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

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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 sub-globose 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 Krascheninnikovia 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 Krascheninnikovia 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; Obba & 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) actually represents a member of the genus Krascheninnikovia. 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 (Linnaeus 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 habitat 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
Fig. 1. Axyris mira – holotype specimen at LE.
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 scieraeidas semper adsunt. In nonnulis specimenibus, et quidem in typo ipso, pericarpium fructuum avellaneorum scleriedas habet, qui character unicus ac nondum testatus, quamquam facultativus, speciei novae nomen dedit. Si scieraeidas in pericarpio exstant, fructus colore rubiginoso sunt, sin minus, avellaneo colore reperirunt.

Species Axyridis mirae speciei hybridae vicaria locum ejus in Imao et in Tibetia tenet.

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 radius 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.


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).
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 only partially and is absent in some fruit parts. Presence or absence of sclerenchyma in the brown fruits does not, however, constitute an intermediate diaspor 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.

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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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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.
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).

### Table 1. Variability of pericarp features in the brown fruits of Axyris mira.

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

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

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

### 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-
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; Twzelev 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. caucasia (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 Sukhov.
   - 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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