### SOLENOSTOMA FUSIFORME: AN ADDITION TO THE NORTH AMERICAN LIVERWORT FLORA AND A REVIEW OF THE GENUS SOLENOSTOMA IN NORTH AMERICA, NORTH OF MEXICO

### VADIM A. BAKALIN

Abstract. This study reviews the taxonomy of the liverwort genus *Solenostoma* Mitt. in North America, including a key to the taxa. Among six species of the genus, a taxon that has not previously been described in North American flora, *Solenostoma fusiforme* (Steph.) R. M. Schust., is described and illustrated. The taxon name *Solenostoma gracillimum* f. *crenulatum* (J. E. Smith) Bakalin, *comb. nov.* is proposed.

Key words: Solenostoma, Solenostomataceae, North American flora, Hepaticae

Vadim A. Bakalin, Institute of Biology and Soil Science and Botanical Garden-Institute FEB RAS, Vladivostok, Makovskogo, 142, 690024, Russia; e-mail: v\_bak@list.ru

The genus Solenostoma was described by W. Mitten (1865a). Two species were recognized: Solenostoma tersum (Nees) Mitt. (= S. sphaerocarpum) and S. crenulatum (Sm.) Mitt., the former being the generic type. The main characteristic of this genus is the presence of a rostellate perianth. That same year, Mitten (1865b) described a new Solenostoma subg. Plectocolea Mitt. for S. radicellosum Mitt. (= Plectocolea radicellosa (Mitt.) Mitt.). For more than one hundred and forty years, Solenostoma was treated as a subgenus within the large and heterogeneous Jungermannia (which includes Solenostoma, Jungermannia, Liochlaena and Plectocolea), with some exceptions in local and not widely recognized literature (Schljakov 1981; Zerov 1964). Sometimes, when a broad generic concept was adopted, Solenostoma was also treated as the priority name for the bulk of Solenostoma, Plectocolea and Jungermannia s.str. as a result of taxonomic confusion. The most widely known example of the latter view point is in Schuster's (1969) Hepaticae and Anthocerotae of North America. Recently, Solenostoma has widely been accepted to belong to a separate genus from Jungermannia and a separate family (Solenostomataceae) (Crandall-Stotler et al. 2009). In most

cases, the genus is treated in a relatively broad sense to include *Plectocolea* at the subgeneric level. In contrast, this study assumes that *Plectocolea* represents a separate genus. Following the convention and evidence described in the Russian literature (Konstantinova *et al.* 2009), *Solenostoma* is considered in the narrow sense, restricted only by subg. *Solenostoma*, as described by Schuster (1969), Váňa (1973), Amakawa (1960), and others. Unlike these authors, however, this study recognizes *Endogemma* and thus excludes *E. caespiticium* from *Solenostoma*.

The taxonomy of the genus *Solenostoma* in North America was discussed in detail for the eastern part of the continent (Schuster 1969) and critically reviewed for the western part (Váňa & Hong 1999). A rather common problem in the study of many liverwort genera in North America (see Bakalin 2011) is that the total taxonomical diversity of the genus is often well studied, but the data on species distribution and ecology are inadequate. Nevertheless, in the course of preparing the treatment of the genus for *The Bryophyte Flora of North America*, a new record of *Solenostoma fusiforme* was found among North American liverwort flora. The main purposes of this study were to describe the new record, to summarise available data on species distribution and to compile a key comprising all taxa currently known in North America.

This paper is based on a literature analysis and the critical study of *ca* 300 specimens, primarily from MO and NY.

### A KEY TO *SOLENOSTOMA* SPECIES FOUND IN NORTH AMERICA, NORTH OF MEXICO

- 1. Plants paroicous, leaves without distinct rim of swollen cells along the margins ...... 2
- - Plants mostly erect, more rarely ascending, green to sepia-brown in colour, never purplish, rhizoids originated from ventral side of stem only ......
    Solenostoma sphaerocarpum
  - 2.\* Plants ascending to creeping, green, greenish, pale green yellowish, yellowish to purplish and brownred in colour, rhizoids originated both ventral side of stem and some cells in lower half of leaves, commonly decurrent downward in the fascicle ...

..... 1. Solenostoma confertissimum

3. Plants whitish to yellowish, without traces of red pigmentation, with the exception of perianth's beaks, plants commonly with endogenous gemmae present within unfertilised perianths, oil-bodies brown to brownish, 1(-2) per midleaf cell .....

..... Endogemma caespicitia

- 3.\* Plant colour varies from yellowish to deep brown-red, gemmae absent, oil-bodies greyish to nearly colourless, more than 3 per midleaf cell ...... 4
  - 4. Plants lax, large (mostly more than 2 mm wide), with undulate leaf margins, leaves vertically oriented, sheathing the stem, blackish to reddish blackish and brownish in colour, but always with the stem whitish, plants mostly erect in dense patches [western flank of the territory] ...... ..... 2. Solenostoma fusiforme

*Endogemma caespiticia* (Lindenb.) Konstant., Vilnet & A. V. Troitsky

Folia Cryptog. Estonica 48: 132. 2011. = Solenostoma caespiticium (Lindenb.) Steph., Sp. Hep. 2: 57. 1901. – Jungermannia caespiticia Lindenb., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 14 (Suppl.): 67. 1829.

Until very recently, this species was invariably placed into *Solenostoma* or *Jungermannia* (if a broad generic concept was adopted), but recently, mostly as a result of genetic evidence, the species was transferred to a separate genus of the monotypic family Endogemmataceae (Vilnet *et al.* 2011). The main morphological feature that separates *Endogemma caespiticia* from *Solenostoma* spp. is the presence of peculiar endogenous gemmae. Because the acceptance of *Endogemma* is not widely known and because plants of the species have obvious 'solenostomoid' appearances, this taxon was retained in this key.

The distribution of this species is confined to the western part of the study area, where its presence has been confirmed in British Columbia and Alaska (Váňa & Hong 1999), but it may be rather more widely distributed there. The species was also found in a rather isolated station in New York (Schuster 1969). Ecologically, the taxon prefers habitats with natively or anthropogenically disturbed vegetation cover, and it is found growing on clayish soil along roadsides and on stream banks in coniferous forest belt, rarely ascending to the tundra. Pechen. Mkhi Severa SSSR 4: 51. 1981. = Jungermannia confertissima Nees, Naturgesch. Eur. Leberm. 1: 277, 291. 1833. – Solenostoma levieri (Steph.) Steph., Bot. Centralbl. 50: 30. 1892. – Solenostoma pyriflorum subsp. purpureum R. M. Schust. & Damsholt, Meddel. Grønland 199: 176. 1974. – Jungermannia pyriflora subsp. purpurea (R. M. Schust. & Damsholt) Stotler & Crandall-Stotler, Bryologist 80: 413. 1977. – Solenostoma pyriflorum var. innovatum R. M. Schust. & Damsholt, Meddel. Grønland 199: 179. 1974. – Jungermannia pyriflora subsp. purpurea var. innovatu (R. M. Schust. & Damsholt, Meddel. Grønland 199: 179. 1974. – Jungermannia pyriflora subsp. purpurea var. innovata (R. M. Schust. & Damsholt) Stotler & Crandal-Stotler, Bryologist 80: 413. 1977. – Solenostoma pyriflora subsp. purpurea var. innovata (R. M. Schust. & Damsholt) Stotler & Crandal-Stotler, Bryologist 80: 413. 1977. – Solenostoma pyriflora subsp. purpurea var. innovata (R. M. Schust. & Damsholt) Stotler & Crandal-Stotler, Bryologist 80: 413. 1977. – Solenostoma pyriflora subsp. purpurea var. innovata (R. M. Schust. & Damsholt) Stotler & Crandal-Stotler, Bryologist 80: 413. 1977. – Solenostoma pyriflora subsp. purpurea var. innovata (R. M. Schust. & Damsholt) Stotler & Crandal-Stotler, Bryologist 80: 413. 1977. – Solenostoma pyriflora subsp. purpurea var. vinaceum R. M. Schust., Hep. Anth. North America 2: 957. 1969.

This taxon is rather sparsely distributed within North America, where it is currently recorded in western North America in Alaska, British Columbia, Nevada and California (Váňa & Hong 1999) and in eastern North America in Quebec, Michigan and Wisconsin (Shuster 1969). The species prefers alpine to subalpine habitats, although it commonly descends into the boreal forest belt and is rather common in lowland tundras. In general, S. confertissimum is one of the most common species of the genus in the northern part of Europe, but it is much rarer in Siberia and the Russian Far East, as well as in North America. The presence of S. confertissimum was confirmed in this study by examining two gatherings from alpine habits in California (NY 00243851, NY 00244362). Previously, this species was recorded in the northern edge of California by Doyle and Stotler (2006), who indicated that the elevation for the species was lower than 1100 m a.s.l.

#### 2. Solenostoma fusiforme (Steph.) R. M. Schust. Fig. 1

Hepat. Anth. North Amer. 2: 944. 1969. = Nardia fusiformis Steph., Bull. Herb. Boiss. 5: 99. 1897 – Jungermannia fusiformis (Steph.) Steph., Sp. Hepat. 2: 77. 1901.

Plants 15–25 mm long and 1.0–2.8 mm wide, ascending to erect in dense patches, pale green to whitish, with characteristically brownish to reddish-brown coloured leaf margins. Stem 315– 420  $\mu$ m wide and 280–390  $\mu$ m high, elliptic in cross section, dorsal surface cells thin- to slightly thick-walled, cells obliquely rectangular to oblong-hexagonal, with small concave or indistinct trigones, 100–125  $\times$  17–33 µm. Rhizoids dense, colourless to brownish, in indistinct fascicles at right angle with stem; in the stem cross-section outer layer 2-stratose mostly composed of moderately thick-walled cells, ca 12-25 µm in diameter, inner cells thin-walled with small to indistinct trigones, in the central part nearly the same size as the outer layer, but larger between the centre and outer layers, up to 45 µm in diameter. Leaves distant to contiguous, commonly sheathing the stem, inserted at an angle of 10-40° with axis, dorsally decurrent for *ca* stem width, ventrally subtransversely inserted, not or barely decurrent, (700-)900-1750  $\times$  (665–)1120–2135 µm [1:0.6–0.95(–1.2)], transversely oval to rounded-widely triangular, mostly flattened to concave, moderately and large-sized frequently undulate at margin; mostly with distinct brown to reddish brown and purplish coloured rim along margin. Cells in the midleaf thin-walled or slightly thickened, colourless, subisodiametric to oblong hexagonal,  $30-45 \times 25-38 \mu m$ , trigones small and concave; near margin 22-33 µm, with mostly thickened, but not strongly, or (rarely) thinwalled but with thickened external wall, brownish to reddish brown or, occasionally, colourless; in basal part cells oblong rectangular to oblong hexagonal, 50–100  $\times$  30–43 µm; cuticle smooth or very loosely striolate. [Sexual condition dioicous. Perianth terminal on main axis, no innovations, emergent for 1/2-2/3 of its length, fusiform, obscurely 3(-4)-keeled, perianth mouth crenulate, composed of elongated cells, perianth unistratose, cells oblong; bracts just below perianth, in one pair, the same size or slightly wider than sterile leaves. Androecia intercalary, in 5-8 pairs, with 2(-3) antheridia per bract, stalk biseriate; bracts similar to sterile leaves, but inflated near the base<sup>1</sup>]. Sporophyte unknown.

Solenostoma fusiforme has mostly borealtemperate East Asian distribution. This taxon was

<sup>&</sup>lt;sup>1</sup> The data in square brackets are based on the study of material from the Russian Far East because generative structures were not found in the American material.



**Fig. 1**. Solenostoma fusiforme (Steph.) R. M. Schust. 1 & 2 – plant habit, 3-7 – leaves, 8 – stem cross section, 9 – dorsal stem epidermis cells, 10, 12 & 13 – leaf margin cells, 11 & 14 – midleaf cells (14 shows papillae). 1, 3-5 & 8-11 from *Cooper D. J.*, U.S.A., Colorado, Mineral County (NY 00580773); 2, 6, 7 & 12–14 from *Halse R. R.*, U.S.A., Oregon, Lincoln County (NY 00693682). Scale bars: a – 1 mm (1 & 2); b – 1 mm (3–7); c – 100 µm (8 & 9); d – 50 µm (10–14).

reported from Japan, and for a long time, it was regarded as Japanese endemic, but it was later (Váňa 1975) synonymised with South Korean Solenostoma koreanum Steph., with S. fusiforme as the priority name. The latter synonymy is quite problematic, and because both taxa have rather remote relations, this study proposes that they should be treated as separate species. This question will be discussed in a future paper. Within the last 15 years, S. fusiforme has been found in many localities in Russia (Blagodatskikh & Duda 2001, and others) and is one of the most common species of the genus in the South Kurils (Bakalin *et al.* 2009). The distribution map of this taxon in Russia was published by Bakalin (2010). In North America, the known distribution of this taxon is confined to Washington, Oregon and Colorado in the U.S.A. and British Columbia in Canada. Therefore, its general distribution resembles that of many species in the boreal circum-Pacific area, e.g., *Macrodiplophyllum plicatum* (Lindb.) Perss. (cf. Bakalin 2010; Hong 1980).

The data on the ecology of the American material are very scant. The material of *Solenos*-

*toma fusiforme* grew in mineral fine-grained soil along the banks of sluggishly flowing streams. In Russia and Japan, this species is mostly confined to similar substrates in the boreal forest belt, rarely ascending to the tundra. The distribution of the species is mostly restricted to areas evidencing extant or extinct volcanic activity. Perhaps Graham Island (British Columbia) and Lincoln County (Oregon) exhibit similar native condition to those found in Russia and Japan (cf. Lefebure 1997; Lund 1974).

Solenostoma fusiforme is characterised by lax plant texture, whitish colour, small to obsolete midleaf cell trigones and noticeably elongated epidermal cells on the dorsal stem surface. Among regional species, this species can be confused with *S. gracillimum*, especially with f. *gracillimum*. This species differs from the *S. gracillimum* f. *gracillimum* in that is has a larger plant size (1.0–2.8 vs. 0.4–0.9 mm), longer stem dorsal surface cells (100–125  $\mu$ m vs. 35–75  $\mu$ m), perianth shape [fusiform, loosely 3(–4)-plicate vs. tubular-conical to short clavate 4–5-pliate], loosely developed leaf rims of swollen cells (vs. commonly well-developed), and growth form of sterile plants (ascending to erect vs. prostrate).

SPECIMENS EXAMINED. U.S.A.: Washington, Rainier County, July 1919, *Jilett J.G.* (NY 00243847); Oregon, Lincoln County, 22 June 2000, *Halse R.R.* (NY 00693682); Colorado, Mineral County, Cooper D.J., 09 August 1999 (NY 00580773). CANADA: Queen Charlotte Islands, Craham Island, *Schofield W.B.*, 19 May 1961 (NY 00099055).

# 3. *Solenostoma gracillimum* (J. E. Smith) R. M. Schust.

Hep. Anth. North Amer. **2**: 972. 1969. = *Jungermannia gracillima* J. E. Smith *in* Sowerby, Engl. Bot. **32**: Tab. 2238. 1811. – *Jungermannia crenulata* J. E. Smith *in* Sowerby, Engl. Bot. **21**: 1463. 1805 non *J. crenulata* Schmidel *in* Paver, Dissert. Jungerm. Charact.: 20. 1760.

Within this species, two forms can be found. They can be distinguished by the following key:

1. Leaves with a rim of swollen thick-walled cells that are 1.5–2.0 times larger than midleaf cells ...... *S. gracillimum* f. *crenulatum* 

# 3a. *Solenostoma gracillimum* f. *crenulatum* (J. E. Smith) Bakalin *comb. nov.*

BASIONYM: Jungermannia crenulata J. E. Smith in Sowerby, Eng. Bot.: Pl. 1463. 1805. = Solenostoma gracillimum f. crenulatum (J. E. Smith) R. M. Schust., Hep. Anth. North Amer. **2**: 980. 1969, nom. illeg. (no reference to basionym).

The North American distribution of the species is mostly confined to the eastern half of the continent, where the frequency of S. gracillimum f. crenulatum vastly prevails over S. gracillimum f. gracillimum. Solenostoma gracillimum f. crenulatum was recorded in the eastern half of the continent in Canada (New Brunswick, Newfoundland, Nova Scotia, Ontario, Prince Edward Island, Quebec) and in the U.S.A. (Alabama, Connecticut, District of Columbia, Florida, Georgia, Illinois, Iowa, Kentucky, Maine, Michigan, Minnesota, Missouri, New Hampshire, New Jersey, New York, North Carolina, Ohio, Pennsylvania, Rhode Island, South Carolina, Tennessee, Vermont, Virginia, West Virginia) (Schuster 1969; Crum 1991). This taxon was also found in California (Jackson County, I. 1987, leg. B. M. Theirs, NY 00244446) and in Indiana (Putman County, IX.1893, leg. L. M. Underwood, MO 5374287). The record of the species from California is rather surprising, because it is the only record of the taxon in western North America.

Ecologically, the taxon is confined to finegrained soil along streams and (more frequently) in human-disturbed areas (roadsides, etc.) in low altitudinal levels in temperate and boreal zones, rarely occurring in the tundra.

#### 3b. Solenostoma gracillimum f. gracillimum

The distribution of this form is poorly known in North America. The form was recorded in New Jersey and in Georgia (Schuster 1969), but as correctly noted by Schuster (1969: 980), it 'actually occurs sporadically through the range of the species'. Specimens of the taxon identified in the present study include material from Arkansas (27.VI.1973, *leg. Redfearn P. L.*, MO 5129594), Kentucky (Boyle County, 6.VIII.1986, *leg. Studlar S. M.*, MO3673846), and Texas (Leon County, 7.IV.1953, *leg. MacGregor R.*, NY00244290).

The ecological preference of the taxon appears to be similar to that of *S. gracillimum* f. *crenulatum* but with a more noticeable inclination to occupy wetter habitats. Given the specimens studied, the form occurs in steep muddy banks of creeks and at the edges of gullies.

#### 4. Solenostoma pyriflorum Steph.

Sp. Hepat. **6**: 83. 1917. = *Jungermannia pyriflora* Steph., Sp. Hepat. **6**: 90. 1917.

This species is fairly rare in North America, currently recorded in Georgia, Michigan, North Carolina, South Carolina and Virginia (Schuster 1969). The current study only examined specimens of this species from North Carolina (MO 5635736, MO 6001431). The ecology of the species in the examined region is restricted to areas containing moist rock crevices or other rocky surfaces and (rarely) bare soil in human disturbed areas in the temperate forest belt. The absence of the taxon in the western part of North America is rather surprising because the taxon is more or less common in south temperate Asia, although it is replaced by *S. pseudopyriflorum* Bakalin & Vilnet north of 40 degrees latitude.

#### 5. *Solenostoma rubrum* (Gottsche *ex* Underwood) R. M. Schust.

Hepat. Anth. North Amer. **2**: 1007. 1969. = *Jungermannia rubra* Gottsche *ex* Underw., Bot. Gaz. **13**: 113. 1888.

The species is restricted to habitats with native or anthropogenically disturbed vegetation cover, where it most frequently occurs on moist soil along streams and clayey roadsides in low to middle elevations (maximal 2160 m a.s.l.; cf. Váňa & Hong 1999). Geographically, the species is a distinctly western American species. It was recently discovered that all previous records of the species in adjacent parts of Russia (Konstantinova *et al.* 2009) should be referred to as another, undescribed taxon (Bakalin, unpublished). In North America, the species has been reported from Canada (Alberta, British Columbia) and from the U.S.A. (Alaska, California, Idaho, Montana, Oregon, Washington, Wyoming) (Váňa & Hong 1999).

#### 6. Solenostoma sphaerocarpum (Hook.) Steph.

Sp. Hep. 2: 61. 1901. = Jungermannia sphaerocarpa Hook., Brit. Jungermann.: Pl. 74. 1815.

This species is distributed across the North American continent but is much more common in the north than in the south. In the southern half of the continent, the species occurs in highly mountainous areas, reaching 3100 m a.s.l. in California (Doyle & Stotler 2006) and 3500 m a.s.l. in Colorado (Larimer County, 14.VII.1956, leg. Weber W. A., NY 00244503). The taxon is mostly found in tundra communities, but it is not rare in the boreal belt, especially in humid regions. Records in the literature of the taxon for North America cite Greenland. Alberta, British Columbia, Newfoundland, Northwest Territories, Nunavut, Quebec, Yukon, Alaska, California, Colorado, Idaho, Maine, Michigan, Minnesota, Montana, New Hampshire, New York, Oregon, Utah, Washington, Wisconsin, and Wyoming (Schuster 1969; Váňa & Hong 1999). In this study, the taxon was also found in Nevada (Washoe County, 19.X.1992, leg. Whittemore A.T., MO 3966883). Ecologically, the species prefers moist soil and rocks near streams, and wet fine-grained soil in anthropogenic or natively disturbed areas.

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