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Fruit anatomy of the genus *Anabasis* (Salsoloideae, Chenopodiaceae)

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Abstract. The fruit anatomy and morphology of 22 representatives of the genus *Anabasis* L. were studied, with the aim of clarifying the taxomomic importance of carpological characters in the genus. As shown in cross-sections, the pericarp of *Anabasis* is differentiated into the following four zones: (i) outer epidermis, (ii) subepidermal hydrated parenchyma, (iii) crystalliferous layer with lignified U-shaped cell walls and (iv) inner epidermis. Anatomical differences mainly relate to the outer epidermal structure. Fruit anatomy does not confirm the separation of the genera *Brachylepis* and *Esfandiaria*. A combination of carpological characteristics separates *A. annua* and *A. setifera* from the other species studied. Also, characters of reproductive organs in representatives of *Anabasis* are shown. When vegetative and reproductive features are considered, the genus *Fredolia* appears rather distant from *Anabasis s.l.* The pericarp histology of almost all the Salsoloideae (incl. *Anabasis*) is fully presented in the upper third of the fruit. In the lower parts of the fruit, some histological layers are either reduced or absent altogether. On the basis of the anatomical structures in the upper third of the fruit, the common carpological features of the Salsoloideae can be defined. These include a pericarp consisting of several, usually well-differentiated layers and the presence of crystalliferous cells with U-shaped walls. The two- to four-cell layered outer epidermis of three *Anabasis* representatives (*A. eriopoda*, *A. jaxartica*, *A. turkestanica*) seems to be an apomorphic feature in the Salsoloideae. The seed coat is thin (two cell layers thick) and non-differentiated. Owing to the pericarp and seedcoat structure, the fruit and seed covers have low resistance to environmental degradation processes and, therefore, are unlikely to be found among fossil remnants.

Introduction

The genus *Anabasis* L. comprises ~28 species. These are distributed in North Africa and arid regions of Eurasia. Most grow in the deserts of central and western Asia. Almost all taxa are nanophanerophytes and chamaephytes, with only *A. annua* Bunge being a therophyte. The representatives of the genus are known to have fleshy annual shoots, usually with reduced or very short, subulate opposite leaves and numerous simple trichomes situated at their leaf bases. When plants have dried, or when individuals die off, annual axes readily break into their separate segments. Because of this, such plants are often called 'articulate', to emphasise this peculiarity of the genus which is also found in many members of Salicornioideae. The flowers of *Anabasis* are located on axils, are solitary or, less often, in threes, with two short bracteoles (missing only in *A. ebracteolata* Korovin ex Botsch.), and with a pentamerous perianth. Free tepals form two circles (3 + 2). At the fruiting stage, tepals of the outer circle (or of both) possess well-developed, vertically aligned wings, or the perianth completely lacks these wing-like projections. Five stamens alternate with staminodes. Fruits are subglobose or broadly ovoid, 2–6 mm in diameter and, as a rule, fleshy with diversely coloured pericarps. The ovary contains one basal ovule. Two (or very seldom three) stylodia are free or fused at the base. The embryo is vertical, contorted by two or three twists, with a sub-basal oriented radicle.

A brief overview on the limit of the genus Anabasis *on the basis of morphological and molecular studies*

The limit of *Anabasis*, as described by Linnaeus (1753), has not yet been fully defined. Meyer (1829) separated *Brachylepis* C.A.Mey. (type—*B. salsa* C.A.Mey.) on the basis of the absence of wing-shaped appendages on the perianth tepals. Some time later, the genus *Fredolia* Coss. & Durieu (Moquin-Tandon and Cosson 1862), with one representative found in the northern Sahara (*F. aretioides* Coss. et Durieu), was established. A pin-cushion habit was named as its main distinctive character. The genus *Esfandiaria* Charif et Aellen (Aellen 1952), with one Iranian species *E. calcarea* Charif et Aellen, was based on the presence of thick, rounded annual shoots, twisted inflorescences and the vertical position of the embryo in the seed.

The structure of the vegetative organs of *Esfandiaria calcarea* became the object of a detailed study (Bokhari and Wendelbo 1978). Despite certain variations in the anatomical structure of the stem, the authors of the same publication transferred *E. calcarea* to *Anabasis*, and placed *A. calcarea* (Charif et Aellen) Bokhari et Wendelbo in the monotypic section *Esfandiaria* (Charif et Aellen) Bokhari & Wendelbo. The merger of *Esfandiaria* with *Anabasis* was accepted later on the basis of both morphological (Hedge 1997) and molecular data (Akhani *et al*. 2007).

Regarding the genus *Brachylepis* C.A.Mey. (only three species), the opinions of various experts are contradictory. The authors of basic floristic and taxonomic treatments considered

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Anabasis sensu lato (Endlicher 1840; Volkens 1893; Iljin 1936; Kühn *et al*. 1993; Czerepanov 1995; Hedge 1997). However, some researchers, mostly those working in the 19th century and the first half of the 20th century (Moquin-Tandon 1840, 1849; Fenzl 1849; Bunge 1862; Ulbrich 1934; Aellen 1949; Vasilyeva 1977), admitted its general rank.

The analysis of nuclear and chloroplast data of *A. aphylla* L., *A. calcarea* (Charif et Aellen) Bokhari et Wendelbo (≡*Esfandiaria calcarea* Charif et Aellen), *A. haussknechtii* Bunge ex Boiss., *A. jaxartica* (Bunge) Benth. ex Volkens, *A. eriopoda* (Schrenk) Benth. (≡*Brachylepis eriopoda* Schrenk), *A. eugeniae* Iljin, *A. setifera* Moq., as well as that of other mainly non-articulated salsoloid representatives, shows the monophyly of the *Anabasis* clade (Akhani *et al*. 2007), excluding *A. setifera*, which was transferred into gen. *Salsola s.str.* (≡*Salsola setifera* (Moq.) Akhani).

In the present paper, *Anabasis* is preliminarily assigned *sensu lato* (incl. *Brachylepis* and *Esfandiaria* + *Anabasis setifera*).

Systematic placement of Anabasis *s.l.*

Anabasis belongs to the subfamily Salsoloideae established by Ulbrich (1934). This subfamily is generally known for the following features: usually terete or half-terete, well developed, less often reduced leaves; special (primarily 'salsoloid') leaf-structure type (Carolin *et al*. 1975) and mostly C_4 photosynthetic pathway (Winter 1981; Akhani *et al*. 1997; Jacobs 2001); lack of perisperm or possessing only traces of it; and spiral position of the embryo in the seed (Meyer 1833). However, the limit of the subfamily has been questioned (e.g. Williams and Ford-Lloyd 1974; Blackwell 1977; Scott 1977). For the first time, and on the basis of molecular evidence, Kadereit *et al*. (2003) proposed to include the tribe Camphorosmeae Moq. in Salsoloideae. These authors also suggested dividing salsoloid representatives into two groups (*Salsoleae* I and *Salsoleae* II); the differences between these are limited to plant pubescence details, cotyledon structure and C_4 biochemical subtypes.

Fruit and seed anatomy of Anabasis

The anatomy of the fruit and seed has been provided only by Butnik (1972), with *A. eriopoda* as an example, and in Butnik's paper the presence of the three- or four-layered pericarp epidermis (exocarp) is pointed out.

The research was undertaken to

(1) clarify the comparative carpology of *Anabasis* representatives;
(2) suggest new carpological traits in this genus, to help solve its systematic and taxonomic problems;
(3) compare the fruit anatomy of *Anabasis* with other Salsoloideae representatives; and
(4) detect carpological differences between Salsoloideae and other subfamilies of the Chenopodiaceae.

Materials and methods

For the present investigation, 22 species of *Anabasis* were used in a comparative carpological study. Material of some *Anabasis* and other representatives of the subfamily Salsoloideae was collected by the author in the south-east of European Russia, Kazakhstan, Uzbekistan and the eastern part of the Mediterranean area. The material was preserved in 70% ethyl alcohol. Fruits of some species were obtained from the Herbaria B, P, LE, MW, TASH (herbarium acronyms are according to Holmgren and Holmgren 1998) and subsequently soaked in a mixture of ethyl alcohol, water and glycerine (equal volumetric proportions) for 1–2 days at 30°C. For comparative carpology, the following genera of Salsoloideae *s.str.* were used: *Agathophora* Bunge, *Arthrophytum* Schrenk, *Girgensohnia* Bunge ex Fenzl, *Hammada* Iljin, *Halothamnus* Jaub. & Spach, *Haloxylon* Bunge, *Iljinia* Korovin, *Lagenantha* Chiov., *Nanophyton* Less., *Noaea* Moq., *Petrosimonia* Bunge, *Salsola* L. and *Seidlitzia* Bunge. The list of specimens investigated is given in Appendix 1. Anatomical sections were cut either by hand or with a microtome. In the latter case, fruits were dehydrated in a graded series of aqueous ethyl alcohol solutions of increasing concentration, then in an alcohol–chloroform mixture and finally in pure chloroform, according to standard procedures (Barykina *et al*. 2004). Sections were cut from the upper third of the fruits where usually all layers are fully represented. For comparison, some sections were cut also from the lower third. For tissue staining, the following solutions were used: 0.2% aqueous toluidine blue, Sudan IV and phloroglucine + HCl. To reveal crystals, sections were viewed under polarised light. The crystals showed no reaction with 3% hydrochloric acid or 40% sulfuric acid so their chemical nature was not revealed. Scanning electron microscope (SEM) observations were made with a JSM-6380 LA microscope (JEOL Ltd, Japan).

Results

Fruit structure in Anabasis *species*

No difference was found in the topology of the pericarp zones among all *Anabasis* species investigated. *A. cretacea* Pall. was chosen for the carpological description.

At the end of the growing season, *A. cretacea* is recognised as one of the most striking calciphilous plants in the steppe and semi-deserts of Asia and south-eastern Europe, owing to the presence of large yellow or reddish-yellow, vertically positioned wing-shaped appendages located on the lower part of the three tepals. Sometimes the two inner tepals can also form outgrowths; however, these are always less developed than the wings formed by the outer tepals. The perianth is half-open, which renders the fruit highly visible (Fig. 1). Immature fruits are found to have yellow or reddish-yellow pericarps, which later turn to red or carmine red and finally become brownish. Their significance for dispersal is the subject of a separate study (Sukhorukov 2009).

Fruit

In a cross-section (Fig. 2), the pericarp of the ripe fruit of *A. cretacea* is clearly differentiated into four zones. The outer epidermis consists of a single cell layer and is 30–45(50) µm thick. By the end of the vegetative period the epidermal cells accumulate a pigment which determines the fruit colour. Some cells contain minute prismatic crystals. Subepidermal layers (2–4 cells thick) are well hydrated and comprise

Fig. 1. *Anabasis cretacea* at the fruiting stage (Russia, province Saratov, Ozinki, IX–X.2006; photo A. Sukhorukov).

isodiametric or radially elongated cells with oily inclusions as spherical granules. The cell sap in the subepidermal layers is yellow. A continuous or slightly interrupted crystalliferous layer (sometimes 2 cell layers thick) is situated just beneath, with rectangular or elliptical cells having thickened, lignified anticlinal and inner periclinal walls and fine-grained crystals of uncertain nature. In a cross-section, these cells appear horse-shoe shaped (the cells having U-shaped wall thickenings), resembling the endodermal cells of the stem cortex of many plants. The inner epidermis is of one cell layer thick (7–10(20) µm) and is represented by cells with thickened walls.

Seed

The seed coat consists of two or three cell layers, being 10–25(35) µm thick, and is separated from the pericarp by a very thin outer cuticle. The seed-coat cells are compressed and usually of a light brown tint owing to the accumulation of tannin-like substances. The perisperm consists of only several peripherical cell layers, hardly noticeable to the naked eye. The embryo is well-developed, green and with a radicle of lighter colour.

No occurrence of fruit or seed dimorphism has been recorded.

Differences in fruit morphology and anatomy in the representatives of Anabasis

The fruit diameter appears to be the most important morphological trait. Small fruits (2.0–2.5 mm) are possessed by *A. annua* and *A. setifera*. The largest fruits (4.0–6.0 mm in diameter) are found only in a few taxa (*A. eriopoda*, *A. ferganica*, *A. jaxartica*, *A. turkestanica*). Fruits of the other species have intermediate dimensions (3.0–4.5 mm).

Anatomical differences relate mainly to the outer epidermal structure. It is one cell thick in almost all species. In some taxa with single-layered epidermis, papillae are found (*A. annua*, *A. articulata*, *A. brevifolia*, *A. ebracteolata*, *A. oropediorum*, *A. pelliotii*, *A. prostrata*, *A. setifera*: Figs 3, 4). Papillae are pronounced either across the entire surface of the fruit (*A. annua*, *A. brevifolia*, *A. setifera*) or are expressed more on the upper half of the fruit (all others of the above-mentioned taxa). Papillae can be cylindrical (*A. annua*, *A. brevifolia*, *A. setifera*: Fig. 4; *A. oropediorum*: Fig. 5) or conical (*A. articulata*, *A. ebracteolata*, *A. pelliotii*, *A. prostrata*: Fig. 6).

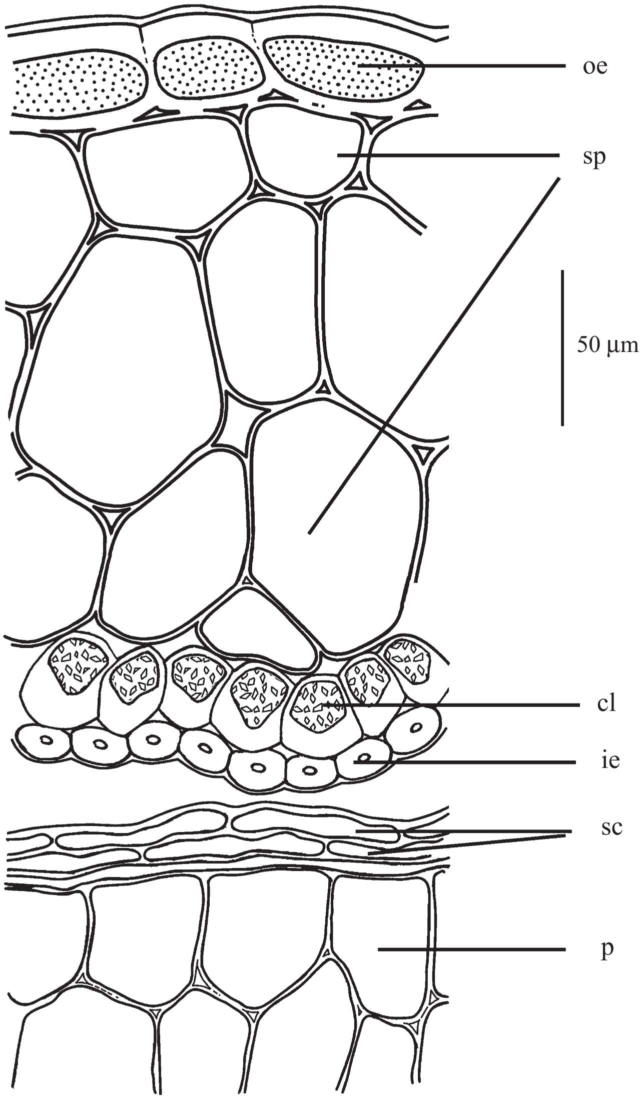

Fig. 2. A cross-section of the pericarp and seed coat of *Anabasis cretacea*. oe = outer epidermis; sp = subepidermal parenchyma; cl = crystalliferous layer; i.e. = inner epidermis; sc = seed coat; p = peripherical cells of perisperm (vestiges).

A multilayered epidermal tissue ((2)3–4 cell layers) has previously been considered a specialised trait of the fruit, characteristic of the entire genus (Butnik 1981). However, in the present study it was found in only three of the species investigated (*A. eriopoda*, *A. jaxartica*: Fig. 7 *A. turkestanica*),

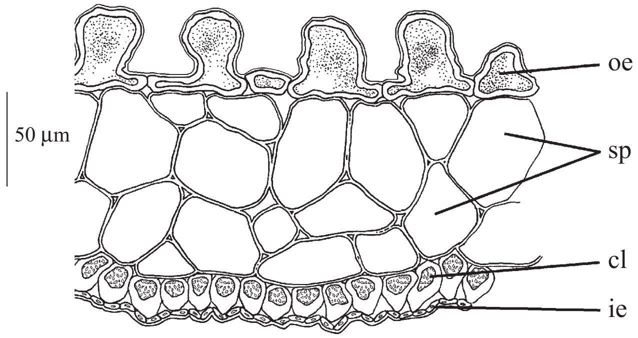

Fig. 3. A cross-section of the pericarp of *Anabasis setifera*. For abbreviations, see caption of Fig. 2.

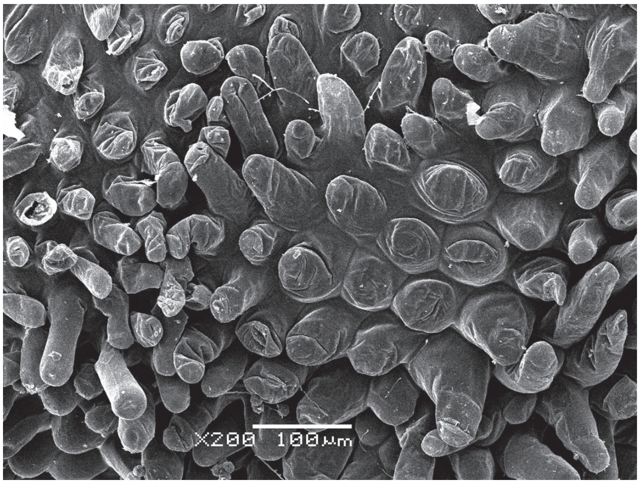

Fig. 4. Papillae on the surface of the upper pericarp of *Anabasis setifera*.

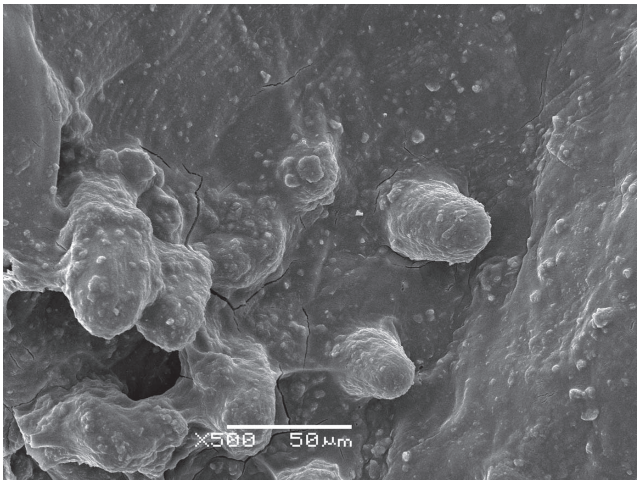

Fig. 5. Papillae on the pericarp surface of *Anabasis oropediorum*.

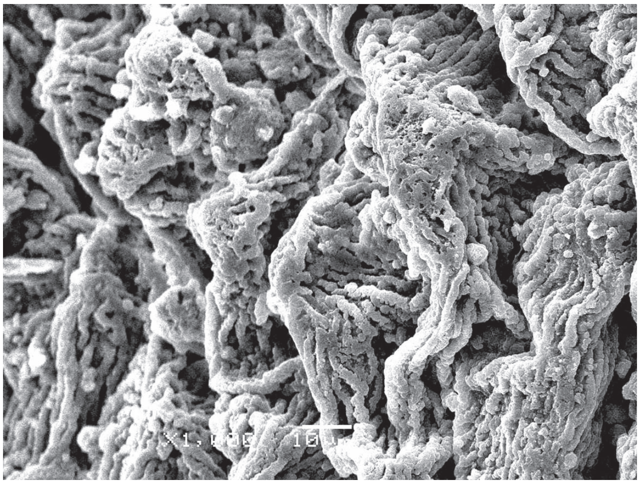

Fig. 6. Papillae on the pericarp surface of *Anabasis prostrata*.

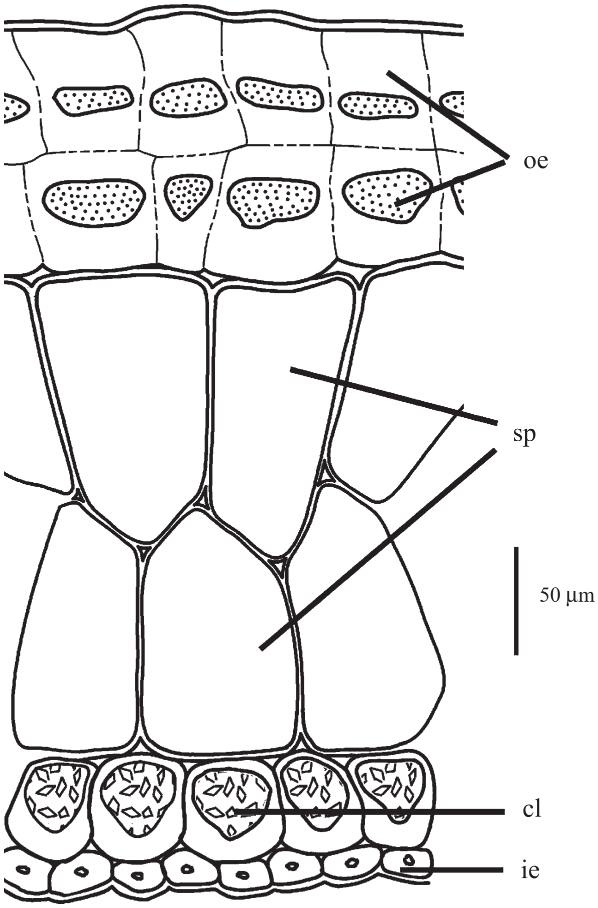

Fig. 7. Pericarp of *Anabasis jaxartica* (the upper part of the fruit). For abbreviations, see caption of Fig. 2.

and therefore is not a consistent characteristic of the genus, but rather an exception. In *A. annua* and *A. setifera*, subepidermal cell layers are generally less developed, and consequently, fruits of these two species can be called fleshy only conditionally. *A. jaxartica* can sometimes possess a two-cell-layered inner epidermis.

Anatomical differences in upper and lower parts of the fruit are well expressed in *Anabasis*. Especially in those species that have rather large fruits with a multilayered outer epidermis in the pericarp (*A. eriopoda*, *A. jaxartica* and *A. turkestanica*). These differences in the upper and lower pericarp parts show gradual transitions (Table 1 and Figs 7 and 8).

In the species with a one-cell-layered outer epidermis, the anatomical differences are also expressed in the decrease of the subepidermal hydrated layers and the omission of the crystalliferous cells. Therefore, the lower parts of the fruits cannot be considered as fleshy as the upper third. Thus, the fruits of *Anabasis* species (excluding fruits of *A. annua* and *A. setifera*) can be referred to as half-berries (semibacca).

The crystalliferous layer has not previously been reported for the Salsoloideae, perhaps because it is often not noticeable or is represented only by solitary cells in ’characteristic’ sections cut from the middle part of the fruit.

The seed-coat structure varies very little around the perimeter.

Discussion

Tentative conclusions regarding the limits of Anabasis *on the basis of morphological characters*

Brachylepis *group*

The reason for alternative taxonomic divisions between *Anabasis* and *Brachylepis* is that the discriminative features have not been sufficiently well considered. Currently, the systematics of *Anabasis* and of closely related genera is based on morphological characters alone (Moquin-Tandon and Cosson 1857; Korovin 1935 (the system of the genus *Anabasis* proposed by E. P. Korovin cannot be considered valid owing to the absence of typification and Latin description (Briquet 1935)); Iljin 1936; Pratov 1976; Vasilyeva 1977). Among these, the presence or absence of bracteoles should be mentioned, as well as the degree of leaf representation, the number of flowers in the bract axils and the presence or absence of papillae on the fruit surface. However, this limited number of traits emphasises the provisional nature of the current systems.

Along with the degree of diversity of the wing-like projections on the perianth segments, Vasilyeva (1977) added a set of distinctions between *Anabasis s.str.* and *Brachylepis* which referred to their reproductive system (the shape of stigmas, perianth : stamen length ratio and the perianth length : fruit diameter ratio). All these characteristics proposed (excluding the absence of wings) should be rejected as genus-specific. In fact, in ‘wingless’ *Anabasis* (≡gen. *Brachylepis s.str.*), the fruits are usually much longer than the non-growing perianth segments. However, the perianth enveloping the fruit in some forms of ‘winged’ *A. jaxartica* may be much shorter than the fruit itself. Furthermore, observations of *A. articulata* from Israel in December 2007 showed that the length of the stamens significantly exceeds the length of the perianth segments. The filiform stigmas can also be found in some ‘winged’ *Anabasis* representatives (e.g. *A. brevifolia*, *A. oropediorum*).

Esfandiaria

The rounded annual shoots and vertical position of the embryo in the seed mentioned by Aellen (1952) are typical characteristics of *Anabasis*. The study of herbarium samples of *Esfandiaria calcarea* in LE and B did not reveal ‘twisted inflorescences’ in this taxon. Apparently, twisting should be treated as normal structural changes in the inflorescences when they dry.

The aspects of fruit anatomy suggest a close affinity among *Brachylepis*, *Esfandiaria* and *Anabasis s.str*.

Fredolia

The fundamental features shown by Hauri (1912) and Killian (1939) suggest a segregation of *Fredolia* from *Anabasis* (Table 2). The life history and alternation in epidermal layers of the stem are apomorphies in the whole Chenopodiaceae family.

In addition to the characteristics named in Table 2, biochemical differences between the genera have also been revealed (Ramaut *et al*. 1984).

Data of Killian (1939) on the subterminal position of the radicle in the seed of *Fredolia aretioides* seem to be erroneous. Similar to that in *Anabasis*, the position of the radicle in *F. aretioides* is sub-basal.

Features of reproductive organs in representatives of Anabasis

The most important reproductive traits to be included in the future revision of *Anabasis s.l.* (including genera *Brachylepis* and *Esfandiaria*) are summarised in Table 3. The present results have highlighted some new carpological characters (i.e. fruit diameter, the number of outer-epidermal cell layers, the form of the papillae) that can be included in the systematics and diagnostics of *Anabasis* species. The most significant changes to the fruit structure, as demonstrated by *A. jaxartica*, *A. turkestanica* and *A. eriopoda* (≡*Brachylepis eriopoda*), are the increases in the number and thickness of the outer epidermal layers in the upper part of the pericarp. Even though the presence of a multilayered epidermis in the pericarp of ‘wingless’ (*Brachylepis*) and ‘winged’ *Anabasis* representatives eliminates the carpological differences between the two genera, further studies are needed to understand the phylogenetic relationship between these taxa.

The fruit colour of most species needs to be clarified because the fruits were studied before the dissemination stage.

Table 1. Differences in the structure of the upper and lower pericarp parts in *Anabasis jaxartica*

Trait	Upper fruit part (Fig. 7)	Lower fruit part (Fig. 8)
Pericarp thickness (µm)	400–550	40–80 (100)
Layer number and thickness (µm) of outer epidermis	2–4 cell layers, 75–120	1 or 2 cell layers, 25–40
Subepidermal layers	Elongated radially	Compressed tangentially
Crystalliferous layer	Well developed, mostly continuous	Missing or represented by solitary cells

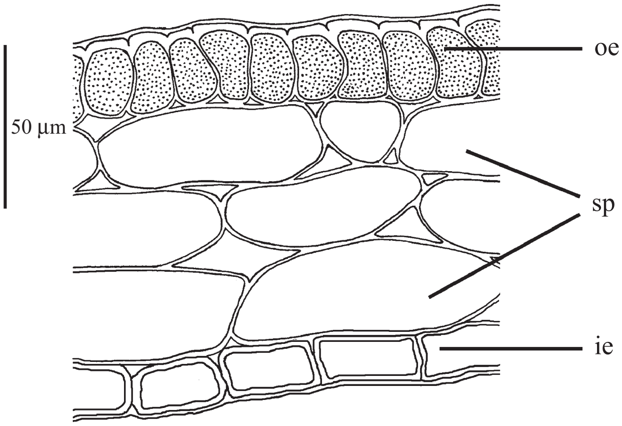

Fig. 8. Pericarp of *Anabasis jaxartica* (the lower part of the fruit). For abbreviations, see caption of Fig. 2.

The data in Table 3 lead to the following conclusions:

(1) the taxa *A. annua*–*A. setifera*, *A. jaxartica*–*A. turkestanica*–*A. eriopoda* (≡*Brachylepis eriopoda*), *A. aphylla*–*A. hausknechtii*, and *A. brachiata*–*A. calcarea* (≡*Esfandiaria calcarea*) possess the closest carpological characters;
(2) merging of *A. ferganica* with *A. jaxartica* (Kinzikayeva 1964) seems to be erroneous;
(3) the combination of reproductive characteristics sets *A. annua* and *A. setifera* apart from the other species studied;
(4) for a small fruit (length 2.2–2.8 mm), *Fredolia aretioides* possesses relatively thick outer and inner periclinal cell walls in the outer epidermis of its pericarp (20–50 μm). This is an additional character helpful in separating this genus. Such thickening of secondary cell walls is common in *Anabasis* species with fruit diameters of 3.0–6.0 mm; however, it is not observed in *A. annua* and *A. setifera* which have small fruits similar to those of *Fredolia*.

The most important morphological and anatomical characters for the future revision of the representatives of Anabasis

For detailed conclusions concerning the relationships among *Anabasis* groups and their position in the Salsoloideae system, a set of vegetative characters can also be considered along with the carpological characters. The following are of principal importance.

Life history

In *Anabasis*, the following types of life history can be distinguished: (1) nanophanerophyte, (2) unspecialised chamaephytes, (3) caudex chamaephytes and (4) therophyte (only *A. annua*).

Stem morphology and anatomy

Almost all taxa possess rounded or terete-quadrangular stems; only in *A. annua* and *A. setifera* (*Salsola setifera*) are the stems linearly striated. The annual stem and branches of several taxa are covered with papillae (*A. pelliotii*, and facultatively *A. jaxartica*) or very short tubercules (*A. oropediorum*).

The branching pattern can also be important for phylogenetic relationships. *A. cretacea* and *A. tianschanica* have a main stem only, whereas most *Anabasis* species are characterised by having annual shoots of second- or third-order branching patterns. Most branched shoots (3 or 4 order), forming a 'tumble-weed' habit, are peculiar to *A. eriopoda*, *A. jaxartica* and *A. turkestanica*.

The anatomical structure of the annual axes, in particular, the number and thickness of outer-epidermal cell layers, as well as the presence of a hypodermis, seems to be of principal importance. A large amount of data on the anatomy of the epidermis of annual axes is available (Olufsen 1912; Keller 1931; Rozhanovsky 1952; Klyshev 1961; Fahn and Dembo 1964; Tutayuk and Khalilova 1967; Voznesenskaya 1976*a*, 1976*b*; Bokhari and Wendelbo 1978; Musayeva 1979; Butnik *et al.* 1991, 2001; Barykina and Chubatova 2005; Smail-Saadoun 2005; Ghadi *et al.* 2006; A. P. Sukhorukov, unpubl. data).

Leaf representation

Only a few representatives of *Anabasis* possess well-developed leaves, including *A. abolinii*, *A. annua*, *A. brevifolia*, *A. eugeniae*, *A. pelliotii*, *A. setifera* (*Salsola setifera*) and *A. turgaica*. All other representatives have either short subulate leaves or leaves that are reduced to fleshy rims. The anatomy of the leaf is of great interest, following the excellent research of Werker and Fahn (1967) and Butnik *et al.* (2001).

Table 2. General differences in the morphology, anatomy and distribution between the genera *Anabasis s.l.* and *Fredolia*

Anabasis s.l. (incl. *Brachylepis*, *Esfandiaria*), ~28 spp.	*Fredolia*, 1 sp.
Plants are not of pin-cushion habit. The leaves are as a rule reduced to rims, short and seldom well developed; slightly connate at the base. Stem epidermis is uniform (single-layered or multilayered) over the whole surface. Flowers solitary or in threes on the axil of the bract, forming generally spike-like inflorescences. Interstaminal lobes glandular. Anthers with scarcely noticeable extension of connective tissue or connective tissue absent. Fruits are subglobose or broadly ovoid. Stylodia are free or fused at the base.	The plant is of pin-cushion habit. The leaves are well developed and connate over considerable lengths. Multilayered areas of stem epidermis alternate with single-layered areas. Flowers solitary on the axils of the uppermost leaves; spike-like inflorescences absent. Interstaminal lobes non-glandular. Anthers with extension of connective tissue. Fruits are narrowly ovoid. Stylodia are fused over greater lengths.
Distribution: central and western Asia, eastern Europe, northern Africa (Mediterranean area), southern Spain.	Distribution: northern Sahara.

Table 3. Characters of reproductive organs of the *Anabasis* representatives

Stigmas: f = filiform; r = ribbon-shaped; colour of perianth wings: w = white or yellowish; c = coloured (red or brownish). References: D = Danin (designated here), observations on 15.XII.2006 in Israel; H = Hedge (1997); I = Iljin (1936); K = Kinzikayeva (1968); M = Mahamov (designated here); P = Pratov (1972); R = Rechinger (1977); S = Sukhorukov (2002), observations on 11.IX in central Kazakhstan; Su = Sukhorukov, designated here, observationes on 3–5.XII in Israel; Z = Zhu *et al.* (2003)

No.	Taxon	Bracteoles	No. of flowers in the bract axils	Presence and number of wings on the perianth	Wing colour	Fruit diameter	Stigmas	No. of cell layers of outer epidermis	Thickness of outer epidermal tissue (μm)[†]	Papillae on the pericarp surface	Pericarp hydratation in its upper part	Fruit colour
1	*A. africana*	+	1	+ (3)	w	3.5	r	1	20–37	–	+	No voucher
2	*A. annua*	+	3	+ (5)	w	2.0–2.7	f	1	12–25	+	–	Purplish or orange (I, sub *A. micradena*)
3	*A. aphylla*	+	1	+ (3)	w	3.0–3.5	r	1	30–50	–	+	Dark red (Z)
4	*A. articulata*	+	1	+ (5)	c	3.0–4.0	r	1	13–25	+	+	Red (Su)
5	*A. brachiata*	+	1	+ (5)	c	3.0–4.0	r	1	35–65	–	+	Brown (K)
6	*A. brevifolia*	+	1	+ (5)	c	2.5–3.0	f	1	12–25	+	+	Reddish (I, sub *A. affinis*); yellow–brown (Z)
7	*A. calcarea*	+	1	+ (5)	c	3.5–4.0	r	1	25–40	–	+	Reddish-brown, purplish or orange (H)
8	*A. cretacea*	+	1	+ (3–5)	c	3.3–4.0	r	1	30–50	–	+	Red or carmine-red (d.h.)
9	*A. ebracteolata*	–	1	–	–	3.0–3.5	f	1	25–50	+	+	Yellow–brown (P); orange (S)
10	*A. elatior*	+	1	+ (3)	c	3.5–4.0	r	1	35–50 (55)	–	+	Yellow or pinky (I); yellow–brown or pink (Z)
11	*A. eriopoda*	+	1	–	–	4.0–6.0	r	3–4	75–130	–	+	Yellow or orange (I; Z); purplish, red or pale brown (R)
12	*A. ferganica*	+	1	+ (5)	c	4.0–5.0	r	1	30–45	–	+	Yellow (I)
13	*A. haussknechtii*	+	1	+ (3)	w	3.0	r	1	25–40	–	+	No voucher
14	*A. jaxartica*	+	1	+ (5)	c	4.0–6.0	r	2–3	75–120	–	+	Red (M)
15	*A. oropediorum*	+	1	+ (5)	c	2.5–3.0	f	1	25–45	+	+	No voucher
16	*A. pelliotii*	+	1	+ (5)	c	4.0–4.5	r	1	30–45	+	+	Dark (K)
17	*A. prostrata*	+	1	+ (5)	c	3.0–3.5	r	1	12–20	+	+	No voucher
18	*A. salsa*	+	1	–	–	3.0–3.5	r	1	25–45	–	+	Red (I); yellow–brown or reddish (Z)
19	*A. setifera*	+	3(4)	+ (5)	c	2.0–2.5	f	1	10–15	+	–	Green & red (D)
20	*A. tianschanica*	+	1	+ (5)	c	3.0–3.5	r	1	20–35	–	+	No voucher
21	*A. truncata*	+	1	+ (5)	c	2.5–3.0	r	1	20–45	–	+	Yellow–brown (I)
22	*A. turkestanica*	+	1	+ (5)	c	3.5–5.0	r	2–3	75–100	–	+	Dark yellow or brown (K)
	Fredolia aretioides (Anabasis aretioides)	+	1	+ (5)	c	2.2–2.8	f	1	25–50	+ (very short tubercules)	+	No voucher

[†] Sections were cut from the upper part of the fruit; the thickness of the outer epidermis did not include the height of papillae.

Chorology

Chorological characters are often combined with morphological and anatomical characters (Sukhorukov 2007*a*). The chorotypes of almost all representatives of *Anabasis* are given by Iljin (1946), Makhmudova (1990) and Heller and Heyn (1994).

The cladistic analysis of all the above-mentioned vegetative and reproductive features, as well as the chorotype data, are presented in a paper by Sukhorukov and Baykov (2009), which shows the monophyly of almost all *Anabasis s.l.* representatives (except *A. annua* and *A. setifera*) and a close relationship between some earlier, phylogenertically distant taxa (e.g. *Anabasis eriopoda* (≡*Brachylepis eriopoda*)–*A. jaxartica*–*A. turkestanica*). To make final conclusions involving all species of the genus, molecular data from at least some *Anabasis* species would be very useful.

General concept of the fruit structure in the members of Salsoloideae sensu *Ulbrich*

In the fruiting stage, the perianth segments enveloping the fruit possess wing-shaped or tuberculate outgrowths in many Salsoloideae taxa. This can be considered an adaptation to anemochorous dissemination of diaspores. Such wings are often white-, red- or yellowish-tinted before full maturation of the fruits and turn brown at dissemination. Fruit dimorphism has been demonstrated for particular taxa (Zappettini 1953; Yamaguchi *et al*. 1990; Kothe-Heinrich 1993; Rilke 1999).

In the case of fruit dimorphism, wing-shaped appendages on the perianth segments may be more or less pronounced, even to complete reduction. Such 'wingless' perianths often become woody (e.g. *Halogeton*, some *Salsola* species). Various dissemination types, more often the barochorous and anemochorous modes, are associated with heterocarpy.

Fruits themselves can be brightly coloured in red, purple or orange across their entire surfaces (*Anabasis* spp. div., *Ofaiston monandrum* (Pall.) Moq.) or at least on their upper parts (*Salsola incanescens*, *S. tamariscina*, *S. tragus*, *Noaea mucronata*). However, neither original observations, nor published data (except for a personal communication by I. F. Momotov, in Butnik (1991), about birds picking *Nanophyton* fruits) suggest endozoochorous dispersal of the diaspores.

In diagnostic keys and taxonomic treatments (e.g. Bochantsev 1976; Tzvelev 1993), salsoloidean fruits are often simply divided into 'dry' and 'fleshy' ('succulent'). Such a rough approach does not reflect the heterogeneity of fruit structure in many Salsoloideae. In succulent fruits, subepidermal (hydrated) layers are distinct only in the upper third or half of the fruit, whereas they are obscure in the lower parts. Such non-uniformity is most pronounced e.g. in *Salsola foliosa*. The upper half of the fruit in this species contains no seed but is 'succulent' and orange, whereas the lower half, which contains a seed with a horizontal embryo, is not hydrated and is coloured green (semibacca). Entire pericarps that have no hydrated layers are represented by the (dry) fruits of *Agathophora*, *Girgensohnia*, *Halothamnus* and *Petrosimonia*.

Results of several studies on the anatomical structure of the fruit and seed covers in Salsoloideae are available (Nigmanova and Payzieva 1973; Werker and Many 1974; Butnik 1979, 1981, 1991; Zhapakova 1979); however, these results have not yet been generalised. The fruit and seed topography of almost all Salsoloideae studied does not differ from that of *Anabasis*. Nevertheless, many taxa are characterised by certain peculiarities in the pericarp structure. The members of *Halothamnus* and *Lagenantha* are the most distinct, owing to the presence of one to several layers of mechanical tissue (brachysclereids or sclerified parenchyma, respectively) underlying the subepidermal layers. The pericarp of *Seidlitzia rosmarinus* Bunge (≡*Salsola rosmarinus* (Bunge) Akhani) and *Iljinia regelii* (Bunge) Korovin possess noticeably thickened (25–40 µm) outer periclinal cell walls in the outer epidermis. In *Girgensohnia*, as well as in many *Salsola* species, subepidermal layers in the upper part of the pericarp are much more poorly developed than those in *Anabasis*. In *Petrosimonia*, the pericarp consists of two or three almost identical layers of parenchymatous cells (Fig. 9); the cells with U-shaped wall thickenings are dispersed and often almost undetectable.

Despite some variations in the pericarp structure in the Salsoloideae, the following common carpological characteristics can be defined:

(1) the pericarp consists of several cell layers and these are usually well differentiated;
(2) a 2–3(4)-cell-layered outer epidermis in the pericarp of some *Anabasis* representatives seems to be an excellent apomorphic feature in Salsoloideae;
(3) crystalliferous cells with U-shaped walls are present in the pericarp of almost all taxa and are visually distinct at least in the upper part of the fruit;
(4) the seed coat is two cell-layers thick, non-differentiated and thin; and
(5) the pericarp and seed coat lack macrosclereids and thick tannin-containing layers. Therefore, the fruit and seed coat are less resistant to environmental degradation and, unlike representatives of the Chenopodioideae (Budantsev 2005), are hardly ever found among fossil remnants (Sukhorukov 2007*a*).

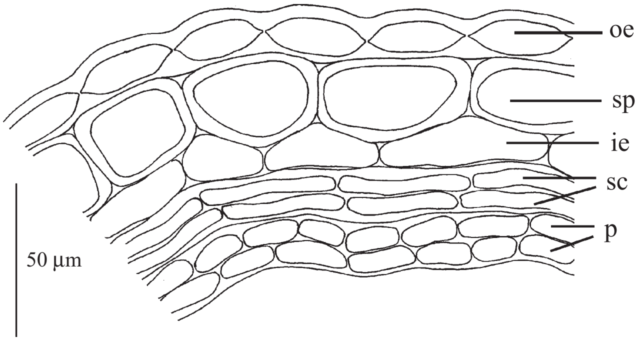

Fig. 9. Pericarp and seed coat of *Petrosimonia brachiata*. For abbreviations, see caption of Fig. 2.

Because of their fruit and seed structure, Salsoloideae *sensu* Ulbrich differ considerably from Salicornioideae (Shepherd *et al.* 2005) and Corispermoideae (Sukhorukov 2007*b*), as well as from the taxa of Chenopodioideae studied having dry or fleshy Chenopodioideae (berry *sensu*: Spjut 1994) fruits (Baar 1913; Cohn 1914; Sukhorukov 2003, 2005, 2006, A. P. Sukhorukov, unpubl. data), and from *Betoideae* (A. P. Sukhorukov, unpubl. data). On the basis of their fruit and seed characteristics, the Salsoloideae could be assigned to a well-distinguished carpological group within the Chenopodiaceae.

The species of *Camphorosmeae* tribe, now placed in Salsoloideae *s.l.* (Pyankov *et al.* 2001; Kadereit *et al.* 2003, 2005; Kapralov *et al.* 2006) or considered as a separate subfamily *Camphorosmioideae* (Scott 1978; Falkovich and Kovalev 2007), have not been thoroughly studied from a carpological point of view (Butnik 1962) and require further investigation.

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Appendix 1. Origin of the material of the Salsoloideae species investigated

Agathophora alopecuroides Bunge: Israel, 5 km S of Jericho, *A. Sukhorukov I-39*, Dec. 2007 (MW)

Anabasis africana Murb. ex H. Lindb.: Marocco, Dar-Drius, *H. Mauricio s.n.*, Sept. 1930 (LE)

A. annua Bunge: Persia borealis, *A. Bunge 68* (LE)

A. aphylla L.: Kazakhstan, ptov. Turgay, Kop-Mulla, *N. Androssov*, exs. *3086*[a], Sept. 1908 (MW)

A. articulata (Forsk.) Moq.: (1) Hispania, Baetica, *Gros 18*, Jul. 1925, (LE) sub *A. hispanica* Pau; (2) Hispania, Murcia, Lorca, *H. Jeronimo 6447*, Nov. 1927 (LE); sub *A. hispanica*; (3) [Egypt], C Sinai, Gebel El-Tih, *N. Tadmor*, *S-729*, Nov. 1969 (LE); (4) Hispania, prov. Murcia, Cartagena, *S. Castroviejo & al. 9572*, Nov. 1984 (MHA)

A. brachiata Fisch. & C.A.Mey. ex Kar. & Kir.: (1) Turkmenistan, prov. Tashauz, Ust-Urt, *A.A. Mesheryakov s.n.*, Oct. 1954 (LE); (2) SW Kazakhstan, Karynzharyk, *D.D. Vyshivkin s.n.*, Sept. 1956 (MW)

A. brevifolia C.A.Mey.: [Russia], Montain Altai region, Kosh-Agach, *M. Danilov & O. Tur s.n.*, Aug. 1982 (MW)

A. calcarea (Charif & Aellen) Bokhari & Wendelbo: Iran, between Kerman and Bam, *E.S. Brown 3428*, Nov. 1960 (LE)

A. cretacea Pall.: (1) [Kazakhstan], Semipalatinsk, city surroundings, *M. Iljin & A. Heinrichsson s.n.*, Sept. 1928, (LE); (2) Russia, prov. Saratov, Ozinki, *A. Sukhorukov, s.n.*, Sept. 2006 (MW)

A. ebracteolata Korov. ex Botsch.: (1) Kazakhstan, Ust-Urt, Ash-Orpa, *F.N. Rusanov s.n.*, Sept. 1926 (LE); (2) Kazakhstan, Ust-Urt, Beyneu, *A. Sukhorukov s.n.*, Sept. 2001 (MW)

A. elatior (C.A. Mey.) Schischk.: East Kazakhstan, Aktogai, *M. Lomonosova & A. Sukhorukov s.n.*, Sept. 2000 (MW)

A. eriopoda (Schrenk) G.Volkens: (1) [Uzbekistan], prov. Bukhara, Kuyu-Mazar, *N. Androsov 1889b*, Sept. 1905 (MW); (2) Kazakhstan, prov. Kzyl-Orda, *N. Pavlov s.n.*, Sept. 1929 (MW)

A. ferganica Drobov: (1) Uzbekistan, Alai range, distr. Khalmion, *Lopotin & Tinkhasov 467*, Oct. 1940 (TASH); (2) Uzbekistan, Fergana valley, between Kadamzhay and Vuadil, *U. Pratov 104*, Nov. 1963 (LE)

A. haussknechtii Bunge ex Boiss.: (LE): N. Iran, prov. Damgan, *M.P. Petrov s.n.*, Dec. 1942 (LE)

A. jaxartica (Bunge) Benth. ex Volkens: 1) Kazakhstan, Karatau, *N. Pavlov 1302*, Sept. 1931, (MW); 2) Uzbekistan, prov. Andizhan, *T. Makhamov s.n.*, Nov. 2006 (MW)

A. oropediorum Maire: Algeria, Chellala, Ras Nokra, *V.P. Bochantsev 236*, Nov. 1967, (LE)

A. pelliotii Danguy: Kirghizia, Alai, Kyzyl-su, Koman, *I. Tyshenko 1037*, Sept. 1933 (LE)

A. prostrata Pomel: (1) Algeria, *A.Pomel s.n.*, Dec. 1861 (P); (2) Dept. d'Oran, Arzew, *R.Cesve 5293*, Dec. 1926 (B)

A. salsa (C.A.Mey.) Benth. ex Volkens: (1) Kazakhstan, distr. Irghiz, *Androsov & Bubyr 3087*, Dec. 1910 (MW) sub *A. ramosissima* Minkw.; (2) Russia, prov. Volgograd, distr. Pallasovka, Elton, *A. Seregin & A. Sukhorukov R-71*, Sept. 2002 (MW)

A. setifera Moq.: (1) Israel, Southern shore of the Dead Sea, *M. Zohary s.n.*, Dec. 1938 (MHA); (2) Iraq, between Shithatha and Hindiya, *K.H. Rechinger 140*, Nov. 1956 (LE)

A. tianschanica Botsch.: Kirghizia, C. Tien-Shan, Akche-tau, *P. Gomolitsky 1094*, Aug. 1932 (LE)

A. truncata Bunge: Kazakhstan, prov. Almaty, Kungey-Alatau, *P. Polyakov 393*, Oct. 1954 (LE)

A. turkestanica Korovin: Uzbekistan, 15 km NE from Dzhizak, *P. Gomolitsky 433*, Sept. 1934 (LE)

Arthrophytum lehmannianum Bunge: [Kazakhstan], distr. Karsakpay, Arys-Kul, *N.V. Pavlov 2266*, Sept. 1929 (MW)

A. subulifolium Schrenk: E Kazakhstan, Ili valley, between Chunzha and Tas-Karasu, *L. Rodin 1655*, Oct. 1931 (MW)

Fredolia aretioides Coss. & Durieu: (1) Algeria, Colomb-Bechar, *ex herb. Bochantsev* s.n. (LE); (2) Algeria, N Sahara, *anonym s.n.*, Nov. 1965 (P)

Girgensohnia bungeana Sukhor.: Uzbekistan, prov. Samarkand, Karakchita, *A. Sukhorukov 250*, Oct. 2006 (MW)

Halothamnus glaucus (M.Bieb.) Botsch.: [Tadzhikistan], Zeravshan valley, *P. Gordienko & L. Chilikina 531*, Sept. 1930 (MW)

H. hispidus (Bunge) Botsch.: W Tien-Shan, Talass valley, *N.V. Pavlov 102*, Aug. 1966 (MW)

Haloxylon persicum Bunge ex Boiss. & Buhse: Uzbekistan, Kzyl-Dzhar, *T.T. Trofimov s.n.*, Oct. 1954 (MW)

H. thomsonii Bunge ex Boiss.: NW India, Jammu & Kashmir, Ladakh, *L.Klimesh 5064*, Sept. 2004 (Pr)

Hammada eriantha Botsch.: Uzbekistan, between Shirabad and Zarabag, *V.P. Bochantsev 18*, Oct. 1970, (LE)

H. leptoclada (Popov) Iljin: Uzbekistan, prov. Surkhandarya, Kuhitang, Aktash, *V.P. Bochantsev 53*, Oct. 1970 (LE)

H. wakhanica (Pauls.) Iljin: Tadzhikistan, W Pamir, *Abdusalyamova 4902*, Aug. 1963 (LE)

Iljinia regelii (Bunge) Korovin: [Kazakhstan], distr. Lepsy, Boin-Nor, *S. Lipshitz 1260*, Sept. 1928 (MW)

Lagenantha gillettii (Botsch.) M.G. Gilbert & Friis: Kenia, *Thompson s.n.*, 1964 (B)

Nanophyton erinaceum (Pall.) Bunge: Kazakhstan, prov. Aktyubinsk, Ust-Urt, Kurusay, *Vostokova s.n.*, Sept. 1948 (MW)

Noaea mucronata (Forsk.) Asch. & Schweinf.: Cypern, Larnaca Bay, *A. Sukhorukov s.n.*, Oct. 2006 (MW)

Petrosimonia brachiata (Pall.) Moq.: Russia, prov. Astrakhan, *A. Sukhorukov s.n.*, Sept. 2002 (MW)

Salsola inermis Forsk.: Cypern, Larnaca Bay, *A. Sukhorukov s.n.*, Oct. 2006, (MW; B)

S. incanescens C.A.Mey.: Uzbekistan, prov. Syr-Darya, road to Tashkent, *A. Sukhorukov s.n.*, Oct. 2006 (MW)

S. komarovii Iljin: Russia, Vladivostok, Russkiy island, *S. Petrova s.n.*, Sept. 2007 (MW)

S. tamariscina Pall.: Russia, prov. Saratov, Ozinki, *A. Sukhorukov s.n.*, Sept. 2006 (MW)

S. verticillata Schousb.: Spain, Costa del Sol, *T. Konovalova & N. Shevyreva s.n.*, Oct. 1996 (MHA)

Seidlitzia rosmarinus Bunge: [Turkmenistan], SE Karakum deserts, *E.V. Korovin s.n.*, Oct. 1926 (MW)