A REVISION OF THE GENUS SCIURO-HYPNUM
(BRACHYTHECIACEAE, BRYOPHYTA) IN RUSSIA

РЕВИЗИЯ РОДА SCIURO-HYPNUM
(BRACHYTHECIACEAE, BRYOPHYTA) В РОССИИ

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Abstract

There are thirteen species of genus Sciuro-hypnum in the Russian bryoflora: S. altaicum, S. brotheri, S. curtum, S. flotowianum, S. glaciale, S. latifolium, S. oedipodium, S. ornellanum, S. plumosum, S. populeum, S. reflexum, S. starkei, and S. uncinifolium. \textit{Hypnum Jeniseense} is synonymized with \textit{Sciuro-hypnum reflexum}. Morphological descriptions and distribution of taxa are given. Analysis of nuclear ITS1-2 data demonstrates the distinct segregation of three groups within the genus: (1) \textit{S. brotheri}, \textit{S. flotowianum}, \textit{S. plumosum}, \textit{S. populeum}, \textit{S. uncinifolium}; (2) \textit{S. curtum}; and, (3) \textit{S. latifolium}, \textit{S. oedipodium}, \textit{S. ornellanum}, \textit{S. glaciale}, \textit{S. reflexum}, \textit{S. starkei}. In the last group, the variability is very low and species differ from each other by just one substitution in nrITS, or are totally identical in this spacer.

Резюме


INTRODUCTION

The genus \textit{Sciuro-hypnum} was segregated from \textit{Brachythecium} by Ignatov & Huttunen (2002). Previously, the species of the genus were placed in \textit{Brachythecium} in two sections: sect. \textit{Reflexa} and sect. \textit{Plumosa} (Brotherus, 1925; Nyholm, 1965, etc.). Species of \textit{Sciuro-hypnum} differ from species of \textit{Brachythecium} in the mostly small size of plants, almost always autoicous sexual condition (except \textit{S. latifolium}, \textit{S. flotowianum}), and rough seta. Among species of \textit{Brachythecium}, the combination of autoicous sexual condition with rough seta is very rare in Russia and is known only in \textit{B. rutabulum} and in some populations of \textit{B. campestre}.

The present paper is based on revision of herbarium materials from the main Russian herbaria (IRK, LE, MHA, MW, SASY, VLA). A discus-

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sion of molecular phylogenetic data is given after the species descriptions. Specimens examined are generally given by one citation for each administrative unit of Russia.


**Chionobryum** Glow., Oesterr. Bot. Z. 63: 279. 1913. Type: *C. venturii* (De Not.) Glow. (= *Bryum venturii* De Not., = *Sciuro-hypnum glaciale*).

**Cratoneurella** H. Rob., Bryologist 65: 140. 1962. Type: *C. uncinifolia* (Broth. et Par.) H. Robinson, syn. nov. (= *Brachythecium uncinifolium* Broth. et Par., = *Sciuro-hypnum uncinifolium*)

Plants small to large, light to deep green, becoming brownish or rarely whitish with age. Stems prostrate, with central strand, loosely, rarely more densely, julaceously or rarely complanately foliate, irregularly to at places regularly pinnately branched, branches straight or curved, foliage somewhat denser than that of stem and more often complanate. Axillary hairs 2-3(-5)-celled, 1-2 basal cells brownish, 1-2(-3) upper cells hyaline, uppermost cell obtuse, rarely indistinctly tapered to distal end. Pseudoparaphyllia acute to shortly acuminate. Stem leaves loosely to closely imbricate, erect to patent or reflexed, ovate to ovate-lanceolate, acuminate or acute, indistinctly plicate to smooth; margin serrate to subentire; costa reaching mid-leaf to percurrent, ending without spine, more rarely in a spine; laminal cells ovate to linear, thin- to moderately thick-walled, smooth (except *S. starkei*); alar cells isodiametric, large and thin-walled or small and thick-walled, alar group isodiametric, gradually transiting to laminar cells, more rarely sharply delimited. Branch leaves narrower than stem leaves, with more strongly serrate margins and costa more often ending in a spine. Autoicous, very rarely dioicus. Perichaetial leaves with reflexed acumina. Seta rough or very rarely smooth. Capsule inclined to horizontal, more rarely erect. Annulus separating by fragments. Operculum conic, more rarely shortly rostrate. Peristome xerocastique, perfect. Spores small. Calyptra naked. Hygromesophytic to xeromesophytic.

The genus includes ca. 40 species, distributed in all continents, but mostly in cold climates of both hemispheres (only one species, *S. plumosum*, is widespread in temperate zone and tropical mountains (at alpine, but also at middle elevations).

Ochyra et al. (2003) claimed that the genus *Sciuro-hypnum* should be abscribed to Hampe, not to (Hampe) Hampe. This change looks small, but leads to a change of generitype from *Hypnum* (*Sciuro-hypnum*) *plumosum* to *Sciuro-hypnum borgenii* Hampe, which would result in a major taxonomic change. Contrary to that, Ignatov & Huttenen suggested invoking Art. 33.2 of the Saint Louis Code, so the generic name is treated as a transfer from *Hypnum* subgen. *Sciuro-hypnum* 1867. Thus, the present circumscription of the genus *Sciuro-hypnum* is given the authority citation (Hampe) Hampe.

1. Costa reaching 0.8-1.0 of leaf length ...... 2
   — Costa reaching 0.3-0.8 of leaf length ...... 8
2. Leaves lanceolate to ovate-lanceolate; basal cells relatively small and uniform across leaf base, forming opaque area across leaf base (rarely below small cells in leaf corners there are few enlarged pellucid cells) ................. 3
   — Leaves ovate to ovate-triangular; basal cells more or less enlarged, but if only weakly so, then they not forming opaque area across leaf base ................................................. 5
3. Leaves reflexed, with acumens secund, or sometimes turned to all sides; Far East ...... 4. *S. uncinifolium*
   — Leaves straight, not secund; throughout Russia ................................................. 4
4. Operculum conic; autoicous; leaves gradually tapered to apex and gradually transiting to acumens; costa percurrent in more or less stiff acumens; plants usually yellow- to brownish-green; throughout Russia ..... 3. *S. populeum*
   — Operculum rostrate; dioicous; leaves lanceolate to broadly lanceolate, rather abruptly shortly acuminate; costa vanishing at base of acumens or within it, but usually not filling it, so the most apical part is rather slender and sometimes twisted, especially in branch leaves; plants usually pure green; Caucasus and Kaliningrad Province ...... 2. *S. flotowianum*
5. Median laminal cells 8-15:1; alar cells enlarged, clearly delimited; stem rather regu-
larly branching; branch leaves rigidly spreading ............................... 13. *S. starkei*

- Median laminal cells 3-7(-10):1; alar cells not enlarged or if enlarged not forming clearly delimited group; branch leaves appressed or more rarely spreading, but not so rigidly and regularly (rather rigidly only in *S. altaicum* that has no regular branching) .................. 6

6. Branch leaves rigid, widely spreading to reflexed; Altai and Kuznetsky Alatau .......... ................................. 9. *S. altaicum*

- Branch leaves appressed to erect, rarely erect-opatent; widespread species .................. 7

7. Plants irregularly and sparsely branched; stem leaves closely imbricate, acute or very short-ly acuminate from broadly ovate or ovate-triangular base, shortly and narrowly decurrent; quadrate alar cells in relatively small group, not much enlarged; arctic-alpine species .... .......................... 10. *S. glaciale* p.p.

- Plants rather regularly pinnately branched; stem leaves rather distant to loosely imbricate, longly acuminate from ovate to deltoid base, broadly and longly decurrent; quadrate alar cells usually enlarged, sometimes not enlarged; widespread species ........... 8. *S. reflexum*

8. Leaves ovate-lanceolate, concave-channeled, straight or occasionally secund; subquadrate cells forming extensive opaque area across entire leaf base (sometimes cells in leaf corners enlarged, but in this case they are separated from laminal cells by more or less broad belt of small cells, similar to juxtacostal basal cells); plants often rich golden or sometimes copper-red ............ 1. *S. plumosum*

- Leaves from ovate or broadly ovate base relatively abruptly acuminate, or broadly ovate and acute or apiculate; plants mostly green, occasionally yellowish or brownish .......... 9

9. Alar cells moderately thick-walled, so alar group or all cells across leaf base look opaque .................................................. 10

- Alar cells thin-walled, forming more or less conspicuous pellucid group in leaf corners or just proximal to decurrency .................. 12

10. Robust moss with reflexed leaves; Far East ........................................... 5. *S. brotheri*

- Leaves erect-appressed (occasionally erecto-patent) ............................................. 11


- Leaves slightly to moderately concave, ovate-lanceolate, acuminate; plants loosely to close-ly foliate, sometimes imbricate; mountain species, growing in Caucasus in upper forest belt and in Chukotka .... 7. *S. oedipodium*

12. Plants medium-sized to large, loosely foliate; branch foliage ±complanate; leaves serrate; alar group slightly to moderately delimited; capsule elongate-cylindric, horizontal to pen- dent ........................................................................ 6. *S. curtum*

- Plants medium-sized, densely foliate, so stem and branches imbricate to julaceous; leaves entire or serrulate; alar group well delimited; capsule relatively shortly elongate to ovoid, inclined to horizontal ........................................ 13

13. Plants pale green or yellow-green to whitish; leaves acuminate to longly apiculate, entire, ovate-triangular, slightly concave, appressed or erect; usually dioicous .......... 12. *S. latifolium*

- Plants green; leaves broadly acute and usually shortly apiculate, serrulate, broadly ovate-triangular, strongly concave, resulting in julaceous habit of plants; autoicous ................ 12. *S. ornellanum*


Illustrations (based on Russian material): Ignatov (1998); Ignatov & Ignatova (2004).

Plants small to medium-sized, in rather dense or loose tufts, deep green, brownish to bronze or reddish golden, not rare with reddish ferruginous spots on some of leaves, usually glossy. Stems prostrate, to 5 cm long, rather densely foliate, irregularly branched, branches ter-ete foliate, to 6 mm long. Axillary hairs 3-4-celled, to 55-80 x 9-11 μm. Stem leaves erect-appressed to erect, dense-
ly to moderately densely imbricate, straight or somewhat falcate, 1.4-2.0 x 0.4-0.9 mm, ovate-lanceolate or lanceolate, widest at 1/4-1/7 of leaf length, concave or in narrower leaves concave-channeled, gradually tapered to apex, shortly acuminate, slightly rounded to base, rather narrowly decurrent, smooth or indistinctly plicate, costa to 0.35-0.65 of leaf length, 35-60 μm wide at base, fastly narrowing in its lower portion, ending smoothly or in a small indistinct spine; margin serrulate, plane or recurved just above leaf insertion; laminal cells 30-80 x 5.5-9 μm, elongate, often somewhat flexuose, smooth; basal cells in 3-7 rows across the base, shortly ovate, ca. 10 μm wide, thick-walled, forming opaque area across the base; sometimes few cells in leaf corners below opaque zone are larger and transparent. Branch leaves smaller, margin more strongly serrate. Autoicous; sporophytes frequent. Seta cherry red, 12-24 mm, rough, but sometimes weakly so. Capsule reddish brown, slightly to moderately inclined, cherry red, 12-24 mm, rough, but sometimes weakly so. Spores 14-19 μm.

SPECIMENS EXAMINED: EUROPE: Bashkoria: Kuyantavskie Bolota, 980 m, 29.VI.1996 Baisheva (MW); Karelia: Pudozh Distr., Vodlo 30.VIII.1976 Volkova (LE); Perm Prov.: Basegi reserve, Vitva Riv-er, Ignatov & Bezgodov #171 (MHA);

CAUCASUS: Kabardino-Balkaria: Malyj Che-gem, 890 m, Ignatov et al., #05-1601 (MHA); Kara-chaevo-Cherkessia: Teberda Reserve, Amanauz Riv-er, 2000 m 7.IX.2005 Ignatov (MHA); Kransnodar Ter-ritory: Temryuk, Golub #557 (MHA);

ASIA: Altai Rep.: Bolshoi Shaltan Creek 540 m, 7.VI.1989 Zolotukhin (MHA); Kayakkatuoryskij Creek 2100 m, Ignatov #7/134 (MHA); Ust-Sema 350 m, Ignatov #24/119 (MHA); Buryatia: Turali Cape, 26.VIII.1956 Bardunov (MHA); Chita Prov.: Batakan 28.VIII.1963 Bardunov (MHA); Chukotsky Autono-mous District: Zalif Kresta, Aegvekinot, 19.VIII.1977 Afonina (LE); Inachpak Cape, Chelyuskin Strait (64°46’N, 172°47’W), 29.VIII.2001 Afonina (LE); Vran-gel Island, upper course of Neizvestnaya River, 26.VII.1987 Sekretareva (LE); Kamechskaya Prov.: Ostryj Tolbachik, 570 m, 6.VIII.2006 Czernyadjeva #8 (LE); Bannaya River, 250 m 12.VIII.2002 Czernyadjeva #67 (MHA); Irkutsk Prov.: Snezhnaya River 17.VII.1960 Dutina (MHA ex IRK); Khakasia: Askiz Distr., Malyj Zub Mt. 850 m 21.VIII.1970 Vasiliev (MHA ex IRK); Khabarovsky Territory: Upper Bureya River, 1600 m, Ignatov #97-131 (MHA); Primorsky Territo-ry: Olkhovaya Mt., 520 m, Ignatov et al., #06-2419 (MHA); Sakhalinskaya Prov.: Kuril Islands, Kunashir, Tyatya Volcano, 1250 m, Ignatov #06-1842 (MHA); Taimyrsky Autonomous District: Kotuy River, Fedosov #05-167 (MW).

Habitats. Wet and shaded rocks, especially cliff and rock outcrops besides creeks, including temporarily flooded ones, occasionally wet soil; in Far East (as well as in China and Japan) also sometimes on bark of tree bases and fallen trunks. From sea level to 2650 m (Caucasus); 2100 m (Altai); 1650 m (Khabarovsky Territory); 1450 m (Kunashir).

Distribution. Nearly cosmopolitan species, known from all continents from Arctic (e.g. in Chukotka) to tropics where it occurs at high and middle elevations (in Hawaii, Papua New Guinea, etc.). In Russia it is widespread in mountain areas, avoiding lowland regions where rocky substrates are rare; records from the Middle European Russia other than from Ural Mts. (Ignatov & Ignatova, 2004) are based on misidentifications or unconfirmed literature records.

Differentiation. In most cases Sciuro-hypnum plumosum can be identified under the stereomicroscope or hand lens by its rich yellow-brown color with ferruginaceous or copper-red strips, frequent presence of sporophytes with rough seta and also the characteristic leaves. The last are ± rigid, ‘very strict’ due to being ‘shallowly channeled’ throughout, and never plicate (although plicae may be seen in microscope slides due to not flat leaf, especially leaf base). Microscopic characters include (1) thick walls of laminal cells; (2) relatively short leaf cells; (3) opaque basal cells; and (4) costa broad in lower part of leaf and quickly narrowing above.

Worldwide this species is very polymorphic, but within each region the variability is relatively small. The species is variable especially in the width of leaves as well as in their falcateness. Plants from dryer habitats (especially from trunks in East Asia, including Russian Far East) have more narrow leaves and narrower cells and were described as ‘Brachythecium densirete’ that however do not require taxonomic recognition (Ignatov & Koponen, 1996). Superficially they are similar to S. populeum.

Northern populations from ± permanently wet rocks have sometimes strongly falcate leaves. Northern and alpine plants often have broad leaves abruptly contracted to narrow acumen. In such phenotypes, small basal cells sometimes are restricted to leaf corners, not reaching the costa.
The intergradation between these extremes does not allow to segregate them in a satisfactory way, although special study on this variability was not yet done.


Type: Germany (see Karttunen, 1990).


Plants rather small to medium-sized, in rather dense or loose tufts, light green, yellowish to brownish with age, glossy. Stems prostrate, to 5 cm long, rather densely foliate, irregularly branched, branches terete foliate, to 6 mm long, but often most branches are sympodial, with indefinite growth. Axillary hairs 3-celled, to 60 x 10 μm. Stem leaves erect-appressed to erect, densely to moderately densely imbricate, straight, 1.2-1.9 x 0.35-0.85 mm, ovate to lanceolate, widest at 1/4–1/7 of leaf length, more or less fastly contracted to short acumen, more or less fastly contracted to short acumen, often twisted below apex, not or only slightly narrowed to insertion, shortly decurrent, concave (broader leaves) or concave-channeled (narrower leaves), smooth, costa to 0.75-0.95 of leaf length, 50-75 μm wide at base and remains quite wide almost throughout, ending in a spine; margin serrulate to serrate, recurved at places, often at considerable distance; laminal cells 45-75 x 6-8 μm, longly rhombic to elongate, thick-walled; basal cells

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Fig. 1. Sciuro-hypnum flotowianum (Sendtn.) Ignatov & Huttunen (from Krasnodar Territory, Khosta, Ignatov & Ignatova: 1-6,8 – from 5.VIII.2002; and 7, 9-11 – from 1.VIII.2002, MHA): 1 – habit; 2 – upper leaf cells; 3-5 – leaves from small-leaved shoot; 6-7 – mid-leaf cells; 8, 11 – basal leaf cells; 9-10 – leaves from large-leaved shoot. Scale bars: 2 mm for 1; 1 mm for 3-5, 9-10; 100 μm for 2, 6-8, 11.
across the base in 2-5 rows shorter, wider in larger leaves or not wider in narrower leaves, and often with 1 row of more enlarged and pellucid cells still below these basal cells (probably at join with the stem); these most basal cells to 50 x 15 μm. Branch leaves only slightly differentiated, smaller and narrower. Dioicus, sporophytes are not known in Russia. [Seta cherry red, 8-12 mm, rough. Capsules reddish brown, inclined, ovate to oblong, slightly curved, 1.4-1.8 mm long; operculum high conic and moderately longly rostrate, sharp. Spores 14-18 μm].

**SPECIMENS EXAMINED:** **CAUCASUS:** Ingushetia: Lyazhginsky waterfall, 12.VII.2004 Bersanov (MHA); Kabardino-Balkaria: Chegem, 1000 m, 5.VIII.2002 Ignatov, Ignatova & Kharzinov (MHA); Krasnodar Territory: Khosta, 5.VIII.2002 Ignatov & Ignatova (MHA).

**Habitats.** On soil, rocks (limestones) and exserted roots in forest; from sea level to 1000 m alt.

**Distribution.** In Russia this species occurs only in Caucasus and is known also from Kaliningrad Province (Napreenko, in prep.). In the former region it is more or less common along the Black Sea coast, with scattered localities in more inland mountains. Mainly a European species, known from most countries of Central and South Europe, and also in Armenia, Azerbaijan, Georgia, Ukraine.

**Differentiation.** The relationship of *S. flotowianum* with *S. populeum* was neglected for a long time by most authors due to placement of the two taxa in different genera, based largely on the shape of operculum. It seems that only Limpricht (1896) noted their similarity, although also placing them in different genera. The operculum of *S. flotowianum* is more or less rostrate, whereas that of *S. populeum* and *S. plumosum* is usually referred to as conic or high conic with a short, broad beak. In fact, some phenotypes of *S. plumosum* have a capsule shape only little different from that of *S. flotowianum*.

Slender phenotypes of *S. flotowianum* with narrow leaves can be confused with *S. populeum*; however, the former species has leaves distinctly concave in their most portion (vs. slightly concave at base only), leaves broadest at 1/3–1/5 of leaf length (vs. ca. 1/10), more shortly and abruptly (vs. longly and gradually) narrowed to leaf apex and often (vs. never) twisted shortly below apex. Differences in leaf structure result in different foliage: shoots of *S. flotowianum* are more or less closely imbricate, whereas in *S. populeum* leaves are erect and their upper parts extend beyond the ‘closed’ outline formed by closely arranged leaf bases. Also, *S. populeum* is often yellowish, whereas *S. flotowianum* is pure green (at least in Russia where it usually grows in rather shaded places). Dioicus sexual condition, broad costa, concave leaf, and short cells together evidence a similarity with *Cirriphyllum crassinervium*, but that species differs in a costa ending at 1/2–2/3 of leaf length.


Type: Sweden, in G (see Hedenäs, 1996).

Illustrations (based on Russian material): Ignatov (1998); Ignatov & Ignatova (2004).

Plants small to medium-sized, in rather dense or loose tufts, green, yellowish green to brownish yellow, sometimes shiny, especially when young. Stems prostrate, to 5 cm, straight to slightly flexuose, rather densely to rather loosely foliate, more or less regularly branched, branches to 7 mm, straight to slightly curved, terete foliate. Axillary hairs 2-3-celled, to 40-70 x 7-11 μm. Stem leaves erect-appressed to erect, imbricate to somewhat loosely arranged, straight, 1.2-2.0 x 0.4-0.6(-0.8) mm, lanceolate to ovate-lanceolate, widest at 1/7–1/10 of leaf length, gradually tapered to apex, shortly acuminate, slightly rounded to base, moderately broadly and longly decurrent, slightly concave in lower leaf, smooth or indistinctly plicate, with two submarginal plicae, costa to 0.8-1.0 of leaf length, 40-60 μm wide at base, gradually narrowing along its length, geniculate below acumen; margin serrulate to subentire, plane or recurved at places (more commonly at base); laminal cells 25-70 x 6-8 μm, rather thick-walled, elongate or sometimes rhomboidal, ranging from 3:1 to 8:1 in different populations, smooth; basal cells subquadrate and ovate in 3-5 rows, relatively small, 7-12(-15) μm wide, thick-walled, forming opaque area across the base, indistinctly delimited from above cells. Branch leaves smaller and narrower, costa somewhat serrate dorsally, margin more strongly serrate. Autoicus; sporophytes frequent. Seta dark to reddish brown, 8-15 mm, rough, sometimes slightly so, especially in lower part. Capsule dark to reddish brown, slightly to moderately inclined, ovate, slightly curved dorsally, 1.3-1.5 mm long; operculum high conic and sometimes somewhat beaked. Spores 12-16 μm.

**CAUCASUS**: Adygeya: Caucasian Reserve, Pseashko 27.VII.1939 Palamarchuk (LE); Dagestan: Khiv, 18.V.1988 Bochkina (MHA); Ingushetia: Leimi, 14.VII.2004 Bersanova (MHA); Kabardino-Balkaria: Belaya Reczka, 650 m, 25.VIII.2005 Ignatov et al. (MHA); Karachaevo-Cherkessia: Teberda Reserve, Amanauz River 1800 m Ignatov et al. 05-3448 (MHA); Krasnodar Territory: Khodzhokh, 21.VII.1960 Tyuremnov (MW); Severnaya Ossetia: Tsei River 1920 m, L.I. Abramova (MHA).

**ASIA**: Altai Republic: Teletskoye Lake, Karagai, 440 m, Ignatov #0/446 (MHA); Altaiysk Territory: Zmeinogorsky Distr., Sautkhino, 3.VII.1913 N.I. Kuznetsov (LE); Buryatia: Bolshaya Cheremshana River, 25.VII.1956 Bardunov (IRK); Irkutsk Prov.: Slyudyanka, 8.VI.2005 Ignatov & Kazanovskiy (MHA); Kemerovo Prov.: Tisulsuk Distr., Kozhukh Creek, 12.IX.1971 Vasilev (IRK); Khabarovsk Territory: Bolshchekhzhirsy reserve, Korovskaya Mt., 9.VIII.1983 Cherdanrseva & Kutovaya (LE); Khakasia: Kharsip (Karasibo) River, 600 m, 12.VII.1968 Bardunov (IRK); Krasnoyarsk Territory: Eniseisk, 1912; Zhuravlev (LE); Primorsky Territory, Oklhovaya Mt., 1450 m, Ignatov & al., #06-2578 (MHA); Sakhalinskaya Prov.: Sakhalin, Aniva Distr., Susunai 24.IX.1966 Ardeeva (IRK); Kunashir, Golovnin Volcano, 150 m, Ignatov #06-3190 (MHA).

**Habitats.** Rocks, especially granite boulders, but sometimes also limestones, not rare on concrete faces, occasionally trunks of deciduous trees. From sea level to 2600 m (Caucasus), 2400 m (Altai), 1550 m (Primorsky Territory).

**Distribution.** Throughout Holarctic except Arctic and boreal regions with no rocky substrates. Records from Chukotka and Kamchatka were not confirmed, so in Siberia this is a rather southern species. In Europe it is reported from most provinces (but is absent in the xeric South-East near Caspian Sea and rare in the north); common also in Caucasus. This species occurs in almost all European countries; in North America from Alaska and Greenland to ca. 35-40°N in U.S.A.; in Asia southwards to China (Yunnan, Hunan), Japan, Turkey.

**Differentiation.** Sciuro-hypnum populeum can be recognized by the combination of percurrent costa with the opaque basal cells. This combination is characteristic also for the next species, which has a restricted distribution in the Russian Far East and differs in smaller, curved or reflexed leaves. Growing on wet rocks, S. populeum may have broader leaves, causing a problem of separation from S. reflexum; the latter species however never has all stem leaves strict and erect, as in S. populeum.


Type: Japan, Honshu, in H-BR (see Czernyadjeva & Ignatov, 2006).

Illustrations (based on Russian material): Czernyadjeva & Ignatov, 2006.

Plants small, in dense or loose tufts, green to yellow brown. Stems to 4 cm, prostrate, flexuose, terete foliate, irregularly pinnate branching, branches to 6 mm, straight to slightly curved, terete foliate, glossy. Axillary hairs 3-4-celled, 60-100 x 7-9 μm. Stem leaves closely imbricate, with appressed basal parts and wide spreading to reflexed acumens which sometimes being secund, 0.8-1.3 x 0.4-0.8 mm, ovate or triangular-ovate, widest at 1/8–1/10 of leaf length, gradually or abruptly narrowly acuminate, moderately to distinctly constricted to base, rather narrowly decurrent, not plicate, margin serrulate, plane or recurved below the broadest point of leaf; laminar cells 25-50 x 5-8 μm, elongate, smooth; basal cells across leaf base subquadrate and shortly ovate in 7-10 rows, relatively small, 7-12(-15) x 6-10(-15) μm, thick-walled, forming extensive opaque area; angular cells somewhat more enlarged, forming indistinct group or not apparent. Branch leaves similar to stem leaves. Autoicous; but sporophytes are rare. Perichaetia conspicuous due to widely reflexed inner perichaetial leaves. Seta dark brown, inclined, ovate, slightly curved
Fig. 2. Sciuro-hyphnum brotheri (Paris) Ignatov & Huttunen (from Kunashir, Ignatov, #06-1779, MHA): 1 – habit (dry); 2 – upper leaf cells; 3-4 – mid-leaf cells; 5-6 – stem leaves; 7-8 – branch leaves; 9 – basal leaf cells. Scale bars: 2 mm for 1; 1 mm for 5-8; 100 μm for 2-4, 9.
dorsally, ca 1.5 mm long; operculum conic. Spores 15-18 μm.

**SPECIMENS EXAMINED:** **ASIA:** Kamchatksaya Prov.: Elovka Creek, 100 m, 31.VIII.2003 Czernyadjeva (LE, MHA); Esso, 1260 m, 12.VIII.2003 Czernyadjeva # 93 (LE); Sakhalinskaya Prov.: Sakhalin, Vaida, 600 m, Ignatov #06-103 (MHA); Kuril Islands, Kunashir, Tyaty, 1250 m, Ignatov #06-1746 (MHA); Ruruy, 20 m, Ignatov #06-1941 (MHA).

**Habitats.** On rocks, rotten logs, tree bases.

**Distribution.** In Russia known only from Pacific Islands (Sakhalin, Kurils) and Kamchatka. Outside Russia in Japan and probably China (judging from illustrations, specimens not seen) and Alaska in North America. From sea level to elevation of elfin forests. Sporophytes only from one collection (Belaya River in Sakhalin, 50 m alt., Ignatov #06-194, 06-200).

**Differentiation.** Sciuro-hypnum uncinifolium can be recognized by narrow shoots due to closely appressed leaf bases with rigidly reflexed to squarrose or secund acumens. This species combines the characters of *S. reflexum* (leaf shape and reflexed acumen) and *S. populeum* (opaque cells across the leaf base); according to molecular phylogenetic analysis (see below), it is more close to the latter species.


Protologue: Yezo: Prov. Ishikari, Yyozankei (Tokobuchi n. 221).

Plants medium-sized to robust, in rather loose tufts, light green to yellowish or brownish with age, glossy. Stems prostrate to arching, to 7 cm long, rather densely terete foliate, remotely and irregularly branched, branches terete foliate, to 10 mm long. Axillary hairs 3-4-celled, to 65-90 x 12-15 μm. Stem leaves moderately densely imbricate, spreading below, often with reflexed acumens, when wet usually squarrose, 2.3-2.9 x 1.1-1.45 mm, broadly ovate or ovate-triangular below, widest at 1/7–1/10 of leaf length, gradually or somewhat abruptly tapered to narrow acumen, rounded to cordate base, rather narrowly decurrent, slightly concave below, smooth or indistinctly plicate, costa to 0.5-0.8 of leaf length, 60-80 μm wide at base, ending smoothly or in a small indistinct spine; margin serrulate, plane or recurved just above leaf insertion; laminal cells 70-140 x 6-8 μm; basal cells wider in 5-8 rows across the base, to 15(-20) μm wide, and especially larger just proximal to decurrency, to 25 μm wide, forming conspicuous pellucid group gradually or quite abruptly delimited from neighboring cells. Branch leaves smaller and narrower, margin more strongly serratate. Autoicous, sporophytes rather frequent. Seta cherry red, 15-25 mm, rough. Capsules reddish brown, inclined to horizontal, ovate to oblong, slightly curved, ca. 2.0 mm long; operculum conic. Spores 9-12 μm.

**SPECIMENS EXAMINED:** **ASIA:** Sakhalinskaya Prov.: Sakhalin, Gornozavodsk, IX.1966, Cherdantseva (VLA); Kuril Islands, Kunashir, Tyaty, 200 m, Ignatov #06-1779 (MHA).

**Habitats.** This species grows on soil on slopes of ravines, under tall-herb canopy, and along roads across dense *Sasa* communities, on rotten logs, trunk bases (on *Picea*). It is sporadic in south Kuril Islands, and more rare in Sakhalin. All records were from low elevations, 0-200 m alt.

**Distribution.** Outside Russia *S. brotheri* is known in Japan; it was also reported from China, but this needs to be confirmed.

**Differentiation.** Sciuro-hypnum brotheri can be recognized by large plants, dense terete foliage, reflexed or wide-spreading leaves, costa ending far below apex, long laminal cells (often >100 μm) and relatively narrow decurrencies, not always easily separated from stem.


Illustrations (based on Russian material): Ignatov (1998, as *Brachythecium oedipodium*); Ignatov & Ignatova (2004, as *Sciuro-hypnum oedipodium*).

NB: Ignatov & Milyutina (2007, present volume) found that the species widely distributed in Eurasia and called in recent literature *Sciuro-hypnum* (*Brachythecium*) *oedipodium* belongs in fact to *S. curtum*.

Plants medium-sized to robust, in loose tufts, often forming extensive covers; deep green, more rarely yellowish or brownish-green, glossy. Stems to 10 cm, prostrate or arching, somewhat flexuose, terete foliate, ±regularly pinnately branched; branches to 10 mm, often curved or flexuose, indistinctly to often distinctly complanate foliate. Axillary hairs 2-4-celled, to 120 x 11 μm. Stem leaves patent, loosely arranged, 1.4-2.4 x 0.8-1.5 mm, ovate or ovate-triangular, widest at 1/7–1/10 of leaf length, gradually acuminate, rounded to base,
with decurrencies proximally broad, but fastly tapered and very narrow along most of their length, slightly concave, not or indistinctly plicate, margins plane, serrulate to serrate; costa weak, reaching 0.4-0.75 of leaf length, 40 μm wide at base, ending without spine or in a small spine; laminal cells linear, 70-140 x 7-11 μm, rather thin-walled, basal cells broader and shorter in ca. 3 rows, cells just proximal to decurrency and in broad proximal part of decurrencies larger than juxtacostal basal cells, to 15-40 x 12-18 μm, forming pellucid group that can be quite abruptly delimited or otherwise very gradually transiting to neighboring cells. Branch leaves smaller, ovate, often asymmetric at base and with margin recurved at base on one side, acute, narrowly decurrent; costa often ending in prominent spine and sometimes with several additional teeth dorsally, but in some leaves weak, vanished without any spines, margin more strongly serrulate to coarsely serrate above; basal cells large across the base. Autoicus; sporophytes frequent. Seta reddish, 17-32 mm, rough. Capsule reddish brown, oblong, horizontal to pendent, curved, especially when young (forming sometimes arch of 180-270°), ca. 2.0 mm long; operculum conic. Spores 13-16 μm.

Specimens examined: see Ignatov & Milyutina (2007).

Habitats. In mesic boreal forests (spruce, pine) and tall-herb meadows on litter, debris, soil rich in humus, rotten logs, occasionally mineral soil and tree bases. In spruce forests (with Oxalis acetosella, ferns, Rhytiadiadelphus subpinnatus, Plagiomnium affine, etc.) of European Russia, this species often dominates. Further to the East it is not so common, but having scattered localities in south Yakutia, Amurskaya Province and Kamchatka, where it grows mostly in tall-herb communities (sometimes mixed with conifer trees), as well as in fern-dominated spruce forests. Mainly lowland plant, reaching 1150 m in South Ural, 2050 m in Altai.

Distribution. In Russia, S. curtum occurs throughout the boreal zone, essentially corresponding to distribution of Picea, and avoiding territories with only Larix forests. Additional discussion on distribution and map are given by Ignatov & Milyutina (2007, present volume).

Differentiation. Sciuro-hypnum curtum is very variable in appearance, becoming very slender and loosely foliate in deep shade. It can usually be recognized by: (1) non-plicate, ovate to ovate-triangular leaves; (2) relatively short costa, often ending at 0.4-0.6 of leaf length; (3) pellucid group just proximal to decurrency or sometimes extending to most of leaf base; (4) frequent presence of sporophytes; and (5) strongly curved capsules. Brachythecium rutabulum specimens from deeply shaded habitats may have nearly plane leaves and a habit that superficially resembles S. oedipodium. Brachythecium rutabulum, however, usually is densely foliate in better developed parts, stem leaves are more shortly acuminate and in general their basal part is more ovate and more concave.

Another problem is the distinction of S. curtum from S. oedipodium, which is discussed by Ignatov and Milyutina (2007, this volume).


Illustrations (based on Russian material): Ignatov & Milyutina (2007, this volume).

NB: Ignatov & Milyutina (2007, present volume) found that the species widely distributed in Eurasia and called in recent literature Sciuro-hypnum (Brachythecium) oedipodium belongs in fact to S. curtum, while S. oedipodium is mainly an American species, with a few localities in Eurasia.

Plants medium-sized to robust, in loose tufts, light green to pale green and stramineous, glossy. Stems to 7 cm, ascending, arching, often curved distally, terete foliate, irregularly pinnate; branches to 7 mm, often curved, terete foliate. Axillary hairs 2-4-celled, to 50-100 x 12-15 μm. Stem leaves erect, imbricate or sometimes erectotopatent, 1.3-2.3 x 0.7-1.1 mm, ovate, widest at 1/5–1/9 of leaf length, acuminate, gradually rounded to base, more or less broadly decurrent; concave, not or slightly plicate; margins plane or often recurved below the broadest part of leaf, serrulate; costa moderately weak, reaching 0.55-0.75 of leaf length, ending without spine; laminal cells 50-100(-120) x 8-12 μm, 5-12:1; basal cells near costa broader and shorter in ca. 3 rows, in leaf corner broader, subquadrature to short rectangular, 15-25 x 12-16 μm, moderately thick-walled, forming extensive alar group of 10-15 x 7-10 cells, extending upward and forming proximal part of decurrency. Branch leaves smaller, gradually acuminate, decurrent; costa strong, ending usually without spine, margin slightly serrulate. Autoicus; sporophytes frequent. Seta reddish-orange, 15-20 mm, rough but often rather indistinctly so. Capsule reddish-orange, usually rather shortly ovoid, inclined
to horizontal, not curved or slightly curved dorsally, ca. 1.2-1.5 mm long, operculum conic. Spores 13-16 μm.

Specimens examined: see Ignatov & Milyutina (2007).

**Habitats.** In Caucasus on soil in pine forest and in grasslands in upper forest and subalpine belts, at 2050-2400(-2750) m; in Chukotka in the hot spring area.

**Distribution.** In Russia, *S. oedipodium* is known from few places in Caucasus, at 2050-2750 m alt. and in one locality in Chukotka. Additional discussion on distribution and map are given by Ignatov & Milyutina (2007).

**Differentiation.** *Sciuro-hypnum oedipodium* is characterized by the large size of the plant, relatively densely arranged leaves, costa ending in mid-leaf, numerous subquadrate and not much enlarged alar cells, rough seta, and short capsule.


Illustrations (based on Russian material): Ignatov (1998); Ignatov & Ignatova (2004).

Plants small to rather robust, in loose to rather dense tufts, green to dark, yellowish or brownish green, not glossy or occasionally glossy. Stems 3-6(-15) cm, prostrate to arching, terete foliate, irregularly to fairly regularly pinnate branched; branches 5-10 mm, often curved, terete foliate. Axillary hairs 3-celled, to 120 x 10 μm. Stem leaves more or less loosely arranged, occasionally to imbricate, appressed to stem by their bases and with spreading to reflexed acumen or more rarely reflexing just from leaf base; 1.0-2.0 x 0.5-1.2 mm, deltoid-ovate or ovate, broadest at 1/5–1/8 of leaf length; gradually to abruptly long-acuminate, rounded to base and longly and broadly decurrent; concave in basal part, not pli- cate; margin plane or recurved below, serrat to serrulate throughout or in acumen entire, occasionally sub- entire throughout; costa reaching 0.8-1.0 of leaf length, 40-50 μm wide at base; laminar cells 25-60(-95) x 6-12 μm, towards base wider and forming extensive laxly areolated area, in leaf corners moderately to distinctly enlarged (to 20 x 15 μm), forming moderately pellucid to moderately opaque area. Branch leaves usually closely imbricate, narrowly ovate to lanceolate; margin more strongly serrat, costa ending in a spine. Autoicous, sporophytes frequent. Seta 8-13 mm, rough. Capsule dark red-brown or occasionally rather light brown, inclined to horizontal, shortly ovate to occasionally ovate-cylindric, and if longer then curved, 1.0-1.5 mm long; operculum conic. Spores 11-21 μm.

SPECIMENS EXAMINED: EUROPE: Archangel, Kargopol, 4.VII.2001 Churakova (MHA); Bashkortostan Republic: Bretyak, 500 m, 12.IX.1990 Ignatova (MHA); Belgorod Prov.: Nature Reserve 'Les na Vorskle’ 1.VII.2003 Nemykin (LE); Chelyabinsk Prov.: Troitsky training forestry station, 14.VII.1989 Bezdgov #34 (MW); Chuvashia: Prisursky Reserve, V.1999 Moshkovsky (MHA); Kaluga Prov.: Zhukovsky Dist., Olkhovo 20.IV.1986 Bochkin (MHA); Karelian Republic: Poyakonda, 30.VII.1985 L.I. Abramova (MW); Komi Republic: Pechero-Ilyshsky Reserve, Smirnova #119 (MW); Kostroma Prov.: Manturovo Dist., Khalbuzh 20.VIII.1997 Lazareva (MHA); Kursk Prov.: Kazatskaya Steppe, 200 m, 14.VIII.1996 Ignatov (MHA); Leningrad Prov.: Shugovitsy 14.V.1985 Ignatov (MHA); Mari El Republic: Nature Reserve ‘Bolshaya Kokshaga’, 23.VIII.1998 Czennaydjava (LE); Moscow Prov.: Solnechnogorsk Dist., Sergeevka 29.V.1986 Ignatov (MHA); Murmansk Prov.: Polar-Alpine Botanical Garden, 31.VII.1998 Ignatov & Ignatova (MHA); Nenetsky Autonomous District: Bolsheyemelskaya Tundra, Varandei-Eeni-Laya, 23.VII.1931 Sambuk & al. (LE); Nizhnij Novgorod Prov.: Kerzhensky Reserve, 100 m, 11.X.1999 Ignatov (MHA); Novgorod Prov.: Valdai Dist., 27.VI.1983 Morozova (MHA); Perm Prov.: Vishera State Reserve, Bolshaya Moiva River, 470 m, 28.VI.1994 Bezdgov (PPU); Pskov Prov.: Mikhailovskoye 17.VII.2005 Afonina (LE exs 243 ex MHA); Ryazan Prov.: Ryazan 19.VII.1996 Ignatov (MHA); Saratov Prov.: Zhiguli, 26.VII.1945 Semenova-Tian-Shanskaya (LE); Sverdlovskaya Prov.: Ivdel Dist., Blagodatsk, 1.VIII.1948 Gorchakovskiy (LE); Tatarstan, Volzhsko-Kamsky Reserve, 50-100 m, 16.VIII.2003 Ignatov & Ignatova (MHA); Tula Prov., Krapivina, Seregin #M-945 (MHA); Udmurtia, Malopurginsky Dist., Gozh- nya, 6.VII.2000 Puzyrev (MHA); Vladimir Prov.:
A revision of the genus Sciuro-hypnum in Russia

Fig. 4. Sciuro-hypnum reflexum ‘var. pacificum’ (1-3 – from Kamchatka, 20.VIII.2004 Czernyadjeva #103, MHA; 4 – from Novosibirsk Prov., 16.VII.1995 Pisarenko, IRK); 1 – stem leaf; 2 – habit; 3 – mid-leaf cells; 4 – basal leaf cells. Scale bars: 2 mm for 2; 1 mm for 1; 100 μm for 3-4.

Vladimir, Seregin #М-137 (MHA); Vologda Prov.: Sokol Dist., Shorega Creek, 22.IX.1990 Ignatov (MHA); Voronezh Prov.: Voronezhsky Reserve, 9.VII.1982 Popova (MHA).

CAUCASUS: Adygea: Oshten Mt., 1700 m, 20.VII.1935 Vasilieva (LE); Kabardino-Balkaria: Adyl-Su River, 2650 m, X-1994 I.Pospelov #33 (MW); Karachaevo-Cherkessia: Tebersdinsky Reserve, 2850 m, Ignatov & Ignatova #05-3228 (MHA); Krasnodar Territory: Caucasian Reserve, Abago Mt., 1860 m, 6.VII.1960 Artamonov (MW); Caucasian Reserve, As-sara Peak, 19.VII.1951 Ariskina (LE).

ASI: Altai Republic: Ayukol, 1450 m, Ignatov #0/1637 (MHA); Altaiisky Territory, Riddera, 25.VIII.1947 Polyakov (MHA); Buyatin: Chivyrkuy, 20.VIII.1991 Anenkonov (MHA); Chita Prov.: Kyrinsky Distr., Sokondo, 1700 m, VI-1990 Arbuza (MW); Chukotsky Autonomous District: Anadyr Distr.: Dlin-naya River 10.VII.1988 Kuzmina (LE); Irkutsk Prov.: Kumerma River, 10.VII.1983 Bardunov (MHA); Khabatskaya Prov.: Pushchino, 13.IX.1978 Afonina (LE); Khabarovsky Territory: Upper Bureya River, Medvezh’e Lake, 1600 m, 9.VIII.1997 Ignatov (MHA); Khanty-Mansiysky Autonomous District: Berezo-

Habitats and Distribution. The species grows on fresh fallen logs, stumps, and tree bases of...
leafy, more rarely coniferous trees, and also on rocks and on soil in forests and under tall-herb vegetation. Up to 2850 m (Caucasus), 1900 m (Altai), 1600 m (Sikhote-Alin).

*Sciuro-hypnum reflexum* is a very common species in many regions of Russia, being absent however in most territory of Yakutia, where it is known only in most southern and western parts of this region. It is apparently absent also in more continental parts of Chukotka and Magadan Province, neighboring to Yakutia. Also *S. reflexum* is absent in xeric regions of Lower Volga River and lowlands of Cis-Caucasus, and, from the other side, in high Arctic islands.

The habitat preference of *S. reflexum* is somewhat shifting from Europe to Asia. In Central European Russia this is a species characteristic to hardwood trunk bases, and in this region it is more
common in hemiboreal and north temperate types of forest, than in boreal ones. In Kola Peninsula and Ural, in wet cold mountain climate, *S. reflexum* is exceedingly common and grows ‘everywhere’ in *Betula* and *Picea* forests, on tree bases, fallen logs, rocks and also litter.

In eastern part of Russia, *S. reflexum* occurs at lower elevations mainly in oceanic climate in Kuril Islands and Kamchatka, whereas in Khabarovsk and Primorsky Territories it occurs at higher elevations, 1000-1600 m, rather avoiding hardwood-coimifer and hardwood forests at lower elevations. This is quite a contrast with European Russia and western part of Siberia (and Eastern North America), where bases of broad-leaved trunks are the most common substrate for this species.

This inconsistency in ecology may indicate the presence of cryptic species; however, our attempts to delimit any group within the *S. reflexum* s.l. were not successful.

Variation. The most common phenotype of the species, occurring throughout Northern Hemisphere and most common in Europe, is that of relatively small plants with curved branches having rather julaceous foliage and short laminal cells.

There are two more or less contrasting phenotypes that correspond with ‘Brachythecium reflexum’ var. *pacificum* (Fig. 4) and ‘Brachythecium *jeniseense*’ (Figs. 3–4), and for ease of discussion called ‘var. *pacificum*’ and ‘*jeniseense*’, whereas the most common phenotype called ‘typical *S. reflexum*’.

‘Var. *pacificum*’ is more common in the western North America and north of Russian Far East. It includes plants with long stems that are regularly but distantly branched. The leaves have a very long acumen and laminal cells 50-80(-95) μm long. Some collections look very different from the ‘typical *S. reflexum*’. However, our attempts to sort out ‘var. *pacificum*’ from ‘typical *S. reflexum*’ was not successful due to too gradual transition between them. According to labels, ‘var. *pacificum*’ grows usually on soil in meadows, in the environment with the stable humidity during the plant development. Plants from other regions in similar habitats also often have longer laminal cells comparatively with plants from trunks, rocks and fresh logs (i.e. developed in the situation of fluctuating humidity).

In analysis of nuclear ITS we found three specimens with one peculiar substitution in ITS2, and all three belong to ‘var. *pacificum*’. However some other collections of ‘var. *pacificum*’ do not belong to this haplotype (Figs 6, 7). Therefore at moment we hesitate to segregate ‘var. *pacificum*’ even at the status of variety due to absence of clear morphological delimitation.

A second phenotype strikingly different from ‘typical *S. reflexum*’ is that of ‘*jeniseense*’. This is a large plant of the size of *Sciuro-hypnum curtum*, with large stem leaves, but usually contrastingly smaller branch leaves. Stem leaves are not appressed by their bases, often spreading at wide angle from their bases and then gradually reflexed; they are rather soft and twisted when dry; branch leaves are appressed to erect. Basal areolation of stem leaves is very lax, cells very variable, often rather narrow, cf. 10:1; branch leaves are usually narrowly acute, and their laminal cells are usually rather short, ca. 4:1. When the whole specimen is composed of shoots with enlarged leaves it looks totally different from the ‘typical *S. reflexum*’. However during our study we saw in some collections of rather ‘typical *S. reflexum*’ individual shoots with much larger leaves reflexing from their base, and also in collection of mostly ‘*jeniseense*’ certain sympodial shoots approaching to ‘typical *S. reflexum*’ (leaves smaller, with appressed bases).

Lindberg & Arnell (1890) indicated close affinity of *Hypnum *jeniseense* to *S. reflexum*, but noted that the former differs from the latter in larger plant size, more lax leaf areolation and longer cells, more weakly serrulate leaf margin, and more weakly roughened seta; however these characters are variable and can not be diagnostic for a separate species. Dioicous sexual condition of *Hypnum *jeniseense*, mentioned in its protologue, was incorrectly identified, as well as costa that was described as ending in mid leaf. Sometimes costa is not reaching leaf apex, but in most leaves it is disappearing in narrow part of acumen, although very weak above and difficult so see as acumen is usually turned and folded in slides.

It seems that the development of phenotype of ‘*jeniseense*’ is also dependent on more wet condition of growth and at least sometimes is raising after a shoot damage. A certain analogy with the vegetative shoots in *Salix* bearing sometimes drastically enlarged leaves would probably be appropriate. Therefore a taxonomic segregation
of these plants is not necessary. As we think that Hypnum (Brachythecium) jeniseense (Fig. 3) is an example of this phenotype, so this name is here reduced to synonymy with S. reflexum. Ignatov, Afonina, Ignatova et al. (2006) incorrectly synonymized Hypnum jeniseense with S. starkei. Plants that more or less agree with ‘jeniseense’ are especially common in Kamchatka, Kuril Islands and wet regions in South Siberian mountains. In Caucasus and Urals, there are plants with the densely arranged and rather rigid, large, broadly ovate stem leaves with narrow laminal cells, while branch leaves are rather similar to ‘typical reflexum’, including short laminal cells. ITS sequence data indicate their position among S. reflexum (see Figs. 6–7, under ‘cf. jeniseense’).


Type: Russia, Altai, in H-BR (cf. Ignatov, 1998).

Illustrations (based on Russian material): Ignatov (1998), as Eurhynchium altaicum and also as Brachythecium reflexum from Kaitanak.

Plants medium-sized, in loose tufts or growing by solitary plants, dark or yellowish or brownish green, not glossy. Stems prostrate, to 8 cm long, loosely foliate, remotely and irregularly branched, branches to 14 mm long, terete foliate. Axillary hairs 2-4-celled, to 40-100 x 9–12 μm. Stem leaves rigid, spreading to squarrose, 1.3–1.9 x 0.6–1.1 mm, broadly ovate-triangular, widest at 1/6–1/10 of leaf length, acuminate, broadly rounded to cordate at base; longly and moderately narrowly decurrent; not concave, not plicate; costa reaching >0.9 of leaf length, 70-100 μm wide at base, ending smoothly or occasionally in a spine; margin recurved below, serrulate throughout; laminal cells 20-60 x 4-10 μm, very uneven, rather thick-walled; towards base cells wider and shorter in several rows; in leaf corner wider, forming more or less distinctly delimited alar group. Branch leaves smaller and narrower, more gradually acute, with costa ending in strong spine or several spines or occasionally without spine. Autoicous; sporophytes frequent. Seta rough, 10–15 mm. Capsule inclined to horizontal, ovate, 1.0–1.4 mm long; operculum conic. Spores 18–20 μm.

SPECIMENS EXAMINED: ASIA: Altaisky Territory: Zmeinogorsk Distr., Malaya Belaya River, 16.VI.1910 Keller (H-BR 3027); same, 17.VIII.2004 M.S. & M.M.Ignatov (MHA); Altai Republic: Tarota Range, 1250 m, 14.VIII.1944 N.Lebedeva (MW);

Kaitanak River, 1500 m, 10.VII.1966 A.G.Krylov & Reezan (LE, MHA); Kemerovo Prov.: Kiya River, 400 m, 6.IX.1971 A.Vasiliev (IRK, MHA).

Habitats and Distribution. This species has been described originally by a single plant found among collections of Keller from 1910 identified by Brotherus as Oxyrrhynchium praelongum [Eurhynchium praelongum, Kindbergia praelonga]. In 2004 M.S.Ignatov & M.M. Ignatov undertook an expedition to the locus classicus and found this species, although only in small quantity. The species grows here in a restricted area where a slightly elevated mountains (ca. 510 m elev. in valleys) are covered by quite soft deposits, and small streams have quite deep beds, surrounded by wall-like banks. All the collections were made from these banks, on humus-rich soils. However, additional collections allow to understand the variation of the species and link to it some unusual specimens placed in S. reflexum with question-mark. The latter are more branched than plants from type locality, and have more strongly reflexed both stem and branch leaves; costa, as has been revealed, is usually percurrent although when ending below is ending in a spine. All the collections are from the especially humid areas of the West-faced macroslope of Altai and Kuznetsky Alatau, at 400-1500 m elevation, on soil in Abies+Pinus sibirica or Betula+Picea forests.

Differentiation. The sequence of ITS of S. altaicum was found to be totally identical with some populations of S. reflexum. This raises the value of similarity between them in at least: (1) short cells; (2) subpercurrent costa; (3) broad decurrency; and (4) short capsule. However, S. altaicum is: (1) usually larger than S. reflexum; (2) has peculiar rigid and strongly spreading both stem and branch leaves; and (3) the costa of the branch leaves ends in a spine or several spines. The distinction from Kindbergia praelonga (with which the species was originally compared) includes: (1) free or loose-pinnate branching with no clear differentiation between stem and branch leaves; (2) very rigidly squarrose leaves; (3) very narrow leaf decurrencies; (4) autoicous sexual condition; and (5) short pseudoparaphyllia.

Widely spreading leaves are characteristic for the S. reflexum ‘jeniseense’ that differs from S. altaicum in (1) not so strongly reflexed stem leaves; (2) erect (vs. reflexed) leaves of well-de-
veloped branches; (3) leaves not so strongly con- 
traced to base; (4) wider area of lax areolation in 
the leaf base, and (5) often elongate stem leaves.


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the leaf base, and (5) often elongate stem leaves.

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veloped branches; (3) leaves not so strongly con-

Variation. The costa is variable in S. glaciale s.l., ranging from ending in mid-leaf to percurrent, the latter described by Limpricht as Brachythecium glaciale var. dovrense (‘ dovrense’). Nyholm (1965) also accepted Brachythecium dovrense as a variety of B. glaciale, Loeske (1910) – as a variety of B. reflexum, Amman (1918) and Schljakov (1952)
– as a separate species.

According to Limpricht (1896) and Nyholm (1965), ‘var. dovrense’ is a small plant (Nyholm suggested also its possible origin through the hybridization of S. glaciale and S. reflexum), whereas in Russia the subpercurrent costa is more characteristic of large plants.

The intraspecific variation of S. glaciale in Russia is difficult to study, as it is known from most of regions only by a few collections, each being relatively uniform, but somewhat different from another ones. Some populations from Caucausus and Kola Peninsula have both plants with short and long costa. This situation precludes segregation of ‘var. dovrense’ as a separate taxon until additional characters will be found.


Lectotype: NW Russia, Kola Peninsula, in H-SOL (Draper & Hedenäs, in perss).

Illustrations (based on Russian material): Ignatov (1998); Ignatov & Ignatova (2004).

Plants medium-sized, in loose tufts, light green to yellowish-green and often to whitish. Stems to 6(-12) cm, prostrate to ascending, terete foliate, irregularly to rather regularly pinnate branching, branches to 8(-15) mm, straight to curved near their ends, terete foli ate. Axillary hairs 2-3-celled, to 60 x 9 μm. Stem leaves imbricate, erect-appressed or occasionally erect-sprea ding, 1.4-2.2 x 0.7-1.3 mm, ovate-triangular, widest at 1/5–1/8 of leaf length, gradually tapered towards apex or broadly rounded, abruptly shortly and narrowly acuminate, sometimes with strongly serrate ‘shoulders’ at base of acumen; rounded to base and decurrent in broad pellucid alars; slightly to moderately concave, not or slightly plicate; margin mostly plane, entire or minutely serrulate in acumen and especially in place of abrupt tapering of leaf below acumen; costa to 0.4-0.7 of leaf length, 30-45 μm wide at base, ending without spine; laminal cells elongate, 30-75(-100) x 6-10 μm, moderately thick-walled, smooth; basal cells near costa short or long rectangular in 2-3 rows, slightly broader than laminal cells, to 12 μm wide, cells in leaf corners to 30-50 x 15-20 μm, pellucid, abruptly delimited, forming conspicuous alar group reaching 1/2–2/3 distance to costa. Branch leaves similar, but smaller and narrower, almost entire, costa ending without spine. Dioicus, sporophytes unknown [Seta reddish orange, 20-25 mm, rough. Capsule orange brown, inclined to horizontal or slightly pendent, ovate, curved dorsally, to 1.8 mm long, operculum high conic. Spores 13-16 μm].


ASIA: Altai Republic: Kobiguyuk Creek, 2550 m, Ignatov #0/400 (MHA); Chukotsky Autonomous District: Gilmimliveem, 18.VII.1977 Afonina (LE); Kamchatskaya Prov.: Klyucheskaya group of volcanoes, 19.VIII.2005 Czernyadyeva #40 (LE); Khabarovsky Territory: Ayan 25.VIII.1989 Cherdantseva (MHA); Khanty-Mansijsky Autonomous District: Ural, Khulga Creek, basin of Severnaya Sosva 21.VIII.1926 Gorokhov (LE); Magadan Prov.: Ola Distr., 7.IX.1977 Blagodatskiikh (LE); Yamalo-Nenetsky Autonomous District: Tazovsky Peninsula, 14.VIII. 1986 Rebristaya (LE); Polar Urals, Sob River, 30.VII.1924 Gorokhov (LE).

Habitats. Soil, rocks, and among other mosses in various mires in arctic, alpine or northern boreal environments.

Distribution. This species has a scattered arcto-alpine distribution in more northern parts of Holarctic. It is rare in mountains of Central Europe, moderately rare in Scandinavia and Kola Peninsula and NE European Russia; in mountains of South Siberia it is known by single collections, but in Kamchatka and some neighboring areas of the Russian Far East this species is common. Similarly it is not very rare in Pacific North America, where it is spreading in high mountains southward up to Colorado and New Mexico. Also S. latifolium occurs in Greenland and Iceland.

Differentiation. Sciuro-hypnum latifolium has alar cells that are ± abruptly differentiated, as in B. rivulare, and the original description compares it to this species. However S. latifolium differs from B. rivulare in its smaller plants, entire leaves, and shortly, but abruptly acuminate leaves. Superficially, S. latifolium is somewhat similar to S. glaciale (especially ‘var. gelidum’ cf. Nyholm, 1965) sharing the characters of concave and appressed leaves. However, the latter species has small alar cells and wider laminal cells.

The narrow laminal cells is a character that is common for S. latifolium and S. starkei. These two species are quite distinct morphologically, but have surprisingly identical ITS sequences.

Variation. Usually S. latifolium is easy to recognize by quite pale color of plants, acute upper leaves, more broad leaves in older parts of stem,
and often having a peculiar small and very narrow acumen that is usually somewhat reflexed. Leaves are often appressed, but when growing among tall herbs (in wet meadows), stem turns to much elongate and leaves erectopatent.

This species has been described as dioicous and all the subsequent authors confirmed this. Most of its collections are sterile or bearing only female inflorescences. However, an autoicous specimen was found: Yamalo-Nenets Autonomous District, 66°N–74°E, Medvezhie, Khaeya-kha Creek, 20.VII.1989 Khusainov (MHA). In all other characters this specimen does not differ from \textit{S. latifolium}. We can add nothing to the moment to discussion of this strange case, except that related species, e.g. \textit{S. glaciale} and \textit{S. ornellanum}, are autoicous but produce sporophytes rather rarely, at least in Russia, probably because of under-expression of male sex. Thus it is difficult to deny that at least some populations of \textit{S. latifolium} are autoicous but with under-represented male gender.


Type: Italian Alps (see Ignatov, 1998).

Illustrations (based on Russian material): Ignatov (1998).

Plants medium-sized, in loose tufts, green to light green, moderately glossy. Stems to 8 cm, prostrate to ascending, terete foliate, irregularly to rather regularly pinnate branching, branches to 10 mm, straight to curved, terete foliate. Axillary hairs 3-celled, to 90 x 9 μm. Stem leaves imbricate, 1.0-1.4 x 0.7-1.1 mm, broadly ovate, widest at 1/5–1/7 of leaf length, broadly acute and often shortly apiculate, rounded to base and broadly decurrent, strongly concave, not or slightly plicate, margin plane or recurved below, serrulate to subentire; costa to 0.2-0.7 of leaf length, ca. 40 μm at base, broad below but fastly narrowing above, ending without spine; laminar cells elongate, 25-90 x 5-8 μm, rather thick-walled; basal cells indistinctly broader and shorter in few rows, cells proximal to decurrency subquadrate to short-rectangular, relatively thin-walled, 20-35 x 15-25 μm, forming conspicuous pellucid alar group rather distinctly delimited from neighboring cells and reaching 1/2–2/3 of distance to costa. Branch leaves similar, but smaller, imbricate, serrulate, costa ending without spine. Autoicous; sporophytes infrequent. Seta reddish brown, 15-20 mm, rough. Capsule reddish to dark brown, ovate-cylindric, curved, to 1.8 mm long, operculum conic. Spores 16-20 μm.

**SPECIMENS EXAMINED:** EUROPE: Bashkortostan Republic: Yamantau Mt., 300 m, 11.VII.1997 Solometch (LE); Komi Republic: North Ural, Pechora River downstream Shezhi Creek mouth, 200 m, Bezgodov & Kucheron #4563 (PPU); Murmansk Prov.: Lavna-Tundra, Likhachev #201-1-97 (KPABG); Nenetsky Autonomous District: Malaya Labygei-Yaga (tributary of Lhorei-Yaga, 8.VIII.1937 Schljakov (LE); Perm Prov.: Okhlovchny Range, 880 m, Bezgodov #4144 (PPU); CAUCASUS: Karachaevo-Cherkessia: Upper course of Bolshoi Zelenchuk, 2000 m, 12.VIII. 1947 Blumental (LE);

ASIA: Altai Republic: Kairu-Bazhi Peak, 2050 m Ignatov #13/107a; 13/114a; 13/115a (MHA); Altai Territory: Sinyukha Mt. 31.VII.1947 Polyakov (LE); Chukotsky Autonomous District: Penkigney Bay 18.VII.1984 Sekretareva (LE); Kamchatskaya Prov.: Pravyy Kikhchik, 240 m, 24.VII.2004 Czernyadjeva #17 (LE); Kemerovo Prov.: Kuznetskiy Alatau, Chemodan Mt., 971 m, Pisarenko op00074 (NSK); Khakasia: Shirinsky Dist., Erovoe, 5.VIII.1961 Kamenskaya (IRK); Khanty-Mansisksky Autonomous District: Lyapin River, 16.VI.1949 Kildyusheskaya #58 (LE); Khakasia Republic: Vorob’ ev #7175 (LE); Krasnoyarsk Territory: Turukhansk Dist., Ketae-oloo Lake, 18.VIII.1992 Schcherbina (MW); Taimyrsky Autonomous District: Byrranga Mts., Bolshaya Bootankagi River, 28.VII.1990 Pospelova (MW); Igarka, 9.VIII.1949 Tyrtikov (MHA); Yamalo-Nenetsky Autonomous District: 25 km N of Polyarny (67°12’N, 65°40’E), 16.VII.2005 Czernyadjeva #58 (LE).

**Habitats.** It grows commonly in tall-herb vegetation or in dwarf Betula and Salix communities with rich composition of herbs that indicates a relatively high snow accumulation in winter. In mountains it is most characteristic to subalpine belt, with maximal snow cover in winter. The species is commonly associated with \textit{Rhytidiadelphus squarrosum}, \textit{Cirriphyllum piliferum}, \textit{Brachythecium erythrorrhizon} ssp. asiaticum, etc. In mountains at 2300-2850 m (Caucasus), 1000-2050 m (Altai), 200-880 m (North Urals).
Distribution. In Russia *S. ornellanum* occurs in the north of European Russia, Ural Mountains, and throughout Asian Russia, mostly in mountains, but with sporadic localities in lowlands as well. Outside Russia it is known from mountains of Central Europe (Italy, France, reported from the former Jugoslavia); Georgia, Kazakhstan, Kyrgyzstan, Alaska; in the latter found only recently by Afonina & Breen (in prep.).

Differentiation. This species can be recognized by its (1) julaceous foliage of stem and branches; (2) broadly ovate, shortly acute to apiculate leaves; (3) rather abruptly differentiated alar group.


Type: SW Poland (Silesia), in H (cf. Piippo, 1983).

Illustrations (based on Russian material): Ignatov (1998); Ignatov & Ignatova (2004); Ignatov & Milyutina (2007, present volume).

Plants medium-sized, in loose tufts, usually light green, glossy. Stems to 4 cm, prostrate to ascending and almost erect, flexuose, curved near apex, terete foliate, usually fairly regularly pinnately branched; branches to 7 mm, slightly curved or flexuose, terete foliate, often somewhat complanate. Axillary hairs 2-3-celled, 60-80 x 7-9 μm. Stem leaves from erect-spreading to spreading at wide angle, more or less spaced, straight or acuminate, slightly falcate or reflexed, 1.0-1.6 x 0.6-0.8 mm, ovate-triangular, widest at 1/7–1/10 of leaf length, gradually tapered to apex or shortly acuminate, more or less abruptly rounded to base, longly and narrowly decurrent; not or indistinctly concave, not plicate; margin ser-rectly rigidly spreading branch leaves. Another nearly unique trait is very narrow laminal cells (probably responsible for this rigidity of leaves), often with length to width ratio 10-15:1.

Narrow-celled phenotype of *Sciuro-hypnum reflexum*, ‘var. pacificum’ and ‘jeniseense’ were often confused with *S. starkei*, apparently due to narrow laminal cells of stem leaves. However, they have short laminal cells of branch leaves, and branch leaves are not rigidly spreading.

Underdeveloped plants of *S. starkei* (from deeply shaded habitats, etc.) has more remote and complanate branch leaves, resembling that of *Bryhnia novae-angliae*. However, the latter species has not so narrow cells, costa ending at 0.7-0.8 of leaf length and is dioecious.
Fig. 6. 50% consensus tree of 58 shortest trees (L=102) found in parsimony ratchet analysis. Jackknife value calculated for 1000 replicates shown below branches; percent of tree where a clade exists shown above branches (L=324; RI=0; CI=1).

Table 1. Number of parsimony informative substitutions between taxa of the *S. reflexum*-group. Countings were made against *S. reflexum* from Vologda; *S. reflexum* var. *pacificum* from Altai, *S. oedipodium* from Caucasus, *S. starkei* from Tatarstan, *S. glaciale* from Caucasus (‘Caucasus 2’). After the number of substitutions are given number of specimens where the substitution occurs; in few cases sequences posses variation C/T and C/G – in those cases they were count as 0.5 against C or T, and C or G respectively). Note that one of specimens of *S. glaciale* has only ITS2 data.

<table>
<thead>
<tr>
<th>N species</th>
<th>reflexum</th>
<th>‘pacificum’</th>
<th>altaicum</th>
<th>oedipodium</th>
<th>starkei</th>
<th>glaciale</th>
<th>latifolium</th>
</tr>
</thead>
<tbody>
<tr>
<td>8 reflexum</td>
<td>1 (in 2/8)</td>
<td>1 (in 2.5/3)</td>
<td>0</td>
<td>1 (in 3.5/4)</td>
<td>1 (in 3/3)</td>
<td>2 (in 2/2)</td>
<td>1 (in 1/1)</td>
</tr>
<tr>
<td>3 ‘pacificum’</td>
<td>0</td>
<td>1</td>
<td>2 (4/4;3.5/4)</td>
<td>2 (in 3/3)</td>
<td>3 (in 2/2)</td>
<td>2 (in 1/1)</td>
<td></td>
</tr>
<tr>
<td>1 altaicum</td>
<td>0</td>
<td>1 (in 3.5/4)</td>
<td>1 (in 3/3)</td>
<td>2 (in 2/2)</td>
<td>1 (in 1/1)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4 oedipodium</td>
<td>1 (in 0.5/4)</td>
<td>3 (in 3/3)</td>
<td>4 (in 2/2)</td>
<td>3 (in 1/1)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3 starkei</td>
<td>0</td>
<td>1 (in 2/2)</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 glaciale</td>
<td>0</td>
<td>0</td>
<td>1 (in1/1)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 latifolium</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
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</tr>
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</table>
As molecular methods have recently demonstrated their usefulness in solving difficult cases in moss taxonomy, we studied nrITS1-2 region of 27 Sciuro-hypnum specimens (Fig. 6, Table 2). The protocol of DNA extraction, PCR and sequencing of ITS data was the same as described by Gardiner et al. (2005). This first set was supplemented by two Genbank sequences of S. brotheri and S. glaciale.

As the most of informative positions were found in ITS2, we built the second set, that includes 7 additional ITS2 sequences from Genbank (ITS1 were not available for them) and one accession with both ITS1&2 for S. plumosum.

Sequences were aligned manually. Parsimony analysis was done with Nona (Goloboff, 1994) within the Winclada (Nixon, 1999a) shell. A multi-ratchet option with five sequential parsimony ratchet runs was used (Nixon,
HEDEN, GARDINER, A., M. IGNA TOV, S. HUTTUNEN & A. GOLOBOFF, P. A. 1994. NONA: A Tree Searching Pro-
CZERNY ADJEV, A. V. & M.S IGNA TOV 2006. The first 
HEDEN, HUTTUNEN, S. & M. S. IGNA TOV 2004. Phylogetic 
BROTHERUS, V. F. 1925. — 
AMMAN, J. 1918. Flore des mousses de la Suisse. Deuxi-
IGNA TOV, M.S. & I.A.MILYUTINA 2007. On 
IGNA TOV, M. S. & I. V. & M.S IGNA TOV 2006. The first 
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tains. VIII. Brachytheciaceae. — Arctoa 7: 85-152.
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al. 2006. Check-list of mosses of East Europe and North 
IGNATOV, M.S. & S. HUTTUNEN 2002. Brachytheciace-
ae (Bryophyta) – a family of sibling genera. — Arct-
11: 245-296.
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Е.А. ИГНАТОВА 2004. Флора мхов средней части 
европейской России. Т. 2. – [Moss flora of the Middle 
European Russia. Vol. 2] M, KMK [Moscow, KMK]: 609-
960.
IGNATOV, M. S. & T. KOPONEN 1996. On the taxon-
omy of some East Asian Brachythecium (Brachytheci-
IGNATOV, M.S. & I.A.MILYUTINA 2007. On Sciuro-
hynum oedipodium and S. curtum (Brachytheciace-
KARTTUNEN, K. 1990. Nomenclatural and taxonomic 
notes on Cirriphyllum (Brachytheciaceae, Bryophy-
LIMPRICHT, K. G. 1896. Die Laubmoose. — In: Raben-
horst, L. Kryptogamen-flora von Duetschland, Oester-

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thanks Elena Ignatova for illustration of species
and Richard Zander for correcting of English. The
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07-04-00013 and 06-04-49493.

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BROTHERUS, V. F. 1925. Musci. — In: Engler, A. & 
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record of Sciuro-hynum unciniifolium (Brachytheciace-
ae, Musci) in Russia. — J.Hattori Bot. Lab. 99: 271-274.
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Pseudoleskeaceae Schimp. and Pylaisiaceae Schimp. 
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analysis of Brachytheciaceae (Bryophyta) based on 
morphology, and sequence level data. — Cladistics 20: 
151-183.

ITS2 only (after cutting off available ITS1). Topolo-
gies and support values were subidentical and 
essentially similar to that obtained from the analy-
sis of the first set. The strict consensus tree of the 
whole alignment is shown in Fig. 7. Three addi-
tional species, not represented in the first set, S. 
plumosum, S. ornellanum and S. hylotapetum 
were found in positions similar to that found in by 
Huttunen & Ignatov (2004): (1) S. plumosum in a 
clade with S. populeum and S. flo towianum; (2) 
S. ornellanum among the unresolved group of S. 
reflexum and S. altaicum; and (3) S. hylotapetum 
in a clade with S. curtum.

The strict consensus tree of the set one (not 
shown) was fairly unresolved, with well segre-
gated only: (1) Sciuro-hynum curtum (sister to all 
other Sciuro-hynum); (2) S. populeum-group: 
S. brotheri, S. populeum, S. plumosum, S. flo-
towianum, S. unciniifolium (sister to S. reflexum-
clade, with all other species, except S. curtum); 
and (3) group of three species: S. glaci ale, S. lati-
folium, S. starkei (nested within S. reflexum-
clade). The two former clades were supported by 
jackknife values. The latter group was not statisti-
cally supported.

The most taxonomically difficult complex of S. 
reflexum, S. altaicum, S. oedipodium was not re-
solved, and the 50% majority rule tree demonstrat-
ed certain clades that appear in the majority of trees. 
Two segregates, however, rather well agree with 
species morphology, and one of them supports the 
clade of all four specimens of S. oedipodium.

The analysis of the second set was done for 
the whole alignment (gaps of ITS1 treated as miss-
ing data for specimens from Genbank) and for the

1999b). Jackknifing with 1000 replications includ-
ing was performed with Nona within the Winclada 
shell.

ing was performed with Nona within the Winclada 
shell.
Table 2. Specimen data of the genus *Sciuro-hypnum* used in analysis, and Genbank accession numbers (* asterisk marked sequences of ITS2 only). If ITS1 and ITS2 have different number they are given correspondingly. Two accessions of *Sciuro-hypnum latifolium* are from the same specimen, but from different extractions.

<table>
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<th>genbank #</th>
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<td><em>Sciurohypnum</em></td>
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<td>curtum New York</td>
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