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ALEXANDER P. SUKHORUKOV[1]

Axyris (*Chenopodiaceae* s.str. or *Amaranthaceae* s.l.) in the Himalayas and Tibet

Abstract

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The genus *Axyris* in the Himalayas and Tibet is revised and only two taxa are recognised: *Axyris prostrata* possesses an extensive distribution range throughout the Himalayas and Tibet; *A. mira* (= *A. hybrida* auct.), with a wider distribution in the Himalayan-Tibetan region, is described as a species new to science. The differences between *A. mira* and *A. hybrida* are given; both are geographically vicarious, with *A. hybrida* actually being distributed in Central Asia. A carpological analysis revealed the facultative presence of sclereids in the pericarp of the brown fruit of *A. mira,* a feature recognised as a peculiarity of the genus. No correctly identified specimens of *A. amaranthoides* were traced from the Himalayas or Tibet. General conclusions for the fruit anatomy of *Axyris* are discussed and a key to all accepted species of *Axyris* is presented.

Additional key words: *Axyris mira, Axyris prostrata, Axyris hybrida,* carpology, taxonomy, identification key

I. Introduction

The species of the small genus *Axyris* L. are mostly widespread in the mountains of Central Asia and eastern Siberia. The centre of species diversity ranges from the Altai to northern Tien-Shan, where four taxa (*A. amaranthoides* L., *A. hybrida* L., *A. prostrata* L., *A. sphaerosperma* Fisch. & C. A. Mey.) are found (Iljin 1936; Grubov 1966; Lomonosova 1992). These are annual monoecious herbs with ovate or oblong leaves and unisexual flowers, well recognisable in situ due to the densely stellate trichomes on the plants. The male flowers are aggregated in terminal, spike-like inflorescences, the female flowers are clustered below them in the axils of bracts, supported by two bracteoles, and consist of three hyaline perianth segments. The fruits are one-seeded with the pericarp tightly adjoining the seed coat. However, distinguishing the species is rather difficult and relies on a limited character set: branching pattern, leaf shape, length of male inflorescence and fruit structure. All investigated species show evident heterocarpy, which is expressed by (1) the presence of sclereids in the pericarp of the black fruits and their absence in the brown fruits, (2) differences in fruit colour caused by heterospermy with respect to the thickness of the testa (terminology after Wunderlich 1967), (3) peculiarities of the pericarp, such as (a) the two ear-like appendices on the top of the fruit, (b) details of fruit surface sculpture, and (c) the shape of both fruit types (Sukhorukov 2005).

The systematics of the genus are not yet fully understood. The species can be divided into two groups: (1) *Axyris amaranthoides*, *A. hybrida* and *A. prostrata* have compressed black fruits with a medium thick (30–50 µm) testa; (2) *A. sphaerosperma* and *A. caucasica* have subglobose black fruits with a very thick (50–100 (or more) µm) testa. The brown fruits of all species always possess a thin testa (8–15 µm, marginally up to 25 µm).

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Within the subfamily *Chenopodioideae, Axyris,* together with the genera *Kraschenninnikovia* Gueldenst. and *Ceratocarpus* L., forms a separate clade that has been recognised as the tribe *Axyrideae* G. Kadereit & Sukhor. The carpological features evidently support the split between *Axyris* and *Kraschenninnikovia* plus *Ceratocarpus* (Kadereit & al. 2010) despite the earlier disposition of tribe members (Heklau & Röser 2008).

In the Himalayan-Tibetan region, which includes the states of Nepal and Bhutan as well as some parts of India, Pakistan and China, *Axyris* species have been found only in the high-altitude belts (at elevations of 2800–4700 m). Moquin-Tandon (1849) reported *A. hybrida* L. and *A. villosa* Moq. for the area (as "Indes Orientales"). Hooker (1890) recognised for the flora of British India only *A. amaranthoides* in the broader sense, including *A. hybrida* and *A. prostrata*. Later, the records of *A. amaranthoides* (without synonyms) were confirmed for NE India by Hemsley (1902) and Strachey & Duthie (1906). All subsequent *Chenopodiaceae* researchers in the 20th and 21st centuries dealing with *Axyris* have accepted the species ranks of *A. hybrida* and *A. prostrata* (e.g. Iljin 1936; Lomonosova 1992; Zhu & al. 2003; Sukhorukov 2005). In recent floristic treatments, 1–3 species (*A. hybrida* L., *A. prostrata* L. and *A. villosa* Moq.) are indicated for the floras of the Himalayas and Tibet (Long 1984; Press & al. 2000; Omer 2001; Zhu & al. 2003; Ohba & al. 2008). The analysis of the type specimen of *A. villosa* (only small fragments of the plant found at P!), however, shows clearly that it actually belongs to the subfamily *Camphorosmoideae* A. J. Scott. Hedge (1997) placed *A. villosa* as synonym to *Kirilowia eriantha* Bunge, which most recently was transferred to the genus *Bassia* as *B. lasiantha* Freitag & G. Kadereit (Kadereit & Freitag 2011). The specimen (K-Wallich!; LE!) named as "*A. moorcroftiana* R. Br. ex Wallich", nom. nud. (Wallich 1828–49) actucally represents a member of the genus *Kraschenninnikovia*. After the exclusion of *Axyris villosa* from the genus, three species, all belonging to the group with compressed black fruits and a medium thick testa, have to be considered for the Himalayan-Tibetan region: *A. amaranthoides, A. hybrida* and *A. prostrata*. Their presence is revised in the present paper.

2. Material and methods

The present study is based on field research carried out in central and western Nepal during expeditions by the author in 2008–10 as well as on the study of herbarium material. The material of *Axyris* in the following herbaria (abbreviations according to Thiers 2008+) was revised: B, BM, E, G, H, K, MW, MHA, MOSP, LE, P, TUCH, W, S-LINN. The anatomical structure of the heterocarpic fruits was investigated through hand cut cross-sections of 2–3 loose fruits from each specimen cited in the results.

3. Results

3.1. Taxonomy of *Axyris* in the Himalayas and Tibet

All specimens identified as *Axyris amaranthoides* from the Himalayan-Tibetan region that were seen by the author were not correctly determined. Judged from the material revised (mainly at LE), the southern distribution limit of this species is apparently somewhere in the northern provinces of China (Xinjiang and Qinghai). The species seems to be also absent from the Pamir mountain range. The main distribution of *A. amaranthoides* is predominantly confined to the Asian steppes and semi-deserts, with secondary occurrences in high-latitude and western regions.

Similarly, all specimens seen by the author from the Himalayan-Tibetan region that were identified as *Axyris hybrida* do not belong to this species, which was originally described from the Altai (Linneaus 1753) and which is widespread in the mountains of Central Asia (including Asian Russia, Mongolia, E Kazakhstan, Kyrgyzstan, Tajikistan, N and NE China). The material so determined from the Himalayas and Tibet actually represents an undescribed species, which is here described as *A. mira,* and which apparently replaces *A. hybrida* in the Himalayan-Tibetan region.

According to the present study, the genus *Axyris* comprises six species, of which only two can be confirmed for the Himalayas and Tibet: *Axyris prostrata* and *A. mira*. A third species that may perhaps occur in N Pakistan, N India and W China, but that was not so far recorded, is *A. sphaerosperma,* which is otherwise known from the dry-cold, high-altitude deserts in the Pamir mountain range of Tajikistan (Sidorenko & al. 1968). It was mentioned as possibly present in W China by Dickoré (1991).

Axyris prostrata L.

This is the only one of the hitherto reported *Axyris* species in the floras of the Himalayas and Tibet, of which the occurrence can be confirmed. It is a species with an extensive distribution range, including NE Pakistan, N and E India, Nepal, W and SW China and Bhutan. It is easily recognised by its prostrate habit, small fruit size (1.5–1.8 mm long) and pear-shaped brown fruits (Sukhorukov 2005). The species is common at least in some territories (Miehe & al. 2009).

Axyris mira Sukhor., **sp. nov.**

Holotypus: [India, Uttarakhand], "Kumaon, Milam glacier, 12500 feet above the Sea", 28.8.1848, *R. Strachey & J. E. Winterbottom 2* (LE). – Fig. 1.

– *Axyris hybrida* auct., non L.; *A. villosa* auct., non Moq.; *A. amaranthoides* auct., non L.

In habitu species nova *Axyridis hybridae* similis sed dense pilositate, tota longitudine perianthii et in semper tenuioribus appendicibus in utrisque typis fructuum (cum avellaneorum tum nigrorum) differt. Appendices

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Fig. 1. *Axyris mira* – holotype specimen at LE.

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pericapii fructuum nigrorum ad 0.1 mm longae, pericarpii fructuum avellaneorum 0.05–0.25 mm longae. Superficies pericarpii fructuum nigrorum rugosa, sine zonis semiconcentricis. In pericarpio nigrorum fructuum sclereidae semper adsunt. In nonnulis speciminibus, et quidem in typo ipso, pericarpium fructuum avellaneorum sclereidas habet, qui character unicus ac nondum testatus, quamquam facultativus, speciei novae nomen dedit. Si sclereidae in pericarpio exstant, fructus colore rubiginoso sunt, sin minus, avellaneo colore reperiuntur. Species *Axyridis mirae* speciei *hybridae* vicaria locum ejus in Imao et in Tibetia tenet.

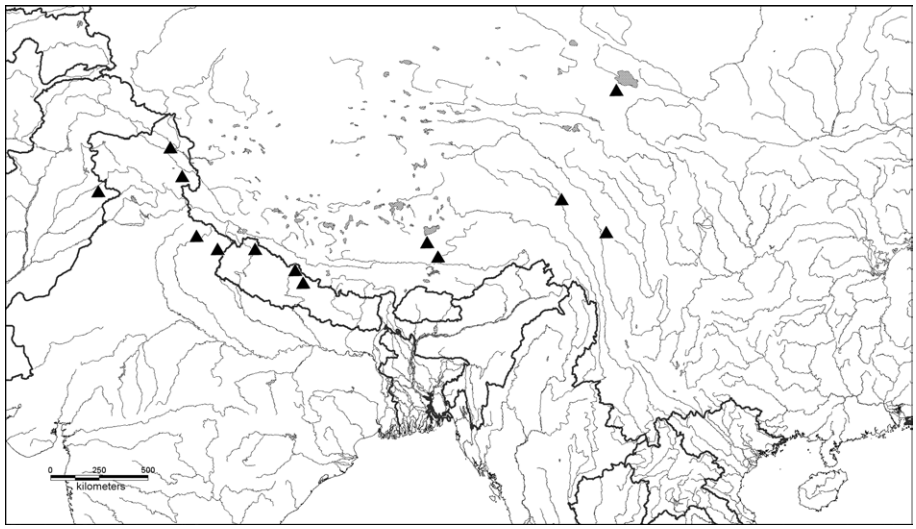


Fig. 2. Distribution of *Axyris mira* according to the specimens revised.

Delimitation. — Usually, the new species is similar to *Axyris hybrida* but differs from the latter by its densely pubescent perianth, the much longer (0.7–2 mm instead of up to 0.6 mm) central ray of its stellate hairs on stem and branches, and the always small to indistinct pericarp appendices in the upper part of both fruit types. The pericarp surface of the black fruits of *A. mira* is rugose but without the radially semiconcentric sculpturing present in *A. hybrida*. Also, there are sometimes sclereids in the pericarps of the brown fruits (in particular in the type specimen).

Distribution. — The records of *Axyris mira* with a more or less precise geographical location are mapped in Fig. 2. The distribution of the new species seems to be localised in the Himalayan-Tibetan region.

Axyris hybrida and *A. mira* are geographically vicarious species. *A. hybrida* is widespread in the mountains of Central Asia.

Additional specimens examined. — Pakistan: [Punjab prov.], distr. Astor, Gudhai valley, 9–10000 ft, 23.7.[18]92, *J. F. Duthie 12231* (E, K, LE).
India: Himalaya, *V. Jacquemont 1642* (P, K) [4]. — Uttarakhand: "Tibet occ[identalis]", Kumaon [div.], 14000 ft, *J. J. Thomson s.n.* (K) [1]; Tehri-Garhwal, 8000 ft, common, 9.[18]82, *J. Duthie 2262* (K) [5]; Kumaon, Kutti, H=13–14000 ft, 8.9.[18]94, *J. F. Duthie 3326* (G) [6]. — Himachal Pradesh: Himalaya, Kunawer [Kinnaur distr.], 10–14000 ft, *J. J. Thomson s.n.* (K) [2]; Himalaya, hab. Kunawer [Kinnaur distr.], alt. 10–14000 ft, 1859, *J. D. Hooker & J. J. Thomson s.n.* (P) [3]; Kangra distr., 7.–10.9.1933, *W. Koelz 7113* (G) [8]. — Jammu & Kashmir: Ladakh, Chortren Chen [Tog Nulla], 18.8.1931, *W. Koelz s.n.* (W-6205) [7]; Ladakh, *Polygonum tortuosum*-Bestand auf schilferigem Schutt, 3940 m, 27.8.1976, *H. Hartmann 2122* (G-152731) [9].
Nepal: Central part: Manang distr., Marsyandi valley, sandy place, 3200 m, 25.9.1969, *T. Wraber 36504* (BM) [1, only black fruits observed in the specimen]; Braga-Thorong pass, 11000 ft, 11.1978, *F. Davis 115* (K) [3]. — Western part: Talung, 2600 m, 3.10.1971, *J. F. Dobremez 71-25* (E 00014374) [2].
China: Qinghai: Nan-Shan [Quilan Shan], 9.1894, *V. I. Roborovsky 420* (LE) [1]; Nangqin Xian, along W side of the Za Qu (upper Mekong), 32°17'N, 96°28'E, 1.9.1996, *T. N. Ho & al. 2972* (E 00064354) [5, only black fruits observed in the specimen]. — Sichuan: neighbourhood of Tatsien-Lu [Tatsienlou], 1924, *R. Cunningham s.n.* (E) [2]; Kangding county, alt. 3000 m, 29.9.1981, *Z. Zhen-Ju 115642* (K) [4]. — Xizang: Reting, 3 marshes north of Lhasa, 14000 ft, 29.9.1942, *F. Ludlow & G. Sherriff 9093* (BM, E) [3].

Ecology and elevation. — *Axyris mira* is a mountain species growing at altitudes of 2800–4300 m in grassy or stony slopes or disturbed areas. In central Nepal, the species seems to be rare (compare Hara 1966, Ohba & al. 2008) and is confined only to the alpine belt between 3600–4500 m, above the hammada deserts.

3.2. Fruit morphology and anatomy of *Axyris mira*

The black fruits of *Axyris mira* (Fig. 3A) are 1.5–1.8 mm long and possess very small (up to 0.15 mm) and easily removed appendices of the pericarp, in most cases they are indistinct. In cross sections (Fig. 3D), the pericarp is 2-layered with a parenchymatous epidermis and sclereids below (the layer topology in the black fruits is the same as in other *Axyris* species). The seed coat consists of 2 layers, the testa is 35–50 μm (only occasionally up to 65 μm) thick. The tegmen is inconspicuous (1–2 μm).

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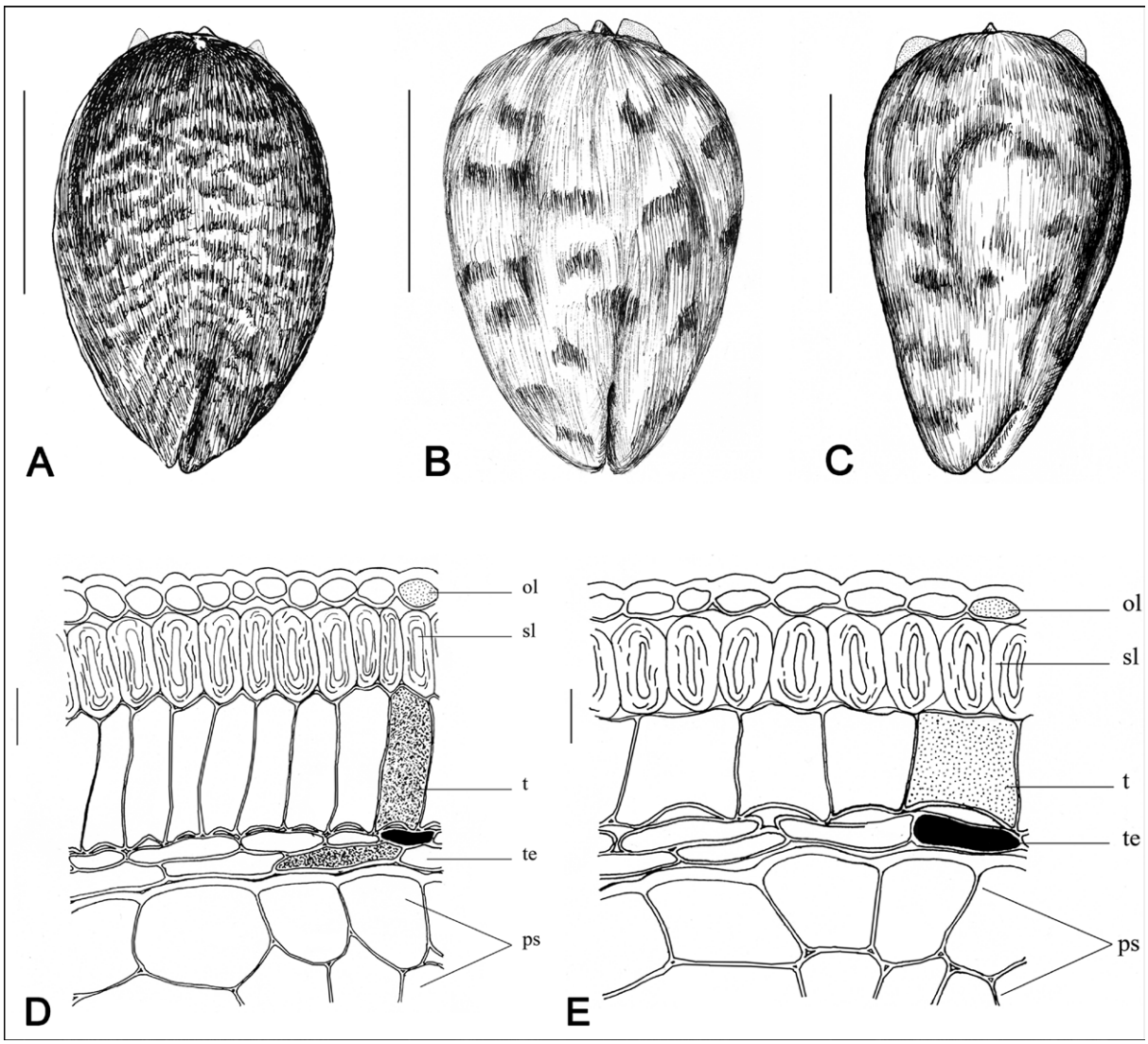


Fig. 3. *Axyris mira* – fruits; A: black fruit; B–C: brown fruits, pericarp appendices adjoining (B) or separate (C); D: cross section of the black fruits; E: cross section of the brown fruits. – Abbreviations: ol = outer pericarp layer, sl = sclereids layer in pericarp, t = testa, te = tegmen, ps = perisperm. – Scale bars: A–C = 1 mm, D–E = 10 µm.

The brown or reddish brown fruits are (1.6–) 2–2.4 mm long. In contrast to the relatively homogenous appearance of the black fruits, the degree of development of the pericarp appendices of the brown fruits, their easy removal and especially the presence of sclereids in the pericarp is variable in the specimens seen (Table 1 and Fig. 3B–C). The presence of sclerenchyma in the pericarp appears to be facultative and varies even within the same individual: some produce two forms of brown fruits, with and without sclereids. In other cases, the sclerenchyma surrounds the pericarp only partially and is absent in some fruit parts. Presence or absence of sclerenchyma in the brown fruits does not, however, constitute an intermediate diaspore type, because the thickness of the testa is similar (7–15 µm) in both forms of the brown fruits. If present (Fig. 3E), the additional sclerenchymatic layer only influences the fruit colour, making it reddish brown.

The carpological variation observed in *Axyris mira* does not show a correlation of features to each other or any geographical pattern (Table 1).

The most important difference in fruit morphology between *Axyris mira* and *A. hybrida* is the sculpturing of the black fruits. Compared with *A. hybrida,* there is also a tendency for reduced pericarp appendices in the fruits of *A. mira* (Table 2).

General conclusions for the fruit anatomy of Axyris. — The presence of sclerenchyma in the pericarp (regularly so in the black fruits and facultatively in the brown fruits) is a unique peculiarity of the genus *Axyris* and not found in other representatives of the *Chenopodioideae* (Sukhorukov, unpubl.). In contrast to *Krascheninnikovia* and *Ceratocarpus, Axyris* possesses evident heterocarpy/heterospermy and a well differentiated seed coat. The obligate absence of tannin-like accumulations in the outer

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Table 1. Variability of pericarp features in the brown fruits of *Axyris mira.* – Specimen numbers within the country of origin refer to the bracketed numbers following their citation in the paragraph Specimens seen.

Specimens	Length of brown fruits [mm]	Length of pericarp appendices [mm]	Appendices distance of each other	Presence of sclereids in pericarp
India 1	2.4	0.2	adjoining	+
2	2.1	0.1	adjoining	–
3	2	0.15	adjoining	–
4	2.2	0.2–0.3	adjoining	±
5	2–2.2	0.1–0.2	separate	±
6	2–2.2	0.1–0.2	adjoining	+
7	1.5–1.8	0.05	separate	–
8	2.1–2.2	0.1	separate	–
9	2.1	0.2	adjoining	+
holotype	2.3–2.4	0.25–0.3	separate	+
Pakistan	2.1–2.4	0.1	adjoining	–
China 1	2.2	0.1	adjoining	–
2	2	0.15	separate	–
3	1.7–2	0.15–0.30	separate	–
4	1.7–2	0.2–0.25	separate	–
5	no data	no data	no data	no data
Nepal 1	no data	no data	no data	no data
2	2	0.2	adjoining	±
3	1.6–1.7	0.1	separate	–

Table 2. The carpological differences between *Axyris mira* and *A. hybrida*.

Species	Sculpturing of black fruits	Length of pericarp appendices of black fruits [mm]	Length of pericarp appendices of brown fruits [mm]	Sclereids in brown fruits
A. hybrida	with distinct semiconcentric lines	0.1–0.3	0.2–0.4	absent
A. mira	rugose, without semiconcentric lines	up to 0.15	0.1–0.3	absent or present

cell walls of the testa and the tight adjunction of the pericarp and the testa are further distinguishing characters. The well developed seed coat can be treated as a plesiomorphic character, common in other members of the subfamily *Chenopodioideae,* but existing only in this genus within the tribe. Following the molecular phylogenies of *Chenopodiaceae/Amaranthaceae* (Kadereit & al. 2003), the presence of the sclerenchyma in the pericarp has developed independently in *Chenopodioideae* and *Corispermoideae*. The similarity in the fruit/seed structure of *Axyris* to *Corispermum* proposed earlier (Sukhorukov 2005) is erroneous (see Sukhorukov 2006, 2007).

Additional material used for the carpological study (supplementary to Sukhorukov 2005).

Axyris hybrida L.: Russia: Irkutsk, ex herb. Henning *s.n.* (MW); Krasnoyarsk prov., Minusinsk, 8.1902, *N. Martyanov 7309* (MW); Altai, Ust-Koksinsk distr., Katanda, 9.1983, M. Maskayev *s.n.* (MW). – Mongolia: East Hangay, Tevshrulag, 9.1978, *I. A. Gubanov 1544* (MW).

Axyris sphaerosperma Fisch. & C. A. Mey.: Kazakhstan, Kunghey-Alatau, Tau-Chilik, 8.1944, *V. P. Goloskokov s.n.* (LE).

3.3. Identification of the species of *Axyris*

A key to the species of *Axyris* based on carpological characters only was given by Sukhorukov (2005). The key below includes new characters based on details of the indumentum that are crucial for the identification of some species at early developmental stages (e.g. *A. hybrida*, *A. sphaerosperma*), or of individuals with a pincushion-like habit (*A. prostrata*) due to underdevel-

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opment of lateral branches. The central ray of the sessile and stalked stellate hairs on the plant can be either equal to and then mostly up to 0.5 mm or much longer than the lateral rays. Some vegetative features, which were used previously (Pratov 1972; Tzvelev 1996) such as leaf indumentum details or length of male inflorescence, are evidently variable. *A. koreana* Nakai is not included in the key due to the poor knowledge of this taxon; the type specimen kept at TI (photo seen) contains a plant fragment similar to *A. amaranthoides*.

Key to the accepted species of Axyris

1. Stellate hairs with a large central ray of 0.7–2.5(–3) mm among others present on the leaves (especially on petioles) and the stem and branches; black fruits subglobose or spheroidal, brown ones compressed 2
– Stellate hairs with similarly large central rays as above present among others on the perianth and only sometimes on the stem and branches but never on the leaves; all fruit types compressed 3
2. Black fruits 1.7–1.9 mm in diameter, brown fruits with small ear-like appendices; Caucasus . . . . . *A. caucasica* (Somm. & Lev.) Lipsky
– Black fruits 1.4–1.6 mm in diameter, brown fruits with unnoticeable appendices. Central Asia & Eastern Siberia. . . . . *A. sphaerosperma* Fisch. & C. A. Mey.
3. Plant without pronounced main stem, all branches (if well-developed) prostrate or ascending; brown fruits 1.3–1.8(–2.2) mm long . . . . . *A. prostrata* L.
– Plants with distinct main stem; brown fruits 1.7–3 mm long 4
4. Stem (at least in upper part) covered with both short- and long-rayed stellate hairs; perianth densely pubescent; pericarp of brown fruits sometimes with sclereids making the fruit surface brownish red, pericarp surface of black fruits rugose, without radially semi-concentric sculpturing . . . . . *A. mira* Sukhor.
– Stem covered with short-rayed hairs only or basally, sometimes also with long-rayed hairs; perianth slightly pubescent; pericarp of brown fruits without sclereids, pericarp surface smooth or with semi-concentric sculpturing 5
5. Leaf length/width ratio 3–5.5 : 1; brown fruits 2.25–3 mm long, their appendices touching each other; pericarp surface of black fruits smooth . . . . . *A. amaranthoides* L.
– Leaf length/width ratio 2–3 : 1; brown fruits 1.8–2.2 mm long, their appendices separate from each other; pericarp surface of black fruits with semi-concentric sculpturing . . . . . *A. hybrida* L.

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