The complex *Sphagnum imbricatum* in Russia is revised basing on the narrow species concept suggested by K.I. Flatberg. According to this approach, *S. austinii* and *S. affine* occur only in European Russia, *S. steerei* is mainly arctic species, distributed from West Siberian Arctic to Yakutia and Chukotka, and *S. imbricatum* s.str. is presently known in the southern part of Russian Far East, northern part of Transbaikalia, South Yakutia and along the Lena River up to 67°N. Species descriptions and illustrations are provided and distribution in Russia is mapped.

The species independence of these taxa was subsequently supported by molecular and genetic markers (Shaw, 2000; Thingsgaard, 2002) and accepted by american (McQueen, 1998; Anderson & Allen, 2001) and european authors (Hill et al., 2006).

In Russia, up to the recent past (e.g. Ignatov & Afonina, 1992), *S. imbricatum* was treated in a broad sense, but in recent years the narrow species concept was accepted, and results of the present revision were partly published in the recent check-

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The present revision is based on all the material from Russia in H, IRK, LE, MHA, MW, PTZ, and SASY, and also on personal field studies in European North and in Yakutia.

According to Flatberg (1984), the important diagnostic characters in the group are (1) the comb-fibrils in stem and branch hyalodermis where they are situated on the inner surface of wall (i.e. adjacent to sclerodermis); 2) the leaf size; 3) the presence of the comb-fibrils in hyalocysts; 4) the presence and the degree of development of comb-fibrils along the length of branch leaves; 5) number of pendent branches per fascicle.

Comb-fibrils in branch hyalodermis can be seen in light microscope after leaf detachment: they are arranged in perpendicular or slightly oblique to branch length, whereas spiral fibrils are arranged in various directions. Comb-fibrils in branch hyalodermis occur in all species of Sphagnum imbricatum–complex, but well-seen only in S. affine and S. austinii. In Sphagnum imbricatum they are less developed and in S. steerei can not be seen without special preparation.

Comb-fibrils in stem hyalodermis are more difficult to observe. This needs a separation of pieces of stem by thin forceps, placement them in water with some glycerol on slide glass, and look at the places where outer layers of hyalodermis were removed.

**KEY FOR SPECIES OF SPHAGNUM IMBRICATUM–COMPLEX IN RUSSIA**

1. Hyalocysts of stem leaves with apparent comb-fibrils; pendent branches 1 per fascicle .................S. austinii
   — Hyalocysts of stem leaves without comb-fibrils (rarely present in hemiisophylous plants of S. steerei); pendent branches 1-3 per fascicle ........................................... 2

2. Inner cells of stem hyalodermis next to sclerodermis with apparent comb-fibrils; branch leaves with or without comb-fibrils; pendent branches 2(-3) per fascicle .............. S. affine
   — Inner cells of stem hyalodermis without comb-fibrils; branch leaves with comb-fibrils; pendent branches 1-2 per fascicle ............. 3

3. Stem leaves 1.2-1.5(-1.6) mm; branch leaves relatively narrow, with width to length ratio 0.6-0.7(-0.8); comb-fibrils well developed throughout branch leaf; inner cell wall of branch hyalodermis adjacent to sclerodermis without comb-fibrils ....................S. steerei
   — Stem leaves 0.8-1.1(-1.2) mm; branch leaves relatively broad with width to length ratio 0.7-0.9; comb-fibrils well developed only in proximal part of branch leaf; inner cell wall of branch hyalodermis adjacent to sclerodermis with comb-fibrils; stems yellow-brownish or occasionally yellow-green ....S. imbricatum


Figs. 1, 5.

Plants of loose tufts, yellow-brown or more rarely yellowish-green or green, not glossy. Stem usually stout, but slender in more wet habitats. Stem hyalodermis 4-5-stratose, outer cells subquadrat to short rectangular, with (1-)2-4 pores and numerous fibrils; inner cells usually with well-developed comb-fibrils. Sclerodermis yellow to fuscous. Stem leaves short rectangular, 1.1-1.5(-1.6) mm long, with width to length ratio 0.7-0.9; distally broadly bordered by decomposed cell remains; hyalocysts above by 2-4(-6) per loop, without comb-fibrils. Branches 4 per fascicle, 2(-3) branches pendent. Branch leaves moderately to loosely imbricate, 1.4-2.2 mm long, with width to length ratio (0.6-)0.7-0.9, broadly ovate to ovate-elliptic; hyalocysts with numerous round and ovate pores on dorsal surface distally; on ventral surface distally with one round pore in distal end of each cell, near margin with 2-4 round pores, in mid leaf on ventral surface without pores; chlorocysts in transverse section triangular, broader to ventral surface; cell walls of hyalocysts at join with chlorocysts with more or less developed comb-fibrils, usually apparent in proximal part of leaf, more rarely only at leaf base to very rarely totally absent. Sporophytes not known in Russia [Spores (27-)28-29(-31) μm].
Differentiation. *Sphagnum affine* has 2(-3) pendent branches per fascicles, i.e. more than other species of the *S. imbricatum*-complex in Russia. Stem leaves are short and relatively broad, usually with broad border of several rows of decomposed cells and hyalocysts are sometimes several per loop of chlorocysts. Also, *S. affine* is unique in having apparent comb-fibrils in the inner cells of stem hyalodermis adjacent to sclerodermis.

SPECIMENS EXAMINED: Karelia: Kyappaselka, 14.VII.1899 Alexeenko (LE); Olonetskiy Distr., Bolshakovo (Il'inskoye) 1.IX.1963 Yurkovskaya (PTZ); Suojarvi Distr., Hiisjarvi, Koitajarvi Lake, Pitkanyemi Cape, 11.VII.1998 Maksimov #А-375; same 4.VII.2002 O.L.Kuznetsov #14 (PTZ); Hiisjarvi Lake, 2.IX.2007 Maksimova & Maksimov (PTZ).

Ecology. Low hummocks and flat covers in mesotrophic sedge–*Sphagnum* mires and sandy
banks of lakes where it grows in small cushions seeping by waves.

**Distribution.** Atlantic and Central Europe, Atlantic North America, Central America, West Indies (Cuba).

Savicz (1936) revealed this species (as *S. imbricatum*) in collections of Alexeenko of 1899, and after that for a long time this species was not collected, despite of extensive studies in the area. Second record was done much later, by Yurkovskaya in 1963 (Yurkovskaya, 1967) and then it was found in Hiisjarvi (Maksimov & Maksimova, 2006).

The species was never recorded during sub-fossil peat analysis, which also supports its status of a rare species.


Figs. 2, 5.

Plants in dense tufts, ferrugineous-brownish, glossy. Stem usually stout and rigid. Stem hyalodermis 4-5-stratose, outer cells rectangular, with
Sphagnum imbricatum complex in Russia

(1-)2-4 (-5) pores and abundant fibrils; inner cells without comb-fibrils. Sclerodermis ferrugineous-brownish. Stem leaves rectangular, 1.0-1.4(-1.5) mm long, with width to length ratio 0.6-0.7; distally narrowed to moderately broadly bordered by decomposed cell remains; hyalocists above by 1(-2) per loop, usually with simple fibrils and comb-fibrils. Branches 3 per fascicle, 1 branch pendent; divergent branches usually curved, tapered to apex. Branch hyalodermis with clear comb-fibrils that sometimes lacking at places. Branch leaves of divergent branches closely imbricate, ovate-elliptic to elliptic, 1.5-2.1 mm long, with width to length ratio 0.6-0.7; upper leaf obviously scabrous dorsally. Hyalocysts of branch leaves dorsally with numerous pores, above with numerous round or ovate pores and pseudopores, ventrally with 1-2 round pores in distal and middle part of leaf, near margin with 2-4 round pores; in basal part pores restricted to 1-2 rows of cells near margin; in inner cell walls adjacent to chlorocysts with clear and numerous comb-fibrils in all parts of leaf. Chlorocysts in transverse section equilaterally triangular; hyalocysts at the adaxial surface intact. Branches 3-4 per fascicle, (1-)2 branches pendent. Branch leaves of divergent branches moderately to loosely imbricate, ovate to round-ovate, 1.1-1.6 mm long, width to length ratio 0.7-0.8(-0.9). Chlorocysts in transverse section equilaterally triangular; hyalocysts in median part of branch leaf on adaxial surface without pores; near margin with large pores almost as broad as hyalocysts; on abaxial surface with numerous elliptic pores near borders with chlorocysts and solitary round pores in upper cell ends; comb-fibrils are clearly seen only in proximal part of leaves. Sporophytes rare. [Spores (22-)24-27(-28) μm].

**Differentiation.** *Sphagnum austini* can be easily recognized both by habit as well as by microscopic characters. It has dense reddish-ferruginous tufts, horn-like curved and densely imbricate divergent branches and 1 pendent branch per fascicle. Microscopically it differs from other species by distinct comb-fibrils in stem leaves, sparse round pores on adaxial surface in central part of branch leaves (that can be absent in wet habitats). Comb-fibrils in branch leaves are the most abundant among other related species, being present also in upper part of leaf.

**SPECIMEN EXAMINED:** Kaliningrad Province: Slavskiy Distr., Kozie Bog (eastern part), 13.X.1996 Napreenko # 553 (PTZ). This specimen was reported as *Sphagnum imbricatum* by Napreenko & Razgulyaeva (1999).

**Ecology.** Hummocks in ombrotrophic bog, with *Calluna vulgaris*.

**Distribution.** Atlantic Europe, northern Atlantic North America and northern Pacific North America.


Fig. 3, 5.
lectotype is closer to *S. steerei*. However, the relatively short and broad leaves, lacking of comb-fibrils in upper part of branch leaves and their total absence in the stem leaves, as well as the presence of comb-fibrils on inner walls in branch hyalodermis, make sure that the lectotype fits the current concept of *S. imbricatum*. In addition, fascicles in lectotype have 2 pendent branches, that agrees with *S. imbricatum* and contradicts with *S. steerei* that has 1 pendent branch per fascicle.

**SPECIMENS EXAMINED:**

**EAST SIBERIA:**

- **Chita Prov.**: Stanovoye Upland, 1963 Mikheev (IRK).
- **Yakutia**: Middle Lena, vicinity of Zhigansk, on Zhiganka River (66°46’N, 123°E), 7.VIII.1901 Cajander (H); Tompo Distr., Bryungoda River 5 km downstream from mouth of Pelkosyg Creek, 9.VIII.1956 Kildyushevsky (LE, SASY); Olekminsk Distr., Tungir River, mouth of Dzyadachi Creek, 29.VI.1910 Sukachev & Poplavskaya # 146 (H, dupl. PTZ); Suktarsky Distr., Vilyuj River, 213 km downstream from Ulokhosh-Vova, 9.VIII.1958 Kildyushevsky (LE, SASY); Olekminsk Distr., Nema-

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**Fig. 3. Sphagnum imbricatum** Hornsch. ex Russow (from Amurskaya Prov., Belaya River, 9.IX.1958 Lipatova, Hepaticae et Musci URSS exiccati, Dec. XIV (1962), # 132, LE): 1 – fascicle of branches; 2 – transverse section of branch leaf; 3 – stem transverse section, showing hyalodermis with pores; 4 – branch hyalodermis; 5 – branch leaf cells from adaxial side; 6 – branch leaf cells from abaxial side in leaf middle part; 7 – stem hyalodermis; 8-10 – stem leaves; 11-12 – branch leaves; 13 – branch leaf cells from adaxial side. Scale bars: 5 mm for 1, 1 mm for 8-12; 100 μm for 2-7, 13.
Fig. 4. *Sphagnum steerei* R.E.Andrus (from Chukotka, Upper Getlyanen River, 2.VIII.1976 Afonina [Bryophyta Rossica... (1995), # 10], LE): 1 – fascicle of branches; 2 – stem leaf cells from abaxial side; 3 – transverse section of branch leaf; 4 – branch leaf cells from adaxial side near leaf margin; 5 – stem hyalodermis; 6 – branch leaf cells from abaxial side; 7 – branch leaf; 8 – stem transverse section, showing hyalodermis with pores; 9-10 – stem leaves. Scale bars: 5 mm for 1; 1 mm for 7, 9-10; 100 μm for 2-6, 8.
ny River 2.5 km from Arylakh, 11.IX.1952 Kuvaev #124 (SASY). FAR EAST: Amurskaya Prov.: Birma Creek, left tributary of Zeya River, 29.VII.1926 Krasnornuzkaya (LE); Upper course of Tom Creek, tributary of Zeya River, 10.VIII.1926 Kuzeneva #32a (c.fr!) (LE); Belaya River, tributary of Zeya River, 9.IX.1958 Lipatova, Hepaticae et Musci URSS exiccati, Dec. XIV (1962), # 132 (LE); Erevskaya Autonomous Prov.: Bira River, 6.VII.1913 Prokhorov & Kuzeneva (LE); Primorsky Territory: Sikhote-Alin Nature Reserve, Chingouza Bay, 4.IX.1936 Kolesnikov (LE); Ussuri area, 1913 Komarov (LE); Vladivostok, Lanchichie Creek, 20.VII.1954 Vasilieva (LE); Khasan Distr., Ryazanova, 14.IX.1985 Ignatov # 82 (MHA); Vladivostok, Lanchichie, 10.X.1950 Woroshilov # 5629 (MHA).

Ecology: Low hummocks and carpets in mesotrophic, sedge–Sphagnum, Betula–sedge–Sphagnum and spring mires, in very wet mires around lakes, and boggy open Larix forest in permafrost areas (“mar’”-type).

Distribution. Outside Russia, this species occurs in China, Korea, Nepal, Japan. In Russia it is known in southern part of Far East, southern part of Eastern Siberia and along Lena River up to Zhigansk (~67°N). Numerous reports from the Arctic (Abramova, 1956; Afonina & Czernyadjeva, 1995; Afonina, 2004; Czernyadjeva, 1994, 2001; Ignatov & Afonina, 1992; Ivanova et al., 2005; Savicz-Ljubitskaya, 1952; Savicz-Ljubitskaya & Smirnova, 1968; Stepanova, 1986; Tyuremnenov, 1963, etc.) belong in fact to S. steerei.


Plants in dense tufts or, more rarely, loose carpets, brownish, with distinct glaucous tones when dry. Stem stout and rigid. Stem hyalodermis 3-4-stratose, outer cells quadrate to rectangular, with 1-2(-3) pores and numerous fibrils; inner cells without comb-fibrils. Sclerodermis dark-brown to yellowish-fuscous. Stem leaves quadrangular to spatulate-quadrangular, or in hemisophyllous forms broadly ovate-spatulate, 1.2-1.5(-1.6) mm long; with width to length ratio 0.55-0.7(-0.8); margin near leaf apex incurred, and narrowly to moderately narrowly bordered by decomposed cells; hyalocysts by 1 per loop of chlorocysts, only rarely by 2, with delicate fibrils or without them, without comb-fibrils or with indistinct ones; hyalocysts on adaxial surface with solitary round pores in upper and middle parts of leaves, sometimes (in hemisophyllous forms) pores like in branch leaves. Branches 3 per fascicle, 1(-2) branches pendent; divergent branches rigid, spreading, curved to erect, somewhat obtuse at apex. Branch hyalodermis usually without comb-fibrils. Leaves of divergent branches imbricate, ovate-elliptic to ovate, 1.6-2.2 mm long, width to length ratio 0.55-0.7; chlorocysts; on abaxial surface in middle part of leaf without pores, near margin with round pores in centres of hyalocysts; on abaxial surface in middle part of leaf with numerous elliptic pores near borders with chlorocysts; comb-fibrils more or less distinct throughout leaf. Sporophytes unknown in Russia.

Differentiation. Sphagnum steerei is similar to S. austinii, but differs in (1) the presence of peculiar glaucous tones of the overwise brownish shoots (glaucous color is absent or indistinct in S. austinii); (2) divergent branches are rigid, more or less erect and distally obtuse (vs. flexuous and distally acute in S. austinii); (3) branch leaves are more loosely arranged, not distinctly imbricate (vs. densely imbricate) and in general are longer than in S. austinii; (4) pores on the adaxial (concave) surface of branch leaves in middle part are absent. Comb-fibrils in stem leaves are absent or weakly developed. Comb-fibrils in inner surface of branch hyalodermis are rare and indistinct (vs. well-developed and easily seen in S. austinii).

SPECIMENS EXAMINED: WEST SIBERIA: Yamal Peninsula: Left shore of Obskaya Guba, 30 km N of Novyy Port, 17.VII.1938 N.Ya. & S.V. Katz (LE); Middle course of Saebyakhe River (69°37′32″N, 69°27′40″E), 27.VII.1992 Czernyadjeva (LE); Gydan Peninsula: Lower course of Chugor-Yakha River (69°07′N, 74°40′E), 26.VII.1991 Czernyadjeva (LE). YAKUTIA: Anabar Distr., Yuelle River 40 km from Kumakh-Yuryakh River, 2.VII.1974 Perfilieva (SASY); Tiksi, Sogo River, 6.IX.1956 Katzen # 73 (LE); Tiksi, behind observatorium, 18.VIII.1982 Perfilieva (SASY); Tiksi Bay, 1962, Mezhenniy (SASY); Tiksi, 1.5 km SE of Polar Station (71°41′N, 129°E), 27.VII.1955 Kildyushevsky (LE); Ust-Yana Distr., Omchikanda, 27.VII.1991 Perfilieva (SASY); Aldan Distr., Tomtom Peak, 17.X.1969 Trufanova (SASY); Tompo Distr., Verkhoyansk Range, upper course of Tompo River, 25.VII.1956 V.Ivanova (SASY); Vato-
Sphagnum imbricatum complex in Russia

- ma River (tributary of Maya River), 20.VII.1912 O.V. Sokolov (PTZ).
- FAR EAST: Chukotka: Upper course of Keiuyveem River, 15 km SW of Kukunevi Mt. (69°-70°N, 172°-174°E), 30.VIII.1951 Grudz'ev (LE); Arakamchechen Island, south coast of Senyavina Bay, 18.VIII.1976 Afonina (LE); Ioni Lake, Ioni Mt., 28.VI.1977 Afonina (LE); Provideniya Bay, 20.VII.1975 Afonina (LE); Belaya Creek, left tributary of Anadyr River, 18.VIII.1929 Sochava (LE); Hot springs Gil'mimleveem, 15 km S of Ioni Lake, 3.VII.1977 Afonina (LE); Egvekinot (in Kresta Bay), 17.VIII.1977 Afonina (LE); Anadyr, near airport, 6.VIII.1950 Andreev (LE); Upper Getlyanen River, 2.VIII.1976 Afonina (Bryophyta Rossica...1995), # 10 (LE); upper course of Anadyr River, Karval'yanyskaya Creek, 21.VII.1982 Afonina (LE); Provedeniya Dist., Chap-linskiye Hot Springs, 30.VIII.1958 V. Gavril'yuk (LE); same, 15.VII.1969 Afonina (LE); Koryaksky Autonomous District: Pechora Dist., 8.VII.1930 Savenk (LE). Magadan Prov.: Tenkinsky Dist., Sibityaellakh, «Aborigen» station, 14.VII.1976 Blagodatskikh (LE); Ola Dist., midlle course of Chelomzha River, zoological station, 10.VII.1982 Blagodatskikh (LE); Kamchatskaya Prov.: Blagodatskikh (LE); Ola Dist., middle course of Chelomzha River, zoological station, 10.VII.1982 Blagodatskikh (LE); Kamchatskaya Prov.: Opalikhinskoe bog, VIII.1958 Koreneva (MW).

**Ecology.** Hummock tundra with Eriophorum; segde—Sphagnum mires in flood plains, shrubby sedge—moss tundras, hummocky shrubby tundras with Eriophorum, sedgy mountain tunras and boggy slopes in alpine areas.

**Distribution.** Arctic Siberia, Yakutia, north of Russian Far East including Kamchatka, North America (Alaska and Canada).

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**LITERATURE CITED**


Fig. 5. Distribution of Sphagnum affine ( ), S. austini ( ), S. imbricatum ( ), S. steerei ( ) in Russia.


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