. 4).

(1) *Outer epidermis* (exocarp). The cells forming the outer epidermis vary in shape. In the body they are often marked by tiny papillae or mamillae invisible to the naked eye. The cell outlines in the beak are mostly smooth. However, the epidermal cells especially in the rib area form stout multi-layered conglomerations. Such so-called spinulae consist of multi-celled aggregates responsible for the tongue-shaped ornamentation of the achene surface (Fig. 5), resembling the fruit of *Annona cherimoya*. In cross-section these outgrowths appear as relatively minute (up to 0.3 mm) with a striate surface on the cell walls, but many of them are oriented obliquely and thus their real length may reach 0.6 mm. In the beak they are more elongated (Fig. 6). The ornamentation of the achene is almost invisible in *T. dubjanskyi*.

(2) *The underlying parenchyma*. The body consists of two differentiated parenchyma cell types: (a) with thin unlignified walls (outer subzone), and (b) with annular cell-wall thickenings (Fig. 7). The thin-walled cells are comparatively very few, and are present in the inter-rib spaces (furrows). At fruit ripening, the walls of such cells are easily ruptured with the formation of air cavities. Most *Tragopogon* species possesses large air cavities in the parenchyma of the achene body (100–150 μm in diameter). Smaller cavities (up to 60–80 μm) are common in the small-diameter bodies (up to 1.5 mm). In some achenes, especially of a smaller diameter, the thin-walled cells do not rupture, and thus air cavities may be hardly noticeable.

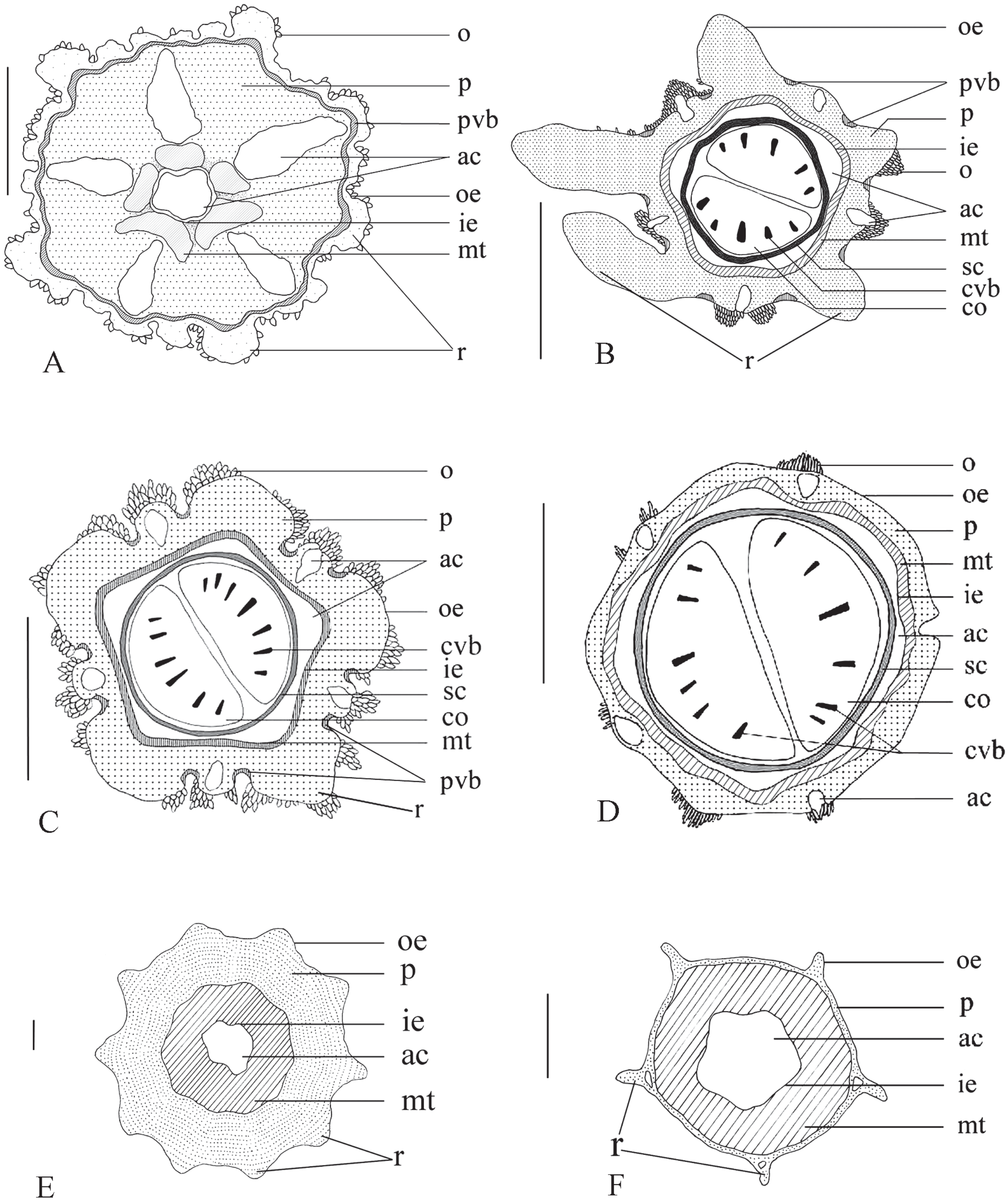

FIGURE 4. Cross section of outer achene base (A), outer achene body of (B, C, D), outer achene beak of (E, F). A, C, E—*T. coloratus*, B—*T. albinervis*, D—*T. dasyrhynchus*, F—*T. dubius*. Abbreviations: ac—air cavity, co—cotyledons, cvb—cotyledon's vascular bundles, ie—inner epidermis, mt—mechanical tissue, o—ornamentation (stout multistage conglomerations), oe—outer epidermis, p—parenchyma, pvb—pericarp vascular bundles (derivates), r—ribs, sc—seed coat. Scale bars: A–D—1 mm, E–F—0.1 mm. Voucher of specimens: *T. coloratus*: Armenia, distr. Kafansky, Chekhi river, 07.1957, V. Alper *962* (MW); *T. albinervis*: Turkey, prov. Erzurum, Tortum Gol, 07.1960, Stainton & Henderson *6116* (W-07775); *T. dasyrhynchus*: Russia, prov. Tambov, Kirsanov, 08.1995, A. Sukhorukov *s.n.* (MW); *T. dubius*: Russia, prov. Tambov, distr. Umyot, Sergievka, 06.2008, A. Sukhorukov *s.n.* (MW).

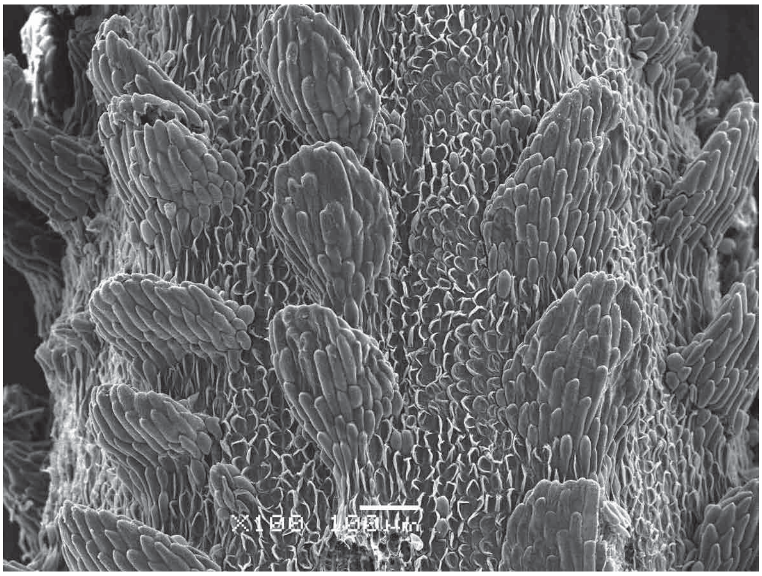

FIGURE 5. Tongue-shaped ornamentation of outer-achene body of *T. badachschanicus*. Scale bars: 100 µm. Voucher of specimen: [Tajikistan] Kaindy river, Suyak-Mazar, 08.1958, N.N. Tzvelev *1473* (LE).

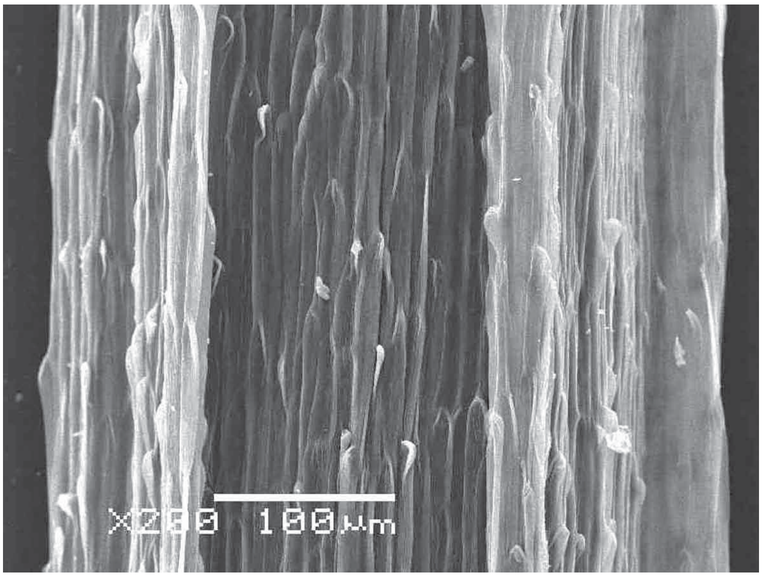

FIGURE 6. Tongue-shaped ornamentation of outer-achene beak surface of *T. badachschanicus*. Scale bars: 100 µm. Voucher of specimen: see caption of Fig. 5.

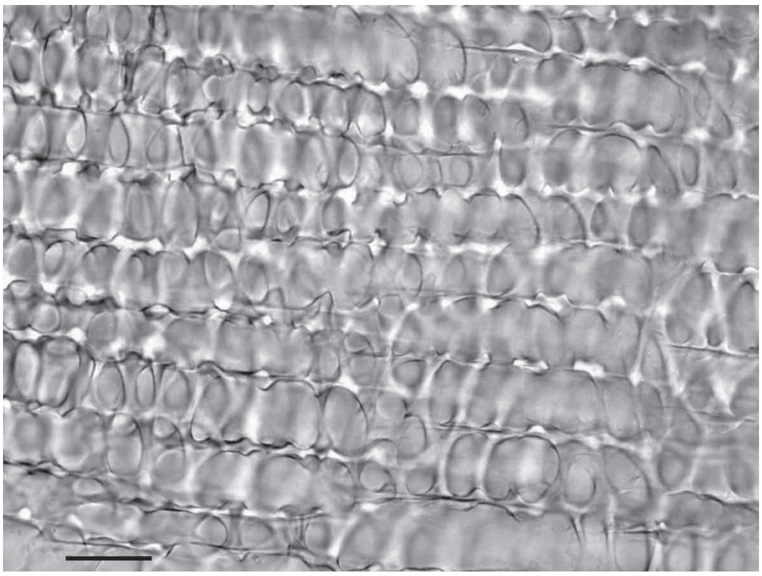

FIGURE 7. Parenchyma with annular cell-wall thickenings of *T. coelesyriacus*. Scale bars: 20 µm. Voucher of specimen: Israel, Jerusalem, 04.2012, A. Sukhorukov (MW).

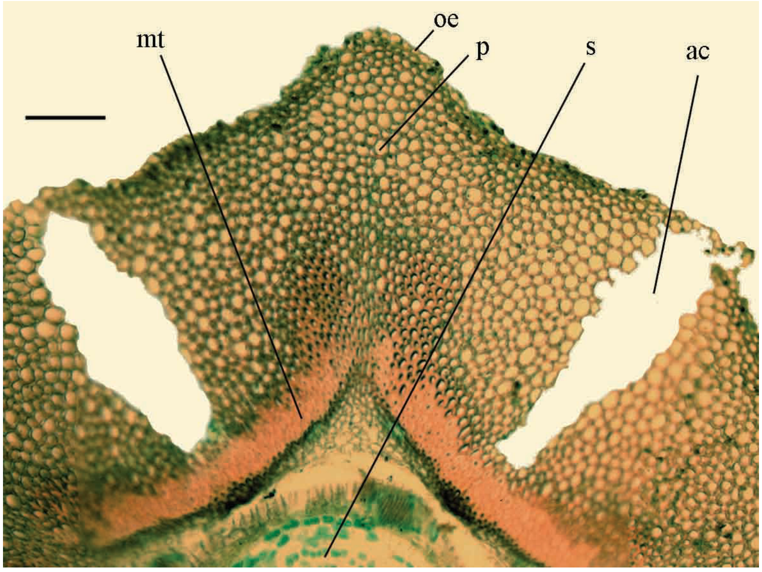

FIGURE 8. Cross section of outer achene base of *T. coelesyriacus*. Abbreviations: ac—air cavity, mt—mechanical tissue, oe—outer epidermis, p—parenchyma, s—seed. Scale bars: 100 µm. Voucher of specimen: see caption of Fig. 7.

In contrast to the thin-walled parenchyma, the parenchyma with annular cell walls is arranged in the pericarp radially. In the rounded achenes it comprises many layers in the base of the body and 4–8 layers in its central part. However, the number of parenchyma layers drastically increases in the ribs of angled achenes (up to 30 layers) and thus the parenchyma plays a key role forming the ribbed outlines in most *Tragopogon* species. Several (2–4) outer layers of this zone are usually transformed into completely lignified cells looking like derivates of the vascular bundles. In rounded or indistinctly 5-ribbed achenes these bundles are mostly radially distributed in the outer layers of the parenchyma as a sheath. In 5-angled bodies, lignified cells are clustered into bundles near the air cavities. However, these mechanical elements in the achene body of many species (e.g. *T. afghanicus*, *T. capitatus*, etc.), as well as in *T. vvedenskyi* with its rounded or indistinctly 5-angled achenes, reveal a tendency to clustering near the air cavities. Towards the fruit apex the air cavities disappear gradually, and the bundles of lignified cells also disappear. At the apex of the fruit the parenchyma has annular cell walls, and the thin-walled parenchyma comprises 2–4 cell layers in thinner beaks (up to 0.5 mm diameter) or 8 or more layers if the beak is of a larger diameter.

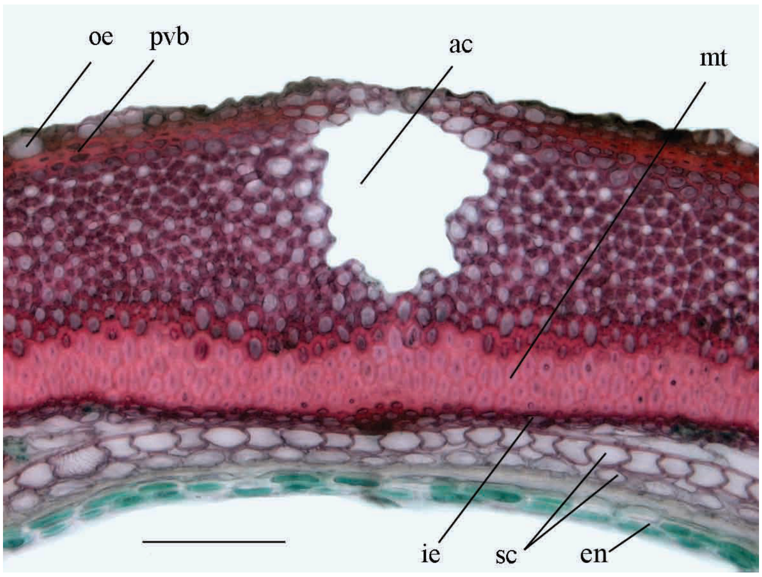

FIGURE 9. Cross section of outer achene body of *T. coelesyriacus*. Abbreviations: ac—air cavity, ie—inner epidermis, mt—mechanical tissue, oe—outer epidermis, pvb—pericarp vascular bundles (derivates), sc—seed coat, en—endosperm. Scale bars: 100 µm. Voucher of specimen: see caption of Fig. 7.

(3) *The mechanical tissue* is always present in the pericarp. In the achene base it forms 5 discontinuous sheaths of sclereids (Fig. 4A, 8), but towards the centre of the body they become fused into a radially oriented tissue consisting of several (usually 3–6) layers (Fig. 9). In the beak their number increases to 7–15 layers (Fig. 10).

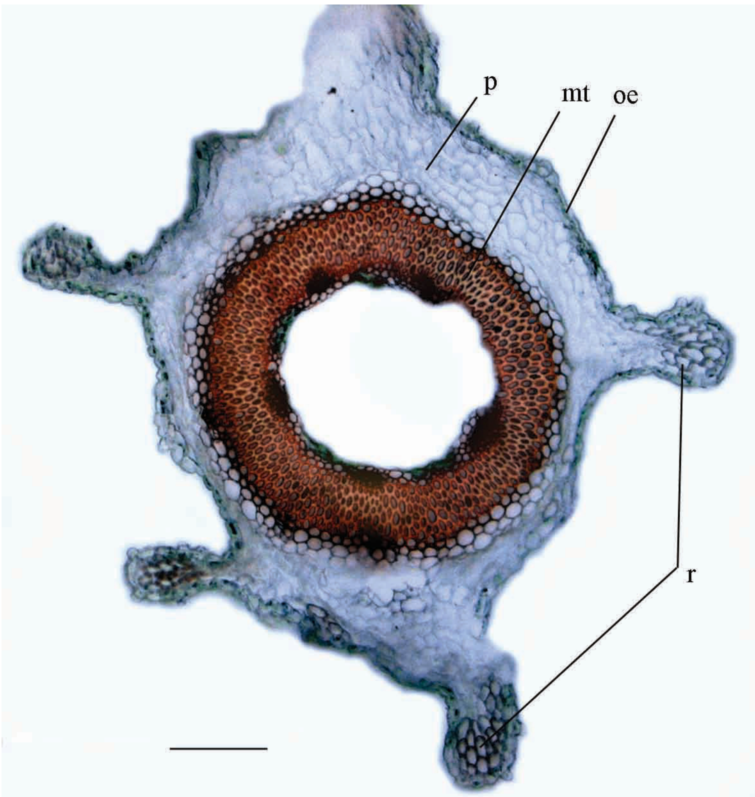

FIGURE 10. Cross section of outer achene beak of *T. coelesyriacus*. Abbreviations: mt—mechanical tissue, oe—outer epidermis, p—parenchyma, r—ribs. Scale bars: 100 µm. Voucher of specimen: see caption of Fig. 7.

(4) *The inner epidermis* (endocarp) consists of 1 or several layers of tangentially compressed cells with unlignified walls. Between the ribs the inner epidermis comprises 1–3(4) layers, whereas in the rib area it increases to 6–7 layers.

Seed. The seed coat comprises (1)2–4(5) equal layers with annular cell walls and adjoins the inner pericarp epidermis in the inter-rib spaces. The derivates of the vascular bundles are 2–3, equally distant from each other. The seed occupies the central part of the body, while its lower or upper parts contain an air cavity. The seed embryo is straight and surrounded by a 2-layered endosperm. The seed structure shows no differences between any of the species and cannot be considered to be relevant for taxonomy.

Differences in the achene morphology and anatomy of outer and inner achenes

The description of the achenes given in the results is based on the outermost achenes. Towards the center of the capitula, the characters of the achenes undergo gradual transitions as shown in Table 1.

TABLE 1. The most common transitions of the morphological and anatomical characters between the outermost and innermost achenes in *Tragopogon*

Character	Outermost achenes	**Innermost achenes**
Degree of curvature	more or less curved	straight or slightly curved
Colour	brownish, reddish or whitish	brighter (whitish)
Ribbing pattern of the body	5 or 10 ribs often expressed, sometimes in the form of wings, rarely ribless and rounded	indistinctly ribbed or rounded
Tongue-shaped ornamentation of the achene surface	clearly expressed at least in the body	smooth or with smaller outgrowths (up to 200 µm)
Diameter of the body	larger	smaller
Air cavities	large or small	small (to 60 µm)
Parenchyma	clearly expressed	reduced to several (7–8) layers

TABLE 2. The most significant differences in the carpological structure of the outer achenes of *Tragopogon* species
If not all specimens of a species show the same character states, they are given separate entries in the table with an indication of the year of collection or other details of the samples (for more information on the samples see Appendix).
Abbreviations: **Pappus**: f – fulvous; w – (dirty) white; wf – dirty white in the lower part, slightly fulvous above; y – yellowish (at least in upper part). **Annulus**: g – glabrous or slightly pubescent; p – pubescent; **achene shape in cross-section**: r – rounded; 5a – (sharply) 5-angled; 5ao – obtusely (indistinctly) 5-angled; 10a – (sharply) 10-angled; 10ao – obtusely (indistinctly) 10-angled. **Air cavities**: b – big; s – small or hardly visible

Species	Achene length (cm), without pappus	Beak length as proportion of total achene length	Thickening at the beak apex	Annulus	Pappus length (cm)	Colour of pappus	Shape of the central portion of the body in cross-section	Diameter of the body, mm (except tongue-shaped appendages)[1]	Length of appendages in the body (maximum, mm)	Air cavities	Mechanical elements in the parenchyma	Diameter of the beak or the achene apex (if beak not present), mm	Beak in cross-section	Outgrowths on the beak (or achene apex), mm (maximum)
Group I														
T. borysthenicus (1909)	1.2–1.3	–	–	p	1.2–1.5	w	r	1.1–1.2	0.1	s	radial	0.7–0.9	10ao	0.13
T. borysthenicus (1923)	1.2	–	–	p	0.6–1.2	w	5ao	1.0–1.1	0.07	s	not visible	0.5–0.7	10ao	–
T. daghestanicus	1.3	–	–	p	1.5–1.8	w	r	1.3–1.4	0.15	b	radial	0.7–0.9	10ao	–
T. dasyrhynchus	1.5	0.2	–	p	1.3–1.5	w	5ao	1.7–1.8	0.15	b	radial	0.7	10ao	0.05
T. dubjanskyi (1928)	1.3	–	–	p	1.5	w	5ao	1.5–1.7	–	b	radial	1.3	10ao	–
T. dubjanskyi (1935)	2.0	–		p	1.7–2.2	w	r	1.9–2.1	0.06	b	radial	1.2–1.4	10ao	0.06
T. dubjanskyi (1936)	1.6	–	–	p	1.3–1.8	w	5ao, r	1.8–2.0	–	b	radial	1.3–1.5	rounded	–
T. podolicus (all specimens)	1.3	0.2	+	p	1.2	w	r	1.3–1.5	0.15	s	radial	0.5–0.6	10ao	0.05
T. sabulosus (all specimens)	2.0–2.3	0.4–0.5	+	p	2.0–2.7	w	5ao	2.0–2.5	0.26	s	radial	1.0–1.2	10ao	–
T. scoparius (all specimens)	1.0–1.2	0–0.3	–	p	1.0–1.5	w	r	1.4–1.6	0.1	b	radial	0.5–0.7	10ao	0.15
T. sindicus (all specimens)	1.4	0.2–0.3	+	p	1.2–1.7	w	r	1.2–1.5	0.15	s	radial	0.5–0.6	10ao	0.13
T. tanaiticus (all)	0.9–1.3	–	–	p	0.8–1.2 (1.5)	w	r	1.4–1.7	0.13	s	radial	0.7–0.9	10ao	–
T. ucrainicus	1.2	0.1–0.2	–	g	1.2–1.3	w	r	1.6–1.7	0.13	s	radial	0.5–0.6	10ao	–
T. undulatus	1.2	0.3	–	p	1.0–1.2	w	r	1.0–1.2	0.1	s	radial	0.6–0.7	10ao	–
Group II														
T. angustissimus	2.1	0.5	+	p	2.2	y	r	1.4–1.5	0.13	b	clusters	0.35–0.40	5a	–
T. vvedenskyi (1931, 1969)	2.0	0.5–0.7	+	p	1.8–2.2	y	r	1.4–1.6	0.2	s	clusters	0.5–0.65	10ao	–
T. vvedenskyi (1976)	2.0	0.4	+	p	1.3–1.7	y	r	1.2–1.3	0.1	s	clusters	0.5–0.6	10ao	–

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1 ‘If the achene has a 5-angled shape, the diameter is measured including the ribs (maximal diameter) and in the furrows (minimal diameter)

TABLE 2. (Continued)

Species	Achene length (cm), without pappus	Beak length as proportion of total achene length	Thickening at the beak apex	Annulus	Pappus length (cm)	Colour of pappus	Shape of the central portion of the body in cross-section	Diameter of the body, mm (sxcept tongue-shaped appendages)[1]	Length of appendages in the body (maximum, mm)	Air cavities	Mechanical elements in the parenchyma	Diameter of the beak or the achene apex (if beak not present), mm	Beak in cross-section	Outgrowths on the beak (or achene apex), mm (maximum)
Group III														
T. afghanicus (all)	3.1–4.0	1.6–2.0	+	p	2.5–3.2	w	5ao	1.6–1.8	0.2	b	clusters	0.3–0.4	5a	–
T. altaicus	1.7	0.6–0.7	–	p	1.5–1.8	w	r	1.4–1.6	0.1	s	radial	0.4–0.6	10ao	–
T. badachschanicus (1955, 1958; 1977)	1.8–2.2	0.7–1.0	+	p	1.4–2.0	w	5ao	1.4–1.6	0.1	s	clusters	0.4–0.5	10ao	–
T. badachschanicus (1968)	2.1	0.8–1.0	+	p	1.5–2.0	w	5ao	1.6–1.7	0.1	b	tendency to form clusters	0.4–0.55	5ao, 10ao	–
T. capitatus (1989)	3.0	1.2–1.5	+	p	3.0–3.5	w	5ao	1.6–1.8	0.15	b	clusters	0.4–0.55	5a	–
T. capitatus (1914)	3.5	2.0	+	p	2.2–2.5	w	5ao	1.3–1.4	0.13	b	clusters	0.25–0.35	5a	–
T. capitatus (1893)=*T. nikitinii* nom. provis.	3.0	1.2–1.5	+	p	3.0–3.4	w	5ao	1.6–1.8	0.15	b	radial	0.6–0.7	5ao	–
T. coelesyriacus (1925)	4.0	2.5	+	p	3.0	w	r	1.3–1.5	0.26	b	radial	0.3–0.4	5a	–
T. coelesyriacus (1954)	4.5	2.5	+	p	2.5-3.0	w	r	1.9–2.0	0.13	b	radial	0.4	5a	–
T. cretaceus (1968)	2.0–2.2	1.0	+	p	1.7–2.0	w	5ao	1.5–1.7	0.2	b	radial	0.6–0.8	10ao	0.07
T. cretaceus (1991)	2.5	1.5	+	p	1.7–2.0	w	5ao	1.1–1.3	0.2	b	tendency to form clusters	0.3	5a	–
T. dubius (2001, 2008)	2.7–3.2	1.3	+	p	2.3–2.7	w	5a	1.4–1.7	0.3	b	radial	0.4–0.5	10a	0.15
T. dubius (Kazakhstan, 1965)	2.7	1.2–1.6	–	p	2.2–2.6	w	5ao	1.5–1.7	0.3	b	radial	0.3–0.4	10a	–
T. dubius (Armenia, 1965)	3.4	2.0	+	p	2.0–2.3	w	5ao	1.4–1.6	0.20	b	radial	0.25–0.30	5a	–
T. kemulariae (1968; 1969; 1974)	3.2–3.8	2.0–2.7	+	p	2.5–3.0	w	5ao	1.4–1.7	0.22	b	tendency to clustering	0.3–0.4	5a	–

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1 ‘If the achene has a 5-angled shape, the diameter is measured including the ribs (maximal diameter) and in the furrows (minimal diameter)

TABLE 2. (Continued)

Species	Achene length (cm), without pappus	Beak length as proportion of total achene length	Thickening at the beak apex	Annulus	Pappus length (cm)	Colour of pappus	Shape of the central portion of the body in cross-section	Diameter of the body, mm (sxcept tongue-shaped appendages)[1]	Length of appendages in the body (maximum, mm)	Air cavities	Mechanical elements in the parenchyma	Diameter of the beak or the achene apex (if beak not present), mm	Beak in cross-section	**Outgrowths on the beak (or achene apex), mm (maximum)**
T. kemulariae (1984)	3.1	1.6–1.8	+	p	2.2–2.5	w	5ao	1.3–1.5	0.2	b	tendency to clustering	0.3	5a	–
T. kindingeri	1.7–1.8	1.0–1.2	+	p	1.5–1.8	w	r	1.4–1.5	0.1	s	radial	0.3–0.35	10a	–
T. kraschenninnikovii (1916, 1943, 1977)	3.2–4.0	1.7–2.5	+	p	2.5–3.0	w	5ao	1.2–1.5	0.15	b	radial	0.25–0.35	5a	–
T. kraschenninnikovii (1936)	3.8	2.0	+	p	2.3–2.8	w	r	1.4–1.5	0.20	b	radial	0.30	5a	–
T. kraschenninnikovii (1948)	3.4	1.7	+	p	2.3–2.5	w	r	1.5–1.6	0.15	b	radial	0.40–0.45	5a	–
T. macrocephalus (1897, 1931 no 15)	3.5–4.0	2.0–2.5	+	p	2.7–3.7	w	r, 5ao	1.7–1.9	0.16	b	clusters	0.3–0.5	5a	–
T. macrocephalus (1931, no 225)	3.5	2.0	+	p	3.5–4.0	w	5a	1.7–2.1	0.30	b	clusters	0.45–0.55	10a	–
T. orientalis (1941)	1.8	0.8	+	p	1.3–1.7	w	r	1.5–1.6	0.1	b	radial	0.3–0.35	5a	–
T. orientalis (1968)	2.3–2.5	1.0–1.3	+	p	2.0–2.5	w	5ao	1.4–1.6	0.1	b	radial	0.40–0.60	5a	–
T. porrifolius (1990)	4.2	2.3–2.5	+	p	2.7–3.2	w	5ao	1.4–1.6	0.2	b	radial	0.3–0.4	10a	–
T. pratensis (both specimens from Central Russia)	1.8	0.7–0.9	+	p	1.3–1.5	w	r	1.8–2.0	0.13	s	radial	0.4–0.5	10a	–
T. pratensis (Finland, 1995)	2.0	0.7	+	p	2.0	w	5a	1.7–2.0	0.15	s	radial	0.4–0.5	10a	–
T. pratensis (England, 2003)	2.3	1.0	+	p	1.8–2.2	w	5a	1.4–1.5	0.13	s	radial	0.4	10a	–
T. pseudomajor (1877)	2.7	1.0–1.2	+	p	2.5–3.0	w	5ao	1.4–1.5	0.15	i	clusters	0.4–0.5	5a	–
T. pseudomajor (1907, 1916)	2.6–3.0	1.2–1.7	+	p	2.2–2.5	w	5ao	1.8–2.0	0.25	b	clusters	0.5–0.6	5a	–
T. samaritani	3.2–3.5	1.2–1.5	+	g	2.5–3.0	w	r	1.4–1.6	0.2	b	r	0.9–1.0	r	–

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1 ‘If the achene has a 5-angled shape, the diameter is measured including the ribs (maximal diameter) and in the furrows (minimal diameter)

TABLE 2. (Continued)

Species	Achene length (cm), without pappus	Beak length as proportion of total achene length	Thickening at the beak apex	Annulus	Pappus length (cm)	Colour of pappus	Shape of the central portion of the body in cross-section	Diameter of the body, mm (sxcept tongue-shaped appendages)[1]	Length of appendages in the body (maximum, mm)	Air cavities	Mechanical elements in the parenchyma	Diameter of the beak or the achene apex (if beak not present), mm	Beak in cross-section	**Outgrowths on the beak (or achene apex), mm (maximum)**
T. serawschanicus (1931)	3.5	1.7	+	p	3.0–3.5	w	5a	2.0–2.3	0.13	b	radial	0.45–0.65	10a	–
T. sinuatus	3.8	1.8	+	p	2.5–3.0	w	5ao	1.5–1.6	0.13	b	radial	0.3	10a	–
T. songoricus (all).	1.8–2.2	0.7–1.0	+	p	1.5–2.0	w	5ao	1.55–1.8	0.15	s	radial	0.3–0.4	5a	–
T. tommasinii	2.2	1.2	+	p	1.6	w	5ao	1.5–1.6	0.13	b	radial	0.3	5a	–
T. trachycarpus (all)	1.8–2.2	0.6–0.8	+	p	1.5–2.0	w	r	1.4–1.6	0.15	s	radial	0.3–0.5	5a	–
T. turkestanicus (all, check only 1931)	2.2–2.5	0.9–1.2	+	p	1.8–2.5	w	r	1.3–1.6	0.1	s	radial	0.30–0.45	10a	–
							Group IV							
T. paradoxus (1932)	4.3	2.0	+	p	3.0–3.5	w	5a	2.5–2.7	0.1	b	radial	0.65	10a	–
T. paradoxus (1953, 1977)	4.5–5.2	2.5–3.0	+	p	3.3–3.8	w	5ao	2.3–2.7	0.07	b	radial	0.8–0.9	10ao	–
							Group V							
T. australis (1926)	4.0–4.2	1.2–1.4	+	p	3.0–3.2	w	r	1.4–1.6	0.26	b	radial	0.9–1.1	10ao	–
T. australis (1952)	5.0–5.2	2.5–3.0	+	p	3.0–3.5	w	r	1.5–1.7	0.15	s	radial	0.8–0.9	10ao	–
							Group VI							
T. albinervis	1.5–1.7	0.2–0.3	–	p	1.3–1.6	w	sharply and unequally 5a	1.3–1.5 (min), ribs to 1 mm	0.15	b	clusters	0.65–0.80	10ao	0.10
T. bornmuelleri	3.0	1.5–1.7	+	p	2.5–3.0	w	sharply 5a, 2 large and 3 smaller ribs	2.0–2.2 (without ribs of max. 2 mm)	0.2	b	clusters	0.5–0.65	sharply ribbed	–
							Group VII							
T. abolinii (nomen)	3.5	1.5	–	p	2.5–3.0	f	5ao	2.2–2.4	0.15	b	clusters	0.7–0.8	10ao	–

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1 ‘If the achene has a 5-angled shape, the diameter is measured including the ribs (maximal diameter) and in the furrows (minimal diameter)

TABLE 2. (Continued)

Species	Achene length (cm), without pappus	Beak length as proportion of total achene length	Thickening at the beak apex	Annulus	Pappus length (cm)	Colour of pappus	Shape of the central portion of the body in cross-section	Diameter of the body, mm (sxcept tongue-shaped appendages)[1]	Length of appendages in the body (maximum, mm)	Air cavities	Mechanical elements in the parenchyma	Diameter of the beak or the achene apex (if beak not present), mm	Beak in cross-section	**Outgrowths on the beak (or achene apex), mm (maximum)**
T. collinus (1967)	2.2	0.7	–	p	2.5–3.0	f	5a	1.6–1.7	0.13	b	clusters	0.65–0.80	10ao	0.06
T. conduplicatus (all specimens)	2.0–2.5	0.5–0.8	–	p	2.2–2.6	f	5a	1.7–2.0	0.25	b	clusters	0.6–0.8	10a	0.07
T. elongatus (1838)	1.8–2.0	0.7–0.8	+	p	1.7–2.5	f	5a	2.1–2.5	0.3	b	clusters	0.9–1.1	10ao	–
T. elongatus (1903)	2.2	0.7	+	p	2.0	f	5a	1.6–2.0	0.25	b	clusters	0.9–1.0	10ao	–
T. karatavicus	2.0	0.8	–	g	2.2	f	5ao	1.7	0.13	b	clusters	0.7–0.8	10ao	–
T. kasachstanicus (all)	2.2–2.7	0.7–0.9	+	p	2.2–2.5	f	5a	1.8–2.2	0.20	b	clusters	0.9–1.0	10ao	–
T. kultiassovii	2.5	0.8–1.1	–	p	2.5	f	5a	2.0–2.5	0.26	b	clusters	0.8–0.9	10ao	–
T. malicus (1960)	2.8	1.1	+	p	2.7–3.2	f	5ao	2.0–2.2	0.10	b	clusters	0.7–0.9	10ao	–
T. malicus (1976)	2.3–2.5	1.0	+	p	2.0–2.3	f	5ao	1.5–1.6	0.30	b	clusters	0.45–0.55	10ao	–
T. malikus (1985)	2.0	0.5	+	p	2.0	f	5ao	2.2–2.6	0.13	b	clusters	1.3–1.4	10ao	–
T. marginifolius (1909; 1931)	2.5	0.4–0.7	+	p	1.8–2.5	f	5a	2.0–2.3	0.20	b	clusters	0.8–0.9	10ao	–
T. marginifolius (1952, 1965)	1.8–2.3	0.6–1.0	+	p	1.8–2.3	f	5a	2.1–2.6	0.26	b	clusters	0.8–1.0	10ao	0.07
T. montanus (1913)	2.4	1.0	+	p	2.0–2.3	f	5ao	1.8–2.0	0.15	b	clusters	0.9–1.1	10ao	0.15
T. montanus (1953)	3.0	1.0	+	p	2.5	f	5a	1.8–2.1	0.15	b	clusters	0.9–1.1	10ao	0.06
T. montanus (1877) sub *T. regelii* (nomen)	2.2	0.5	+	p	2.0	f	5a	1.7	0.15	b	clusters	0.9–1.1	10ao	–
T. montanus subsp. *tjanschanicus*	2.5	1.0	+	g	2.5	f	5a	2.1–2.5	0.15	b	clusters	0.9–1.1	10ao	0.15
T. ruber (1934. 1986)	2.5	1.0	–	p	2.5	f	5a	1.8–2.2	0.3	b	clusters	0.8–0.95	10ao	–
Group VIII														
T. colchicus	1.1–1.3	0.2	+	p	0.8–1.1	w	r	1.5–1.7	–	b	radial	0.4–0.5	5a (10a)	–
T. filifolius	1.2	0.3	+	p	1.0–1.4	w	r	1.45–1.7	0.13	s	radial	0.5	10ao	–
T. gracilis (1901, 1944)	1.6–2.0	0.4-0.6	+	p	1.3-1.6	w	r	1.1-1.4	0.2	s	radial	0.3-0.4	5a, 10a	–
T. gracilis (1935)	1.3-1.4	0.3	+	p	1.5–1.7	w	r	1.8–1.9	0.15	s	tendency to clustering	0.8–0.9	5a, 10a	0.1
T. graminifolius (1925)	1.5	0.5	+	p	1.5–1.7	w	r	1.05–1.2	0.15	s	radial	0.35-0.55	5a	–
T. graminifolius (1936)	1.2–1.5	0.3–0.4	+	p	1.0–1.2	w	r	1.3	0.1	b	radial	0.4	5a	–

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1 ‘If the achene has a 5-angled shape, the diameter is measured including the ribs (maximal diameter) and in the furrows (minimal diameter)

TABLE 2. (Continued)

Species	Achene length (cm), without pappus	Beak length as proportion of total achene length	Thickening at the beak apex	Annulus	Pappus length (cm)	Colour of pappus	Shape of the central portion of the body in cross-section	Diameter of the body, mm (sxcept tongue-shaped appendages)[1]	Length of appendages in the body (maximum, mm)	Air cavities	**Mechanical elements in the parenchyma**	**Diameter of the beak or the achene apex (if beak not present), mm**	**Beak in cross-section**	**Outgrowths on the beak (or achene apex), mm (maximum)**
T. graminifolius (1970)	1.5	0.5	+	p	1.5–1.8	w	r	1.4–1.6	0.2	s	radial	0.65	10ao	–
T. pusillus	1.5	0.3	+	p	2.0	w	r	1.5–1.6	0.15	b	radial	0.4–0.55	10a	–
T. reticulatus	1.5–1.7	0.5–0.6	+	p	1.5–1.7	w	r	1.5–1.7	0.4	s	not visible	0.5–0.7	10ao	0.15
T. subalpinus	1.0	0.5–0.7	+	p	1.5–1.7	w	r	1.2–1.4	0.13	s	radial	0.25–0.35	10a	–
Group of species/specimens of unclear position														
T. acanthocarpus (1974)	2.6	1.1–1.3	+	p	2.7–3.0	wf	5a	1.8–2.1	0.35	b	radial	0.65–0.8	10ac	–
T. collinus (1957)	1.6	0.2–0.3	–	g	1.5–2.0	w	5a	1.6–1.8	0.20	b	not visible	0.9–1.0	10ao	–
T. buphthalmoides var. *humilis*	2.6	1.0		p	2.0	w	5a	1.7–1.9	0.15	b	radial	0.4–0.55	10a	–
T. caricifolius	2.2–2.4	0.7	–	p	2.5–2.7	w	5a	2.0–2.2	0.25	b	clusters	0.8–0.9	10ao	–
T. coloratus (1957)	2.4–3.0	0.8-1.0	+	p	2.8–3.0	f	5a	1.6–2.0	0.3	b	clusters	0.9–1.5	10ao	0.13
T. coloratus (1967)	2.5	0.6	+	p	2.2–2.7	f	5a	1.6–1.9	0.3	b	clusters	0.5–0.65	5a	0.20
T. gaudanicus	1.7–2.2	0.2–0.6	+	p	2.2–2.7	f	5a	1.7–2.2	0.20	b	radial	0.7–0.9	10ao	0.2
T. graminifolius (1963)	1.5	0.3–0.4	+	p	1.5–2.0	w	5ao	1.7–2.0	0.2	b	radial	1.0–1.2	10ao	0.2
T. marginatus	1.8	0.4–0.5	–	p	2.2–2.5	w	5ao	1.4–1.5	0.15	b	not visible	0.9–1.0	10ao	–
T. maturatus	2.5	1.0	+	p	1.8–2.2	w	r	1.35–1.6	0.13	b	clusters	0.5–0.65	10ao	–
T. porrifolius (1895)	3.7–4.5	1.7–2.3	+	p	3.0	w	r	1.5–1.6	0.2	b	radial	0.8–0.9	10ao	–
T. pseudomajor (1915)	2.2–2.5	0.7–1.0	+	p	2.5–3.0	w	5a	1.7–1.9	0.15	b	clusters	0.7–0.9	10ao	–
T. pseudomajor (1964)	3.1	1.3	+	p	2.5–3.0	w	5a	2.2–2.4	0.24	b	clusters	0.9	10ao	–
T. pterocarpus	3.5	2.0	–	p	2.5–3.0	w	5a	2.6–2.8	0.2	b	clusters	0.7–0.9	10ao	–
T. serawschanicus (1908)	3.0	1.2	+	p	3.0–3.5	w	5a	2.3–2.5	0.1	b	clusters	0.9–1.1	10ao	–
Geropogon														
Geropogon hybridus (outer achenes)	5.0	3.0	–	g	0.3–1.2 (awns)	–	r	2.0	–	s	radial	0.5–0.65	r	–
G. hybridus (inner achenes)	3.2	1.3	–	g	2.2	w	r	1.0–1.2	0.1	s	radial	0.3	r	–

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1 ‘If the achene has a 5-angled shape, the diameter is measured including the ribs (maximal diameter) and in the furrows (minimal diameter)

Carpological variability in the outer achenes

This study has identified 14 characters useful in describing the morphology and anatomy of the outer achenes in *Tragopogon* (Table 2). The most informative parts of the achene in respect of the carpological investigation include the central part of the seed-containing body and the beak. The most indicative characters of the groups are mostly qualitative traits: (1) colour of the pappus, (2) shape of the central part of the body in cross-section, (3) shape of mechanical elements in the parenchyma, and (4) shape of the beak. Some quantitative characters such as diameter of the body or presence of outgrowths on the beak may be used to distinguish between species. *Geropogon hybridus* is also included in Table 2 for comparison.

Discussion

Carpological differences within one species and their possible causes

Our data show that many species (e.g. *T. capitatus*, *T. collinus*, *T. dubius*, *T. dubjanskyi*, *T. gracilis*, *T. graminifolius*, *T. orientalis*, *T. paradoxus*, *T. porrifolius*, *T. pratensis*, *T. pseudomajor*, *T. serawschanicus*) may be characterized by a wide range of carpological character states, especially with respect to achene diameter and beak outline in cross-section. These differences are especially noticeable in specimens from geographically distant regions (e.g. West or East Europe; Pamir or Tien-Shan). This variability is not evaluated taxonomically in the present article due to the lack of extensive studies of other morphological characters that might be involved in future taxonomic revisions. However, DNA sequences from leaf fragments obtained from the same specimens that were included in the present study reflect the presence of cryptic species with diverse systematic position, especially in *T. porrifolius*, *T. capitatus*, *T. dubius* or *T. pseudomajor* aggregates (Mavrodiev *et al*. 2007, 2012; E.V. Mavrodiev, pers. comm.). The differences in body diameters of outer achenes or (in some cases) in beak outlines in cross-section may appear to be taxonomically significant in future taxonomic studies of these aggregates, but the extremely limited number of specimens is insufficient to trace possible diagnostic characters and variability of such cryptic species.

The major morphological groups in Tragopogon and their correlation with the existing molecular phylogeny

In the last decade extensive molecular investigations have shown that *Tragopogon* appears to be monophyletic, but the subdivision of the genus based on different markers is still not congruent. In one of the first comprehensive trees based on ITS+ETS markers, the clades were named in accordance with the existing morphological subdivision (Mavrodiev *et al.* 2005), and the composition of some clades roughly corresponded with the sectional circumscription based on morphology (e.g. Borisova 1964), with positional amendments of critical taxa like *T. krascheninnikovii* or *T. coelesyriacus*. One of the most important results was that corolla colour differences are not supported as a diagnostic character at the rank of section.

The latest trees based on seven loci involve splitting the genus into several large clades, and many species represented by 3–4 samples are clearly non-monophyletic (Mavrodiev *et al.* 2012). However, the relationships among some sections and their circumscriptions are still unresolved (Bell *et al*. 2012), and the species investigated here were united into nominal groups to demonstrate the diversity of carpological traits within the genus and comparision with the existing molecular phylogeny.

Group I comprises *T. borysthenicus*, *T. daghestanicus*, *T. dasyrhynchus*, *T. dubjanskyi*, *T. podolicus*, *T. undulatus*, *T. scoparius*, *T. sindicus* (nomen nudum), *T. tanaiticus* and *T. ucrainicus*. The achenes of these taxa are up to 1.5(2) cm long, with a short or indistinct beak; pappus dirty-white; annulus slightly hairy. In cross-section the outer-achene bodies are rounded or slightly 5-angled, small in diameter (1.0–1.6 mm), with radially located mechanical elements in the pericarp parenchyma and with mostly small or barely visible air cavities. The beaks have obtuse outlines and are often covered with tongue-shaped ornamentation. *Tragopogon sabulosus*, which is close to this group, possesses larger achenes with a thickened annulus and a larger body diameter.

This group of biennial herbs with yellow flowers, distributed in the steppes of Eurasia including the Black Sea area (Regel 1955), is united into the clade 'Brevirostres' (Mavrodiev *et al.* 2005) and is in the large 'Clade I' sensu Mavrodiev *et al*. (2012).

Group II includes *T. angustissimus* and *T. vvedenskyi*. Achenes ca. 2 cm long, beak 1/3–1/4 of the body length, apex with a club-shaped tip and a hairy annulus; pappus dirty white in the lower half and yellowish in the upper part. In cross-section the outer-achene bodies are obtusely 5-angled, 1.4–1.6 mm in diameter, with medium-sized air cavities and clusters of sclerenchyma fibres in the parenchyma zone; beak 0.5–0.7 mm in diameter, with obtuse margins. The most indicative attributes of this group are (1) reddish achenes; (2) pappus yellowish in its upper part, and also (3) presence of clusters of mechanical elements in the parenchyma, which is unusual for the relatively small and rounded achene body.

The two species are usually synonymized (Borisova 1964, Li 1993); however, Mavrodiev *et al.* (2012) prefer to maintain the specific rank of *T. angustissimus*. Both these closely related species are in 'Clade E'.

Group III (*T. afghanicus*, *T. altaicus*, *T. badachschanicus*, *T. capitatus*, *T. cretaceus*, *T. dubius*, *T. kemulariae*, *T. kindingeri*, *T. krascheninnikovii*, *T. macrocephalus, T. orientalis*, *T. pratensis*, *T. pseudomajor*, *T. samaritani*, *T. serawschanicus, T. sinuatus*, *T. songoricus, T. tommasinii*, *T. trachycarpus*, *T. turkestanicus*) unites the species with large achenes (3–4 cm long) thickened at the top; bodies rounded or obtuse 5-angled; beak well-developed, equaling to or even being longer than the body, sharply angled, thin, 0.3–0.5 mm in diameter; annulus long-haired; pappus dirty-white; mechanical elements in the pericarp parenchyma radial, rarely tending to clustering. The two specimens of *T. coelesyriacus* differ in the body diameter.

Group III unites species of the 'Majores' clade (Mavrodiev *et al.* 2005) with variably colored (yellow and mauve) flowers, but the species represented by many samples in the recent analysis (Mavrodiev *et al.* 2012) were non-monophyletic.

Group IV (*T. paradoxus*). Achenes large (4.3–5.3 cm long); body 5-angled, very large in diameter (2.3–2.7 mm), with radially arranged mechanical elements in the pericarp parenchyma. Beak thick, 0.7–0.9 mm in diameter, apically inflated, with obtuse outlines; pappus dirty-white. This biennial species with yellow flowers appears to be non-monophyletic in the molecular trees.

Group V (*T. australis*). Achene length 4–5.2 cm; body rounded, 1.4–1.7 mm in diameter; beak well-developed, obtuse 5-angled, with apical thickening; annulus pubescent; pappus dirty-white. Carpologically, *T. australis* is closely related to one of the samples of *T. porrifolius* collected in Hercegovina.

Tragopogon australis (biennial herb with mauve flowers) is in 'Clade B' sensu Mavrodiev *et al.* (2012), but its exact position is not yet resolved.

Group VI (*T. albinervis*, *T. bornmuelleri*). The achenes are sharply angled with unequal or equal ribs; maximal body diameter ca. 1 mm, with clusters of mechanical elements in the parenchyma; beak short, thick, with obtuse angles, without apical thickening. These species with yellowish flowers are distributed in East Turkey (*T. albinervis*), Iraqi Kurdistan and W Iran (*T. bornmuelleri*).

In the molecular trees (Mavrodiev *et al.* 2012), almost all specimens investigated are closely related and are in 'Clade F'.

Group VII (*T. collinus*, *T. conduplicatus*, *T. elongatus*, *T. karatavicus*, *T. kasachstanicus*, *T. kultiassovii*, *T. malicus*, *T. marginifolius*, *T. montanus* s.l., *T. ruber*) is distinguished by whitish achenes (at least in the upper part), 1.8–3.0 cm long; body 5-angled, 1.8–2.6 mm in diameter, with large air cavities and clusters of mechanical elements in the parenchyma, gradually tapering into the obtusely 5-angled beak (ca. 1 mm in diameter) which is apically thickened (except in *T. elongatus*); pappus whitish-violet or fulvous.

This group mostly corresponds to the circumscription of the 'Collini' clade s.str. (Mavrodiev *et al.* 2005), and all its species are part of the large 'Clade F' sensu Mavrodiev *et al.* (2012). All the species are distinguished by being perennials, with peduncles not inflated apically, mauve or violet flowers and distinct achenes, and the center of their chorological diversity is mostly associated with the western part of Central Asia (mainly the Tien-Shan and Pamir mountains), with radiation into the plains of Central and West Kazakhstan (*T. ruber* and *T. marginifolius*) and the Caucasus.

Group VIII (*T. filifolius*, *T. gracilis*, *T. graminifolius*, *T. pusillus*, *T. reticulatus*, *T. subalpinus*) is characterized by small, rounded achenes with a small beak (up to 0.7 cm) with 5- to 10-angled outlines. Morphologically these species are distinguished by being perennials with diverse flower colours (from yellow to mauve or differently colored adaxial and abaxial corolla surfaces). According to the recent molecular phylogeny (Mavrodiev *et al.* 2012), many species of this group are non-monophyletic, but some specimens of *T. filifolius*, *T. gracilis*, *T. graminifolius*, *T. subalpinus* involved in the molecular analysis belong to one clade.

Carpology of the genus Geropogon

According to the recent revision, the large tribe Cichorieae is divided into five clades (Kilian *et al.* 2009). One of them, with the subtribal rank Scorzonerinae, comprises ca. 10 genera distributed in the (semi)arid or mountainous regions of Eurasia and North Africa. One of them is the genus *Geropogon* with a single species *G. hybridus*, which is morphologically close to *Tragopogon* but differs by being annual and having a distinct pappus consisting of awns on the outer achenes (lacking in all *Tragopogon* species) and of hairy plumose outgrowths as in *Tragopogon* on the inner achenes. Such a heteromorphic pappus structure within one capitulum is evidently connected with two different modes of dispersal: anemochory as in *Tragopogon* and epizoochory (Voytenko 1989).

In previous floristic accounts *Geropogon* was considered to be a separate genus (e.g. Boissier 1875, Borisova 1964, Rechinger 1977, Meikle 1985) and was only sometimes included in *Tragopogon* (Richardson 1976, Imbert 2002). However, in recent decades, *Geropogon* has been intensively studied, and many further details in cytological, pollen or reproductive characters show additional differences between the genera (Wilson 1982, Diaz de la Guardia & Blanca 1986, 1988). According to extensive molecular studies (Mavrodiev & al. 2005, 2012), *Geropogon* is a sister clade to *Tragopogon*. The fruit anatomy of *Geropogon* was not studied in previous works, and the newly revealed differences in the fruit structure of *Geropogon* and *Tragopogon* are summarized in the Table 3.

TABLE 3. Newly established carpological differences between *Geropogon* and *Tragopogon*

Character	***Geropogon***	***Tragopogon***
Multi-celled aggregates on the fruit surface	thin, elongated (Fig. 11)	thick, tongue-shaped
Shape of the body and beak of outer achenes	rounded (Fig. 12A)	5-angled, rarely rounded
Parenchyma/ sclerenchyma ratio of inner achenes	parenchyma drastically reduced (up to 4 layers) and normally not exceeding 30 µm, thinner than sclerenchyma (Fig. 12B)	parenchyma consisting of 7 or more layers and clearly thicker than the sclerenchyma

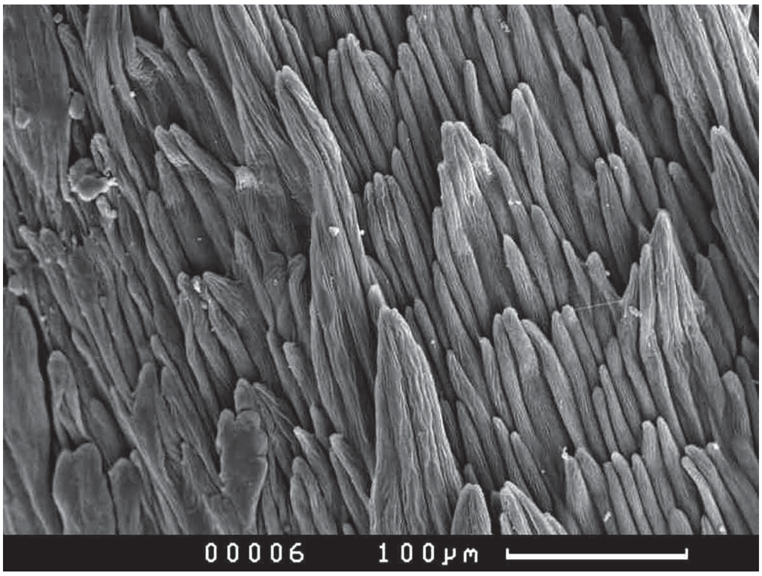

FIGURE 11. Ornamentation of outer achene body of *Geropogon hybridus*. Scale bars: 100 µm. Voucher of specimen: Morocco, 04.1989, G. Blanca & al. *39881* (dry fruits from the field).

Acknowledgements

We are grateful to Alexander Sennikov, Evgeny Mavrodiev, Norbert Kilian, Alexander Chechurov, Geoffrey Harper, Evgeny E. Makarov for useful discussion, and the herbarium staffs for permission to obtain the material for the present investigation. The study is supported by grant RFBR 14-04-01852-a (collection of the plant material and field observations) and Russian Science Foundation 14-50-00129 (carpological investigations).

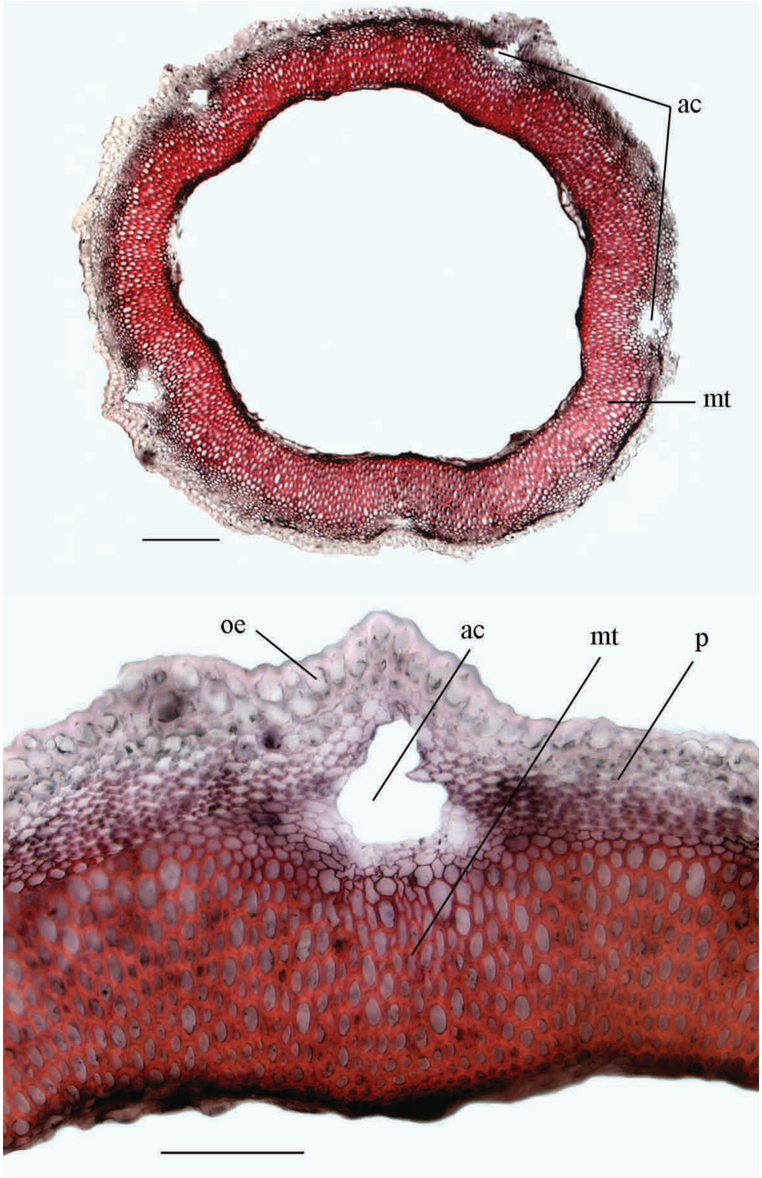

FIGURE 12. Cross section of inner achene body of *G. hybridus* (A), close-up view (B). Seed deleted. Abbreviations: ac—air cavity, mt—mechanical tissue, oe—outer epidermis, p—parenchyma. Scale bars: A—200 µm, B—100 µm. Voucher of specimens: see caption of Fig. 11.

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Appendix

Origin of materials

Tragopogon abolinii S.A. Nikitin (nomen): Tajikistan, distr. Khodjent, Mogol-tau, IV.1924, M. Popov & A. Vvedensky *10* (MW);

T. acanthocarpus Boiss.: Iran, prov. Mazandaran, Lar valley, VII.1974, P. Wendelbo & Assadi *13322* (W-05146);

T. afghanicus Rech.f. & Koie: 1) Afghanistan, Aoi Kurak, VIII.1939, W. Koelz *13798* (W-3122); 2) Afghanistan, Bamian, valley of Foladi river, VII.1974, I.A. Gubanov *et al*. *597* (MW);

T. albinervis Freyn & Sint.: Turkey, prov. Erzurum, Tortum Gol, VII.1960, Stainton & Henderson *6116* (W-07775);

T. altaicus S. A. Nikitin & Schischk.: 1) "Songaria", [anno] 1842, A. Schrenk *s.n.* (LE);

T. angustissimus S.A. Nikitin: Tajikistan, Zeravshan range, VII.1931, S.A. Nikitin *454* (MW);

T. australis Jord.: 1) Morocco, Atlas magnum, prope pag. Asni, VI.1926, H. Lindberg *s.n*. (H); 2) Spain, prov. de Jaén, VI.1952, H. Roivainen *s.n.* (H);

T. badachschanicus Boriss.: 1) Badakhshan, between Khory & Osh, IX.1955, S.S. Ikonnikov *5101* (LE); 2) [Tajikistan] Kaindy river, Suyak-Mazar, VIII.1958, N.N. Tzvelev *1473* (LE); 3) Tajikistan, Alay range, Kichik-Karamyk valley, VIII.1976, G.M. Ladygina, S.S. Ikonnikov *1884* (LE);

T. bornmuelleri Ownbey & Rech.f.: Iraq, distr. Mosul, VII.1957, K.H. Rechinger *12028a* (W-19532);

T. borysthenicus Artemczuk: 1) Ukraine, Aleshki, VI.1909, V. Transhel *s.n.* (LE); 2) Ukraine, Dzharylagach, VIII.1923, S.A. Dzevanovsky *s.n.* (LE);

T. buphthalmoides var. *humilis*: Syria, Mt. Hermon, Ein Jinna, VII.1924, A. Eig *s.n.* (HUJ);

T. capitatus S. A. Nikitin: 1) [Kazakhstan] near Verny (Almaty), VI.1893, I. Killoman *s.n.* (LE); 2) Kazakhstan, distr. Atbasar, VI.1914, I. M. Krascheninnikov *5339* (LE); 3) Kirghizia, valley of Ala-archa river, VII.1989, T. Ostroumova *7* (MW);

T. caricifolius Boiss.: Iran, Tehran, Mt. Elburz, V.1975, K.H. Rechinger *52121* (W-01363);

T. coelesyriacus Boiss.: 1) [Israel] Mt. Carmel, IV.1925, E. Smoly *s.n.* (HUJ); 2) Israel, Judaean Mts., Qiryat Anavim, V.1954, I. Amdursky *s.n.* (HUJ); 3) Israel, Jerusalem, V.2012, A. Sukhorukov *s.n.* (MW);

T. colchicus Albov ex Grossh.: [Russia] Caucasus protected area, VIII.1930, A. I. Leskov *546* (LE);

T. collinus DC.: 1) Azerbaijan, Nakhichevan, Karabaglar, VI.1957, N.N. Tzvelev & S.K. Cherepanov *180* (LE); 2) Israel, C. Negev, Nahal Nitzana, V.1967, A. Danin *s.n.* (HUJ);

T. coloratus C.A.Mey.: 1) Armenia, distr. Kafansky, Chekhi river, VII.1957, V. Alper *962* (MW); 2) Turkey, Erzurum, Kop Dagh, VIII.1967, K.H. Rechinger *37700* (W-*5785*);

T. conduplicatus S.A. Nikitin: 1) Uzbekistan, Fergana distr., V.1913, G.I. Dolenko *583* (LE); 2) Kirghizia, Khizyr-Chashma river, VIII.1931, S.A. Nikitin *1360* (LE);

T. crantzii Dichtl: [Russia] Moscow, VIII.1925, M. Nazarov *9838* (MW);

T. cretaceus S.A. Nikitin*:* 1) [Russia] Zhiguli, K. Florenskaya *s.n.* (MW); 2) [Russia] Mordovia Rep., distr. Bolsheberesnikovsky, VIII.1968, K.G. Malyutin *s.n.* (MW); 3) [Russia] Ulyanovsk prov., Novaya Bekshanka vill., V.1970, K.G. Malyutin *s.n.* (MW); 4) Ulyanovsk prov., Nikolaevsky distr., Praskovino, VI.1991, S. Polevova *et al. 89* (MW);

T. daghestanicus (Artemczuk) Kuth.: [Russia], Daghestan, distr. Buynaksk, Manas-aul, A. Radzhi *5947* (LE);

T. dasyrhynchus Artemczuk: Russia, prov. Tambov, Kirsanov, VIII.1995, A. Sukhorukov *s.n.* (MW);

T. dubius Scop.: 1) [Ukraine] Odessa, VI.1825, anonym *s.n.* (MW); 2) West Kazakhstan, prov. Aktyubinsk, Uil, VI.1965, G.I. Cherkasova *s.n.* (MW); 3) Armenia, distr. Sevan, Tsovagukh village, VII.1965, Sh. Aslanyan *et al*. *s.n.* (LE); 4) Kalmykia, Iki-Burul distr., VI.2001, M.A. Novikova *s.n.* (MW); 5) Russia, prov. Tambov, distr. Umyot, Sergievka, VI.2008, A. Sukhorukov *s.n.* (MW);

T. dubjanskyi Krasch. & S.A. Nikitin: 1) West-Kazakhstan, near Kara-tube, VII.1928, S.A. Nikitin *888* (LE); 2) West Kazakhstan, Ak-kum, VIII.1935, Z. Akaemova & T. Poyarkova *s.n.* (LE); 3) Kazakhstan, Ural-Emba area, Kara-Agach, VII.1936, M. Deulina *s.n.* (LE);

T. elongatus S.A. Nikitin: 1) Eastern Kazakhstan, VIII.1838, anonym *339* (LE); 2) Eastern Kazakhstan, Zaisan lake, Orta-Terekty, VI.1903, V. Reznichenko *s.n.* (LE);

T. filifolius Rehmann ex Boiss.: South Osetiya, Ermani, 2000 m, VIII.1935, E. & N. Bush *s.n.* (LE);

T. gaudanicus Boriss.: Turkmenistan, Kopet-Dag, Dushak Mt., VI.1961, V.V. Nikitin *s.n.* (LE);

T. gracilis D. Don: 1) [Kirghizia] Alay range, Ak-Basaga, VIII.1901, B. Fedchenko *s.n.* (LE); 2) [Tajikistan] West Pamir, VIII.1935, P.N. Ovchinnikov & K.S. Afanasyev *1940* (LE); 3) Kirghizia, Kapka, IX.1944, E. M. Iljina *103* (LE);

T. graminifolius DC.: 1) Turkmenistan, Sumbar river, Koyne-Kyasyr, VI.1925, V. Kutyeva, N. Androsov *s.n.* (MW); 2) Turkmenistan, Kopet-Dag, 1936, O.A. Enden *s.n.* (LE); 3) Turkmenistan, Central Kopet-Dag, V.1963, Gubanov & Mesheryakov *381* (LE); 4) Georgia, Lelovani, VII.1970, Yu.L. Menitsky *s.n.* (LE);

T. karatavicus N. Pavl.: Kazakhstan, Kainar-kul, V.1939, N.V. Pavlov *139* (MW);

T. kasachstanicus S.A. Nikitin: 1) [Eastern Kazakhstan] Ayaghuz, [sensu anno] ex herb. C.F. Ledebour *580.15* (LE); 2) [Kazakhstan] Turgay distr., Irghiz, V.1904, V. Dubjansky *235* (LE); 3) Kazakhstan, Zaisan, V.1914, B.K. Shishkin *s.n.* (LE);

T. kemulariae Kuth.: 1) Armenia, Erevan, VI.1968, T. Popova *s.n.* (LE); 2) Georgia, Tbilisi, VI.1969, Yu.L. Menitsky *s.n.* (LE); 3) Iran, W Azerbaijan, Zehzad & Siami *3377a* (W-05176); 4) Armenia, distr. Kamo, VII.1984, E.A. Nazarova *s.n.* (W-01314);

T. kindingeri Adamov: Macedonia, inter Krucje & Kosel, VI.1955, K.H. Rechinger *15909* (W-6362);

T. krascheninnikovii S.A. Nikitin: 1) [Uzbekistan] distr. Andizhan, Arslanbob, V.1916, V. I. Lipsky *445* (LE); 2) Turkmenistan, Kopet-Dag, 1936, O.A. Enden *s.n.* (LE); 3) Tajikistan, Pamiro-Alai, Stalinabad [Dushanbe], V.1943, Yu. Grigoriev *137* (LE); 4) Armenia, Erevan, VI.1948, S. Kuthatheladze *s.n.* (LE); 5) Uzbekistan, between Sherabad & Guzar, V.1977, V.P. Bochantsev *284* (LE);

T. kultiassovii Popov: Kirghizia, Alay range, Langar, VI.1901, B. Fedchenko *s.n.* (LE);

T. macrocephalus S.A. Nikitin & Zak. (nomen): 1) Uzbekistan, Bukhara, Kafirnigan-darya valley, V.1897, S. Korzhinsky *443* (LE); 2) [Tajikistan] Zeravshan range, VII.1931, S.A. Nikitin *15* (MW); 3) [Tajikistan] Farab-say, VII.1931, S.A. Nikitin *225* (MW);

T. malikus S.A. Nikitin: 1) Uzbekistan, prov. Samarkand, Alay-say, V.1960, N. Zaprometov & S. Niyarov *75* (LE); 2) [Kirghizia] West Tian-Shan, Talas range, Orto-Tokoy, VI.1976, Kluykov *et al. 748* (MW); 3) Kirghizia, prov. Osh, Susamyr range, Torkent river, VII.1985, Kluykov *61* (MW)

T. marginatus Boiss. & Buhse: Azerbaijan, Nakhichevan, V.1932, T. Heideman *s.n.* (LE);

T. marginifolius N. Pavl.: 1) [Russia] prov. Astrakhan, Baskunchak, V.1909, V. Artsimovich *s.n.* (LE); 2) [Kazakhstan] Karatau, Saya-su, VI.1931, N.V. Pavlov *312* sub *T. marginatus* N. Pavl. nom. inval. (MW; typus); 3) [Kazakhstan] Kara-tau, Byr-Isek river valley, V.1952, N. Parfentyeva *s.n.* (MW); 4) Kazakhstan, prov. Aktyubinsk, Uil, VI.1965, G.I. Cherkasova *s.n.* (MW);

T. maturatus Boriss.: Turkmenistan, Kopet-Dag, Kara-Kala, VI.1931, I.A. Linchevsky *192* (LE);

T. montanus S.A. Nikitin: 1) [China] Kuldzha, V.1877, A. Regel *s.n.* (LE, sub *T. regelii* S. A. Nikitin, nomen); 2) [Uzbekistan] prov. Fergana, distr. Kokand, IV.1913, Z. Minkvits *s.n.* (LE); 3) Kazakhstan, Zailiysky Alatau, Syugaty, V.1953, V.P. Goloskokov *s.n.* (LE);

T. montanus subsp. *tjanschanicus* S. A. Nikitin: Kirghizia, Kara-Archa, VI.1931, G.I. Igolkin *274* (LE);

T. orientalis L.: 1) Kazakhstan, prov. Pavlodar, Yamyshevo, VII.1941, N.V. Pavlov *4* (MW); 2) [Russia] Mordovia, Gart, VIII.1968, K. G. Malyutin *s.n.* (MW);

T. paradoxus S.A. Nikitin: 1) Tajikistan, Vakhsh range, VII.1932, N. Goncharov *et al 711* (LE); 2) Tajikistan, Parkharsky distr., Kara-Agach, VII.1953, I.A. Linchevsky & T.I. Maslennikova *251* (LE); 3) Uzbekistan, Babatag Mts., V.1977, V.P. Bochantsev *351* (LE);

T. podolicus Besser ex DC.: 1) Russia, prov. Voronezh, Divnogorye, VII.1989, V.N. Tikhomirov & al. *s.n.* (MW); 2) Russia, prov. Tambov, Novoye Depo, VII.2000, A. Sukhorukov *s.n.* (MW);

T. porrifolius L.: 1) Hercegovina, Mostar, VI.1895, H. Raap *104* (H); 2) Turkey, Tekirdag, Sarköy, V.1990, R. Lampinen *7327* (H);

T. pratensis L.: 1) Russia, Kaluga prov., Satino, VII.1975, I. Podobedov & L. Lobanova *s.n.* (MW); 2) Finland, Mellilä, VI.1995, U. Nummela-Salo & P. Salo *1588* (H); 3) England, Surrey, Richmond, VI.2003, A. Seryogin *E-40* (MW); 4) Russia, Tver prov., Torzhok, VIII.2007, Yu.E. Alexeev *s.n*. (MW);

T. pseudomajor S.A. Nikitin: 1) [China] Kuldscha, V.1877, A. Regel *s.n.* (LE); 2) [Uzbekistan] prov. Samarkand, Shakhristan, VIII.1907, anonym *278* (LE); 3) Kazakhstan, Tarbagatay range, Keldy-Murat river, VI.1915, V. Sapozhnikov & T. Tripolitov *s.n.* (LE); 4) Kyrghyzstan, Pishpek, VI.1916, M. Sovetkina & S. Chausova *1355* (LE); 5) Kyrghyzstan, Ala-too river, VI.1964, Nikitina & Sudnitsyna *510* (LE);

T. pterocarpus DC.: Iran, prov. Kazvin, Keredj, VI.1974, Gauba *1474* (W-05266);

T. pusillus M.Bieb.: Crimea, Planerskoe, V.1978, N.K. Shvedchikova s.n. (MW);

T. reticulatus Boiss. & A. Huet: [Russia] Daghestan, VII.1970, A. Gadzhiomarov *s.n*. (MW);

T. ruber S.G. Gmel.: 1) Kazakhstan, Dau-tau, VII.1934, M. Khomutova *s.n*. (MW); 2) Kazakhstan, Akshatau, VI.1986, V.I. Grubov *et al*. *47* (LE);

T. sabulosus Krasch. & S.A. Nikitin: 1) Kazakhstan, Sary-su, V.1914, N. Krasheninnikov *s.n.* (LE); 2) West Mongolia, Cherny Irtysh river, VI.1914, B. Shishkin *s.n.* (LE); 3) Kazakhstan, prov. Aktyubinsk, Irghiz, VI.1976, R.V. Kamelin *et al*. *5746* (LE);

T. samaritani Heldr. & Sart.: Greece, Attika, Mt. Pentelikon, V.1976, T. Pichler *s.n*. (LE);

T. scoparius S.A. Nikitin: 1) Kazakhstan, Kolpakovskoye, IX.1930, L.E. Rodin *702* (MW); 2) Kazakhstan, Dshungarsky Alatau, Ush-Kain, VII.1934, S.A. Nikitin *s.n.* (LE);

T. serawschanicus S.A. Nikitin: 1) Uzbekistan, prov. Samarkand, V.1908, Fedotov & Golbek (LE) *s.n*.; 2) Uzbekistan, Yagnob river, VIII.1931, S.A. Nikitin *1331* (LE);

T. sindicus Chechurov (nomen): 1) [Russia] NW Caucasus, Spokoynaya settlement, VII.1946, E. Shiffers *s.n*. (LE); 2) [Russia] prov. Krasnodar, distr. Mostovskoy, Psebay, VII.1990, Yu.L. Menitsky *et al. 15-1* (LE);

T. sinuatus Avé-Lall.: Cyprus, Aya Napa, IV.2006, A. Seryogin & I. Privalova *A-819* (MW);

T. songoricus S.A. Nikitin: 1) Kazakhstan, Dshungarian Alatau, Lepsy, VIII.1934, S.A. Nikitin *50* (LE); 2) Kazakhstan, Dshungarian Alatau, Kshi-Argaly, VIII.1934, S. Nikitin *7449* (MW); 3) Kazakhstan, Dshungarian Alatau, between Lepsy & Tentek, VIII.1934, S.A. Nikitin *1307* (LE); 4) Mongolia, Dshungaria, Baytag-Bog-Do, VIII.1988, I.A. Gubanov *et al. 2632* (MW);

T. subalpinus S.A. Nikitin: Kirghisia, Atbashi, VII.1973, G.M. Ladygina, S.S. Ikonnikov *13219* (LE);

T. tanaiticus Artemczuk: 1) Russia, prov. Voronezh, distr. Petropavlovka, Dedovka, VII.1986, V.N. Tikhomirov *et al. s.n*. (MW); 2) Russia, prov. Tambov, Michurinsk, as alien, VI.2004, A. Sukhorukov & S. Kolesnikov *s.n.* (MW);

T. tommasinii Sch. Bip.: [Italia] Mt. Spaccato, [sensu anno] Kammerer *3400* (MW);

T. trachycarpus S.A. Nikitin: 1) Mongolia, Tsagan-Khairkhan, VIII.1982, I.A. Gubanov *et al*. s.n. (MW); 2) Mongolia, Selengynsky aimak, VIII.1985, I.A. Gubanov *9748* (MW);

T. turkestanicus: S.A. Nikitin: 1) Kazakhstan, Talas Alatau, VIII.1931, N.V. Pavlov *959* (MW, typus); 2) Kazakhstan, Almaty, Medeo, VI.1936, N.V. Pavlov *167* (MW); 3) [Kazakhstan] Tersky Alatau, Tuzkul lake, VI.1950, L.I. Medvedeva *et al*. *252* (LE);

T. ucrainicus Aretemczuk: Russia, prov. Tambov, Muchkap, VIII.2005, A. Sukhorukov *s.n.* (MW);

T. undulatus Jacq.: Crimea, Sevastopol, VIII.2002, V. Nikiforova & A. Belov *s.n.* (MW);

T. vvedenskyi Popov: 1) [Kazakhstan] Karatau, Bukut-tau, VI.1931, N.V. Pavlov *424* (MW, syntypus); 2) Turkmenistan, Central Kopet-Dag, Prokhladnoye, VI.1969, A.A. Mescheryakov *s.n.* (H); 3) Tajikistan, Turkestan range, Ayni, VII.1976, G.M. Ladygina & S.S. Ikonnikov *541* (LE);

Geropogon hybridus (L.) Sch. Bip.: 1) [Portugal] prov. Estremadura, 1848, Welwitsch *s.n.* (LE); 2) Spain, prov. De Malaga, San Julian, V.1952, Y. Roivainen *s.n.* (H); 3) Morocco, IV.1989, G. Blanca *et al. 39881* (dry fruits from the field).