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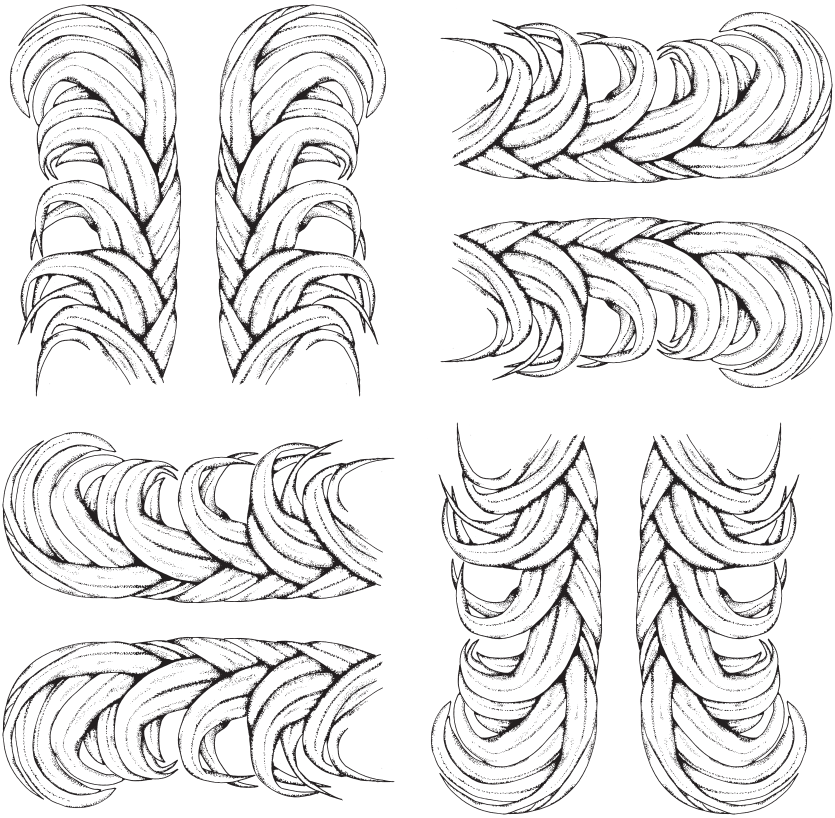

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Bryolich

Schweizerische Vereinigung für Bryologie und Lichenologie
Association suisse de bryologie et de lichénologie
Associazione svizzera di briologia e lichenologia
Associaziun svizra per la scienza da mistgel e lichen
Swiss Association of Bryology and Lichenology

Meylania ist die Zeitschrift der Schweizerischen Vereinigung für Bryologie und Lichenologie und erscheint zweimal jährlich zu Beginn der Monate April und November. Die Herausgabe der Zeitschrift wird unterstützt von der Schweizerischen Akademie der Naturwissenschaften SANW. Die Autoren-Beiträge werden nicht referiert. Die in der Zeitschrift vertretenen Meinungen müssen nicht mit jener der Bryolich übereinstimmen.

Die Mitgliedschaft bei der Bryolich steht allen Interessierten im In- Und Ausland offen. Der Jahresbeitrag beträgt Fr. 30.- (CHF) (20 Euro) ; für Studentinnen und Studenten Fr. 15.-. Der Einzahlungsschein wird jeweils der Aprilausgabe der Meylania beigelegt. Mitgliederbeiträge aus dem Ausland sollten auf das Postcheck-Konto der SVBL in Bern, Nr. 30-36350-7, oder bar in einem Umschlag am den Kassier überwiesen werden.

Hinweis für Autoren

Beiträge müssen in definitiver Form bis Ende Januar bzw. Ende August bei der Redaktion eintreffen. Wissenschaftliche Beiträge werden nicht begutachtet, die Verantwortung (für Inhalt, Sprache und Stil) liegt beim Verfasser bzw. bei der Verfasserin. Für die Präsentation gelten keine bestimmten Regeln. Die Beiträge sollten in der Regel 6 Seiten nicht überschreiten, längere Artikel sind mit der Redaktion abzusprechen. Erwünscht sind Manuskripte auf Diskette oder als E-Mail (Text- oder MS Word-Dokumente), plus ein Ausdruck auf Papier. Auf Formatanweisungen soll wenn möglich verzichtet werden, die Artikel werden beim Satz gestaltet. Für die Planung der Hefte ist eine vorgängige Ankündigung der Artikel bei der Redaktion erwünscht.

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The European species of the Calliergon-Scorpidium-Drepanocladus complex, including some related or similar species

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Introduction

Species belonging to the moss family Amblystegiaceae are important components in many wetland habitats. Besides *Sphagnum*, species within this family are probably those which most frequently dominate among the mos-ses in non-forested wetland habitats in large parts of the northern temperate region. In addition, several species are frequent in Arctic, sub-Arctic, Antarctic, and sub-Antarctic areas, as well as at high altitudes in tropical and subtropical mountains (Hedenäs 1999). Species belonging to the genera of the *Calliergon-Scorpidium-Drepanocladus* complex, to *Campyliadelphus*, *Campy-lium*, *Cratoneuron*, or *Palustriella* are most likely the ones that, besides *Sphagnum*, most often dominate or occur abundantly in temperate wetlands, excluding running waters.

Our knowledge about habitat requirements of *Sphagnum* species allows us to estimate several habitat parameters in relatively acid environments and paleohabitats from the species composition. Because most members of the Amblystegiaceae inhabit mineral-richer habitats than *Sphagnum*, these are suitable for assessing water chemistry characteristics and wetness of habitats in intermediately mineral-rich to calcareous wetlands.

Unfortunately, several species of the mentioned genera are often difficult to identify with certainty in the field, or even in the laboratory. This is partly depending on difficulties with describing some features which are seen with a trained eye and partly on the variability of many species in relation to factors such as water level, nutrient richness, or light availability in the habitats where they are found. The present overview, which is an expanded and elaborated version of the earlier "Field and microscope keys to the Fennoscandian species of the *Calliergon-Scorpidium-Drepanocladus* complex" (Hedenäs 1993a), is an attempt to overcome some of these problems. The main taxonomic additions, compared with the earlier overview, are that the genus *Drepanocladus s.* str. is completely revised, and the genera *Campylium* and *Campyliadelphus* are now included. The geographical area covered is Europe rather than Fennoscandia. In addition all North American species except the rare *Drepanocladus cardotii* are keyed out, and species that are only known from outside these areas are mentioned with distinguishing

characters under the species they are closest to. The European species are more completely described than in earlier key, and substantially more habitat and distributional data are included.

Habitat factors

Mires have been divided into different categories according to various criteria, and the terminology is therefore not always consistent. It is thus important to define what is meant by different terms in this publication in order to provide understandable habitat descriptions. Among variables that have been considered important for mire classification are (1) water availability, (2) pH, (3) mineral richness, (4) nutrient richness, and (5) the amount of solar radiation. The gradient from ombrotrophic (fed only by rainwater) to minerotrophic (fed by groundwater) environments is often considered important in mire ecology, but because this gradient is of importance mainly because of its influence on variables 2-4 above it is not considered separately here. The same habitat parameters that are of importance in mires are likely to be important also in other wetland habitats.

(1) Water availability. Different wetland species are found at different levels in relation to the water table. Some species, such as *Calliergon megalophyllum* and *Warnstorfia trichophylla* are mostly found submerged. In the other end of the gradient, *Tomentypnum nitens* and *Straminergon stramineum* tend to grow relatively high in relation to the water table. A number of species, such as *Pseudocalliergon lycopodioides* and *P. turgescens* are able to grow submerged in shallow pools or depressions, but can also survive long periods during the summer in a completely dried out state.

(2) pH. Only a few of the species included in this treatment grow in wetlands with a very low pH. *Warnstorfia fluitans*, and to some degree *W. procera*, *Straminergon stramineum*, and possibly *W. pseudostraminea* are able to survive acid habitats, with a pH below 4.0 or 4.5, whereas most species occur in habitats with a pH above 5.0.

(3) Mineral richness. The most important kations in terms of concentrations in the water are usually calcium (Ca), magnesium (Mg), iron (Fe), and sodium (Na), with the corresponding anions bicarbonate (HCO_3) and chloride (Cl). Species that seem to be more or less restricted to extreme habitats as far as mineral richness is concerned (e.g., calcareous fens) may actually not prefer these habitats but do rather stand them better than other taxa.

(4) Nutrient richness. The main nutrients are nitrogen (N), phosphorus (P), and potassium (K). Nitrogen and phosphorus compounds are likely to be limiting to the growth of wetland mosses in many cases because the available amounts are sometimes small during the growth season, especially concerning phosphorus.

(5) Solar radiation. Perhaps the most clearly visible effect of high levels of solar radiation is the appearance of secondary pigments in the plants. The secondary colours may be brownish, yellowish, or red, and their function

is in most cases likely to be protection from damaging levels of radiation. Which colour the plants get is most likely due to inherited characteristics. For example, red colours are found in species of *Hamatocaulis*, *Scorpidium*, several *Warnstorfia* species, and to some degree (pinkish) in *Calliergon giganteum*, whereas species of *Pseudocalliergon* get yellow-brown with a golden gloss and many other species get brownish. In species of *Warnstorfia* that may get red, such as *W. exannulata* and *W. sarmentosa*, one may find a distinct zonation in coloration when they grow in certain habitats. Plants in the coldest parts of very cold springs have frequently markedly less of red pigments (or lack red completely) than those in warmer parts of the same springs.

Some Fennoscandian wetlands habitats

Although most people associate the term "wetlands" with mires, wetlands as understood here include a diverse array of habitats, from mires of diffe-rent kinds to lake bottoms and periodically dry depressions. Running waters, such as brooks and rivers, are also wetlands, but are not covered by the present treatment, although Amblystegiaceae species of genera such as *Hygrohypnum* and *Amblystegium* grow there. Some species included in this treatment may, however, sometimes grow in slowly flowing water.

The present short overview is intended to give an idea of which of the species included in this book can be expected in different common or special habitats in northern Europe, rather than to give a full overview of all types of wetlands that exist in Europe. Some wetland types that do not occur in the north may occur in other parts of Europe, but since I have limited personal field experience of these, the following concerns mainly Fennoscandia. Because most Amblystegiaceae species occur in relatively mineral-rich habitats, the variation in mineral-poor wetlands is not completely covered. It should also be remembered that transitional or mixed habitat types are abundant in some areas, which means that such wetlands are sometimes as frequent as the "typical" expressions of the following wetland types.

I. Non-forested wetlands that form no or little peat

(1) Periodically wet depressions. Periodically wet depressions are usually relatively shallow (up to ca. 1 m deep) and located in more or less flat or slightly sloping ground. Usually they are water-filled during autumn-winter-spring and during shorter periods with higher precipitation during the summer, whereas they dry up more or less completely for longer periods in the summer during normal years. Species that grow in these depressions are able to stand complete drying up and temporary wetting during the hottest part of the year, and often complete submergence during the colder periods of the year. Naturally occurring periodically wet depressions may be found in meadows, in glades in forests on thin soil, on alvar-ground, and on shores of different kinds. However, also rock-pools and road-side ditches frequently belong to this category of wetland habitats.

In the calcareous alvar areas of the Baltic Sea area, the water of temporary depressions has often very high levels of calcium (up to 220 mg/l) and a high pH ((6.5-) 7.0-8.2). Such depressions are partly inhabited by a few strongly specialised Amblystegiaceae species, such as *Campyliadelphus elodes*, *Drepanocladus sendtneri*, *Pseudocalliergon lycopodioides*, or *P. turgescens*, but *Calliergon giganteum*, *Campylium stellatum*, *Drepanocladus aduncus*, *D. polygamus*, *Scorpidium cossonii*, and *S. scorpioides* are also frequent in this habitat. *Drepanocladus aduncus* and *D. polygamus* tend to occur in depressions with a slight nutrient enrichment, and are, for example, relatively rare on many oligotrophic calcareous alvars of Öland and Gotland (S Sweden). *Palustriella falcata* is also found in connection with some calcium-rich depressions, but then often associated with springs or otherwise at least periodically moving water. A species that is sometimes found in connection with depressions in calcareous areas in southern Fennoscandia and that is sometimes confused with *Tomentypnum nitens* is *Brachythecium turgidum*.

In other strongly calcareous areas in the southern and eastern parts of Fennoscandia, the species composition is more or less similar, although *Pseudocalliergon turgescens* has very few lowland occurrences outside Öland and Gotland. On the other hand, *Pseudocalliergon angustifolium* occurs in similar habitats in the northern Finnish lowlands. In mineral-rich lowland areas further north or west, *Campyliadelphus elodes*, *Pseudocalliergon lycopodioides*, and *P. turgescens* are rare or absent, but on the other hand *Calliergon richardsonii* is sometimes or frequently found. In the mountains, depressions that dry out during the summer are frequent, and in calcareous areas *P. angustifolium* and *P. turgescens* can occur, often together with species such as *Campylium stellatum*, *Scorpidium cossonii*, or *S. scorpioides*.

In mineral-poor places the conditions may approach those of bog-pools or other ombrotrophic habitats, and species such as *Straminergon stramineum*, *Warnstorfia fluitans*, or occasionally *W. pseudostraminea* may be the only Amblystegiaceae ones found. Under somewhat more mineral-rich conditions, *Calliergon cordifolium* or *Warnstorfia exannulata* can thrive, and also *Sanionia uncinata* sometimes grows in the margin of such periodically wet places.

(2) Submerged habitats. Mosses of the family Amblystegiaceae can be found submerged in lakes of different sizes, in ponds, kettle holes, and oxbow lakes. A few species, such as *Calliergon megalophyllum*, *Drepanocladus longifolius*, *D. sordidus*, and *Warnstorfia trichophylla* have a large proportion, probably the majority of their known occurrences in submerged habitats, whereas many other species, such as *Calliergon richardsonii*, *Drepanocladus polygamus*, *Scorpidium scorpioides*, and *Warnstorfia exannulata* (or in limited areas possibly *W. procera*) are frequent in lakes but occur more commonly in terrestrial wetland habitats. Many of the other Amblystegiaceae species treated here are occasionally found submerged (cf. Hedenäs 1997d), but even species that occur only rarely in lakes, such as *Campyliadelphus elodes* or *Pseudocalliergon trifarium* are most likely part of the natural flora there. The first of these species was found in a central Swedish lake at two occasions

with 55 years in between, and both species are known to be widespread in at least some of the lakes where they occur.

The floras of different lakes in the lowlands differ depending on the same chemical habitat factors as in terrestrial wetlands, although the niche overlap between the species seems to be much greater than in the latter habitats.

(3) Shores of lakes, watercourses, and the sea. Most terrestrial wetland types can naturally reach the shores of different kinds, and these wetlands are here treated as ordinary terrestrial ones. However, a few wetland types are more or less restricted to shores of different kinds, and two of these will be discussed. In Fennoscandia the first type is restricted to sea shores, also around the Baltic Sea, whereas the other occurs both along freshwater and brackish water shores.

Along sea shores, especially in more or less calcareous areas, a small group of Amblystegiaceae species is often found in the transition zone between shore meadows and the sea, in the part of the shore that is submerged during high-water and more or less dry during normal- and low-water. Usually the vascular plant vegetation, consisting mainly of grasses and sedges, is rather sparse, at least in portions, and part of the vegetation has often eroded away due to wave action. *Drepanocladus aduncus* and sometimes *Conardia compacta* are found in this habitat, and in addition *Amblystegium serpens* is frequent. Slightly further inland, the wetland habitats soon become more similar to normal inland wetlands, but the nutrient levels are frequently relatively high, and species such as *Drepanocladus aduncus* and *D. polygamus* (more rarely *D. longifolius*) are found. In the arctic, *Drepanocladus arcticus* also belongs to the flora of sea shore wetlands.

Reed belts, dominated by *Phragmites*, *Typha*, *Scirpus*, etc., are found along shores of both freshwater and brackish water. When occurring along shores of more or less eutrophic and relatively mineral-rich (though not extremely calcareous) waters, species such as *Calliergon cordifolium*, *C. megalophyllum*, *Drepanocladus aduncus*, *D. longifolius*, and *D. polygamus* are sometimes or frequently found in reed belts. In more northern areas, *Calliergon richardsonii* is also found in this habitat now and then. *Amblystegium radicale*, which may look like small individuals of *D. polygamus*, sometimes occurs in this habitat. In relatively nutrient-poor places, species such as *Scorpidium scorpioides*, *Straminergon stramineum*, and *Warnstorfia exannulata* can also be found in shore reed belts.

(4) Wet meadows. Wet meadows with a vegetation that allows bryophytes to compete successfully are frequently kept open by grazing or other kinds of human management. Only in mountainous areas or sometimes along shores with fluctuating water levels or where the ice causes abrasion during the winter, wet meadows of a more natural kind cover larger surfaces. Among other things, wet meadows differ from fens by the absence or near absence of peat formation, and in many cases more or less large areas of bare soil can be found in this habitat. Species that are found in calcareous wet meadows include *Calliergon giganteum*, *Campyliadelphus chrysophyllus*, *C. elodes*, *Campylium stellatum*, *Cratoneuron filicinum*, *Drepanocladus sendtneri*, *Pseudocal-*

liergon lycopodioides, *Scorpidium cossonii*, and *S. scorpioides*. Another species which is relatively frequent in this habitat is *Ctenidium molluscum*, some shoots of which may look like a *Campylium* or *Campyliadelphus* species. In intermediately mineral-rich wet meadows, species such as *Campylium stellatum*, *Scorpidium revolvens*, *S. scorpioides*, *Straminergon stramineum*, and *Warnstorfia exannulata* are often found, and if the meadows are nutrient-rich enough *Drepanocladus aduncus* and *D. polygamus* may occur.

II. Non-forested peat-forming wetlands (mires)

(5) Bogs. Bogs are mires which only or main supply of minerals and nutrients comes from atmospheric water and dry deposition (ombrotrophic mires). Because the input of minerals and nutrients from the atmosphere is frequently low, except in areas relatively close to sea coasts, bogs are normally mineral- and nutrient-poor in their natural state. The water in bogs is poor in buffering minerals, and because *Sphagnum* species produce acidifying substances, this means that bog water is normally both acid (pH < ca. 4.5) and poor in minerals. In recent times, the input of antropogenously produced nitrogen compounds via atmospheric deposition has caused artificially high nitrogen levels in some bogs. Bogs in the natural state are usually dominated by *Sphagnum* species, but a few members of the Amblystegiaceae can also survive in this extreme environment, especially *Straminergon stramineum* and *Warnstorfia fluitans*.

(6) Fens. Fens are mires that are supplied with minerals and nutrients both from atmospheric sources and from the groundwater (minerotrophic mires). Fens, like other wetlands, can be subdivided both according to the pH or availability of minerals, and according to the availability of nutrients (oligotrophic or nutrient-poor, vs. eutrophic or nutrient-rich), and the position of different kinds of fens in relation to these parameters is given in Fig. 1 (cf. Wheeler & Proctor 2000). As can be seen from this figure, the different fen types overlap. This is normal when quantitative parameters are important factors in determining the species composition and development of the vegetation. However, the terminology is still useful for descriptive purposes.

Poor fens. Poor fens have a low pH (< ca. 4.5-5.0 (-5.5)), low mineral levels, and in the natural state usually low nutrient levels. Few Amblystegiaceae species can survive or compete successfully in this environment, which is instead dominated by *Sphagnum* species. However, *Warnstorfia fluitans* is a typical species of poor fens, and, especially when the water is slightly moving or the habitat is disturbed, *W. pseudostraminea* occasionally occurs. *Straminergon stramineum*, which occurs in a relatively wide range of habitats is frequent also in poor fens, and *Warnstorfia procera* occurs particularly in fens transitional between poor fens and intermediate fens.

Intermediate fens. In the central and northern parts of Fennoscandia, this kind of fens belong to the more frequent and widely distributed ones. They are characterised by intermediate pH (ca. (4.5-) 5.0-6.5) and mineral levels, and mostly relatively low nutrient levels. The buffering capacity is

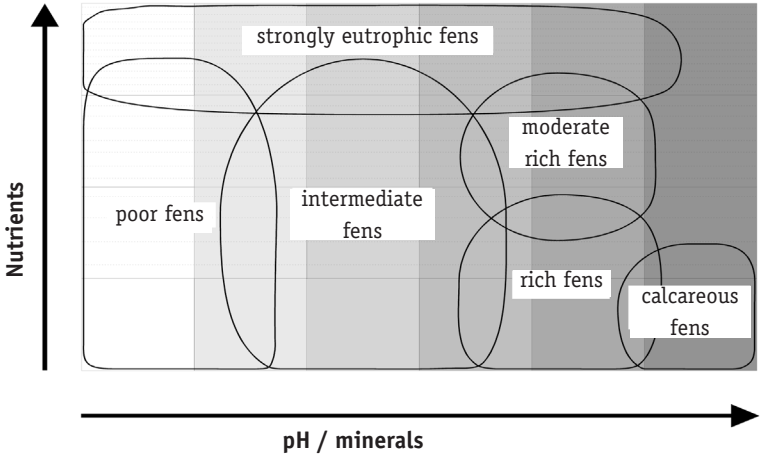


Fig. 1. Classification of fens according to the relative mineral and nutrient content of the water. See text for further explanations.

low, which may be one reason why this kind of fens are at present rare or almost absent in many areas of southernmost Fennoscandia, as well as in other areas of Europe where the influence of human management is stronger than in the north. The most frequent Amblystegiaceae species in this kind of fens are *Loeskypnum badium*, *Scorpidium revolvens*, *Straminergon stramineum*, *Warnstorfia exannulata*, and *W. sarmentosa*. Sometimes *Campylium stellatum* and *Scorpidium scorpioides* are also found, especially in those intermediate fens that approach rich fens. In fens transitional to the poor fens *Warnstorfia procera* can be found.

Rich fens. Rich fens, as the term is used here, are fens where the water has a high mineral content or a high pH (ca. 6.0-7.5), but where the nutrient amounts are relatively low. Rich fens in southern Fennoscandia have generally got higher mineral levels than those in northern Fennoscandia, but the pH does not differ between the north and the south. The most common species in the rich fens are *Calliergon giganteum*, *C. richardsonii* (northern), *Campylium stellatum*, *Pseudocalliergon trifarium* (frequently among *Scorpidium scorpioides*), *Scorpidium cossonii*, *S. scorpioides*, and *Tomentyp-num nitens*.

Moderate rich fens. Besides the ordinary rich fens of the kind just described, there is another kind of rich fens, with its characteristic set of species. This kind of rich fens is much rarer than the previous kind, and corresponds with what has been described as moderate rich fens in North America (Chee & Vitt 1989, Vitt & Chee 1990). It is here suggested that this term is adopted also for the European fens of this kind. At least some of the species characteristic for this kind of fens, both among the bryophytes and among the vascular plants, indicate slightly elevated levels of nutrients (often together with Fe, 0.1-12,4 mg/l ; Ca levels are often low, 2.5-30.0 (-57.0) mg/l ; pH ca. 6.0-7.5). Among the bryophytes especially *Drepanocladus aduncus*, and in the

south *Calliergonella cuspidata*, which occur in many fens of this kind, could be mentioned. Other species typically found in this kind of fens, with varying frequencies, are *Calliergon giganteum*, *C. richardsonii*, *Campylium laxifolium* (uncommon), *Drepanocladus sordidus* (seemingly rare), *Hamatocaulis vernicosus*, *Straminergon stramineum*, *Tomentypnum nitens*, and *Warnstorfia tundrae*. Also *Helodium blandowii* (F. Weber & D. Mohr) Warnst. and sometimes *Brachythecium mildeanum* (Schimp.) Milde can be found in fens of this kind.

Calcareous fens. This kind of fens, which are also called *extreme rich fens*, have often got a surprisingly species-poor bryophyte flora, because few species are able to survive the extremely high levels of minerals, mainly calcium, and the high pH (> ca. 7.0-7.5) in this habitat. The nutrient levels are mostly low or sometimes very low. In strongly oligotrophic calcareous fens, the vascular plant cover is often also sparse or in extreme cases almost absent, and bare soil is clearly visible between the plants. Many, perhaps most natural calcareous fens are found in connection with springs or moving water, which may be a prerequisite for maintaining the high calcium levels in the absence of human management. Species found in calcareous fens include *Calliergon giganteum*, *Campyliadelphus elodes*, *Cratoneuron filicinum*, *Pseudocalliergon angustifolium* (in the mountains and in the northern boreal zone in Finland), *P. lycopodioides* (in the S and E), *P. turgescens* (rare), *Scorpidium cossonii*, *S. scorpioides*, *Palustriella* species, and sometimes *Tomentypnum nitens*. The latter species may be confused with *Brachythecium turgidum* which sometimes grows in this kind of fens or in the mineral-richest rich fens.

Strongly eutrophic fens. This kind of fens are frequently the result of farming activities or they occur in connection with outlets of waste-water. Natural strongly eutrophic fens occur mainly close to sea shores, sometimes also along lake shores or in other locations where organic material accumulates. Because of the high nutrient levels, vascular plants mostly dominate and form such a dense vegetation that few bryophytes manage to survive. Thus, this category of fens partly overlaps with the kinds of wetlands found along sea and lake shores. Bryophytes that can be found in this habitat are especially *Calliergonella cuspidata* and *Calliergon* and *Drepanocladus* species. Also *Amblystegium radicale* (cf. above) is sometimes found in this habitat.

III. Some special wetland types

(7) Springs. Springs in the strict sense are concentrated outlets of groundwater, and the vegetation around springs often deviates strongly from the surrounding vegetation. The latter is true both when the springs are situated in wetlands and elsewhere. However, every transition between strongly localised springs and a diffuse outlet of groundwater over a larger surface exist, and the mineral content and pH of the spring water varies a lot. The vegetation of springs is thus almost as heterogeneous as that of fens (cf. Fig. 1). The size of springs varies a lot, from less than 1 m^2 to 1 km^2, although the size is usually closer to the first than the latter of these values. A continuous spring vegetation area covering about 1 km^2 has been found in the Swedish province Norrbotten.

In springs with calcareous water, species such as *Campyliadelphus elodes* (mainly S Fennoscandia), *Campylium stellatum*, *Cratoneuron filicinum*, *Palustriella commutata* (very calcium-rich water ; mainly S Fennoscandia), *P. decipiens* (mainly N Fennoscandia), *P. falcata*, *Scorpidium cossonii*, and *S. scorpioides* are found, sometimes also *Breidleria pratensis* and in some areas *Pseudocalliergon turgescens*. In somewhat less mineral-rich places, *Campylium stellatum*, *Scorpidium cossonii*, and *S. scorpioides* are still frequent, and mosses such as *Calliergon* spp. and *Tomentypnum nitens* are also common. Under mineral-rich and apparently slightly nutrient-enriched conditions *Calliergon* spp., *Drepanocladus aduncus*, *Hamatocaulis vernicosus*, and *Straminergon stramineum* occur. Under intermediately mineral-rich conditions, *Scorpidium revolvens*, *Loeskypnum badium*, *Straminergon stramineum*, and especially *Warnstorfia exannulata* and *W. sarmentosa* are often abundant in the springs. Mainly in the latter kind of springs and in slightly mineral-richer ones, *Brachythecium rivulare* Schimp., which because of its large and well differentiated alar groups could be confused with, for example, green phenotypes of *Calliergon* or *Warnstorfia* species, is sometimes also frequent. In the mineral-poorest springs the number of species is small, although *Straminergon stramineum* and *Warnstorfia fluitans* can occur. In slightly sloping poor fens with a very slight spring influence, *Warnstorfia pseudostraminea* may be found.

(8) Swampy forests. Naturally, all transitions between treeless mires and swampy forests exist, and in transitional habitats, species typical of both may be found. However, a few Amblystegiaceae species are much more common in swampy forests than in open wetlands, or are sometimes almost restricted to swampy forests. Three such species are *Calliergon cordifolium*, *Campylium protensum*, and *Sanionia uncinata*. The *Drepanocladus polygamus*-like *Amblystegium radicale*, as well as *Leptodictyum riparium* are also sometimes found in swampy forests. Species that can occur both in more open wetlands and in swampy forests of different kinds, such as *Drepanocladus aduncus*, *D. polygamus*, or *Warnstorfia exannulata*, do sometimes look very different in the two habitats. For example, *W. exannulata*, which frequently gets strongly red in more open habitats, is almost invariably green in forested wetlands.

(9) Man-made wetlands. Man-made wetlands is a variable category, including everything from dams intended to improve the breeding conditions for ducks and fishes, or for hydroelectric power plants, to fen-like wetlands of different kinds. The latter, which are nowadays sometimes created in order to catch nutrients, are frequently relatively eutrophic, and have a relatively species-poor flora. *Drepanocladus aduncus* is one of the more frequent species in the latter kind of habitats. Otherwise, the flora in man-made wetlands varies like that in other wetlands, depending on the mineral and nutrient conditions. Especially in somewhat older, stabilised wetlands, the flora may approach that of more natural environments.

Taxonomic treatment and included species

The taxonomic treatment is based on studies by Hedenäs (1987a, b, 1989a, b, c, d, e, 1992a, b, c, 1993b, 1996, 1997a, b, 1998, 2001, 2003, Hedenäs & Kooijman, 1996), for *Cratoneuron* and *Palustriella* partly on Ochyra (1989). Although this means that many names in this work differ from what is found in most of the currently used floras, I have preferred to follow a system which seems to reflect the phylogenetic relationships between the species rather than one which groups the species in a few genera because of similarities in a few arbitrarily chosen "key characters". The studies by Vanderpoorten et al. (2002), where molecular as well as morphological and anatomical characters are included, suggest that the genera recognised in the present treatise reflect the evolutionary history of the taxa better than the traditionally circumscribed genera. In the present treatise, the species of the *Calliergon-Scorpidium-Drepanocladus* complex, *Breidleria*, *Calliergonella*, *Campylium*, *Campyliadelphus*, *Cratoneuron*, and *Palustriella* are included in the keys. Other species that could be confused with the treated ones are discussed in connection with those of the treated ones they are most similar to. All species included, are listed in Table 1.

Notes on keys and descriptions

The main purpose with this treatment is to provide keys and descriptions for the identification of the European species of the genera mentioned above, but in addition all other known species of the included genera are either keyed out or mentioned with distinguishing characters in connection with the most closely related species. Two main keys are provided, one field key and one key that uses both macro- and microscopic characters. Several auxiliary tables that list species with certain characteristics are included after the field key. Although some of the best separating characters for the genera are found in the sporophyte, the keys presented here are almost exclusively based on gametophyte characters, because sporophytes are often not available. Sporophyte characters that are present in all or most members of the included Amblystegiaceae with horizontal capsules and unreduced (well developed, perfect) peristomes are usually not mentioned in the descriptions of genera and species. These common sporophytic character states include a (1) smooth seta, (2) long-pored stomata of the capsule, (3) a conical lid, (4) brownish yellow or yellow-brown exostome teeth, (5) an exostome border that is ± distinctly widened at the zone of transition in the outer peristomial layer pattern (least distinctly widened in *Palustriella* and *Breidleria*), (6) normally developed exostome teeth trabeculae (i.e., the transverse ridges of the primary peristomial layer, or inner exostomial layer), i.e., neither strongly developed as in many members of the Hookeriaceae or the Sematophyllaceae nor weakly developed, like in many species with reduced or specialised exo-stomes, (7) nodose endostome cilia, except in *Calliergonella*, *Campylium*,

Campyliadelphus, and *Drepanocladus* (which have sometimes or mostly appendiculate cilia) ; (8) not or narrowly perforate endostome processes, (9) and spores that mature during late spring to early autumn. In the few cases where the capsules are more upright and the peristomes are more or less reduced or specialised, the character states deviate from the above and are mentioned in the descriptions when relevant.

Table 1. Species included in the *Calliergon-Scorpidium-Drepanocladus* complex, and in other genera included in the keys.

Breidleria erectiuscula
B. pratensis
Calliergon cordifolium
C. giganteum
C. megalophyllum
C. richardsonii
Calliergonella cuspidata
C. lindbergii
Campyliadelphus chrysophyllus
C. elodes
Campylium laxifolium
C. longicuspis
C. protensum
C. stellatum
Conardia compacta
Cratoneuron curvicaule
C. filicinum
Drepanocladus aduncus
D. arcticus
D. brachiatus
D. cardotii
D. latinervis
D. longifolius
D. perplicatus
D. polygamus
D. sendtneri
D. sordidus
Hamatocaulis lapponicus
H. vernicosus
Loeskypnum badium
L. wickesiae
Palustriella commutata
P. decipiens
P. falcata
Pseudocalliergon angustifolium
P. brevifolium
P. lycopodioides
P. trifarium
P. turgescens
Sanionia georgico-uncinata
S. orthothecioides
S. symmetrica
S. uncinata
Scorpidium cossonii
S. revolvens
S. scorpioides
Straminergon stramineum
Tomentypnum falcifolium
T. nitens
Warnstorfia exannulata
W. fluitans
W. laculosa
W. luipichensis
W. procera
W. pseudosarmentosa
W. pseudostraminea
W. sarmentosa
W. trichophylla
W. tundrae

The illustrations show features that are difficult to describe accurately with words and no attempt was made to fully illustrate all characters of each species. For each European species one or a few stem leaves are figured to give an idea of how they look. It should be stressed that one or a few leaves can never show the entire range of variation found within a species.

Habitat and distribution

After the description of each species, a description of its habitat follows, including information about pH, electric conductivity (EC ; corrected for the contribution by H^+), calcium concentration (Ca), and the Ionic Ratio (IR ; cf. van Wirdum 1991) of the water, when known for its European habitats. The Ionic Ratio (IR), an indicator for water type, is calculated as 2[Ca] / (2[Ca] + [Cl]) (van Wirdum 1991). On a scale from 0 to 1, this value indicates the similarity to ground water versus rain water and sea water. Ground water is characterised by a high IR due to the dissolution of $CaCO_3$ in the mineral soil. The reference value for ground water, based on samples from The Netherlands, is 0.95 (van Wirdum 1991). Rainwater or, at very high mineral levels, sea water, is characterised by a low IR due to the dominance of Cl in sea water and thus in rain. The reference value for rain water, based on samples from The Netherlands, is 0.19. Intermediate values represent a mixture between ground water and rainwater. The sources of the water chemistry information are given in Table 2. Simple distribution maps for Europe excluding the Arctic, indicating in which countries, or for eastern Europe sometimes earlier countries or portions of earlier countries, the species have been found are provided for those species that occur on the European mainland. Besides checked specimens, mainly located in S, I have consulted literature information (in particular Abolin 1968, Augier 1966, Blockeel 1991, Casas 1991, Çetin 1988, Cortini Pedrotti 1992, Düll 1985, 1992, Frahm & Frey 1983, Geissler et al. 1998, Hill et al. 1994, Ignatov & Afonina 1992, Ingerpuu & Vellak 1998, Jóhansson 1998a, b, Kubinská & Janovicová 1996, Preston 1984, Sérgio et al. 1994, Söderström 1996, 1998, Touw & Rubers 1989, Werner 1993). The maps are to be used as indications for where species occur if suitable habitats are available. The patterns and symbols used in the maps are explained in Fig. 2.

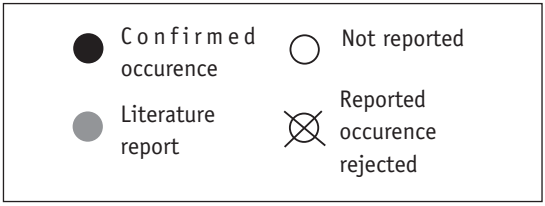


Fig. 2. Symbols used in the distribution maps.

Table 2. Sources for chemical habitat data included under the species.

pH

Albertson (1946)
Apinis & Lacis (1936)
Arts (1990)
Bell & Lodge (1963)
Gläser (1994)
Hedenäs & Kooijman (unpublished data)
Holz (1997)
Karttunen & Toivonen (1995)
Lohammar (1938 ; together with specimens checked by the author)
Malme (1976, 1978)
Maristo (1941)
Rintanen (1976, 1977)
Sjögren (1964)
Sjörs (1946, 1961)
Sørensen (1948)
Stetzka (1994)
von Krusenstjerna (1945)
Witting (1949)

EC, Ca, IR

Hedenäs & Kooijman (unpublished data)
Lohammar (1938 ; together with specimens checked by the author)

Methods for the identification of the plants

The methods used in the field and in the laboratory are necessarily of quite different kinds. In both cases it is, however, important to remember that there is often considerable variation both within and between plants or tufts of the same species growing in what may at first seem to be a homogeneous habitat. Thus, it is important to study as much as possible of the variation available in a given sample or within a given locality. Some phenotypes may be more easily identified than other ones, because of their colour, some state of their rhizoid characters or some other character where a certain state is not universally present even in species that may have it.

I. Identification in the field

Most characters are visible with a hand lens ((10-) 12-20x magnification), without dissection of the moss plant. However, sometimes it is necessary to tear off a few leaves to expose paraphyllia, decurrent leaf bases, perichaetia, or perigonia. It may also help to remove some leaves to study the appearance of the alar groups, either on the torn off leaves (if reasonably entire) or on leaves that are still attached to the stem. It is usually possible to make these field dissections with your fingers. In the field key, illustrations are only given to explain what an alternative in a dichotomy means, when this is difficult to convey or might be misunderstood with words only. Additional descriptions and illustrations of the species, as well as information regarding their habitat preferences and distributions are provided in connection with the more detailed descriptions of the species.

II. Identification in the laboratory

To be able to fully use the included keys with microscopic characters, it is necessary to have both a dissecting microscope, for making preparations, and a compound microscope with magnifications between ca. 30-400x. To make good preparations easily, it is also almost indispensable to have two good pairs of tweezers, preferably of the finer kinds used by surgeons or watchmakers. For transverse sections of stems it is usually enough with a razor-blade, whereas for sections of other structures, like leaves, a very fine knife is necessary for making good sections with precision. Such knives can be made of small pieces of razor-blade that are glued to tooth-picks or matches (be sure to get razor-blades of the kind that break easily rather than those that can be bent).

For leaf characters it is advisable to study at least 10-15 stem leaves (if it is not specifically stated that branch leaves are concerned). As was indicated above, it is not possible to define "typical" leaves in plants which are as plastic as many wetland mosses are (cf. Hedenäs 1996). On the contrary, any leaves except the youngest, immature leaves, could in principle be studied. However, in practice it is mostly best to study the most recently mature stem leaves, a short distance below the shoot apex, in medium-sized species in the uppermost centimetre of the shoot. Such leaves are mature but have not yet begun to disintegrate, and have mostly got no overgrowth of algae. It is important to tear off entire leaves, i.e. with all the basal and alar leaf cells left. This is usually accomplished under the dissecting microscope by holding the moss shoot, with the shoot apex towards the left, with your left hand pair of tweezers (if you are right-handed) and then get a hold of one leaf base as close to its insertion as possible with your right hand pair of tweezers. Then just move the right hand pair of tweezers (holding the leaf base) gently downwards along the moss stem until the leaf gets loose. Attempts to tear off leaves by drawing them away outwards from the stem usually result in breaking the leaves above the leaf base. In most species with curved leaves, median lamina cells should be studied as indicated in Fig. 3. In the same figure the place to measure costa width is also indicated. The median leaf lamina cells tend to have different lengths on the two sides, relative to the costa, in species with curved leaves. It is thus sometimes important that measurements are always made in the same area to make comparisons possible. This concerns the genus *Scorpidium* among the taxa included here.

Transverse sections of the stem are best made in not too old parts of the shoot and good sections are usually easily made between a half and one centimetre below the shoot apex. Most other characters of the gametophyte are also best studied in this region of the shoot but in some cases, as with pseudoparaphyllia, it may be difficult to find the structures in this region and additional shoot parts have to be searched.

Terminology

Alar cells = The cells in the basal angles of the leaves. The alar cells may be undifferentiated or may form a small or large group, which may or may not be sharply differentiated from the surrounding cells. In the literature, the alar cells are sometimes called "angular cells".

Antheridium = The male sex organ (cf. Fig. 5B). Antheridia develop in the perigonia (cf. "Perigonium") and are cylindrical and stalked in the species treated here.

Apiculate = With apiculus, a short, abrupt point.

Archegonium = The female sex organ. Archegonia develop in the perichaetia (cf. "Perichaetium") and are flask-shaped.

Autoicous = With perichaetia and perigonia on the same shoot. Autoicous species have mostly got the perigonia below the perichaetia on the shoot. In cases when only young perigonia are found relatively close to the shoot apex it is not safe to assume that the species is dioicous, since in this case the current season's perichaetia may not yet have started to develop. However, in such cases perichaetia from the previous year are often found further down on the shoot in autoicous species (cf. "Dioicous").

Axillary hairs = Hair-like structures inserted in the leaf axils. Axillary hairs usually consist of a basal, one- or few-celled portion and an apical one- or several-celled portion. Whereas the basal cells are usually short and often brownish, the apical cells are more variable, but in the species treated here mostly ± elongate and hyaline, or in some species yellowish to brownish.

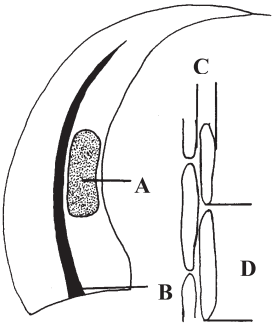


Fig. 3. Schematic figure showing where to make measurements in leaves, and how to measure cells. A : Median lamina cells (be sure to measure on correct side of costa in *Scorpidium* ; cf. text). B : Position to measure costa width. C : Cell width. D : Cell length.

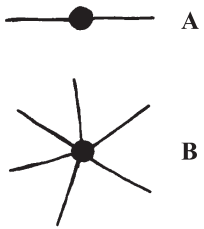


Fig. 4. Showing distichous (A) and radial (B) branching of shoots viewed from the shoot apex downwards.

Basal leaf lamina cells = The cells near the leaf base. In some species these cells are homogeneous throughout the leaf base, in some the alar cells are differentiated from the other basal cells and form a small or large group. Where the alar cell group reaches the leaf costa, the term basal cells refers to the cells just above the alar cells near the costa.

Branching pattern = Species in the groups treated here may be branched in one plane (distichously branched ; Fig. 4A), radially branched (when viewed from the top of the shoot : with branches pointing outwards from the stem in all directions ; Fig. 4B) or sparsely branched, in which case it is not possible to refer them to either of the two other patterns.

Costa width = The costa width is measured as indicated in Fig. 3.

Dioicous = With perichaetia and perigonia on different shoots (cf. "Autoicous").

Distichously branched = See "Branching pattern".

Hyalodermis = An epidermis of inflated, thin-walled cells outside the normal, more or less incrassate cells of the stem cortex (e.g., Fig. 16A, p. 32).

Median leaf lamina cells = If not otherwise stated, these are measured in the area indicated in Fig. 3.

Ontogeny = Pattern of development of a structure (here : of the alar cells ; Fig. 19, p. 35).

Papillose = With papillae, i.e. with projections from the cell wall.

Paraphyllia = Green, leaf-like or filiform (sometimes branched) structures, inserted randomly or in obliquely transverse rows on the stem or branches (cf. "Pseudoparaphyllia").

Perichaetium = Short branch with archegonia (and often paraphyses) surrounded by perichaetial leaves. When unfertilised, the perichaetia are usually more elongate and narrower than the perigonia (Fig. 5A ; cf. "Perigonium"). In case of doubt it is best to dissect the branch to see whether archegonia or antheridia are present.

Perigonium = Short branch with antheridia (and paraphyses) surrounded by perigonial leaves (Fig. 5B ; cf. "Perichaetium").

Peristomial layers = The peristome consists of the remaining cell walls of three cell layers, namely the inner, the primary, and the outer peristomial layers. The exostome consists of parts of the outer and primary layers and the endostome of parts of the primary and inner layers.

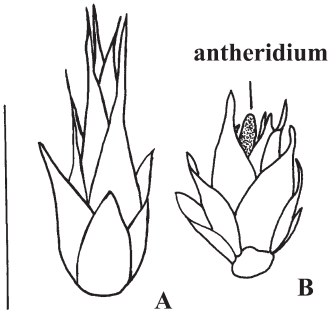


Fig. 5. Perichaetium (A) and perigonium (B) of *Warnstorfia tundrae*. Scale : 1 mm.

Prorate cells = Cells with one or both ends projecting above the general (otherwise smooth) leaf surface.

Pseudoparaphyllia = Green, leaf-like or filiform structures inserted on the stem around branch buds or branch bases (cf. "Paraphyllia").

Radially branched = See "Branching pattern".

Rhizoid initials (nematogones) = Special cells, usually with little or no chlorophyll and usually somewhat wider and more thin-walled than the surrounding cells (e.g., Fig. 33C, p. 58). From the rhizoid initials, rhizoids are sometimes growing. In *Conardia*, both rhizoids and gemmae may develop from the initial cells.

Rhizoids = Simple or branched, red-brown (in the species treated here), uni-seriate structures which may grow from the stem in various places, or from the leaves. The rhizoid positions stated for the stem are those where rhizoids appear in free shoots that are not in contact with wood, rocks, etc., in which case rhizoids may grow from other portions of the stem. The rhizoids may be smooth or, more rarely, warty papillose (or granular-papillose in species not included in this key).

Submerged = Under the water surface.

Supra-alar cells = One or several rows of differentiated cells just above the alar cells, along the basal leaf margin.

Tomentum = Felt-like covering consisting of abundant, much branched rhizoids.

Vaginula = A sheath around the base of the seta, derived from the base of the archegonium and surrounding stem tissue. The vaginula may have paraphyses (sterile hairs) or be naked. Note that the perichaetial leaves have axillary hairs which may be confused with paraphyses, but the latter are not inserted in the leaf axils.

Field key

The field key includes all European and North American species, except *Drepanocladus cardotii*, which is known from a single North American locality. The page numbers given after each species refer to their descriptions. In connection with the latter, stem leaves of the species are figured, and the habitats and distributions of the species are provided.

1. Stem leaves ± straight, ovate, broadly ovate or rounded-triangular, in upper part ± suddenly rounded / narrowed or apiculate (Fig. 6A, B, p. 19 ; note that inflexed upper leaf margins may give the apex a more acuminate appearance ; occasional specimens of *Scorpidium scorpioides* may key out here). **2**

-. Stem leaves straight, falcate, or spreading to squarrose, from ovate or triangular basal portion gradually narrowed towards leaf apex (Fig. 6C, p. 19). . . . **11**

2. Stem leaf costa short, double or single, not or hardly visible with a hand lens (e.g., Fig. 10A, p. 23). Shoots sometimes flattened. **3**

-. Stem leaf costa long, reaching leaf middle or further, single or branched, usually easily seen with a hand lens (e.g., Fig. 7, p. 19). Shoots not flattened. . . . **4**

3. Shoots flattened, mostly ± regularly and somewhat sparsely pinnate. Alar cells hyaline, in well delimited group (Fig. 62B, p. 107). . . . . ***Calliergonella cuspidata*** **(p. 107)**

-. Shoots turgid, not flattened, slightly and irregularly branched. Alar cells not hyaline, in indistinctly delimited group (Fig. 52B, p. 88). . . . . ***Pseudocalliergon turgescens*** **(p. 88)**

4. Stem leaves broadly ovate to almost orbicular, densely imbricate along most of the shoot. Shoots somewhat stiff, unbranched or with very few branches. Never with leaf-borne rhizoids. . . . . ***Pseudocalliergon trifarium*** **(p. 89)**

-. Stem leaves broadly ovate, ovate or narrowly ovate, spreading to erect, but never densely imbricate. Shoots sparsely to densely (usually ± radially) branched. Leaf-borne rhizoids can be found in all species and are common in some. **5**

5. Medium-sized species, usually with ovate, narrowly ovate (Fig. 7A, p. 19), oblong, or obovate stem leaves. Red to green, or pale- to yellow-green species, more rarely golden to coppery brown. **6**

-. Stem leaves usually broadly ovate or broadly rounded-triangular (Fig. 7B, p. 19). Green, brown-green, or brown species, sometimes with a pale pinkish hue. **8**

6. Stem leaves ovate or narrowly ovate. Pale- or yellow-green to green, sometimes with red secondary colours. (Widespread taxa). **7**

-. Stem leaves ovate, oblong, or obovate. Secondary colours golden to coppery brown, rarely entirely yellow-green. (Relatively narrowly distributed in North America and easternmost Asia ; subfossil in Europe). . . . . ***Loeskypnum wickesiae*** **(p. 61)**

7. Red colours common, otherwise green to dark green. Usually ± branched plants. Stem leaf apex usually distinctly apiculate (Fig. 6B), at least in young leaves, leaf point often bent inwards. Very rarely found with leaf-borne rhizoids. . . . . ***Warnstorfia sarmentosa*** **(p. 54)**

-. Pale- or yellow-green. Usually sparsely branched or unbranched. Stem leaf apex rounded or rounded-obtuse (Fig. 7A). Leaf-borne rhizoids common. . . . . .***Straminergon stramineum*** **(p. 62)**

8. Stem leaf costa usually ending well below leaf apex, with short branches or forked near apex (Fig. 8, p. 20). (Shoots with rather long, thick branches, more sparsely branched and with branch leaves more erect or imbricate than in *Calliergon giganteum*, cf. below). . ***Calliergon richardsonii*** **(p. 48)**

-. Stem leaf costa ending almost in leaf apex (appears to reach apex when seen with a hand lens). **9**

9. Stem leaf costa strong, (Fig. 7B). Alar groups of stem leaves large, triangular, and sharply delimited from surrounding cells, extending from leaf margin to costa or almost so (70-95 % of distance from leaf margin to costa). Stem leaves broadly rounded-triangular. Sometimes pale pink. (Shoots when well developed densely branched like a spruce tree, with ± spreading branch leaves except near branch apices, cf. *Calliergon richardsonii*, above). . . . . ***Calliergon giganteum*** **(p. 47)**

-. Stem leaf costa weaker, (Fig. 25, p. 46 ; Fig. 28, p. 49). Alar groups of stem leaves either smaller (extending from margin 35-60 % of distance from leaf margin to costa), or large and diffusely delimited from surrounding cells. Shape of stem leaves varying. Never pink. (Shoots when well developed more sparsely branched than in *Calliergon giganteum*). . . . **10**

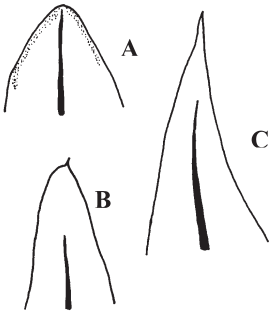


Fig. 6. Different kinds of leaf apices. A : Suddenly narrowed to rounded apex. B : Suddenly narrowed to rounded-apiculate apex. C : Gradually narrowed to acuminate leaf apex.

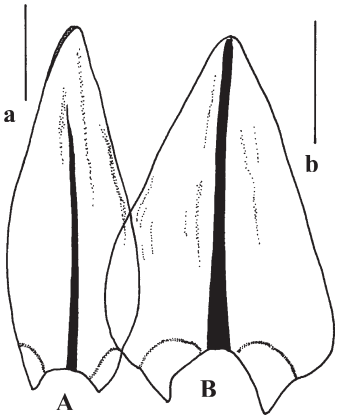


Fig. 7. Stem leaves of *Straminergon stramineum* (A) and *Calliergon giganteum* (B). Scales : a : 0.5 mm, A. b : 1 mm, B.

10. Medium-sized to large species with rounded-triangular stem leaves. Alar groups of stem leaves large, extending from leaf margin to costa or almost so, diffusely delimited from surrounding cells. Rarely found in permanently submerged habitats. . . . . .***Calliergon cordifolium*** **(p. 46)**

-. Large or very large species with broadly ovate stem leaves. Alar groups of stem leaves small, extending 35-60 % of distance from leaf margin to costa, sharply delimited from surrounding cells. Mostly growing submerged or with the uppermost parts of the shoots above the water surface. . . . . .***Calliergon megalophyllum*** **(p. 49)**

11. Stem leaf costa short, usually double, not or hardly visible with a hand lens (e.g., Fig. 10A, p. 23). **12**

-. Stem leaf costa long, reaching middle of leaf or further, normally single, usually easily seen with a hand lens (e.g., Fig. 7, p. 19). **24**

12. Stem leaves spreading to squarrose (Fig. 9), with distinctly furrowed leaf acumina. When viewed from above, the shoots sometimes look like miniature "stars".. . . . . **13**

-. Stem leaves falcate-secund, rarely straight, with or without distinctly furrowed leaf acumen. Shoots not "star-like". **18**

13. Relatively small species. Stems creeping, irregularly pinnately branched. Leaf acumen constituting 55-80 % of leaf length.. . . . . .***Campylium protensum*** **(p. 104)**

-. Plants small, medium-sized, or large. Stems erect or creeping, irregularly or irregularly pinnately branched. Leaf acumen constituting up to 65 % of leaf length, in the large arctic species *Drepanocladus arcticus* up to 70 %. . . **14**

14. Large arctic species. Stem leaf base strongly concave, subclasping. . . . . .***Drepanocladus arcticus*** **(p. 82)**

-. Usually medium-sized species occurring in temperate to arctic areas. Stem leaf base sometimes concave, but not strongly so and not subclasping. . **15**

15. Plants usually with distinctly spreading or squarrose leaves more or less throughout. Leaf costa always short and double. **16**

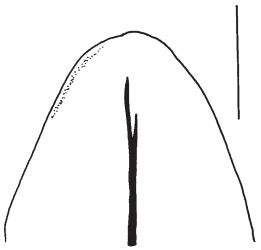


Fig. 8. Upper part of stem leaf of *Calliergon richardsonii*. Scale : 1 mm.

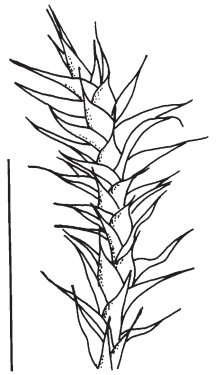


Fig. 9. Apical part of shoot of *Campylium stellatum*. Scale : 2 mm.

-. Plants usually partly with spreading or squarrose leaves, partly with straight or falcate-secund leaves. Leaf costa mostly single and long in some leaves.. . . . . **17**

16. Stem leaf base cordate or rounded-triangular. Dioicous and relatively rarely found with sporophytes. . . . . ***Campylium stellatum*** **(p. 102)**

-. Stem leaf base cordate-ovate or broadly so. Autoicous and frequently found with sporophytes. . . . . ***Campylium laxifolium*** **(p. 101)**

17. Plants small. Alar groups relatively small and indistinct. Dioicous and relatively rarely found with sporophytes. . . . . ***Campyliadelphus chrysophyllus*** **(p. 97)**

-. Plants usually medium-sized. Alar groups large and usually distinct. Autoicous and relatively frequently found with sporophytes. . . . . ***Drepanocladus polygamus*** **(p. 81)**

18. With long and narrow, more or less distinctly furrowed stem leaf acumen. **19**

-. Long and narrow stem leaf acumen not differentiated, but the acumen is sometimes furrowed.. . . . . **21**

19. Stem leaves straight or slightly homomallous ; a short and relatively sharply differentiated leaf acumen present, constituting 15-35 % of leaf length. Arctic species.. . . . . ***Campylium longicuspis*** **(p. 102)**

-. Stem leaves straight or falcate-secund ; leaf acumen gradually differentiated from rest of leaf. Widespread species. **20**

20. Plants small. Alar groups relatively small and indistinct. Dioicous and relatively rarely found with sporophytes. . . . . ***Campyliadelphus chrysophyllus*** **(p. 97)**

-. Plants usually medium-sized. Alar groups large and usually distinct. Autoicous and relatively frequently found with sporophytes. . . . . ***Drepanocladus polygamus*** **(p. 81)**

21. Large or medium-sized species. Shoots often ± turgid, not flattened ; green or often with brown, yellow-brown, red, or blackish colours. . . **22**

-. Medium-sized species. Shoots often somewhat flattened ; green or pale to yellow-green species. **23**

22. Widespread species. Usually large, red, blackish red, green, or dark green species. Shoots turgid, with claw-like apex. Stem leaves strongly concave, with usually small and indistinct groups of alar cells ; costa almost invariably short . . . . . ***Scorpidium scorpioides*** **(p. 64)**

-. Arctic species. Medium-sized, brown, yellow-brown, or green species. Shoots sometimes ± turgid, but without claw-like apex. Stem leaves concave with often large groups of weakly differentiated alar cells ; costa often variable, in some leaves short and double, in some single and longer.. . . . . ***Pseudocalliergon brevifolium*** **(p. 87)**

23. Stem leaves with large and distinct groups of alar cells (Fig. 10A, p. 23) . . . . . ***Calliergonella lindbergii*** **(p. 105)**

-. Stem leaves with small and indistinct groups of alar cells (Fig. 10B, p. 23) . . . . . ***Breidleria pratensis*** **(p. 108)**

24. Stem leaves spreading to squarrose (Fig. 9, p. 20), with furrowed leaf acumen. When seen from above, the shoots often look like miniature "stars". **25**

-. Stem leaves falcate-secund, rarely straight. Shoots not "star-like". . . **26**

25. Plants small. Alar groups relatively small and indistinct. Dioicous, sporophytes relatively rare. . . . . ***Campyliadelphus chrysophyllus*** **(p. 97)**

-. Plants usually medium-sized. Alar groups large, usually distinct. Autoicous, sporophytes relatively frequent . . . . . ***Drepanocladus polygamus*** **(p. 81)**

26. Plants small **27**

-. Plants medium-sized to large. If small, then with tomentum on lower back of costa in at least some leaves (*Conardia compacta*, which grows on sea shores and on calcareous rocks). **28**

27. Stem leaves relatively short and broad, 0.9-1.5 mm long, 0.4-0.7 mm wide ; acumen mostly recurved in at least parts of shoots ; costa always ending well below leaf apex. . . ***Campyliadelphus chrysophyllus*** **(p. 97)**

-. Stem leaves relatively long and narrow, 1.0-2.4 mm long, 0.2-0.6 mm wide ; leaves sometimes falcate, but acumen not recurved, costa sometimes percurrent or excurrent. . . . . ***Campyliadelphus elodes*** **(p. 98)**

28. Stem leaves usually ± broadly triangular to very broadly cordate, rather quickly narrowed towards leaf acumen (e.g., Figs 20, p. 37 ; 23, p. 42). Costa strong (e.g., Fig. 23, p. 42). Alar groups large, triangular, and well delimited, reaching from leaf margin to costa. Plants usually ± densely pinnate (Fig. 23A, p. 42). Paraphyllia present (sometimes difficult to see with a hand lens). Tomentum may occur in all species. **29**

-. Stem leaves differently shaped (rounded-triangular, ovate-triangular, ovate or broadly ovate), more gradually narrowed towards leaf apex (e.g., Fig. 31, p. 55). Costa strong or weak. Alar groups usually less distinct. Branching rarely densely pinnate. Paraphyllia present only in *Palustriella falcata* and tomentum may occur in *P. falcata*, *Tomentypnum nitens*, and *Conardia compacta*. **30**

29. Stem leaves plicate. Paraphyllia linear or lanceolate-linear (Fig. 21, p. 40). Tomentum dull when dry. . . . . ***Palustriella commutata*** **(p. 42) or *P. decipiens*** **(p. 41)**

(These species are difficult to separate in the field. The first is usually more regularly branched, with longer branches than in the latter. The longer leaf cells of *P. commutata* than in *P. decipiens* give the first species a stronger gloss than the second, especially when dry).

-. Stem leaves not plicate. Paraphyllia ovate or narrowly ovate (Fig. 20, p. 37). Tomentum glossy when dry. . . . . ***Cratoneuron filicinum*** **(p. 36)**

30. Paraphyllia present (tear off a few leaves, usually distinctly visible with a hand lens). Large species with falcate, distinctly plicate stem leaves. Costa strong. Tomentum frequently present. ***Palustriella falcata*** **(p. 39)**

-. Paraphyllia absent. Tomentum lacking except in *Tomentypnum nitens* and the small or very small *Conardia compacta* (size like *Amblystegium serpens*). Other characters not in the same combination as in *Palustriella falcata*. . **31**

31. Tomentum usually present in some stem leaves on lower back of costa (check several shoots) ; leaves ± straight, outside Europe sometimes falcate, either narrowly triangular and plicate (Fig 40C, p. 70), or very small and not plicate (Fig. 24, p. 44). **32**

-. Tomentum lacking (but plenty of unbranched or slightly branched rhizoids may be present). Stem leaves with different combination of characters. **34**

32. Medium-sized or robust species in fens. Leaves plicate ; leaf-borne rhizoids only on lower back of costa. **33**

-. Small or very small species (size like *Amblystegium serpens*) on sea shores or calcareous rocks. Leaves not plicate ; leaf borne rhizoids from back of costa or from leaf apex.. . . . . ***Conardia compacta*** **(p. 43)**

33. Stem leaves straight or slightly homomallous. Rhizoids on both stem and abaxial leaf (Widespread in N America and Eurasia). . . . . ***Tomentypnum nitens*** **(p. 71)**

-. Stem and branch leaves falcate-secund. Rhizoids only on abaxial leaf (N America and E Asia).. . . . . ***Tomentypnum falcifolium*** **(p. 72)**

34. Medium-sized or large species, often rather weakly branched, yellow-brown, golden yellow, or green. Shoots often ± turgid. Stem leaves broadly or very broadly ovate (Fig. 50, p. 86). Costa narrow in comparison with the leaf width (Fig. 50, p. 86). Alar cells weakly differentiated. (*Loeskypnum badium*, which could perhaps key out here, has leaves more shortly narrowed towards apex, is mostly smaller than the *Pseudocalliergon* species, and is growing in intermediately mineral-rich habitats, whereas the *Pseudocalliergon* species grow in strongly calcareous places).. . . . . **35**

-. Small to large species with various colours. Usually not turgid. Leaves narrowly ovate to ovate, sometimes broadly ovate. Costa width varying. Appearance of alar cells varying. **36**

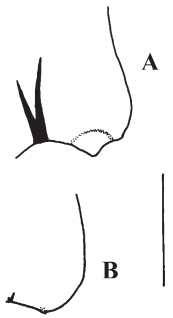


Fig. 10. Stem leaf base in *Calliergonella lindbergii* (A) and *Breidleria pratensis* (B). Scale : 0.5 mm.

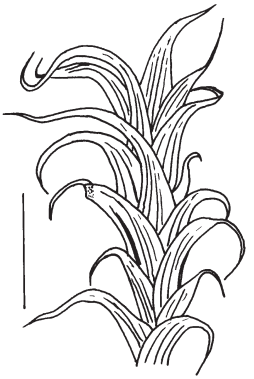


Fig. 11. Shoot of *Sanionia uncinata* seen from dorsal side. Scale : 1 mm.

35. Southern, mainly European species. Large and with more longly acuminate stem leaves (Fig. 50, p. 86) ; costa single. . . . . ***Pseudocalliergon lycopodioides*** **(p. 86)**

-. Arctic species. Medium-sized and with more shortly acuminate stem leaves (Fig. 51, p. 87) ; costa single or double (often varying within the same specimen). . . . . ***Pseudocalliergon brevifolium*** **(p. 87)**

36. Stem leaves plicate (least distinct in *Sanionia georgico-uncinata*, which occurs only in larger late snow-beds or along glacier brooks or rivers in mountainous and arctic areas). **37**

-. Stem leaves not or indistinctly plicate. **42**

37. Autoicous. Stem leaves evenly curved ± along their entire length (Fig. 53, p. 92), with longly or very longly acuminate apex (most shortly acuminate in *Sanionia georgico-uncinata*, occurring in larger late snow-beds or along glacier brooks or rivers in mountainous and arctic areas) ; alar cells inflated, in ± distinct groups. Never with red colours. Shoot apex not curved like a walking stick. **38**

-. Dioicous. Stem leaves rather suddenly curved in their upper part (Fig. 39, p. 69), with acute to longly acuminate point (never in late snow-beds) ; alar cells not differentiated from the other basal cells. Often with red colours, sometimes only in transverse band shortly above leaf insertion or in leaf costa. Shoot apex often curved like a walking stick **41**

38. Small, medium-sized, or large species. Stem leaves longly or very longly acuminate ; inflated alar cells in transversely triangular group, distinctly delimited from cells above. Inner perichaetial leaves (frequently present in these species) gradually narrowed to longly acuminate apex **39**

-. Large species (stem leaves 0.48-1.70 mm wide). Stem leaves acuminate or longly acuminate ; inflated alar cells in ± isodiametric group which together with the hyaline cells above often form a longitudinal group along lower leaf margin (Fig. 55D, p. 95). Inner perichaetial leaves ± suddenly narrowed to acute or shortly acuminate apex . . . . . ***Sanionia georgico-uncinata*** **(p. 95)**

39. Small or medium-sized species (stem leaves 0.35-1.05 mm wide). Shoots usually ± pinnately branched, with the stem leaves typically "combed" when seen from dorsal side of shoot (Fig. 11, p. 23). Capsules horizontal or erect. Found in various habitats, also on sea shores. (When growing outside the wetland habitats, weakly plicate or smooth leaves are sometimes found). **40**

-. Large species (stem leaves 0.62-1.45 mm wide). Shoots usually sparsely or irregularly branched, without "combed" leaves. Capsules erect or inclined. Grows in relatively coastal areas, mostly close to the sea shore . . . . . ***Sanionia orthothecioides*** **(p. 93)**

40. Capsules horizontal or occasionally erect to inclined. Endostome in recently dehisced capsules pale, brownish to yellowish ; basal membrane 36-45 % of total endostome height ; cilia well developed. Widespread species. . . . . ***Sanionia uncinata*** **(p. 91)**

-. Capsules erect to slightly inclined. Endostome in recently dehisced capsules strongly yellow ; basal membrane 25-33 % of total endostome height ; cilia rudimentary. Endemic to western N America. . . . . .
. . . . . .***Sanionia symmetrica*** **(p. 93)**

41. Smaller species (stem leaves 0.61-1.10 mm wide). Stem leaf base erect (and then often ± adpressed to the stem) or slightly spreading (Fig. 12C, D, p. 26), ovate and not or slightly constricted at insertion. . . . . .
. . . . . .***Hamatocaulis vernicosus*** **(p. 68)**

-. Larger species (stem leaves 0.78-2.01 mm wide). Stem leaf base ± patent (Fig. 12A, B, p. 26), broadly ovate and distinctly constricted at insertion.
. . . . . ***Hamatocaulis lapponicus*** **(p. 69)**

42. Stem leaves from basal part suddenly or shortly narrowed towards apex, strongly concave, falcate. Usually sparsely branched, golden yellow, yellow-green, or brownish yellow species, often blackish in older parts. . . .
. . . . . .***Loeskypnum badium*** **(p. 61)**

-. Stem leaves more gradually narrowed upwards, usually not strongly concave (exception : *Warnstorfia procera*, which is mostly distinctly red or blackish red, if not growing submerged), falcate or straight. Branching pattern varying, but mostly ± richly branched. Colour varying. **43**

43. Stem leaves from ± straight and (except in *Hamatocaulis lapponicus*) rather erect basal portion with rather strongly curved upper part (Figs 12B, D, p. 26, 13B, D, p. 27). Alar groups undifferentiated or very small and not visible in the field. **44**

-. Stem leaves curved ± along their entire length, or straight (see cover of book). Alar groups distinctly differentiated and usually visible on torn off leaves (indistinctly differentiated in *Pseudocalliergon angustifolium*, which occurs in the mountains and in parts of the northern boreal zone). **47**

44. Stem leaves slightly to distinctly plicate. Shoot apex often distinctly curved like a walking stick (Fig. 12A, C, p. 26). Green or greyish green, often (check several shoots) with red transverse band shortly above leaf insertion, sometimes entirely red or dark red. Alar cells not differentiated. **45**

-. Stem leaves not or hardly plicate. Shoot apex usually not curved like a walking stick (if the shoot apex has not been growing upwards from a secondary horizontal stem position). Red, brown-red, blackish red, green, yellow-green, or brownish species. Alar cells few (to 15), inflated, hyaline (mostly invisible with a hand lens). **46**

45. Smaller species (stem leaves 0.61-1.10 mm wide). Stem leaf base erect (and then often ± adpressed to the stem) or slightly spreading (Fig. 12C, D, p. 26), ovate and not or slightly constricted at insertion. . . . . .
. . . . . .***Hamatocaulis vernicosus*** **(p. 68)**

-. Larger species (stem leaves 0.78-2.01 mm wide). Stem leaf base ± patent (Fig. 12A, B, p. 26), broadly ovate and distinctly constricted at insertion. . . . . ***Hamatocaulis lapponicus*** **(p. 69)**

46. Dioicous. Shoots usually relatively weak and relatively richly branched (Fig. 13C, p. 27). Green, yellow-green, brown or brown-red. Unique colour

combination compared with *Scorpidium revolvens* : Leaves green or yellow-green with brown-red costa and often also leaf base. Somewhat dull (due to short leaf cells with square to shortly narrowed ends). (Often difficult to separate from the following species in the field)..... ***Scorpidium cossonii* (p. 65)**

-. Autoicous. Shoots usually relatively large and relatively sparsely branched (Fig. 13A, p. 27). Red, blackish red, (brown-red) or green. Unique colour compared with *Scorpidium cossonii* : deep red to blackish red. Glossy (due to long cells with gradually narrowed ends). . ***Scorpidium revolvens* (p. 67)**

47. Stem leaves broadly and longly decurrent (Fig. 29B, C, p. 52 ; visible with a hand lens). Never red. ..... ***Warnstorfia tundrae* (p. 52)**

-. Stem leaves not decurrent. Colour variable, several species have often got red colours. **48**

48. Stem leaf costa excurrent. Shoot and branch apices sometimes pencil-like (Fig. 14A, p. 29). Usually growing submerged and not in mires, except in connection with passing brooks or rivers. **49**

-. Costa not excurrent ; in case of doubt (occurring in species with radially branched shoots) the shoot and branch apices are not pencil-like. Growing submerged or not. **50**

49. Shoot and branch apices pencil-like (Fig. 14A, p. 29). Leaves straight or curved. Shoots which are exposed above the water surface usually become partly red. Young axillary hairs long and brown (visible also with a hand lens if a few leaves are torn off). Shoots radially branched..... ***Warnstorfia trichophylla* (p. 53)**

-. Shoot and branch apices not pencil-like (Fig. 14B, p. 29). Leaves usually curved. Shoots never becoming red. Young axillary hairs small, hyaline (not visible with a hand lens). Shoots distichously branched. ..... ***Drepanocladus longifolius* (p. 76)**

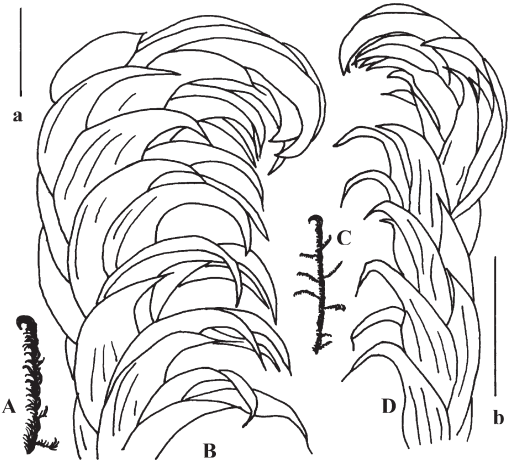


Fig. 12. Habit (A, C) and close-up figures (B, D) of *Hamatocaulis lapponicus* (A, B) and H. *vernicosus* (C, D). Scales : a : 1 mm, B, D. b : 2 cm, A, C.

50. Yellow-brown, brownish yellow or green species, typically with golden gloss when dry. Alar groups of stem leaves indistinctly differentiated. Occurring in ± strongly calcareous habitats in the mountains and parts of the northern boreal zone. . . . . ***Pseudocalliergon angustifolium*** **(p. 84)**

-. Colour varying, not with golden gloss when dry. Alar groups usually large and ± distinctly differentiated. Except for *Cratoneuron curvicaule* and *Drepanocladus sendtneri* rarely occurring in more strongly calcareous habitats. **51**

51. Shoots distichously branched. Never red. Rhizoids never growing from the leaves. Often found in ± nutrient-rich and / or calcareous habitats. . . **52**

-. Shoots ± radially branched, most distinct when growing with stem in vertical position. Sometimes with red colours. Sometimes with rhizoids growing from the leaves (this may occur in all species under this alternative and is frequent in some species). Not especially in nutrient-rich habitats, even if some species tolerate nutrient enrichment. **55**

52. Alar cells of stem leaves thin-walled ; alar group reaching costa or almost so (Fig. 42, p. 75). **53**

-. Alar cells of stem leaves thin-walled or incrassate ; alar group not reaching costa (Fig. 45, p. 79). . . . . ***Drepanocladus latinervis*** **(p. 80),** ***D. sendtneri*** **(p. 79),** ***D. sordidus*** **(p. 78)**

These three species are not possible to separate in the field. They are best separated by the ratio between the leaf lamina cell length and the leaf length (see the key to the species of *Drepanocladus* on p. 73-74).

53. Dioicous. Stem leaves straight or falcate, but not distinctly spreading to squarrose, acumen in straight leaves not markedly furrowed. **54**

-. Autoicous. Stem leaves in parts of shoots frequently spreading to squarrose, in parts straight to falcate, acumen usually distinctly furrowed in straight leaves.. . . . . ***Drepanocladus polygamus*** **(p. 81)**

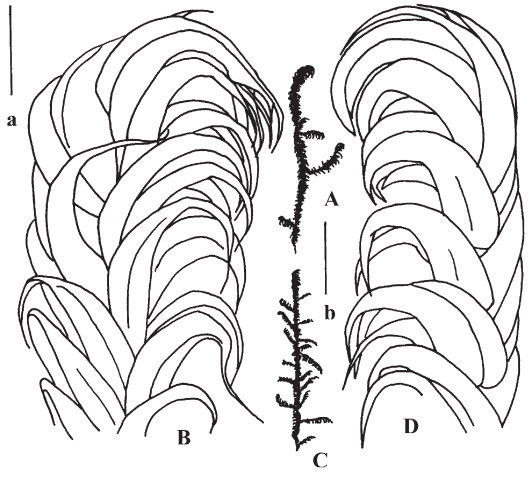


Fig. 13. Habit (A, C) and close-up figures (B, D) of *Scorpidium revolvens* (A, B) and *S. cossonii* (C, D). Scales : a : 1 mm, B, D. b : 1 cm, A, C.

54. Stem leaves straight or falcate ; margin entire or almost so. Widespread and common species in various nutrient-rich wetland habitats, rarely on wet rocks (Fig. 15).. . . . . .***Drepanocladus aduncus*** **(p. 74)**

-. Stem leaves straight ; margin often denticulate or serrulate almost throughout. Rare species on calcareous ground, often on rocks with trickling water. . . . . .***Cratoneuron curvicaule*** **(p. 38)**

55. Dioicous. Alar groups of stem leaves mostly large, triangular, and well delimited. Costa relatively strong (Fig. 31, p. 55). Green or partly to entirely red to blackish red plants.. . . . . **56**

-. Autoicous. Alar groups of stem leaves either large, triangular and well delimited, or indistinct or ± ovate. Costa weak or strong (Figs 33, p. 58 ; 34, p. 59). Plants usually green to brownish, hardly ever with clear red colours, but sometimes brown-red. **58**

56. Stem leaves concave, but not strongly so, and at most shallowly channelled near apex. Leaf margin ± distinctly denticulate (often visible with a hand lens, especially near leaf base and leaf apex. Green or often with clear or sometimes deep red colours.. . ***Warnstorfia exannulata*** **(p. 55)**

-. Stem leaves strongly concave, often deeply channelled near apex. Leaf margin entire (rarely weakly and indistinctly, obtusely denticulate when studied in the microscope). Usually deep red to blackish red, green only in very protected habitats or when growing submerged. (Often difficult to separate from *W. exannulata* in the field) **57**

57. Stem leaves falcate or rarely almost straight, in acumen ± deeply furrowed. (Only known from Eurasia) . . . . . ***Warnstorfia procera*** **(p. 56)**

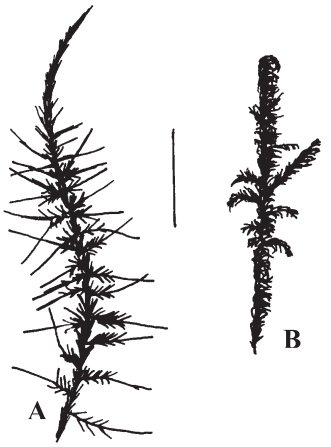


Fig. 14. Habit of *Warnstorfia trichophylla* (A) and *Drepanocladus longifolius* (B). Scale : 1.5 cm.

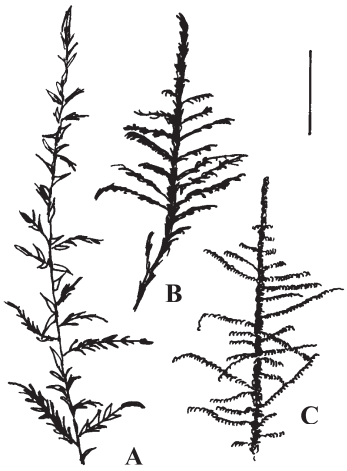


Fig. 15. Habit of *Drepanocladus aduncus*. (A) a submerged plant, (B) an emergent plant, and (C) a plant from an iron spring. Scale : 1 cm.

-. Stem leaves straight, in acumen furrowed to almost tubular. (Only known from northern North America).. ***Warnstorfia pseudosarmentosa*** **(p. 57)**

58. Alar cells of stem leaves in triangular or narrowly triangular group along leaf insertion, often indistinctly delimited. Leaf apex longly to shortly acuminate, very rarely bent inwards over the leaf. . . . . ***Warnstorfia fluitans*** **(p. 58)**

-. Alar cells of stem leaves in all or most leaves together with the supra-alar cells forming an ovate group along leaf margin, usually rather distinctly delimited (in some leaves the group may be ± triangular). Leaf apex usually short, often bent inwards over the leaf (cf. Fig. 29E, p. 52). (In habit and colour reminding of *Straminergon stramineum* or something in between this species and *Warnstorfia fluitans*). . . . . ***Warnstorfia pseudostraminea*** **(p. 59)**

Auxiliary tables

In the following tables, European and North American taxa that have or may have certain characteristics are listed. Thus, when a specimen has the character state indicated in the table heading, it belongs to one of the listed taxa. On the other hand, the absence of a certain character state, such as red colour, in a specimen does not always mean that it cannot belong to the taxa in the respective table.

Table 2. ***Species which may get distinctly red colours.*** The red colour is best developed in habitats exposed to sunlight (never found in submerged specimens) and is most frequently found in relatively northern areas.

Hamatocaulis spp.	*Warnstorfia procera*
Scorpidium spp. (brown-red in *S. cossonii*)	*Warnstorfia pseudosarmentosa*
Calliergon giganteum (pale pinkish hue)	*Warnstorfia sarmentosa*
Warnstorfia exannulata	*Warnstorfia trichophylla*
Warnstorfia fluitans (brown-red, hardly ever with clear red colours)	

Table 3. ***Species which may have leaf-borne rhizoids or rhizoid initials.***

Calliergon spp.	*Tomentypnum* spp. (lower back of costa)
Conardia compacta	
Loeskypnum spp.	*Warnstorfia* spp.
Straminergon stramineum	

Table 4. ***Species which may develop tomentum.*** These species may have abundant and strongly branched rhizoids, which form a tomentum. Check that the tomentum does not belong to some intermixed species, e. g., of *Plagiomnium* or *Cinclidium*.

Campylium laxifolium	*Cratoneuron filicinum*
Campylium protensum	*Palustriella* spp.
Campylium stellatum	*Tomentypnum* spp.
Conardia compacta	

Table 5. *Species with paraphyllia.* Note that sometimes the paraphyllia are rare, and in these cases easily overlooked, especially with a hand lens.

Campylium protensum (rare)	*Palustriella* spp.
Cratoneuron filicinum	

Table 6. *Species which often or normally have distinctly plicate leaves.*

Hamatocaulis spp.	*Sanionia* spp.
Palustriella spp.	*Tomentypnum* spp.

Table 7. *Species which often or normally have prorate, mamillose, or papillose leaf lamina cells.* Note that also *Ctenidium molluscum*, which can grow in wetlands, has distally prorate cells on the dorsal leaf lamina.

Palustriella spp.	*Sanionia* spp. (except *S. orthothecioides*)
Pseudocalliergon angustifolium	

Table 8. *Autoicous species.* These species have sporophytes more often than dioicous species. Below the perichaetia (Fig. 5A, p. 16 ; the short branches from which sporophytes develop), perigonia (Fig. 5B, p. 16) are found in these species (either on the stem or on the base of some branches). Note that perichaetia and / or perigonia are often found also in specimens without sporophytes, and that it is thus frequently possible to judge the sexual condition when capsules are not available.

Calliergon cordifolium	*Drepanocladus polygamus*
Calliergon richardsonii	*Sanionia spp.*
Campylium laxifolium	*Scorpidium revolvens*
Campylium longicuspis	*Warnstorfia fluitans*
Drepanocladus arcticus	*Warnstorfia pseudostraminea*

Table 9. *Species with an excurrent stem leaf costa.*

Campyliadelphus elodes (sometimes)	*Drepanocladus longifolius*
Cratoneuron filicinum (sometimes)	*Warnstorfia trichophylla*

Table 10. *Species with spreading to squarrose leaves.* These species have a "*Campylium*-like" appearance (cf. Fig. 9, p. 20).

Campyliadelphus chrysophyllus (sometimes)	*Campylium stellatum*
Campylium laxifolium (sometimes)	*Drepanocladus arcticus*
Campylium protensum	*Drepanocladus polygamus* (mostly)

Key using both macro- and microscopic characters

I. Key to the genera in Europe

1. Paraphyllia present on stem (best seen close to shoot apex when the leaves are removed and the shoot is studied in the compound microscope). If paraphyllia are very sparse or absent, then axillary hairs very weak and narrow, with 1-2-celled, 4.5-7.0 µm wide upper part (Fig. 20C, p. 37). Rhizoids often forming tomentum. **2**

-. Paraphyllia absent. Axillary hairs frequently with more upper cells and > 7.0 µm wide, only in *Straminergon* sometimes narrower. Rhizoids forming tomentum or not. **4**

2. Stem leaves plicate ; at least some median lamina cells usually prorate or papillose on back. Paraphyllia linear or lanceolate-linear (Fig. 21C, p. 40) . . . . . ***Palustriella*** **(p. 38)**

-. Stem leaves not plicate, median lamina cells smooth. Paraphyllia varying around lanceolate (Fig. 20B, p. 37). **3**

3. Leaves straight or falcate ; costa single, strong, ending far above mid-leaf. ***Cratoneuron*** **(p. 36)**

-. Leaves spreading to squarrose ; costa mostly double, extending at most 35 % way up leaf. . . . . ***Campylium protensum*** **(p. 104)**

4. Stem with at least a partial hyalodermis (Fig. 16A, p. 32). **5**

-. Stem without hyalodermis (Fig. 16B, p. 32). **10**

5. Stem leaf costa long and single. **6**

-. Stem leaf costa short and double. **8**

6. Inflated alar cells numerous and forming a large transversely triangular group which reaches from leaf margin to costa or almost so (Fig. 31B, p. 55). Rhizoid initials frequently present in stem leaves (study several leaves, and especially the upper acumen). . . . . ***Warnstorfia*** **(some species) (p. 50)**

-. Inflated alar cells in smaller transversely triangular or isodiametric group which reaches at most about half way from leaf margin to costa. **7**

7. Stem leaves not or hardly plicate, from ± straight base rather suddenly curved in upper part ; alar groups small or very small (of 2-10 (-15) cells ; Fig. 38B, p. 66) ; supra-alar cells not or hardly differentiated. Red or brown-red colours often present. . . . . ***Scorpidium*** **(p. 63)**

-. Stem leaves usually distinctly plicate, gradually curved along their entire length ; alar groups well developed (Figs 53-55, p. 92-95) ; supra alar cells differentiated, often numerous. Red or brown-red colours never present. . . . . ***Sanionia*** **(p. 90)**

8. Stem leaves orbicular to broadly ovate-lanceolate, strongly concave. Plants medium-sized to very robust, turgid, not flattened ; often with red colours. Hyalodermis of stem often incomplete, i.e., not present around entire stem. . . . . ***Scorpidium*** **(p. 63)**

-. Stem leaves oblong-ovate or ovate, concave. Plants medium-sized, not turgid, usually ±flattened ; never with red colours. Hyalodermis complete. . **9**

9. Pseudoparaphyllia broad (Figs 61-62, pp. 106-107). Alar groups large and distinct. . . . . .***Calliergonella*** **(p. 105)**

-. Pseudoparaphyllia narrow, lanceolate (Fig. 63, p. 109). Alar groups of stem leaves small and indistinct. . . . . .***Breidleria*** **(p. 108)**

10. Plants small or very small (size like *Amblystegium serpens*). Rhizoids warty-papillose ; much branched and often forming tomentum. Alar cells of stem leaves small (Fig. 24B, p. 44).. . . . . ***Conardia*** **(p. 43)**

-. Plants medium-sized to robust, if small, then with inflated alar cells and / or with smooth rhizoids that are slightly branched and do not form a tomentum.. . . . . .**11**

11. Stem leaves usually plicate, if plication weak to indistinct then leaves from ± straight basal portion rather suddenly curved above ; alar cells not differentiated from other basal lamina cells (e.g., Fig. 39B, p. 69).. . . .**12**

-. Stem leaves not or hardly plicate, straight, recurved-squarrose, or gradually curved along their entire length ; alar cells differentiated from other basal lamina cells, but transition to surrounding cells sometimes gradual.. . . .**13**

12. Stem leaves straight or relatively weakly and gradually curved along entire length, often with yellowish or brownish yellow colours, never red. Stem with central strand ; cortex of several layers of incrassate cells (Fig. 17A). . . . . ***Tomentypnum*** **(p. 70)**

-. Stem leaves from ± straight basal portion rather suddenly curved above, often with red colours. Stem without central strand ; cortex of 1-2 layers of slightly incrassate cells (Fig. 17B). . . . . .***Hamatocaulis*** **(p. 68)**

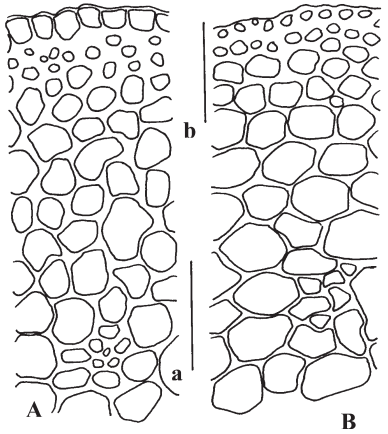


Fig. 16. Partial transverse sections of stem in *Scorpidium cossonii* (A) and *Pseudocalliergon angustifolium* (B). Scales : a : 50 µm, A. b : 50 µm, B.

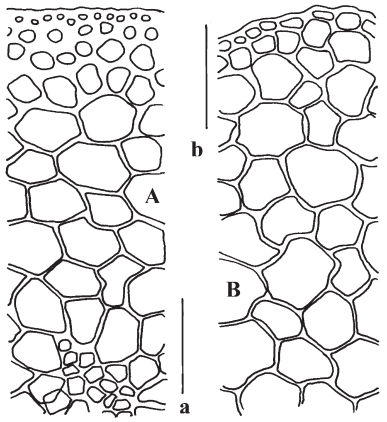


Fig. 17. Partial transverse sections of stem in *Tomentypnum nitens* (A) and *Hamatocaulis vernicosus* (B). Scales : a : 50 µm, A. b : 50 µm, B.

13. Stem leaf costa short and double; alar cells inflated (widest cells 17.0-29.5 µm wide), in well differentiated ovate or ovate-rectangular group along basal leaf margin (cf. Fig. 57C, p. 101). . . . . ***Campylium*** **(p. 99)**

-. Stem leaf costa long and single; if short and double then alar groups either transversely triangular or alar cells smaller (widest cells 10.5-17.5(-21.0) µm wide). **14**

14. Stem leaves recurved to squarrose, at least along some shoot portions, with distinctly furrowed leaf acumen. When viewed from above, the shoots frequently look like miniature "stars". **15**

-. Stem leaves falcate-secund, more rarely straight, with or without distinctly furrowed leaf acumen. Shoots not "star-like". **16**

15. Stem leaves to 1.7 mm long, alar cells slightly inflated, widest cells 10.5-17.5(-21.0) µm wide. Dioicous.. . . . . ***Campyliadelphus*** **(p. 96)**

-. Stem leaves at least (1.3-)1.6 mm long, alar cells strongly inflated, widest cells 17.0-31.5 µm wide. Autoicous. .***Drepanocladus polygamus*** **(p. 81)**

16. Stem leaves narrowly decurrent. Plants small to almost medium-sized, often with distinctly set off, channelled acumen with acuminate apex. Never with red colours. . . . . ***Campyliadelphus*** **(p. 96)**

-. Stem leaves decurrent or not ; when decurrent plants either medium-sized to large or leaf apex broadly acuminate to rounded or rounded-apiculate. Sometimes red. **17**

17. Alar cells of stem leaves inflated or slightly so, mostly incrassate to strongly so, rarely thin-walled in mature leaves, indistinctly delimited from surrounding cells. Axillary hairs well developed, abundant, with early yellowish or brownish cells. Brownish yellow, yellow-brown, or copper-brown colours often present, never red. **18**

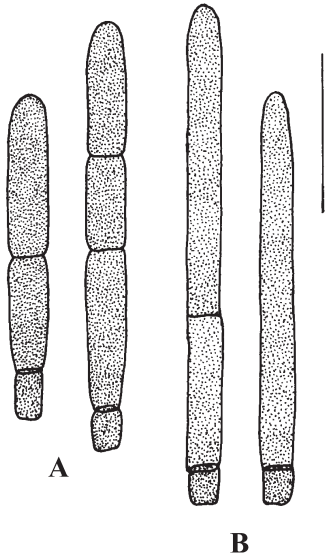


Fig. 18. Axillary hairs in *Loeskypnum badium* (A) and *Pseudocalliergon lycopodioides* (B). Scale : 50 µm.

-. Alar cells of stem leaves inflated or strongly so, thin-walled or sometimes incrassate (in *Drepanocladus sendtneri* often strongly incrassate), distinctly delimited from surrounding cells, except in *Calliergon cordifolium* (Fig. 25, p. 46) and *Warnstorfia fluitans* (Fig. 33, p. 58). Axillary hairs well developed and abundant or small and rare, hyaline except in *Warnstorfia trichophylla* (brownish). Colours, except often in *D. sendtneri*, different, sometimes red. **19**

18. Plants mostly medium-sized. Stem leaves strongly concave ; rhizoid initials frequent in lamina, especially near leaf apex. Apical cell of axillary hairs not markedly elongate (Fig. 18A, p. 33). All leaf and stem cells ± incrassate. . . . . ***Loeskypnum*** **(p. 60)**

-. Plants medium-sized or large. Stem leaves concave or strongly concave ; rhizoid initials always absent from leaf lamina. Apical cell of axillary hairs usually comparatively elongate (Fig. 18B, p. 33). Stem cells between central strand and cortex ± thin-walled, leaf cells thin-walled or incrassate. . . . . ***Pseudocalliergon*** **(p. 83)**

19. Stem leaves broadly ovate to broadly rounded-triangular, with broadly obtuse or rounded apex. Axillary hairs 2-8 (-10)-celled, hyaline when young, large and abundant. . . . . ***Calliergon*** **(p. 45)**

-. Stem leaves ovate to rounded-triangular, with acuminate, shortly apiculate, or rounded apex ; if apex rounded, then axillary hairs 1-2-celled (*Straminergon*) or 1-4 (-5)-celled (*Warnstorfia sarmentosa*), weak and usually sparse. **20**

20. Stem leaves straight, oblong, ovate or narrowly ovate, suddenly narrowed to rounded and often cucullate apex. Alar group ovate or broadly ovate, along basal leaf margin. Plants usually sparsely branched. Red colours absent. . . . . ***Straminergon*** **(p. 62)**

-. Stem leaves straight or falcate, triangular to ovate or narrowly so, gradually narrowed to acuminate or obtuse apex, or shortly narrowed to rounded-apiculate or rarely rounded apex. Alar group usually ± transversely triangular ; if alar and supra-alar cells together form an ovate group along basal leaf margin, then leaves triangular or ovate and gradually narrowed towards apex. Plants usually more strongly branched. Red colours sometimes present. **21**

22. Plants distichously branched. Axillary hairs with 1-2 (-3)-celled upper part. A stage with a ± square group of undifferentiated alar cells, when the surrounding cells have already differentiated, present in the ontogeny of the alar cells (Fig. 19A, p. 35; study the youngest stem leaves). Never with red colours and never with rhizoid initials in leaves. Usually in somewhat eutrophic habitats. . . . . ***Drepanocladus*** **(p. 72)**

-. Plants radially branched. Axillary hairs with 1-7-celled upper part. "Square group stage" absent from alar cell group ontogeny (Fig. 19B, p. 35). Sometimes with red colours and frequently with rhizoid initials present in leaves (most often near leaf apex). In nutrient-poor or sometimes in somewhat eutrophic habitats. . . . . ***Warnstorfia*** **(p. 50)**

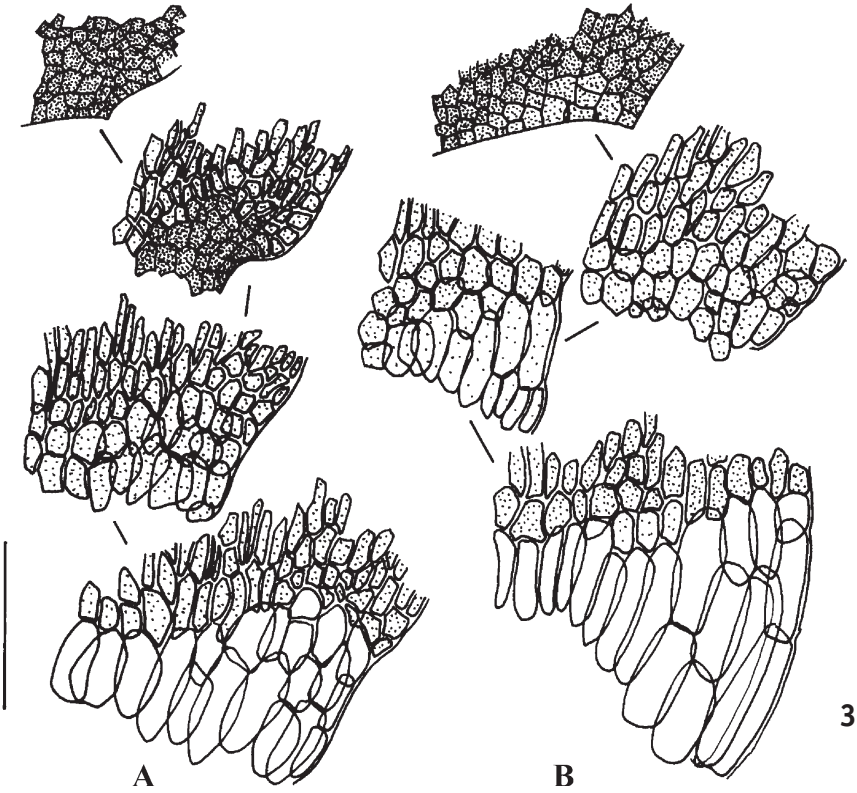


Fig. 19. Ontogeny of alar cells in *Drepanocladus aduncus* (A) and *Warnstorfia exannulata* (B). Scale : 100 µm. For both species the series of stages in the ontogeny should be followed from the upper part of the figure downwards. In the first stage the basal cells are undifferentiated and parenchymatous throughout in both species. In the next stage all cells except those in a more or less square or isodiametric area of parenchymatous and relatively strongly chlorophyllose cells differentiate in the *aduncus*-type of ontogeny (the 'square group stage'). Next, the cells of the square group start to differentiate and finally expand, sometimes together with other basal cells, to form the mature alar group. In the *exannulata*-type of ontogeny all basal cells begin to differentiate more or less simultaneously. The alar cells differentiate until a stage where they are somewhat larger and less chlorophyllose than the other basal cells is reached. After this the alar cells expand and reach their mature size.

II. Genera and species

Cratoneuron (Sull.) Spruce

Dioicous. Plants branched ± in one plane, never with red colours. Stem leaves plane or slightly concave, narrowly to broadly triangular or rounded triangular, gradually or rather suddenly narrowed to short or long acumen, acuminate, straight or falcate ; costa strong, usually percurrent or excurrent, sometimes ending some distance below leaf apex ; margin denticulate or serrulate almost throughout ; median lamina cells smooth, mostly short, alar cells usually strongly inflated and hyaline, forming a large transversely triangular group, decurrent ; rhizoid initials never present in leaves. Paraphyllia present and few to numerous, varying around lanceolate, or absent. Axillary hairs rare and weak, 4.5-7.0 µm wide, with 1-2-celled upper portion (Fig. 20C). Rhizoids usually much branched and often forming tomentum, red-brown, smooth (glossy when dry), inserted at or just below leaf costa insertion. Stem with central strand, cortex of 2-3 layers of incrassate cells. Inner perichaetial leaves straight and erect, plicate. Seta tall ; capsule ± horizontal ; annulus separating. Peristome well developed ; outer layer of exostome cross-striolate in lower part.

Key to the species of Cratoneuron

1. Stem leaves mostly varying around triangular ; median lamina cells 12.0-53.0 µm long, rectangular or elliptic, sometimes linear ; alar cell group usually strongly expanded in marginal portion. Paraphyllia almost invariably present, but sometimes only in youngest shoot portions. Rhizoids frequently forming tomentum. . . . . **1. *C. filicinum***

-. Stem leaves varying around ovate ; median lamina cells (16.0-) 21.0-80.0 µm long, linear or shortly so ; alar cell group transversely triangular. Paraphyllia absent. Rhizoids usually sparse. . . . . **2. *C. curvicaule***

1. Cratoneuron filicinum (Hedw.) Spruce (Fig. 20A-C)

***Amblystegium tenax* var. *spinifolium* (Schimp.) H. A. Crum & L. E. Anderson ; *Cratoneuron filicinum* var. *atrovirens* (Brid.) Ochyra ; *Cratoneuron filicinum* var. *fallax* (Brid.) G. Roth ; *Cratoneuron formianum* (Fior. Mazz.) G. Roth ; *Cratoneuron punae* Müll. Hal. ; *Hygroamblystegium crassicostatum* E. B. Bartram ; *Hygroamblystegium meridense* E. B. Bartram**

Stem leaves plane or slightly concave, not plicate, narrowly to broadly triangular, rounded-triangular, or sometimes ovate, gradually to rather suddenly narrowed to acumen, straight or falcate, branch leaves usually narrower and more strongly falcate ; margin denticulate or serrulate almost throughout ; costa strong, 38.0-157.0 (-170.0) µm wide at base, constituting 9-20 (-33) % of leaf width where leaf is widest, ending in leaf apex to longly excurrent, more rarely ending a short distance below leaf apex ; median lamina cells 12.0-

53.0 µm long, rectangular or elliptic, smooth ; alar cells usually numerous, usually strongly inflated and hyaline, forming a well defined group which is mostly strongly widened in its marginal part. Paraphyllia few or numerous, rarely absent, varying around lanceolate to narrowly triangular, sometimes found only in youngest part of shoot. Rhizoids smooth, frequently abundant and forming tomentum. Axillary hairs few, very weak. - Usually medium-sized, pinnately or irregularly branched and somewhat stiff plants, green or yellowish green, more rarely brownish. In the field often easily recognised by pale shoot and branch apices. The species is found in moist or wet habitats in calcareous districts, on rocks, on tree bases beside streams, in springs, on moist soil, or in calcareous fens, from the sea level to the alpine region of the mountains. [pH 6.7-8.2 (n = 64) ; EC 106-706 mS/m (n = 12) ; Ca 18.3-121,0 mg/l (n = 10) ; IR 0.72-0.96 (n = 10)]. *Cratoneuron filicinum* is widely distributed in the northern temperate to arctic regions, in Macaronesia, in mountains of tropical Africa, in South America, and in New Zealand.

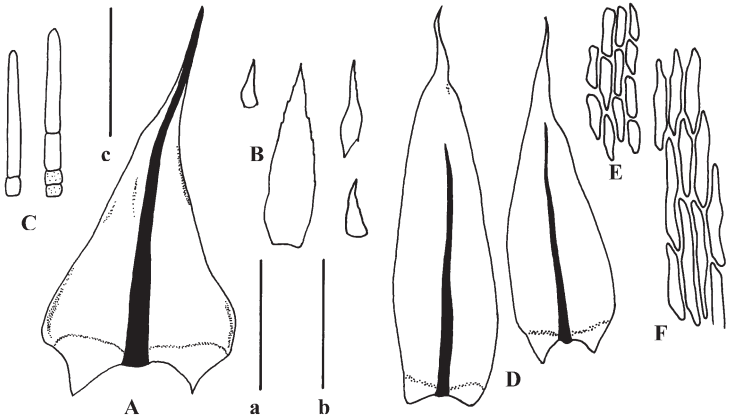
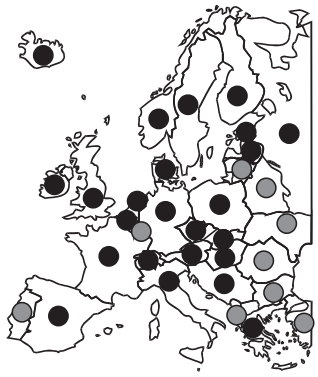


Fig. 20. *Cratoneuron filicinum* (A-C) and *C. curvicaule* (D-F). A, D : Stem leaves. B : Paraphyllia. C : Axillary hairs. E, F : Median lamina cells from two leaves. Scales : a : 0.5 mm, A, D. b : 200 µm, B. c : 50 µm, C, E, F.

Cratoneuron filicinum is very variable in habit. Especially in Macaronesia and the Mediterranean areas, strikingly rigid plants with extremely strong costae are sometimes found. These are sometimes recognised as *Cratoneuron filicinum* var. *atrovirens* (Brid.) Ochyra. They have narrowly triangular or narrowly ovate-triangular leaves that are gradually narrowed to an acuminate or often obtuse point. The costae are

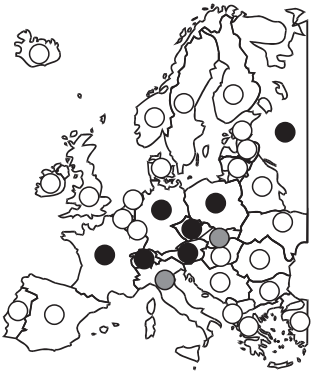


up to 8-stratose, 101.0-170.0 µm wide, and constitute 20-33 % of the leaf width where the leaf is widest. The excurrent part of the costa may constitute up to 50 % of the leaf length. However, quite "normal" *C. filicinum* leaves are sometimes found in parts of such plants, or shoots that grow from old plants of this kind may have a "typical" *C. filicinum* appearance. Thus, it seems like this extreme variation may be due to habitat modifications only. On Madeira, plants with extremely broad costae are typically found in connection with waterfalls, whereas plants with relatively narrower costae are found in moist or wet places where the water is neither falling nor running fast.

Cratoneuron filicinum is frequently confused with species of *Palustriella*, which, however, have plicate leaves, mostly at least some prorate or papillose leaf lamina cells (especially on dorsal side), rhizoids that are mostly warty-papillose, large axillary hairs, and which paraphyllia are linear or lanceolate-linear.

2. Cratoneuron curvicaule (Jur.) G. Roth (Fig. 20D-F)

***Callialaria curvicaulis* (Jur.) Ochyra**



Stem leaves plane or concave, not plicate, narrowly to broadly ovate or triangular-ovate, gradually to rather suddenly narrowed to often shortly set off acumen, straight and erect, branch leaves usually narrower ; margin denticulate or serrulate throughout to almost entire ; costa strong, 42.0-80.0 µm wide at base, ending in lower part of acumen or somewhat below ; median lamina cells (16.0-) 21.0-80.0 µm long, linear or shortly so, smooth ; alar cells usually numerous, inflated and hyaline, forming a well defined transversely triangular group. Paraphyllia absent. Rhizoids smooth, few. Axillary hairs few, very weak. – Medium-sized, pinnately or irregularly branched and rather soft plants, green or yellowish green. The species is found in calcareous districts, usually on rocks with trickling or dripping water, in central Europe mainly in the higher regions of the mountains. *Cratoneuron curvicaule* occurs in arctic and mountainous areas of Eurasia.

Cratoneuron curvicaule is close to *C. filicinum*, from which it differs by the characters given in the key.

***Palustriella* Ochyra**

Dioicous. Plants branched ± in one plane, never with red colours. Stem leaves plicate or strongly plicate, triangular-cordate to ovate-lanceolate, sud-

denly or gradually narrowed to short or long acumen, straight or falcate ; costa strong, ending far up in acumen or percurrent ; margin denticulate in lower part or throughout ; at least some median lamina cells usually prorate or papillose on back, more rarely smooth throughout, alar cells usually strongly inflated and hyaline (at least when young) and forming a ± large transversely triangular group, sometimes strongly expanded in its marginal portion, ± decurrent ; rhizoid initials never present in leaves. Paraphyllia present, few or numerous, linear to lanceolate-linear. Axillary hairs numerous, well developed, with (1-) 2-6-celled upper portion (Fig. 22C). Rhizoids usually much branched and often forming tomentum, red-brown, warty-papillose (dull when dry), inserted at or just below leaf costa insertion. Stem with or without weak central strand, cortex of incrassate cells. Inner perichaetial leaves straight and erect, plicate. Seta tall ; capsule ± horizontal ; annulus separating. Peristome well developed ; outer layer of exostome cross-striolate in lower part.

Species of *Palustriella* could be confused with *Cratoneuron filicinum* or *Helodium* species. The differences between *Palustriella* and *C. filicinum* are discussed under the latter. While the shoots of *Palustriella* are clearly distichously branched, those of *Helodium* usually have the branches in two opposite 'zones', but not strictly in only two directions. Contrary to the condition in *Palustriella*, the paraphyllia in *Helodium* are much branched and frequently inserted on the lower leaf margin.

Key to the species of *Palustriella*

1. Stem leaves ± broadly cordate-triangular, above ± suddenly narrowed to short and recurved or elongate and falcate acumen (ventral leaves usually wider and with shorter acumen than dorsal leaves). Alar cell group large (Figs 22A, 23B, C), usually strongly expanded in marginal portion. **2**

-. Stem leaves ovate, above gradually narrowed to usually long and falcate (rarely straight) acumen. Alar cell group comparatively small (Fig. 21B), not or slightly expanded in marginal portion. . . . . **1. *P. falcata***

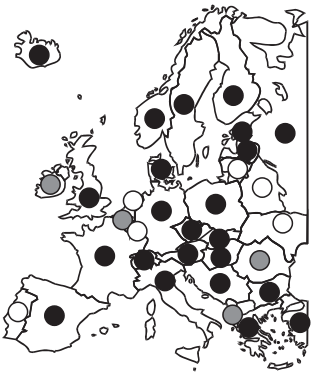
2. At least some of the more basal median lamina cells (above alar cells) papillose, or papillose cells mixed with prorate and / or smooth cells.. . . . . **2. *P. decipiens***

-. Basal lamina cells only prorate, sometimes ± smooth throughout.. . . . . **3. *P. commutata***

1. Palustriella falcata (Brid.) Hedenäs (Fig. 21)

***Cratoneuron commutatum* var. *falcatum* (Brid.) W. Mönkemeyer ; *Cratoneuron commutatum* var. *sulcatum* (Lindb.) W. Mönkemeyer ; *Cratoneuron falcatum* (Brid.) G. Roth ; *Palustriella commutata* var. *falcata* (Brid.) Ochyra**

Stem leaves usually strongly plicate, from ovate base lanceolate, gradually narrowed to long or more rarely short acumen, strongly falcate to ± straight, branch leaves smaller than stem leaves but differing only slightly



in shape ; margin distinctly denticulate only below ; costa strong, ending in leaf apex, in weak modifications sometimes weaker and shorter ; median lamina cells 17.5-155.0 µm long, mostly at least some basal cells dorsally prorate ; alar cells inflated, hyaline when young but early yellow, forming a rather small group which is not expanded in its marginal part. Paraphyllia few or numerous, linear to lanceolate-linear. Rhizoids warty-papillose. Axillary hairs numerous, well developed. - Mostly rather coarse, sparsely pinnately to irregularly branched plants, green, yellowish, or brownish, in calcareous springs, fens, irrigated calcareous rocks or beside small brooks, from the sea level to the alpine region. [pH 5.0-8.4 (n = 152) ; EC 53-706 mS/m (n = 113) ; Ca 6.4-121,0 mg/l (n = 31) ; IR 0.68-0.97 (n = 31)]. *Palustriella falcata* is widespread in the northern temperate to arctic regions, and occurs also in northern Africa, including Macaronesia.

This species is frequently confused with *P. commutata*, a species that seems to be confined to Eurasia. However, the latter is somewhat smaller, its shoots are usually densely branched in a feather-like fashion, the stem leaves

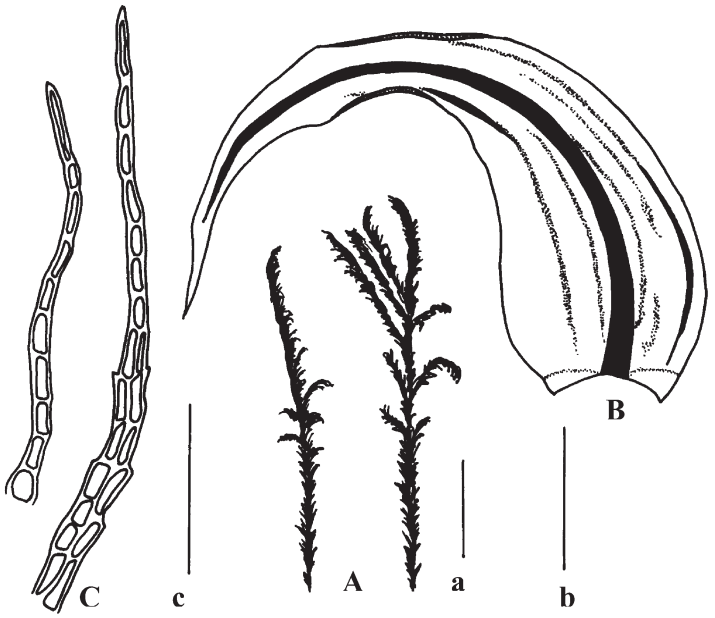


Fig. 21. *Palustriella falcata*. A : Habit. B : Stem leaf. C : Paraphyllia. Scales : a : 1 cm, A. b : 0.5 mm, B. c : 100 µm, C.

are broadly cordate-triangular, and its alar groups are strongly widened in their marginal portion. The stem and branch leaves are relatively similar in shape in *P. falcata*, whereas they are clearly different in most expressions of *P. commutata*. In addition, *P. commutata* is more restricted than *P. falcata* in its habitat, occurring only in the most strongly calcareous habitats. The differences between *P. falcata* and *P. decipiens* are given under the latter.

2. Palustriella decipiens (G. De Notaris) Ochyra (Fig. 22)

***Cratoneuron decipiens* (G. De Notaris) Loeske**

Stem leaves usually strongly plicate, from broadly cordate-triangular base ± suddenly narrowed into short and recurved or more elongate and falcate acumen, branch leaves smaller and narrower than stem leaves ; margin denticulate throughout ; costa broad, ending in leaf apex ; median lamina cells 14.0-26.0 µm long, in dorsal leaves sometimes up to 35.0 µm long), below shorter and wider, at least the more basal cells papillose on back, sometimes some basal cells prorate or smooth ; alar cells inflated and mostly hyaline, forming a large distinct group which is ± strongly expanded in its marginal part. Paraphyllia usually numerous, linear to lanceolate-linear. Rhizoids warty-papillose. Axillary hairs numerous, well developed. - Mostly medium-sized, pinnately or irregularly pinnately branched plants, green, yellowish, or brownish, in calcareous springs and fens and beside small brooks, avoiding habitats that are strongly exposed to the sun, from the lowlands to the alpine region. [pH 5.8-8.0 (n = 24) ; EC 80-538 mS/m (n = 20) ; Ca 4.2-87,8 mg/l (n = 18) ; IR 0.53-0.97 (n = 18)]. *Palustriella decipiens* is widespread in Eu-

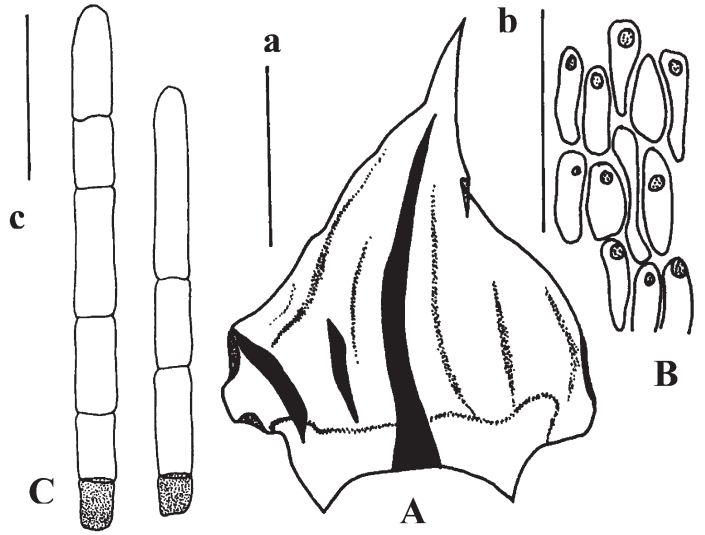
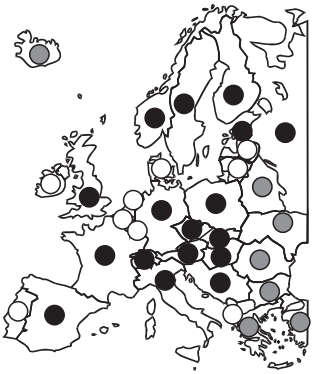


Fig. 22. *Palustriella decipiens*. A : Stem leaf. B : Lamina cells above alar group. C : Axillary hairs. Scales a : 0.5 mm, A. b : 50 µm, B. c : 50 µm, C.

rasia, whereas no certain finds are known from North America. In Europe the species is frequent in calcareous areas in the north, for example in connection with the Scandinavian mountain range, whereas it is apparently less common in mountains further south.



Palustriella decipiens is similar to *P. commutata* in leaf shape, but the plants are on the average slightly smaller and more irregularly branched, the median lamina cells are shorter (14.0-26.0 vs. 22.0-147.0 µm long), and at least some of the basal cells have distinct papillae. In *P. commutata* the basal cells are often prorate, but never papillose. *Palustriella falcata* differs from *P. decipiens* in its distinctly larger size, differently shaped stem leaves and alar groups, and in never having papillose cells.

3. Palustriella commutata (Hedw.) Ochyra (Fig. 23)

***Cratoneuron commutatum* (Hedw.) G. Roth. ; *Cratoneuron glaucum* (Lam. & DC.) G. Roth**

Stem leaves usually strongly plicate, from broadly cordate-triangular base ± suddenly narrowed into short and recurved or more elongate and falcate acumen, branch leaves smaller and narrower than stem leaves ; margin denticulate ± throughout and often strongly denticulate near leaf base ; costa strong, ending in leaf apex ; median lamina cells 22.0-147.0 µm long, below

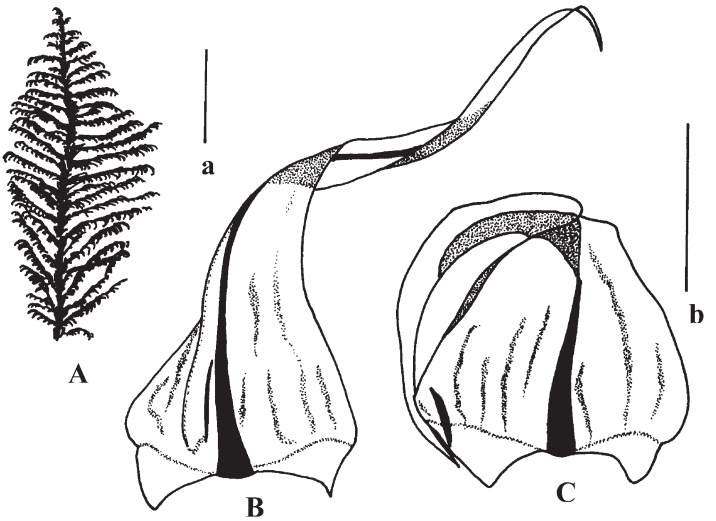
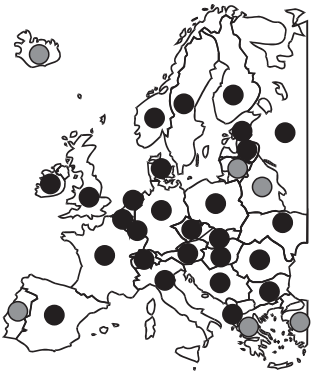


Fig. 23. *Palustriella commutata*. A : Habit. B : Dorsal stem leaf. C : Ventral stem leaf. Scales : a : 1 cm, A. b : 0.5 mm, B, C.

shorter and mostly distinctly widened, mostly at least some basal cells dorsally prorate ; alar cells inflated and mostly hyaline, forming a large distinct group which is usually ± strongly expanded in its marginal part. Paraphyllia few or numerous, linear to lanceolate-linear. Rhizoids warty-papillose. Axillary hairs numerous, well developed. - Mostly medium-sized, regularly pinnately branched plants, green, yellowish, or brownish, in strongly calcareous springs, on irrigated calcareous rocks, and beside small calcareous brooks. [pH 4.9-8.1 (n = 31) ; EC 280-538 mS/m (n = 16) ; Ca 48.6-103,5 mg/l (n = 15) ; IR 0.72-0.96 (n = 15)]. Seemingly widespread in Eurasia, including Madeira, but lacking in North America.



For the differences between *P. commutata*, *P. falcata*, and *P. decipiens*, see the notes after the latter two.

Conardia H. Rob.

Dioicous (Europe) or autoicous. Plants branched ± in one plane, never with red colours. Stem leaves erect-spreading and straight or slightly falcate, lanceolate or ovate-lanceolate, not plicate ; costa single, ending in acumen or percurrent ; margin finely denticulate or near leaf base often coarsely so ; median lamina cells shortly linear, alar cells usually numerous, small, quadrate or rectangular and extending from leaf margin almost to costa, indistinctly delimited from surrounding cells ; rhizoid initials sometimes present in the leaf lamina near leaf apex, slightly inflated and paler than other lamina cells. Gemmae sometimes produced from initial cells near leaf apex. Paraphyllia absent. Axillary hairs usually abundant, with hyaline, 1-4-celled upper part, well developed. Rhizoids warty-papillose, red-brown, strongly branched and often forming tomentum, inserted on stem below leaves or on back of leaf costa or growing from rhizoid initials near leaf apex. Stem with central strand and a cortex of incrassate cells. Seta tall ; capsule inclined ; annulus separating ; operculum conical to shortly rostrate. Peristome slightly reduced ; outer layer of exostome reticulate in lower part, mostly with portions cross-striolate. [Sporophytes not known from Europe].

1. Conardia compacta (Drumm.) H. Rob. (Fig. 24)

***Amblystegium compactum* (Drumm.) Austin ; Rhynchostegiella compacta (Drumm.) Loeske**

Stem leaves erect-spreading and straight or slightly falcate, lanceolate or ovate-lanceolate ; margin finely denticulate or near leaf base often coarsely

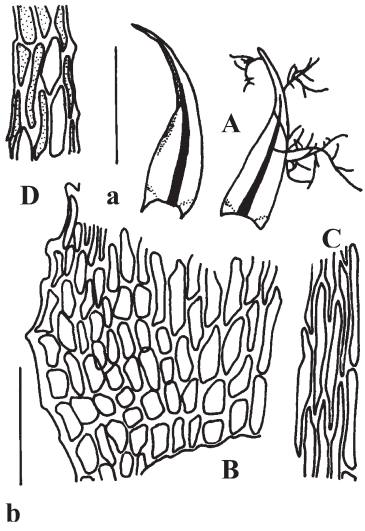
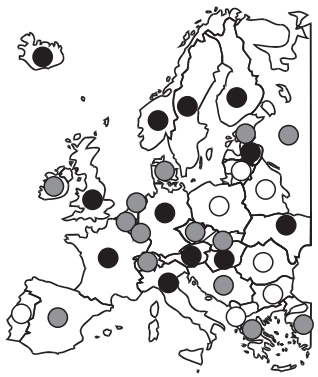


Fig. 24. *Conardia compacta*. A : Stem leaves. B : Alar cells. C : Median lamina cells. D : Portion of leaf apex, with rhizoid initials. Scales : a : 0.5 mm, A. b : 50 µm, B-D.



denticulate ; costa ending in acumen or sometimes percurrent ; median lamina cells 21.0-77.0 µm long, thin-walled or slightly incrassate, near base shorter, wider and more strongly incrassate ; alar cells usually numerous, small, quadrate or rectangular, extending from leaf margin almost to costa. Rhizoids warty-papillose, red-brown, strongly branched and often forming tomentum, inserted on stem below leaves, on back of leaf costa, or growing from rhizoid initials near leaf apex. - Minute plants (size approximately as in *Amblystegium serpens* (Hedw.) Schimp.), irregularly branched and usually in soft, dense green or yellow-green mats, in northern Europe mostly on rocks and soil on sea shores, in other areas also on moist calcareous rocks or soil. [pH 7.7 (n = 2)]. Widespread in Europe and North America, in addition known from South America, North Africa, and Kashmir.

Amblystegium serpens, which also can grow on sea shores, differs from *C. compacta* in more indistinct alar groups, in having less strongly denticulate leaf margins, in having smooth and unbranched rhizoids that are inserted only on the stem, and in never having gemmae. *Rhynchostegiella durieui* (Mont.) P. Allorge & V. Allorge is another small pleurocarpous species with warty-papillose rhizoids that may grow on richer rocks. However, the rhizoids in the latter species are never inserted on the leaves, the leaves are lanceolate-triangular to narrowly triangular and gradually narrowed to a longly or very longly acuminate apex, the lamina cells are (63.0-) 73.0-151.0 µm long, and the costa ends below mid-leaf.

Calliergon (Sull.) Kindb.

Autoicous or dioicous. Plants ± radially branched, never with clear red colours, but sometimes (*C. giganteum*) pinkish. Stem leaves straight, ± broadly ovate to broadly rounded-triangular with rounded or obtuse apex, not plicate ; costa single, unbranched and ending just below leaf apex, or branched or in upper part forked and ending well below apex ; margin entire or occasionally slightly sinuose ; median lamina cells linear, smooth, cells near margin often clearly narrower than in middle of lamina ; alar cells rectangular to elongate-rectangular, strongly inflated and hyaline, thin-walled, in large triangular to broadly ovate group, distinctly or indistinctly delimited from lamina cells above, broadly decurrent ; rhizoid initials common in leaves, especially near leaf apex and along costa, slightly wider and paler than other lamina cells. Paraphyllia absent. Axillary hairs abundant, large, with hyaline, 2-8 (-10)-celled upper part. Rhizoids red-brown, slightly branched, smooth, inserted at various points on leaves, or on scattered points or in rows on stem. Stem with central strand and a well differentiated cortex of incrassate cells. Inner perichaetial leaves straight and erect, not plicate, margin entire or with an occasional tooth at shoulder ; vaginula naked. Capsule ± horizontal ; annulus not separating. Peristome well developed ; outer layer of exostome reticulate in lower part.

Besides the species mentioned below, Steere (1941) described *Calliergon aftonianum* from fossil material. His description suggested large and pinnately branched plants with the habit of *Calliergon giganteum*, at the same time mentioning that only isolated branches were known. His photographs of branch leaves and the description indicate that it is indeed a species of *Calliergon*, albeit with a short or sometimes absent costa. Weakly developed costae are not that uncommon in weak plants of many species treated here and the description of a new species only from isolated branches may thus seem premature. On the other hand, Janssens and Glaser (1986) reported that plants with short costae in the stem leaves still occur in North America. Further studies are therefore necessary before deciding about the correct treatment of *Calliergon aftonianum*.

Key to the species of Calliergon

1. Alar groups large, extending from leaf margin to costa or almost so ; transition between alar cells and surrounding cells gradual and alar groups thus diffusely delimited (Fig. 25).. . . . . **1. *C. cordifolium***

-. Alar groups large or small ; transition between alar cells and surrounding cells sudden and alar groups thus sharply delimited (e.g., Fig. 26).. . . .**2**

2. Stem leaf costa strong or very strong, (88.0-) 95.0-282.0 µm wide at base, normally unbranched and ending near leaf apex ; alar groups reaching 70-95 % of distance from leaf margin to costa (Fig. 26). . . **2. *C. giganteum***

-. Stem leaf costa weaker, 52.5-119.0 µm wide, either single and ± reaching

leaf apex, or single, branched, or forked and ending well below leaf apex ; alar groups reaching 35-80 % of distance from leaf margin to costa (Figs 27A, 28A). **3**

3. Autoicous. Stem leaf costa reaching 50-90 % way up leaf and usually branched or in upper part forked. Axillary hairs with long apical cells (Fig. 27B).. . . . . **3. *C. richardsonii***

-. Dioicous. Stem leaf costa ± reaching leaf apex, normally unbranched. Axillary hairs with short apical cells (Fig. 28B). . . **4. *C. megalophyllum***

1. Calliergon cordifolium (Hedw.) Kindb. (Fig. 25)

Autoicous. Stem leaves erect to almost spreading, concave, ovate-cordate to triangular-ovate or narrowly elongate-cordate, broadly obtuse or rounded at apex ; costa 54.0-117.0 (-132.0) µm wide at base, usually ending shortly below leaf apex ; median lamina cells 33.5-138.5 (-157.0) ((-192.5)) µm long ; alar groups large, extending from leaf margin to costa or almost so, transition between alar cells and surrounding cells gradual and alar groups thus diffusely delimited. - Medium-sized to large, sparsely radially branched, green, pale green, or brownish plants, growing in moist or wet, ± nutrient-rich habitats, in fens, on shores of lakes or pools (more rarely submerged), in ditches, or in swampy forests. It is mainly a lowland plant, but is found up to the low-alpine belt of the mountains. [pH 3.8-8.2 (n = 40) ; EC 23-324 mS/m (n = 21) ; Ca 1.4-57,8 mg/l (n = 19) ; IR 0.39-0.96 (n = 19)]. *Calliergon cordifolium* is widespread in the northern temperate zone.

This species is most frequently confused with *C. giganteum*, which has also got alar groups that frequently reach or almost reach the leaf costa. However, *C. giganteum* is dioicous, and the transition between the alar cells and the lamina cells above is sudden, whereas *Calliergon cordifolium* is autoicous and shows a gradual transition between the alar cells and the lamina cells above. The latter species has also got a weaker stem leaf costa (54.0-117.0 (-132.0)

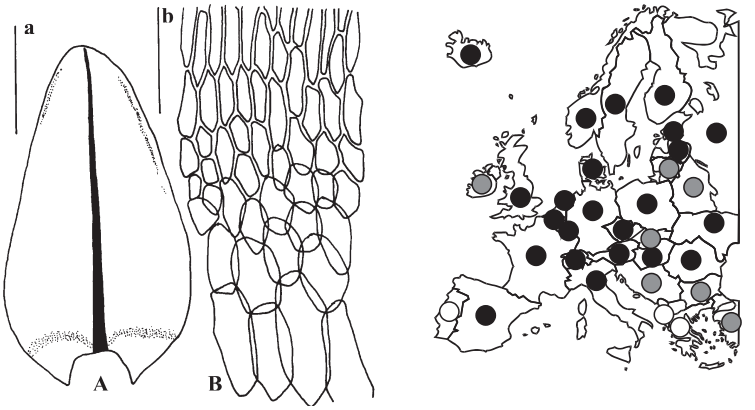


Fig. 25. *Calliergon cordifolium*. A : Stem leaf. B : Cells at transition between alar cells and cells above. Scales : a : 1 mm, A. b : 100 µm, B.

µm wide near base) than *C. giganteum* ((88.0-) 95.0-282.0 µm), and never gets pinkish like some expressions of the latter. Finally, *C. cordifolium* grows in nutrient richer and on the average slightly less mineral rich habitats than *C. giganteum*. *Calliergon orbiculari-cordatum* (Renauld & Cardot) Broth. from northern North America is close to *C. cordifolium*. The type material of *Hypnum orbiculari-cordatum* Renauld & Cardot differs from *C. cordifolium* mainly in having large and very broad stem leaves. Differences between *C. cordifolium* and *C. richardsonii* are treated under the latter.

2. Calliergon giganteum (Schimp.) Kindb. (Fig. 26)

***Calliergon subsarmentosum* Kindb.**

Dioicous. Stem leaves erect to spreading, concave, broadly ovate-cordate and rounded or broadly obtuse at apex ; costa (88.0-) 95.0-282.0 µm wide at base, usually ending shortly below leaf apex ; median lamina cells ((25.0-)) (31.5-) 40.0-164.0 (-189.0) µm long ; alar groups large, extending from leaf margin to costa or almost so, transition between alar cells and surrounding cells sudden and alar groups thus sharply delimited. - Usually large and then mostly densely radially branched with ± spreading branch leaves, brownish, pale pink, or sometimes green or yellowish plants, growing in wet and ± mineral-rich habitats in fens, ditches, on lake or pool shores, or sometimes floating or submerged in lakes. It occurs from the lowlands to the low-alpine region of the mountains. [pH 5.2-8.5 (n = 123) ; EC 35-499 mS/m (n = 66) (in lakes 2-18 mS/m ; n = 3) ; Ca 1.6-65,8 mg/l (n = 34) ; IR 0.32-0.97 (n = 34)]. *Calliergon giganteum* is widespread in the northern temperate zone. From the southern hemisphere, the species is known from southernmost South America and from New Zealand.

Calliergon giganteum is usually easily recognised by its frequently occurring dense radial branching pattern, which makes the plants look like

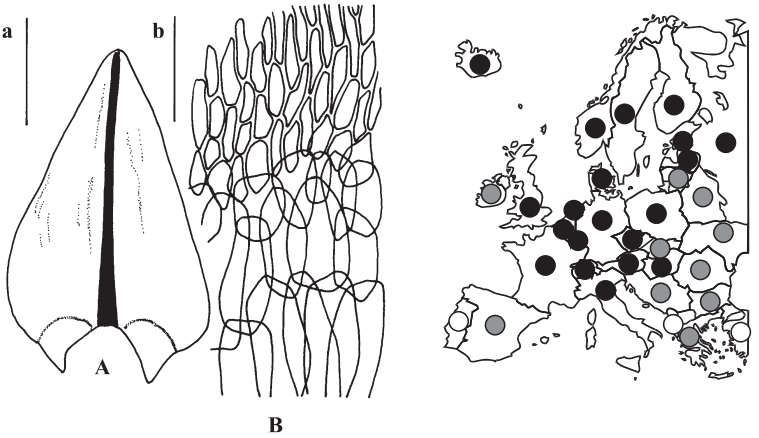


Fig. 26. *Calliergon giganteum*. A : Stem leaf. B : Cells at transition between alar cells and cells above. Scales : a : 1 mm, A. b : 100 µm, B.

miniature spruce trees, its usually broadly ovate-cordate stem leaves, its broad costa, and its large and sharply delimited alar groups. In addition *C. giganteum* has often got a characteristic pale pink colour. The differences between this species, *C. cordifolium* and *C. richardsonii* are mentioned under the latter two.

3. Calliergon richardsonii (Mitt.) Kindb. (Fig. 27)

***Calliergon macounii* Karczmarz ; *Calliergon obtusifolium* Karczmarz ; *Calliergon subgiganteum* Kindb.**

Autoicous. Stem leaves erect to spreading, concave, rounded ovate or broadly rounded ovate to rounded ovate-cordate ; costa 52.5-119.0 µm wide at base, ending 50-90 % way up leaf and usually forked or branched in some or all leaves ; median lamina cells (20.0-) 50.0-132.0 µm long ; alar groups reaching 60-80 % of distance from leaf margin to costa, transition between alar cells and surrounding cells sudden and alar groups thus sharply delimited. - Usually large and then mostly rather sparsely radially branched, brownish, yellowish, or sometimes green plants, growing in wet, ± mineral-rich and somewhat nutrient-rich habitats in fens, ditches, on lake or pool shores, sometimes floating or submerged in lakes. It occurs from the lowlands to the alpine region of the mountains. [pH 5.2-7.8 (n = 54) ; EC 14-264 mS/m (n = 36) ; Ca 1.3-30,7 mg/l (n = 17) ; IR 0.36-0.93 (n = 17)]. *Calliergon richardsonii* is widespread in the northern part of the northern temperate zone and in the arctic, more scattered or absent further south in the temperate zone. It is also known from New Zealand, under the name *Calliergon subpapillosum* Karcz.

Calliergon richardsonii is usually easily separated from the other *Calliergon* species by its comparatively short, usually branched or forked stem leaf costa. From *C. giganteum* and *C. cordifolium* it also differs in its mostly smaller alar groups and from *C. giganteum* in that the plants are autoicous and generally

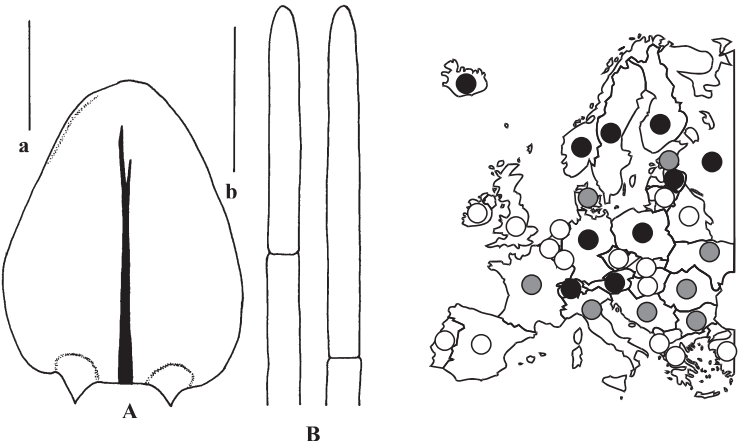


Fig. 27. *Calliergon richardsonii*. A : Stem leaf. B : Apices of axillary hairs. Scales : a : 1 mm, A. b : 60 µm, B.

more sparsely branched, with coarser branches having less spreading leaves than in the latter. The differences between *C. richardsonii* and *C. megalophyllum* are given after the latter.

4. Calliergon megalophyllum Mikut. (Fig. 28)

Calliergon richardsonii* var. *pungens* Bryhn, *nom. nud.

Dioicous. Stem leaves erect to spreading, concave, rounded ovate or broadly rounded ovate to rounded ovate-cordate ; costa 73.5-105.0 µm wide at base, ending shortly below leaf apex ; median lamina cells (68.0-) 84.0-195.0 (-231.0) µm long ; alar groups reaching 35-60 (-65) % of distance from leaf margin to costa, transition between alar cells and surrounding cells sudden and alar groups thus sharply delimited. - Usually large or very large, rather sparsely radially branched, green, brownish, or yellowish plants, usually growing submerged in somewhat nutrient-rich lakes, ox-bow lakes and other small waters, sometimes floating or among *Phragmites* or sedges along lake shores. It occurs from the lowlands to the sub-alpine region of the mountains. [pH 5.5-8.1 (n = 110) ; EC 1-138 mS/m (n = 63) ; Ca 0.6-16,6 mg/l (n = 62) ; IR 0.22-0.95 (n = 62)]. This species is probably overlooked in many areas due to its habitat. It is frequent in many areas of the northern temperate zone, rare or absent in the southern part.

The dioicous *C. megalophyllum* is sometimes confused with large phenotypes of the autoicous *C. richardsonii*. However, in *C. megalophyllum*, the stem leaf costa is usually single and reaches almost to the leaf apex, whereas it is branched or forked and ends well below the leaf apex in *C. richardsonii*. In the first species the alar groups reach 35-60 (-65) % of the distance from the leaf margin to the costa, in the latter 60-80 %, and the axillary hairs are generally having shorter cells, at least in their apical part, in *C. megalophyllum* than in *C. richardsonii* (see Figs. 28 and 27, respectively).

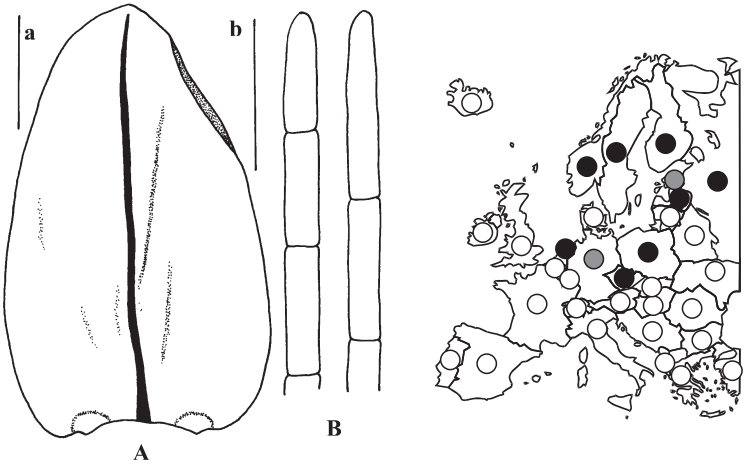


Fig. 28. *Calliergon megalophyllum*. A : Stem leaf. B : Apices of axillary hairs. Scales : a : 1 mm, A. b : 60 µm, B.

Warnstorfia Loeske

Autoicous or dioicous. Plants ± radially branched, sometimes with red colours. Stem leaves straight or falcate, triangular to ovate or narrowly ovate, either gradually narrowed to a longly acuminate, acuminate, or obtuse apex, or more suddenly narrowed to a shortly acuminate to broadly rounded and usually apiculate apex, concave or strongly concave, not or hardly plicate ; margin entire, sinuose or denticulate ; costa single, ending ca. 60 % way up leaf to longly excurrent ; median lamina cells linear, smooth ; alar cells quadrate or shortly to longly rectangular, inflated or strongly inflated, hyaline, thin-walled or (especially when old) somewhat incrassate, in transversely triangular, narrowly transversely triangular or almost quadrate group, distinctly or indistinctly delimited from surrounding cells, not or hardly decurrent or (in *W. tundrae*) longly and broadly decurrent, supra-alar cells ± undifferentiated or well differentiated, sometimes (*W. pseudostraminea*) together with alar group forming an ovate or broadly ovate group along basal leaf margin ; rhizoid initials in leaves scarce or common, most abundant near leaf apex and along costa, slightly inflated and paler than other lamina cells. Paraphyllia absent. Axillary hairs abundant, large or rather weak, with hyaline or early brown, 1-7-celled upper part. Rhizoids red-brown, slightly branched, smooth, inserted at various points on leaves, or on scattered points or in rows on stem. Stem with central strand and a well or weakly differentia-ted cortex (epidermis sometimes partly of more thin-walled cells than rest of cortex). Inner perichaetial leaves straight and erect, not plicate, margin ± entire or with an occasional tooth at shoulder ; vaginula naked. Capsule ± hori-zontal ; annulus not separating. Peristome well developed ; outer layer of exostome reticulate in lower part.

Key to the species of *Warnstorfia*

1. Stem leaves longly and ± broadly decurrent (Fig. 29B, C, p. 52). Plants never red. . . . . **1. *W. tundrae***

-. Stem leaves not or hardly decurrent. Plant colour variable, sometimes with red colours present. **2**

2. Stem and branch leaves with strong, shortly or longly excurrent costa (excurrent part up to ca. 1/3 of leaf length). Branch apices (and often shoot apex) pencil-like (Fig. 14, p. 28). Axillary hairs medium-sized, 2-7-celled, getting brown early (Fig. 30B, p. 53). . . . . **2. *W. trichophylla***

-. Leaf costa not excurrent. Branch and shoot apices not pencil-like. Axillary hairs small or medium-sized, 1-4 (-5)-celled, hyaline when young. **3**

3. Stem leaves oblong, ovate, or narrowly ovate, in upper part ± suddenly narrowed to rounded-apiculate or acute-apiculate apex, very rarely shortly acuminate (Fig. 30C, p. 53), the short apiculus (almost invariably present in young leaves) often bent inwards over the leaf. . . . . **3. *W. sarmentosa***

-. Stem leaves from ovate, ovate-lanceolate, or ovate-triangular base gradually narrowed to acuminate, or (in *W. pseudostraminea*) sometimes obtuse apex, without apiculus. **4**

4. Dioicous. Clear red colours often present. Pseudoparaphyllia broad (Figs 31D, p. 55 ; 32C, p. 56). Alar cells forming a large transversely triangular group which is distinctly delimited from the surrounding cells and ± reaches the costa (Figs 31, 32 ; in late snow beds or in cold springs in mountainous areas, modifications with less well delimited alar groups occur). **5**

-. Autoicous. Clear red colours extremely rare ; red colours when present usually covered by brown pigments, giving a reddish brown colour. At least some pseudoparaphyllia narrow, often lanceolate (Figs 33D, p. 58 ; 34C, p. 59). Alar cells forming a rather narrowly transversely triangular group which may reach the costa, or an isodiametric group which, together with the supra-alar cells, often form an ovate group along basal margin, alar groups somewhat indistinctly delimited from the surrounding cells (Figs 33, 34). **7**

5. Stem leaf margin distinctly denticulate in upper and / or lower part ; marginal cells at widest part of leaf usually differentiated from the cells further in, often rectangular or distinctly widened and forming ± distinct border (Fig. 31C, right, p. 55). Leaves ± concave, acumen flat or furrowed, but not strongly so. Cells of stem epidermis sometimes distinctly wider than other cortex cells in part of stem circumference, forming a partial hyalodermis. . . . . **4. *W. exannulata***

-. Stem leaf margin entire or partly very indistinctly and then usually obtusely denticulate ; marginal cells at widest part of leaf usually similar to the cells further in, rarely slightly differentiated (Fig. 32B, p. 56). Leaves strongly concave, acumen deeply furrowed to almost tubular (in submerged plants this may be less distinct). Cells of stem epidermis differentiated or not. **6**

6. Stem leaves falcate or rarely almost straight, in acumen ± deeply furrowed. Cells of stem epidermis not or hardly differentiated from other cortex cells. (Only known from Eurasia). . . . . **5. *W. procera***

-. Stem leaves straight, in acumen strongly furrowed to almost tubular. Cells of stem epidermis distinctly wider than other cortex cells in up to 50 % of stem circumference, forming a partial hyalodermis. (Only known from northern North America). . . . . **6. *W. pseudosarmentosa***

7. Alar cells in ± indistinctly delimited, transversely triangular or narrowly transversely triangular group which ± reaches the costa ; supra-alar cells rather small and not forming a group together with the alar cells (Fig. 33, p. 58). Stem leaf apex acuminate, rarely incurved. . . . . **7. *W. fluitans***

-. Alar cells forming an isodiametric or, more rarely, transversely triangular group ; supra-alar cells large and together with the alar cells often forming an oval or rectangular group along lower leaf margin (Fig. 34, p. 59). Stem leaf apex acuminate or obtuse, often incurved (cf. Fig. 29E, p. 52). . . . . **8. *W. pseudostraminea***

1. Warnstorfia tundrae (H. W. Arnell) Loeske (Fig. 29)

***Drepanocladus tundrae* (H. W. Arnell) Loeske**

Dioicous. Stem leaves from ovate or ovate-triangular base gradually narrowed to rather broadly acuminate apex, apex often incurved over leaf, leaves straight or slightly falcate ; margin distinctly denticulate below, entire or sparsely denticulate above ; costa relatively strong, reaching 70-85 % way up leaf ; median lamina cells 25.0-92.5 µm long ; alar cells in distinctly delimited, transversely triangular group which ± reaches costa, cells in marginal portion often distinctly more inflated than those in more central portion of group, longly and broadly decurrent. - Medium-sized, radially or sparsely radially branched plants, green, yellow-green, or brownish, branch and shoot apices not pencil-like. The species grows in mineral-richer habitats than the other *Warnstorfia* species and is in this respect similar to species of *Calliergon*. Its habitat is mostly slightly nutrient-enriched. It is found in rich fens, on lake shores, or sometimes submerged, from the lowlands to the alpine region and in the arctic. [pH 5.9-7.5 (n = 49) ; EC 39-213 mS/m (n = 17) (in lakes 1-12 mS/m ; n = 16) ; Ca 1.6-24,0 mg/l (n = 26) ; IR 0.54-0.91 (n = 26)]. *Warnstorfia tundrae* is widespread in the northern part of the northern temperate zone and in the arctic, more scattered or absent further south in the temperate zone.

Warnstorfia tundrae is easily separated from the other species of the genus by its longly and widely decurrent stem leaf bases. Other features that aid in distinguishing this species are the relatively weakly falcate stem leaves and the total lack of red colours.

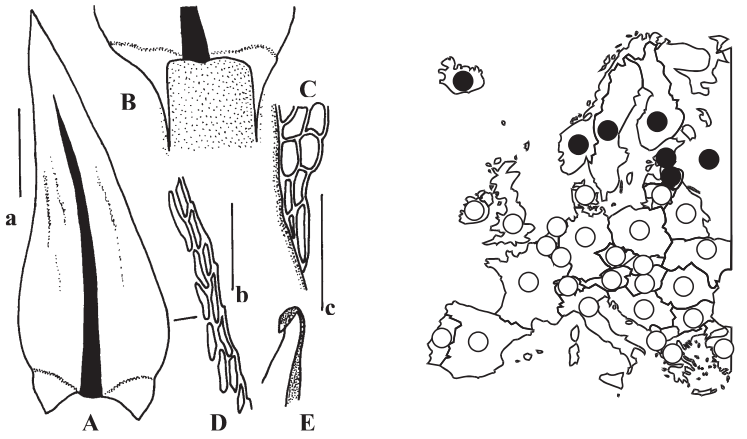


Fig. 29. *Warnstorfia tundrae*. A : Stem leaf. B : Stem leaf insertion. C : Decurrent portion of leaf base. D : Leaf margin. E : Leaf apex from another leaf. Scales : a : 0.5 mm, A, B, E. b : 50 µm, D. c : 100 µm, C.

2. Warnstorfia trichophylla (Warnst.) Tuom. & T. J. Kop. (Figs 14, p. 28 ; 30A, B)

***Drepanocladus rotae* var. *trichophyllus* Warnst. ; *Drepanocladus trichophyllus* (Warnst.) J. Podpěra**

Dioicous. Stem leaves from ovate to triangular base gradually narrowed to very longly acuminate apex, straight or more rarely falcate ; margin denticulate ; costa in stem and branch leaves strong, shortly or longly excurrent (excurrent part up to ca. 1/3 of leaf length) ; median lamina cells 54.5-189.0 (-231.0) µm long ; alar cells in large, distinctly delimited, transversely triangular group which reaches costa ; rhizoid initials in leaves rare. Axillary hairs medium-sized, 2-7-celled, abundant, early getting brown. - Medium-sized to almost large, usually rather densely radially branched plants, green, brown, or when emergent above the water surface sometimes red, branch apices, and often shoot apex, pencil-like. This species is found submerged or with emergent shoot apices in water, mostly in small lakes, in water-filled kettle holes, ox-bow lakes, and other small water bodies (sometimes dry plants that were deposited during high-water periods, are found in shore vegetation). It occurs from the lowlands to the low-alpine region. [pH 4.8-8.7 (n = 81) ; EC 1-87 mS/m (n = 30) ; Ca 0.9-14,1 mg/l (n = 30) ; IR 0.27-0.92 (n = 30)]. The species is widespread, and in some areas common, in the northern parts of the temperate region in Eurasia. In North America the species is rare in Canada, more frequent in western Alaska. In South America a single locality is known in Colombia.

Warnstorfia trichophylla sometimes reminds about *W. exannulata*, but the more distinctly pencil-like branch and shoot apices, the excurrent leaf costa and the early brown axillary hairs (weaker and normally hyaline in *W. exannulata*) separate *W. trichophylla* from the latter.

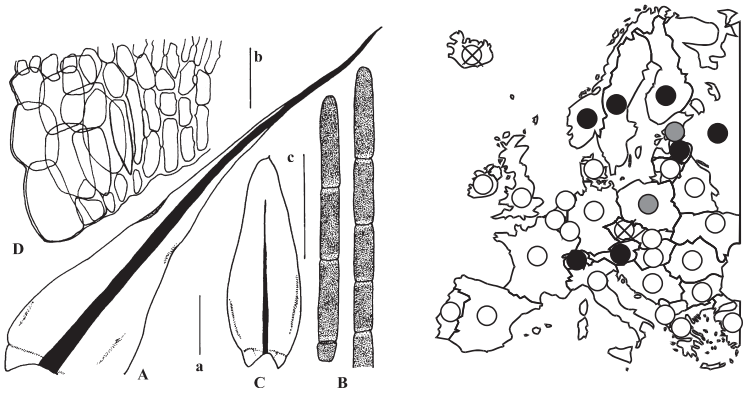


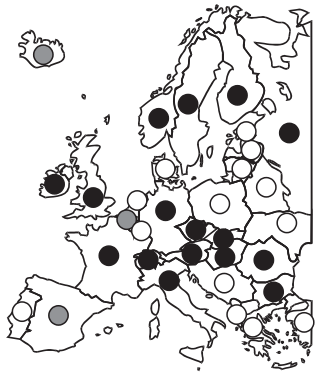
Fig. 30. *Warnstorfia trichophylla* (A, B) and *W. sarmentosa* (C, D). A, C : Stem leaves. B : Axillary hairs. D : Alar cells. Scales : a : 0.5 mm, A, C. b : 50 µm, D. c : 60 µm, B.

3. Warnstorfia sarmentosa (G. Wahlenberg) Hedenäs (Fig. 30C, D)

***Calliergon sarmentosum* (G. Wahlenberg) Kindb. ; *Sarmentypnum sarmentosum* (G. Wahlenberg) Tuom. & T. J. Kop.**

Dioicous. Stem leaves straight, concave, loosely imbricate or erect-spreading, oblong, ovate, or narrowly ovate, in upper part ± suddenly narrowed to rounded-apiculate or acute-apiculate apex, very rarely shortly acuminate, the short apiculus (rarely lacking) often bent inwards over the leaf ; margin entire or almost so ; costa usually ending 80-95 % way up leaf ; median lamina cells 25.0-136.5 (-157.5) µm long ; alar cells hyaline or when old pigmented, in distinctly delimited, transversely triangular group which ± gradually passes into basal cells near costa, not or hardly decurrent ; rhizoid initials in leaves rather rare and when present usually only one or two cells near leaf apex differentiated. - Medium-sized, sparsely radially branched plants, red, dark red, or green. This species is found in intermediately mineral-rich habitats, around springs, in spring-influenced fens, and in late snow-beds, from the lowlands to the high-alpine region, and in arctic as well as Antarctic areas. [pH 4.6-7.7 (n = 95) ; EC 15-152 mS/m (n = 69) ; Ca 0.7-12,8 mg/l (n = 23) ; IR 0.17-0.80 (n = 23)]. It is widespread in the northern and southern temperate to sub-polar zones, and occurs in many mountain areas in the tropical and subtro-pical zones.

Warnstorfia sarmentosa is easily separated from most other species of the genus by its oblong or ovate stem leaves that are suddenly narrowed to a rounded-apiculate or acute-apiculate apex. The apiculus is most distinct in young leaves and is rarely lacking. The species could possibly be confused with *Calliergon* species, which, however, are larger, have broader leaves and never get clear red colours, or *Straminergon stramineum*, which is usually pale or whitish green to yellow-green (never red) and lacks the apiculus near the leaf apex. In addition, the alar groups are ovate or broadly ovate in *Straminergon*, transversely triangular in *W. sarmentosa*.



In the Andes and rarely also in southernmost South America the closely related *W. luipichensis* (R. S. Williams) Hedenäs (*Calliergon luipichense* R. S. Williams) occurs in similar habitats as *W. sarmentosa*. It can be separated from *W. sarmentosa* by means of the following key.

1. Stem leaf margins entire or at most with an indistinct, obtuse denticle near base of apiculus. Leaves ± suddenly narrowed to short apiculus or more rarely apex acute or even shortly acuminate. . . . . ***W. sarmentosa***

-. Stem leaf margins at least partly and in some leaves distinctly denticulate, for

a short distance near apex frequently coarsely denticulate. Leaves gradually or suddenly narrowed to acuminate or shortly acuminate, sometimes acute-apiculate, or rarely rounded-apiculate apex. . . . . ***W. luipichensis***

4. Warnstorfia exannulata (Schimp.) Loeske (Fig. 31)

***Drepanocladus exannulatus* (Schimp.) Warnst. ; *Warnstorfia exannulata* var. *purpurascens* (Schimp.) Tuom. & T. J. Kop. ; *W. purpurascens* (Schimp.) Loeske**

Dioicous. Stem leaves falcate or sometimes straight, concave, ovate or ovate-triangular, gradually narrowed to acuminate apex ; margin distinctly denticulate in upper and / or lower part, marginal cells at widest part of leaf usually differentiated from cells further in, often rectangular or distinctly widened and forming ± distinct border ; costa strong, reaching 60-95 % way up leaf ; median lamina cells (21.0-) 28.0-194.0 (-215.0) µm long ; alar cells strongly inflated, hyaline or when old brownish, in distinctly delimited, transversely triangular group which reaches costa or almost so, not decurrent. Pseudoparaphyllia triangular, broadly triangular or broadly irregular. Cells of stem epidermis often widened and thin-walled in part of stem circumference. - Medium-sized, radially or sparsely radially branched, green, yellow-green, or when exposed to the sun often red or dark red plants. Found in intermediately mineral-rich fens, often around springs or in late snow-beds, sometimes submerged in lakes, from the lowlands to the high-alpine region of the mountains, and in arctic as well as Antarctic areas. [pH 4.0-8.0 (n = 212) ; EC 10-243 mS/m (n = 122) (in lakes 1.6-17.5 mS/m ; n = 38) ; Ca 0.7-34,5 mg/l (n = 68) ; IR 0.17-0.82 (n = 30) (in lakes 0.54-0.95 ; n = 38)]. The species is widespread in the northern and southern temperate to sub-polar zones, and occurs in many mountain areas in the tropical and subtropical zones.

Warnstorfia exannulata is separated from *W. procera* by at least partly denticulate leaf margins, mostly with the marginal lamina cells widened at

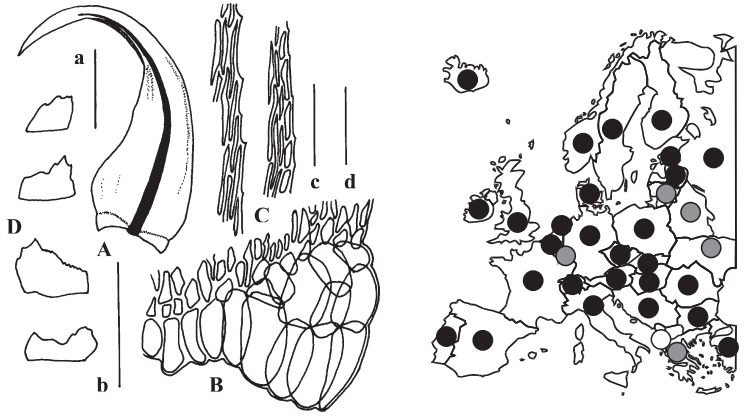


Fig. 31. *Warnstorfia exannulata*. A : Stem leaf. B : Alar cells. C : Leaf margin at widest part of leaf. D : Pseudo-paraphyllia. Scales : a : 0.5 mm, A. b : 300 µm, D. c : 50 µm, C. d : 75 µm, B.

widest part of leaf, and by having less strongly concave leaves than the latter. In addition, *W. exannulata* has stem epidermis cells that are often inflated in parts of the stem circumference, this not being the case in *W. procera*. *Warnstorfia fluitans* and *W. pseudostraminea* differ from *W. exannulata* in being autoicous, in having narrower, triangular to lanceolate, pseudoparaphyllia, in hardly ever getting pure red colours and in having more weakly differentiated alar groups. The alar groups in *W. fluitans* usually extend less far up the leaf than in *W. exannulata*, whereas those in *W. pseudostraminea* often form ovate groups together with the supra-alar cells. For the differences between *W. exannulata* and *W. pseudosarmentosa*, *W. tundrae*, and *W. tricho-phylla*, see the notes after the latter three.

Certain phenotypes from springs with the inflated alar cells more or less in only one row along the leaf base have sometimes been called var. *purpurascens*. However, all transitions between these phenotypes and those from other habitats exist, and if these phenotypes are cultivated together with other phenotypes the resulting plants cannot be separated from each other (Hedenäs, unpublished results). Thus, the "*purpurascens*"-plants are likely to be mere modifications of *W. exannulata*.

5. Warnstorfia procera (Renauld & H. W. Arnell) Tuom. (Fig. 32)

***Drepanocladus procerus* (Renauld & H. W. Arnell) Warnst.**

Dioicous. Stem leaves falcate or rarely almost straight, concave or strongly concave, in acumen ± deeply furrowed (less distinct in submerged plants), ovate or ovate-triangular, gradually narrowed to acuminate apex ; margin entire or in small parts very indistinctly and obtusely denticulate, marginal cells at widest part of leaf usually similar to cells further in, rarely slightly differentiated ; costa strong, reaching 60-95 % way up leaf ; median lamina cells 31.5-147.0 µm long ; alar cells ± strongly inflated, hyaline or especially when old brownish or reddish, forming a well delimited, transversely triangular group which reaches

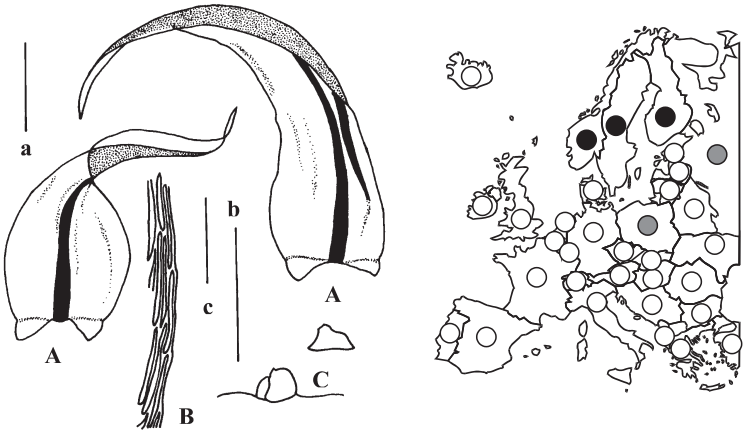


Fig. 32. *Warnstorfia procera*. A : Stem leaves. B : Leaf margin at widest part of leaf. C : Pseudoparaphyllia. Scales : a : 0.5 mm, A. b : 300 µm, C. c : 50 µm, B.

costa or almost so, not decurrent. Pseudoparaphyllia triangular, broadly triangular or broadly irregular. Cells of stem epidermis not widened. - Medium-sized, radially branched plants, red or mostly dark red, rarely green plants. It is found in intermediately mineral-rich habitats, in fens (often in flarks, but usually not in markedly spring-influenced habitats), on lake shores, rarely submerged, from the sea level to the low-alpine region. [pH 4.2-6.6 (n = 24) ; EC 13-58 mS/m (n = 15) (in lakes 1-2 mS/m ; n = 2) ; Ca 0.0-5,1 mg/l (n = 10) ; IR 0.00-0.69 (n = 8) (in lakes 0.64-0.89 ; n = 2)]. The species is widespread, but seemingly never very common, in the boreal and boreo-nemoral zones of Europe and Asia.

For the differences between *Warnstorfia procera* and *W. exannulata* and *W. pseudosarmentosa*, see the notes after the latter two species.

6. Warnstorfia pseudosarmentosa (Cardot & Thér.) Tuom. & T. J. Kop.

***Calliergon pseudosarmentosum* (Cardot & Thér.) Broth. ; *Drepanocladus pseudosarmentosus* (Cardot & Thér.) N. P. H. Persson**

Dioicous. Stem leaves straight and erect or weakly homomallous, concave, ovate, or triangular-ovate, gradually narrowed to acuminate or shortly acuminate, sometimes blunt apex, apex sometimes incurved over apical leaf, near apex furrowed to almost tubular ; margin entire or at most slightly sinuose, marginal cells at widest part of leaf usually similar to cells further in, rarely slightly differentiated ; costa long, ending shortly below leaf apex ; median lamina cells 34.5-92.5 µm long ; alar cells strongly inflated, thin-walled or near costa sometimes incrassate, forming a sharply delimited transversely triangular group that extends from leaf margin to costa or almost so, not decurrent. Pseudoparaphyllia broadly ovate to slightly wider than long, with rounded to irregular apex. Cells of stem epidermis often widened and thin-walled in up to 50 % of stem circumference. - Plants medium-sized, pinnately to irregularly pinnately branched, with deep red secondary coloration. Appears to grow in spring-influenced habitats or along brook shores in the north. Probably endemic to northern North America (N.W.T., Yukon, Alaska).

Warnstorfia pseudosarmentosa is superficially similar to *W. sarmentosa* in habit, with rather thick shoots and short and often curved branches with obtuse endings due to densely inserted and relatively shortly acuminate leaves. However, the upwards more gradually narrowed leaves in *W. pseudosarmentosa* than in *W. sarmentosa*, and the usually acuminate or shortly acuminate apices in the first of these species make the separation easy. The species also resembles the Eurasian *W. procera*, which, however, usually has falcate leaves and stem epidermal cells that hardly differ from the cortical cells further in. *Warnstorfia pseudosarmentosa* is closest to *W. exannulata*, from which it differs mainly in having more strongly concave leaves that are mostly deeply furrowed to almost tubular in their upper part, and in having entire leaf margins. Sometimes the stem leaf lamina is weakly plicate (in moist condition) in *W. pseudosarmentosa*, something which does not occur in *W. exannulata*. Because few specimens of *W. pseudosarmentosa* were seen it is difficult to judge whether it is a good species or an extreme, arctic modification of *W. exannulata*.

7. Warnstorfia fluitans (Hedw.) Loeske (Fig. 33)

***Drepanocladus berggrenii* (Lange & C. E. O. Jensen) G. Roth ; *Drepanocladus fluitans* (Hedw.) Warnst. ; *D. fluitans* var. *falcatus* (C. E. O. Jensen) G. Roth. ; *D. h-schulzei* (Limpr.) Loeske ; *Warnstorfia h-schulzei* (Limpr.) Loeske**

Autoicous. Stem leaves falcate or sometimes straight, concave or slightly so, narrowly ovate to triangular-ovate and gradually narrowed to acuminate apex ; margin denticulate, sometimes only in parts or indistinctly so ; costa weak or rather strong, ending in mid-leaf to 80 % way up leaf (in occasional specimens or leaves shorter and / or double) ; median lamina cells 31.5-182.0 µm long ; alar cells ± inflated and hyaline, forming a transverse, narrowly triangular group which more or less reaches costa, usually rather indistinctly delimited from surrounding cells, not decurrent. Pseudoparaphyllia triangular to lanceolate, sometimes irregular. - Medium-sized, radially or sparsely radially branched, green, yellow-green, or brownish to brown-red plants. (Clear red colours rarely present in extreme, exposed habitats). Found in mineral-poor, acid, but sometimes nutrient-rich habitats, in poor fens or bog pools, in depressions in rocks (rarely on vertical rocks with trickling water), from the sea-level to the alpine region, and in arctic areas. [pH 3.2-6.3 (n = 84) ; EC 0-84 mS/m (n = 19) ; Ca 0.2-5,4 mg/l (n = 17) ; IR 0.06-0.61 (n = 17)]. Widespread in the northern and southern temperate zones, in the Arctic, and occurs in many mountain areas in the tropical and subtropical zones.

Warnstorfia fluitans differs from the other autoicous species of the genus, *W. pseudostraminea*, by having transverse, ± narrowly triangular alar groups in the stem leaves. In *W. pseudostraminea*, the alar groups are sometimes transversely triangular (though more broadly so than in *W. fluitans*), but in some or most leaves, the alar and the large supra-alar cells together form an oval or rectangular group along the lower leaf margin. *Warnstorfia pseudostraminea* has usually ± straight to slightly falcate stem leaves, often with obtuse leaf apices having short cells, and the leaf apex is commonly hoo-

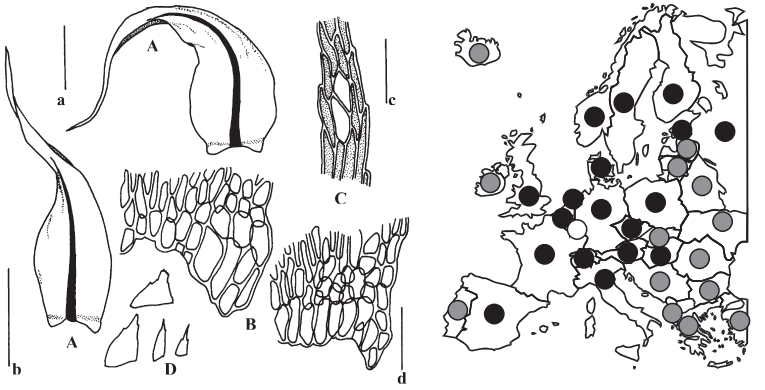


Fig. 33. *Warnstorfia fluitans*. A : Stem leaves. B : Alar cells. C : Part of leaf apex, showing rhizoid initials. D : Pseudoparaphyllia. Scales : a : 0.5 mm, A. b : 300 µm, D. c : 50 µm, C. d : 75 µm, B.

ked. However, neither of the last mentioned features are quite constant in *W. pseudostraminea*, and occasional (rare) specimens of *W. fluitans* have the same character states. For the differences between *W. fluitans* and *W. exannulata*, see the note after the latter. Sometimes specimens with relatively strongly developed costae were treated as a separate species, *Warnstorfia h-schulzei*. However, the characters which were used to separate *W. h-schulzei* from *W. fluitans* show a continuous variation between the extreme phenotypes and are not correlated with each other. Sometimes a variety of *W. fluitans*, as *Drepanocladus fluitans* var. *falcatus* (*Hypnum fluitans* var. *falcatum*, *hom. illeg.*) is recognised. However, because no type material seems to be extant, the status of this taxon cannot be judged.

8. Warnstorfia pseudostraminea (Müll. Hal.) Tuom. & T. J. Kop. (Fig. 34)

***Calliergidium plesistramineum* (Renauld) Grout ; *Drepanocladus pseudostramineus* (Müll. Hal.) G. Roth**

Autoicous. Stem leaves almost straight or slightly falcate (rarely more strongly falcate), narrowly ovate-triangular or ovate, gradually narrowed to acuminate or often obtuse to blunt point, leaf apex often incurved over leaf ; margin ± entire or finely denticulate ; costa weak or rather strong, ending 65-80 % way up leaf ; median lamina cells 35.5-138.5 µm long ; alar cells inflated and forming an isodiametric or, more rarely, transversely triangular group, supra-alar cells often large and then together with alar cells forming an oval or rectangular group along lower leaf margin, not decurrent. Pseudoparaphyllia (broadly triangular), triangular, or lanceolate. - Medium-sized, sparsely or sparsely radially branched, green, yellow-green, or brownish plants. The species is apparently favoured by some disturbance, and typical habitats are slightly sloping poor fens, ditches, or periodically water-filled depressions. [pH 5.2 (n = 2) ; EC 15-42 mS/m (n = 2) ; Ca 4.8 mg/l (n = 1) ; IR 0.48 (n = 1)]. Probably widespread in the arctic to boreal lowlands in the north, rarer further south in the northern temperate zone.

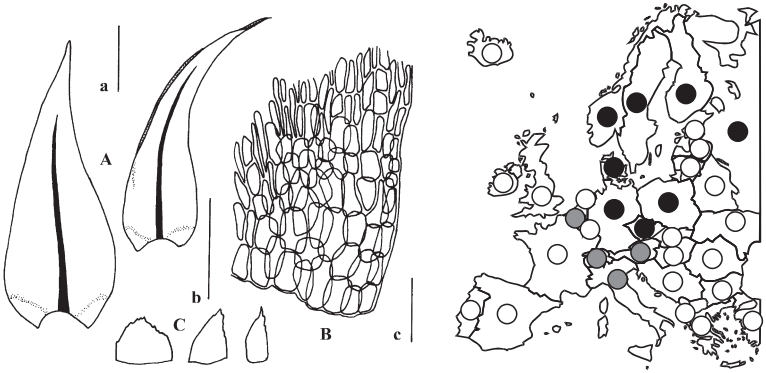


Fig. 34. *Warnstorfia pseudostraminea*. A : Stem leaves. B : Alar cells. C : Pseudoparaphyllia. Scales : a : 0.5 mm, A. b : 300 µm, C. c : 75 µm, B.

Warnstorfia pseudostraminea is usually recognisable already in the field, where it gives an impression between *W. fluitans* and *Straminergon stramineum*. The differences between *W. pseudostraminea* and *W. fluitans* are given in the note after the latter.

In Antarctic and subantarctic areas *Warnstorfia laculosa* (Müll. Hal.) Ochyra (syn. *W. austrostraminea* (Müll. Hal.) Ochyra) occurs. This taxon is closely related to *W. pseudostraminea*, and the relationship between these two taxa needs to be further evaluated.

Loeskypnum H. K. G. Paul

Dioicous. Plants medium-sized and somewhat turgid, sparsely and irregularly branched, yellow-green, golden brown, or coppery brown, lower parts of shoot often blackish, never with red colours. Stem leaves strongly concave, not plicate, either falcate, ovate or broadly so, and gradually narrowed to acuminate or shortly acuminate apex, or straight, ovate, oblong, or obovate and above suddenly narrowed to rounded-apiculate apex, with apiculus often curved in over leaf ; margin entire or rarely sinuose ; costa single, occasionally branched above, weak, ending 55-85 % way up leaf ; median lamina cells linear, strongly incrassate or incrassate, porose, smooth ; differentiated alar cells few, rectangular or shortly rectangular, slightly inflated, incrassate, porose or indistinctly so, in approximately triangular, indistinctly delimited group, not or shortly decurrent, supra-alar cells indistinctly delimited ; rhizoid initials in leaves frequent, especially near leaf apex, slightly wider and paler than other lamina cells. Paraphyllia absent. Axillary hairs abundant, well developed, with early brownish or yellow-brown, 1-5 (-7)-celled upper part. Rhizoids red-brown, slightly branched, smooth, inserted at various points on leaves, or on scattered points or in rows on stem. All stem cells incrassate, stem with central strand and a well differentiated cortex of strongly incrassate cells, no hyalodermis. Inner perichaetial leaves straight and erect, not plicate, margin entire or with an occasional tooth at shoulder ; vaginula naked or occasionally with 1-2 paraphyses. Capsule (unknown in *L. wickesiae*) cylindrical, small, horizontal, occasionally almost inclined ; annulus not separating. Peristome well developed ; outer layer of exostome reticulate below.

Key to the species of Loeskypnum

1. Stem leaves falcate, erect-spreading to sub-imbricate, ovate or broadly ovate, gradually narrowed to acuminate or shortly acuminate apex, not cucullate.. . . . . **1. *L. badium***

-. Stem leaves straight, ± imbricate, ovate, oblong, or obovate, suddenly narrowed to broadly acute to rounded, apiculate apex, often cucullate and with apiculus curved in over leaf. . . . . **2. *L. wickesiae***

1. *Loeskypnum badium* (Hartm.) H. K. G. Paul (Fig. 35)

***Drepanocladus badius* (Hartm) G. Roth.**

Stem leaves erect-spreading to sub-imbricate, ± falcate, ovate or broadly ovate, above suddenly or gradually narrowed to acuminate or shortly acuminate apex, not cucullate ; median lamina cells 24.5-119.0 (-130.0) µm long ; alar cells few, rectangular or shortly so, slightly inflated, incrassate, porose or indistinctly so, in indistinctly delimited approximately triangular group. - Plants medium-sized, rarely robust, yellow-green, golden brown, or coppery brown, often blackish in lower shoot. The species grows in intermediately mineral-rich to relatively mineral-rich, nutrient-poor fen habitats, often on top of other mosses and thus relatively dry. It is found from the lowlands to the low-alpine region, and in the arctic. [pH 4.2-6.8 (n = 43) ; EC 14-158 mS/m (n = 30) ; Ca 0.9-19,0 mg/l (n = 16) ; IR 0.28-0.79 (n = 16)]. The species is mainly boreal, reaching into the arctic, and few localities are known further south.

Usually easily recognised because of its characteristic colour, relatively shortly acuminate leaves, and the fact that all cells of the plant are incrassate. It can be confused with the following species, from which it differs in the characters of the key.

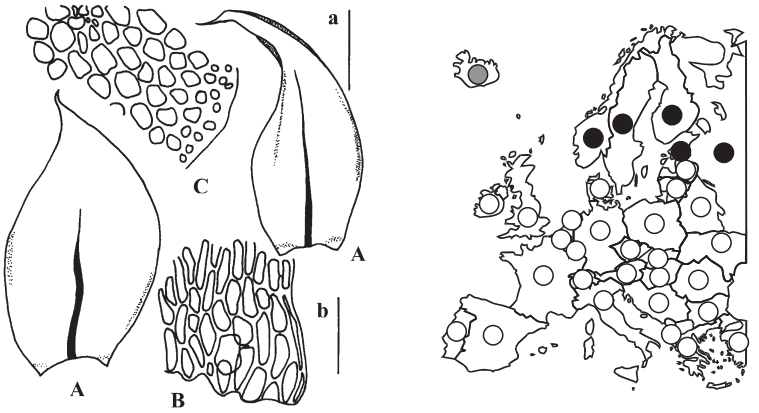


Fig. 35. *Loeskypnum badium*. A : Stem leaves. B : Alar cells. C : Partial transverse section of stem. Scales : a : 0.5 mm, A. b : 75 µm, B, C.

2. Loeskypnum wickesiae (Grout) Tuom.

Calliergon wickesiae* Grout ; *Hypnum* (*Cuspidaria*) *inflatum* Müll. Hal., *hom. illeg.

Stem leaves ± imbricate, straight, ovate, oblong, or obovate, above suddenly narrowed to broadly acute or rounded, apiculate apex, often cucullate and with apiculus curved in over leaf ; median lamina cells 27.3-94.5 µm long. - Plants medium-sized, yellow-green, golden brown, or coppery brown, often blackish in lower shoot. *Loeskypnum wickesiae* grows in intermediately mineral-rich, mostly relatively dry wetland habitats, in fens, usually in places with some seepage, mainly in the border zone between the arctic and boreal

regions. It has extant localities in Greenland, Canada, Alaska, Japan, and the Bering Strait area of Russia, and has been found in interstadial deposits in northernmost Sweden (Hedenäs 1994).

Straminergon Hedenäs

Dioicous. Plants sparsely branched, never with red colours. Stem leaves straight, oblong, ovate, or narrowly ovate, with rounded and often cucullate apex, concave, not plicate ; margin entire ; costa single, weak, ending in upper half of leaf ; median lamina cells linear, smooth, cells near margin ± narrower than in middle of lamina ; alar cells (quadrate), shortly rectangular, or rectangular, inflated and hyaline or when old brownish, thin-walled or ± incrassate, in well differentiated ovate or broadly ovate group along basal margin, decurrent, but often narrowly so, upwards passing gradually into a group of rectangular or elongate-rectangular supra-alar cells which extend up along leaf margin ; rhizoid initials in leaves common, especially near leaf apex and along costa, slightly inflated and paler than other lamina cells. Paraphyllia absent. Axillary hairs few, weak, with hyaline, 1-2-celled upper part. Rhizoids red-brown, slightly branched, smooth, inserted at various points on leaves, or on scattered points or in rows on stem. Stem with central strand and a well differentiated cortex of incrassate cells. Inner perichaetial leaves straight and erect, gradually narrowed to obtuse, acute or shortly acuminate apex, not plicate, margin irregularly dentate above ; vaginula naked. Capsule ± horizontal ; annulus not separating. Peristome well developed ; outer layer of exostome reticulate in lower part.

1. *Straminergon stramineum* (Brid.) Hedenäs (Fig. 36)

***Calliergon stramineum* (Brid.) Kindb.**

Stem leaves straight, loosely imbricate, more rarely somewhat spreading, concave, oblong, ovate, or narrowly ovate, with rounded and often cucullate apex ; costa single, weak, ending 60-90 % way up leaf ; median lamina cells (38.0-) 40.0-88.0 (-122.0) µm long ; alar cells inflated and hyaline or when old brownish, in well differentiated ovate or broadly ovate group along basal margin, upwards passing gradually into a group of rectangular or elongate-rectangular supra-alar cells which extend up along leaf margin. - Plants medium-sized, sparsely branched, pale or whitish green to yellow-green. Found in mineral-poor to mineral-rich and nutrient-poor to nutrient-rich wetland habitats, in fens, on shores, or on irrigated rocks. It occurs from the lowlands to the middle-alpine region of the mountains, and in the arctic. [pH 3.2-7.3 (n = 97) ; EC 7-264 mS/m (n = 59) ; Ca 0.7-28,7 mg/l (n = 31) ; IR 0.21-0.89 (n = 31)]. The species is widespread in the northern temperate to arctic zones, rare in the southern temperate zone, and occurs in some mountain areas in the tropical and subtropical zones.

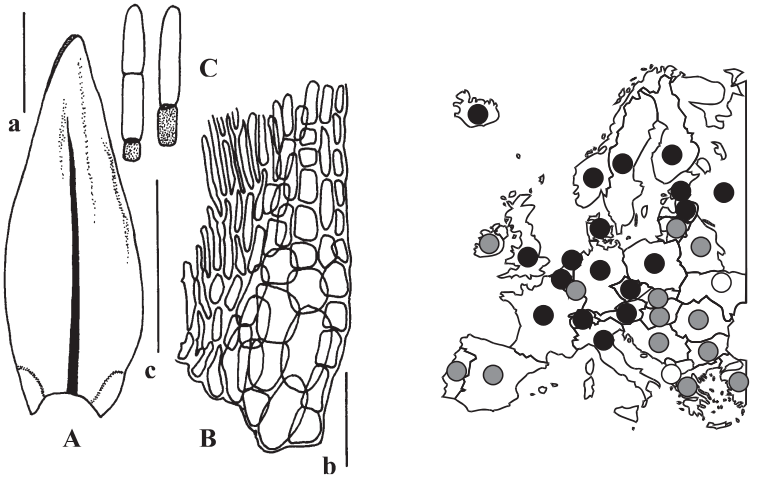


Fig. 36. *Straminergon stramineum*. A : Stem leaf. B : Alar cells. C : Axillary hairs. Scales : a : 0.5 mm, A. b : 75 µm, B. c : 60 µm, C.

Usually easily recognised by its pale and sparsely branched shoots with oblong, ovate, or narrowly ovate leaves with rounded apices. Occasionally *Straminergon stramineum* can be confused with *Calliergon cordifolium* in the field. However, modifications of the latter with comparatively narrow leaves have indistinctly delimited, large groups of alar cells, which reach from the leaf margin to the costa or almost so, whereas the alar groups of *S. stramineum* are well delimited and ovate or broadly ovate, along the basal margin. For the differences between *S. stramineum* and *Warnstorfia sarmentosa*, see the note after the latter.

Scorpidium (Schimp.) Limpr.

Dioicous or autoicous. Plants branched ± in one plane, sometimes with red colours. Stem leaves concave or strongly concave, from erect-patent to patent, ovate-lanceolate to broadly ovate (sometimes almost orbicular) base suddenly curved in upper part and narrowed to obtuse, apiculate, acute, or acuminate apex, sometimes (in *S. scorpioides*) indistinctly curved or ± straight, smooth or sometimes slightly plicate ; margin plane, entire below, finely denticulate or ± entire near leaf apex ; costa single and ending in upper half of leaf or short and then single or double (rarely absent) ; median lamina cells linear, alar cells few, strongly widened, hyaline, in transversely triangular group, extending shortly inwards from margin, not or hardly decurrent, supra-alar cells not or hardly differentiated from other basal cells ; rhizoid initials never present in leaves. Paraphyllia absent. Axillary hairs abundant and well developed, with 2-9 (-11) upper, hyaline cells. Rhizoids rare, reddish brown, smooth, slightly branched, inserted at or just below leaf costa insertion. Stem with weak central strand (rarely lacking), a well developed

cortex of incrassate cells and at least a partial hyalodermis. Inner perichaetial leaves slightly concave, straight and erect, lanceolate to ovate and gradually or suddenly narrowed to acuminate apex, plicate ; margin not or indistinctly bordered at shoulder, entire or sometimes denticulate above ; vaginula with paraphyses. Seta tall ; capsule cylindrical, curved and ± horizontal ; annulus separating. Peristome well developed ; outer layer of exostome reticulate or reticulate-striolate, sometimes partly (rarely entirely) cross-striolate in lower part.

Key to the species of Scorpidium

1. Stem leaves strongly concave, either almost orbicular and obtuse to apiculate, or from broadly ovate to broadly ovate-lanceolate base narrowed to apiculate, acute or acuminate point, falcate or rarely straight ; costa usually double, more rarely single or lacking, rarely reaching above mid-leaf. Hyalodermis of stem often incomplete (but always covering > 25 % of stem circumference). Usually large species (stem leaves (0.73-) 0.95-2.41 mm wide). . . . . **1. *S. scorpioides***

-. Stem leaves concave, from ovate to ovate-lanceolate base narrowed to shortly or longly acuminate apex, often near apex narrowed to apiculus, falcate ; costa single, ending in upper half of leaf. Hyalodermis of stem complete. Usually medium-sized species (stem leaves 0.45-1.09 mm wide). **2**

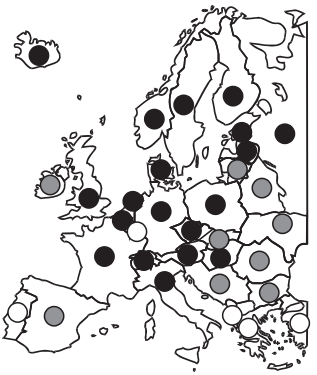
2. Dioicous. Median lamina cells of stem leaves 14.0-95.0 (-120.0) µm long, with square to shortly tapering cell ends. Outer peristomial layer of exostome predominantly (70-100 %) reticulate in lower part. . . **2. *S. cossonii***

-. Autoicous. Median lamina cells 61.0-140.0 (-178.5) µm long, predominantly with shortly to longly tapering cell ends. Outer peristomial layer usually predominantly (>(40-) 50 %) cross-striolate in lower part. . **3. *S. revolvens***

1. Scorpidium scorpioides (Hedw.) Limpr. (Fig. 37)

Stems with partial or complete hyalodermis (>25% of stem circumference). Stem leaves from erect-patent to patent base usually rather suddenly curved in upper part, rarely straight or almost so, varying in shape from almost orbicular to broadly ovate-lanceolate, suddenly narrowed to obtuse and mostly apiculate point or more gradually narrowed to acute or acuminate point, (0.73-) 0.95-2.41 mm wide, strongly concave ; costa double or occasionally single (rarely absent), reaching somewhere below to very rarely slightly above middle of leaf, when single often branched ; median lamina cells 32.0-200.0 (-210.0) µm long, cell ends square, rounded or shortly fusiformly narrowed ; differentiated alar cells 5-20. Dioicous. Lower outside of exostome varying from almost entirely cross-striolate to almost entirely reti-culate. - Robust or very robust, occasionally medium-sized, turgid plants, mostly sparsely or irregularly pinnately branched, often with a characteristic claw-like shoot apex, green, brown, or often red to blackish red. Found in strongly calcareous to intermediately mineral-rich habitats, in fens, pools, on lake

shores, or submerged in lakes, from the lowlands to the alpine region, and in the arctic. [pH 5.2-8.5 (n = 359) ; EC 14-582 mS/m (n = 171) (in lakes 1-18 mS/m ; n = 44) ; Ca 1.2-141,0 mg/l (n = 106) ; IR 0.34-1.00 (n = 106)]. Widespread and often common in the temperate to arctic regions of the northern hemisphere, in the Andes of South America, and in a few places in Australia.



Scorpidium scorpioides is usually easily known by its large size and strongly concave, broad and usually shortly pointed leaves with a short single or double costa. Straight-leafed phenotypes are rare in most areas, but seem to be more frequent in some arctic areas, in the Andes, and in Australia. These plants look very different from the falcate-leafed ones (see Fig. 37A, B), but except for the leaf curvature there does not seem to be any difference between these phenotypes. For differences between this species and *Pseudocalliergon turgescens*, see the notes after the latter.

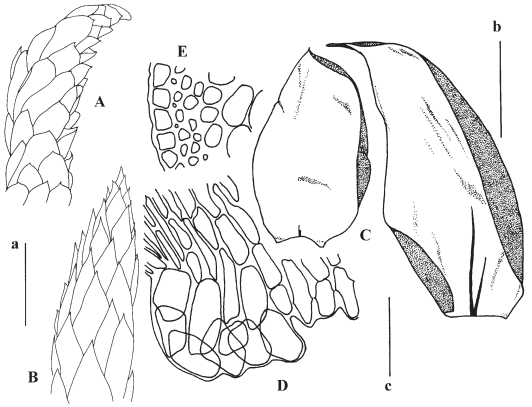


Fig. 37. *Scorpidium scorpioides*. A, B.Shoot apices from falcate- and straight-leafed plants. C : Stem leaves. D : Alar cells. E : Partial transverse section of stem cortex and hyalodermis. Scales : a : 2 mm, A, B. b : 1 mm, C. c : 50 µm, D, E.

2. Scorpidium cossonii (Schimp.) Hedenäs (Figs 13C, D, p. 27 ; 16A, p. 32 ; 38A-C)

***Drepanocladus intermedius*_(Lindb.) Warnst. ; *Drepanocladus revolvens* var. *intermedius* (Lindb.) Grout ; *Limprichtia cossonii* (Schimp.) L. E. Anderson ; *Limprichtia revolvens* var. *tenuis* (Turn.) Ochyra & Zarnoviec**

Stems with well developed, complete hyalodermis. Stem leaves from erect-patent or patent base ± suddenly curved in upper part, ovate or rather broadly ovate, gradually narrowed to shortly or longly acuminate apex, near apex often suddenly narrowed to apiculus, 0.45-1.09 mm wide, concave ; costa single, ending in upper half of leaf ; median lamina cells 14.0-95.0

(-120.0) µm long, cell ends square, rounded or shortly fusiformly narrowed ; differentiated alar cells 2-10 (-15). Dioicous. Lower exostome outside predominantly (>70%) reticulate in lower part. – Medium-sized to robust, more rarely slender plants, rather irregularly or more commonly pinnately branched, not turgid, with shoot apex sometimes slightly hooked, green, yellow-green, brown, or brown-red. The species grows in mineral-rich (often calcareous) habitats in fens, springs, periodically water-filled depressions, on shores, or more rarely submerged. [pH 5.0-8.1 (n = 307) ; EC 18-681 mS/m (n = 238) ; Ca 2.3-130,0 mg/l (n = 82) ; IR 0.42-1.00 (n = 82)]. Widespread and often common in temperate to sub-polar areas of the northern and southern hemispheres, and in the Andes.

Scorpidium cossonii is frequently confused with *S. revolvens* or *Hamatocaulis vernicosus*. From the latter it is easily separated by its hyalodermis and the usually present central strand of the stem, and by its differentiated hyaline and inflated alar cells of the stem leaves. *Hamatocaulis vernicosus*, which lacks all these features has usually got distinctly plicate stem leaves, whereas these are smooth in *S. cossonii*. In *H. vernicosus* a pure red colour is often present in a band shortly above the base of the leaves, whereas in *S. cossonii* the leaf base and sometimes costa are often brown-red in plants that are not entirely red or brown-red. *Scorpidium cossonii* differs from *S. revolvens* in being dioicous (the latter is autoicous) and in having shorter median stem leaf lamina cells. The ends of these cells are square to shortly fusiformly narrowed in the first species whereas they are shortly to longly fusiformly narrowed in the latter. Note that in order to separate *S. cossonii* and *S. revolvens* it is important to measure lamina cell length in the shorter 'half' of the leaves, as indicated in Fig. 3 (p. 15). Both species may have red or strongly red colours, and in such cases *S. cossonii* is usually brownish red while *S. revolvens* is mostly blackish or purplish red. Due to a large variation in both species, especially when herbarium material is also considered, colour should, however, be used with care in identifying specimens. Dark purplish plants usually belong to *S. revolvens* and

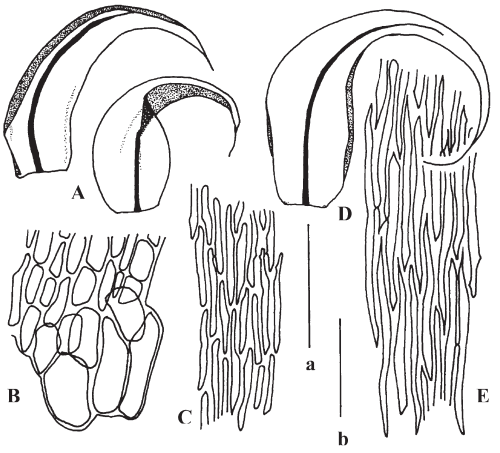
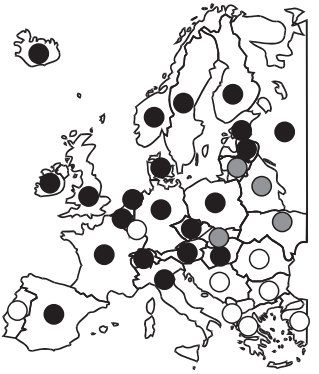


Fig. 38. *Scorpidium cossonii* (A-C) and *S. revolvens* (D, E). A, D : Stem leaves. B : Alar cells. C, E : Median lamina cells. Scales : a : 1 mm, A, D. b : 50 µm, B, C, E.

predominantly green or yellow-green plants with a brown-red costa or costa and leaf base belong to *S. cossonii*. The difference in leaf areolation between the two species makes *S. cossonii* less glossy than *S. revolvens*, but this character, like the difference in size and branching pattern (*S. cossonii* is slightly smaller and more richly and regularly branched than *S. revolvens*) which is obvious in mixed collections is often difficult to use in identification without much experience. In mixed collections *S. cossonii* has more shortly acuminate stem leaves than *S. revolvens*, but both species are variable in this character and the overlap between them is great.

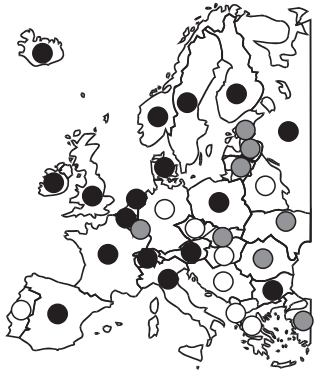


3. Scorpidium revolvens (Sw. ex Anonymo) Rubers (Figs 13A, B, p. 27 ; 38D, E)

Drepanocladus revolvens **(Sw. ex Anonymo) Warnst. ;** ***Limprichtia revolvens*** **(Sw. ex Anonymo) Loeske**

Stems with well developed, complete hyalodermis. Stem leaves from erect-patent or patent base ± suddenly curved in upper part, ovate or ovate-lanceolate, gradually narrowed to acuminate or longly acuminate apex, sometimes near apex suddenly narrowed to apiculus, 0.45-1.01 mm wide, concave ; costa single, ending in upper half of leaf ; median lamina cells 61.0-140.0 (-178.5) µm long, cell ends shortly or longly fusiformly narrowed (rarely rounded to almost square) ; differentiated alar cells 2-10. Autoicous. Lower outside of exostome predominantly (>(40-) 50 %) cross-striolate in lower part. – Medium-sized to robust, not turgid plants, sparsely and irregularly or, more rarely, ± pinnately branched, shoot apex not hooked, green, red, purplish red, dark brownish red, or blackish red. Occurs in intermediately mineral-rich and often spring-influenced habitats, in fens, in small periodically water-filled depressions, on shores, or more rarely submerged. This species is absent from the most calcium-rich regions. [pH 5.1-7.1 (n = 84) ; EC 16-166 mS/m (n = 64) (in lakes 1.8-3,7 mS/m ; n = 3) ; Ca 0.7-27,7 mg/l (n = 40) ; IR 0.17-1.00 (n = 40)]. Widespread and often common in temperate to sub-polar areas of both hemispheres, and in Papua New Guinea.

This species has often been confused with *S. cossonii*, and the differences between these species are discussed under the latter.



Dioicous. Plants branched ± in one plane, sometimes with red colours. Stem leaves concave or strongly concave, from ± erect or patent, ovate to broadly ovate base suddenly curved in upper part, upwards narrowed to acute or acuminate point, near apex often suddenly narrowed to short apiculus, usually distinctly plicate ; margin plane, often finely but irregularly denticulate near leaf apex, otherwise entire ; costa single, ending in upper half of leaf ; median lamina cells linear, cell ends rounded or tapering, alar cells not differentiated, not or hardly decurrent ; rhizoid initials never present in leaves. Paraphyllia absent. Axillary hairs abundant and well developed, with 2-6 upper, hyaline cells. Rhizoids rare, smooth, reddish brown, slightly branched, inserted at or just below leaf costa insertion. Stem without central strand, with a cortex of 1-2 layers of slightly incrassate cells, without hyalodermis. Inner perichaetial leaves slightly concave, straight and erect, ovate-lanceolate and gradually or suddenly narrowed to acuminate point, plicate ; margin plane or slightly recurved, not or indistinctly bordered at shoulder, entire or sometimes finely denticulate above ; vaginula with paraphyses. Seta tall ; capsule cylindrical, curved and ± horizontal ; annulus separating. Peristome well developed ; outer layer of exostome reticulate in lower part.

Key to the species of Hamatocaulis

1. Stem leaf base erect (and then often ± adpressed to the stem) or slightly spreading, ovate and not or slightly constricted at insertion. Smaller species (stem leaves 0.61-1.10 mm wide). . . . . **1. *H. vernicosus***

-. Stem leaf base ± patent, broadly ovate and distinctly constricted at insertion. Larger species (stem leaves 0.78-2.01 mm wide). .**2. *H. lapponicus***

1. Hamatocaulis vernicosus (Mitt.) Hedenäs (Figs 12C, D, p. 26 ; 17B, p. 32 ; 39)

***Drepanocladus vernicosus* (Mitt.) Warnst. ; *Limprichtia vernicosa* (Mitt.) Loeske ; *Scorpidium vernicosum* (Mitt.) Tuom.**

Stem leaves from ± erect base rather suddenly curved in upper part, slightly narrowed at leaf insertion, ovate and ± gradually narrowed to shortly or longly acuminate point, near apex often suddenly narrowed to short apiculus, 0.61-1.10 mm wide, often with red colour in transverse sub-basal ribbon, more rarely larger parts of leaf red, strongly or, less commonly, slightly plicate, concave ; median lamina cells (28.0-) 30.0-130.0 (-140.0) µm long ; alar cells not differentiated. Spores 10.5-22.0 µm, finely papillose, mature in summer. - Medium-sized to almost robust plants, mostly ± pinnately branched and with the shoot apex often hooked like a walking stick, not turgid, green, greyish green, brownish, or variegated green and red, rarely entirely red. In mineral-rich (though usually not calcium-rich) and often slightly nutrient-enriched, spring-influenced habitats, or on lake shores. [pH 5.4-7.8 (n = 61) ; EC 16-396 mS/m

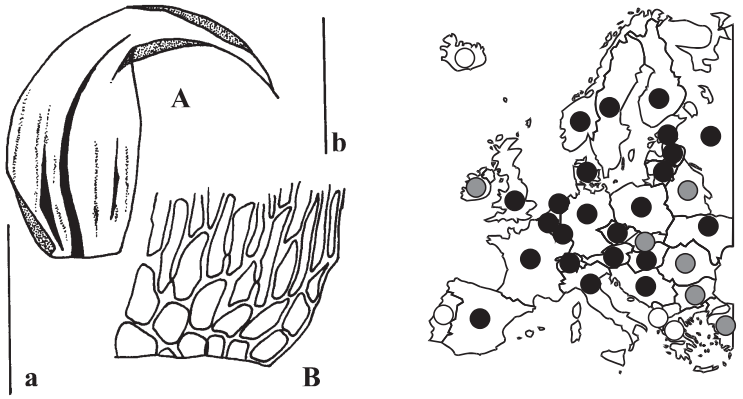


Fig. 39. *Hamatocaulis vernicosus*. A : Stem leaf. B : Alar cells. Scales : a : 1 mm, A. b : 50 µm, B.

(n = 48) ; Ca 2.5-56,8 mg/l (n = 21) ; IR 0.41-0.95 (n = 21)]. Widely distributed but rarely common in the northern temperate to arctic zones, scattered in mountains of Central and northern South America (Africa ?). The species is either rare or lacking in strongly oceanic and arctic areas.

Usually easily recognised by the distinctly plicate stem leaves having erect bases and suddenly curved upper parts. The stem leaves lack differentiated alar cells and the stem lacks central strand and hyalodermis. For differences between this species, *Hamatocaulis lapponicus* and *Scorpidium cossonii*, see the notes after the latter two.

2. Hamatocaulis lapponicus (Norrl.) Hedenäs (Figs 12A, B, p. 26 ; 40A, B)

***Drepanocladus lapponicus* (Norrl.) Smirn. ; *Scorpidium lapponicum* (Norrl.) Tuom. & T. J. Kop.**

Stem leaves from ± patent base rather suddenly curved in upper part, distinctly constricted at leaf insertion, broadly ovate and ± gradually narrowed to acute or acuminate point, near apex sometimes suddenly narrowed to short apiculus, 0.78-2.01 mm wide, often with red colour present in large parts of leaf or in transverse, sub-basal ribbon, plicate or almost smooth, concave or strongly concave ; median lamina cells (32.0-) 35.0-165.0 (-170.0) µm long ; alar cells not differentiated. Spores 13.5-24.5 µm, finely papillose, mature in summer. – Robust to very robust plants, occasionally medium-sized, turgid, mostly sparsely and irregularly branched, shoot apex sometimes hooked, variegated red and green, brownish red, or blackish red, more rarely green or greyish green throughout. In wet, mesotrophic and often spring-influenced mires or on lake shores, sometimes submerged in lakes. Widely distributed in the boreal and, rarely, in the arctic zones of Eurasia and western North America. Earlier it occurred in a few localities in southern Germany. The species appears to be rare in northern Europe and western North America, whereas its frequency in Asia is poorly known.

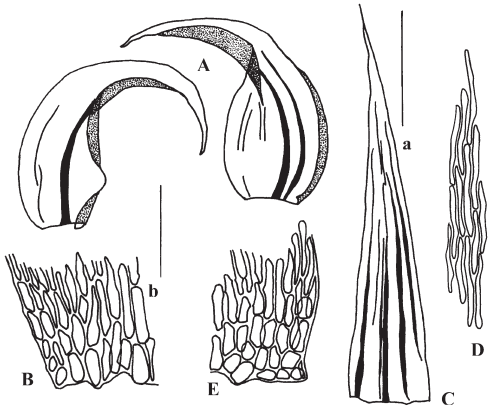
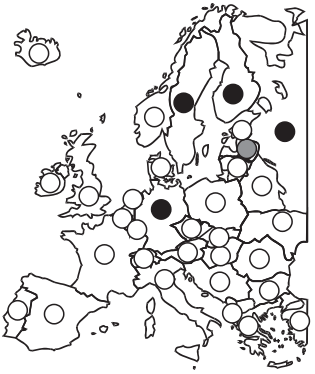


Fig. 40. *Hamatocaulis lapponicus* (A, B) and *Tomentypnum nitens* (C-E). A, C : Stem leaves. D : Median lamina cells. B, E : Alar cells. Scales : a : 1 mm, A, C. b : 50 µm, B, D, E.



Usually easily recognised by its large size (approximately as large as *Scorpidium scorpioides*), its usually slightly plicate stem leaves without differentiated alar cells, and a stem with neither central strand nor hyalodermis. Besides the larger size, it differs from *H. vernicosus* in having ± patent stem leaf bases, and in that the stem leaves are broadly ovate and more distinctly constricted at their insertion. *Hamatocaulis lapponicus* is usually also more sparsely and irregularly branched than *H. vernicosus*, has somewhat less plicate leaves than the latter, and large parts of its shoots are more often red than is the case in the latter.

Tomentypnum Loeske

Dioicous. Plants usually branched ± in one plane, occasionally indistinctly so, never with red colours. Stem leaves longly lanceolate, triangular-lanceolate, or narrowly ovate-lanceolate, shortly or longly acuminate, straight or falcate-secund, strongly plicate ; margin plane or recurved, entire or sinuose, near leaf apex sometimes obtusely denticulate ; costa single, ending in upper half of leaf ; median lamina cells linear, incrassate or strongly incrassate, slightly flexuose, alar cells not differentiated, not or hardly decurrent ; rhizoid initials in leaves often present on lower back of costa. Paraphyllia absent. Axillary hairs abundant and well developed, with 2-6 upper, hyaline cells. Rhizoids usually abundant, smooth, reddish brown, strongly branched, inserted on back of leaf costa (in lower 1/2-3/4 of costa) or on stem at or just below leaf costa insertion. Stem with central strand and a well developed cortex of incrassate cells. Inner perichaetial leaves straight and erect, longly lanceolate,

acuminate, plicate ; margin entire, unbordered ; vaginula with paraphyses. Seta tall ; capsule cylindrical, curved and ± horizontal ; annulus separating. Peristome well developed ; outer layer of exostome reticulate in lower part.

Key to the species of Tomentypnum

1. Stem leaves straight or slightly homomallous ; leaves lanceolate or triangular-lanceolate, widest close to insertion. Rhizoids on both stem and abaxial leaf. . . . . **1. *T. nitens***

-. Stem and branch leaves falcate-secund ; leaves narrowly ovate-lanceolate, widest ca. 1/5 way up leaf. Rhizoids only on abaxial leaf. **2. *T. falcifolium***

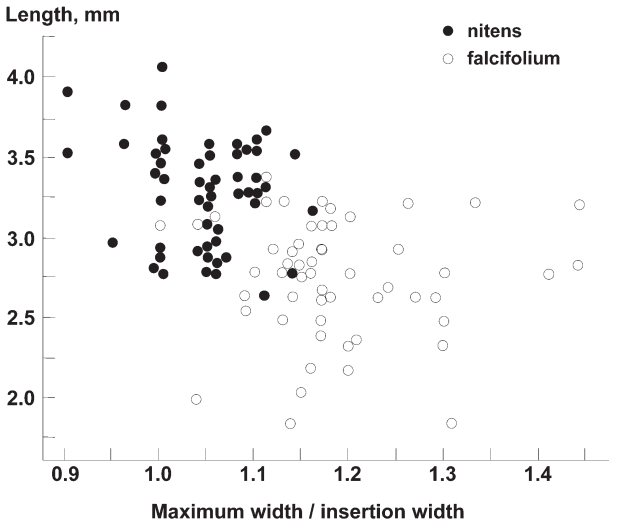
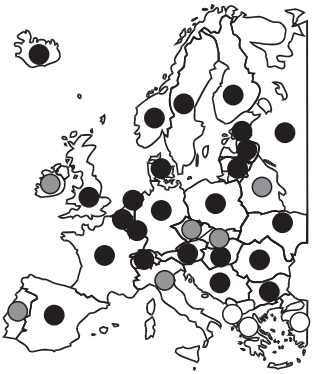


Fig. 41. Plot of leaf length against the ratio between maximal leaf width and leaf width at insertion for *Tomentypnum nitens* and *T. falcifolium* (after Vitt & Hamilton 1975).

1. Tomentypnum nitens (Hedw.) Loeske (Figs 17A, p. 32 ; 40C-E)

***Camptothecium nitens* (Hedw.) Schimp. ; *Homalothecium nitens* (Hedw.) H. Rob.**

Stem leaves straight and erect or slightly homomallous, longly lanceolate or triangular-lanceolate, widest near insertion, shortly or longly acuminate, strongly plicate ; median lamina cells 42.0-88.5 (-105.0) µm long ; alar cells not or hardly differentiated. Rhizoids on both stem and abaxial leaf. Spores 15.0-21.0 µm. - Medium-sized or usually robust plants, ± pinnately branched, green, yellowish, or brownish. In ± mineral-rich and sometimes somewhat nutrient-rich fens, sometimes in other rich wetland habitats. [pH 5.7-8.0 (n = 60) ; EC 24-509 mS/m (n = 36) ; Ca 2.1-73,7 mg/l (n = 23) ; IR 0.48-0.97 (n = 23)]. Widespread and in many areas common in the northern temperate and arctic zones.



The usually yellowish colour, the straight, strongly plicate stem and branch leaves without differentiated alar cells, and the strongly branched rhizoids that are usually numerous in the lower parts of the plants, and which are partly inserted on the lower back of the costa make this species easily recognisable. At high altitudes in the mountains and in the far north the leaves are often more shortly acuminate than in other areas of the territory. *Tomentypnum nitens* could possibly be confused with *Brachythecium turgidum* (Hartm.) Kindb. which in Europe is frequent in richer mountain areas, with scattered or rare occurrences also in the lowlands. The latter species is, however, more turgid and mostly paler than *T. nitens* and has got somewhat wider, more ovate, and somewhat less strongly plicate stem leaves with distinct small groups of differentiated and decurrent alar cells. Usually, *Brachythecium turgidum* is also more sparsely branched than *T. nitens* and has never got rhizoids on the back of the costa. The differences between *T. nitens* and *T. falcifolium* are given under the latter.

2. Tomentypnum falcifolium (Renauld ex Nichols) Tuom.

***Tomentypnum nitens* var. *falcifolium* (Renauld ex Nichols) Podp.**

Stem leaves falcate-secund, narrowly ovate-lanceolate, widest ca. 1/5 way up leaf, shortly or longly acuminate, strongly plicate ; median lamina cells 42.0-86.0 µm long ; alar cells not or hardly differentiated. Rhizoids only on abaxial leaf. Spores 12.0-21.0 µm. - Medium-sized plants, ± pinnately branched, green, yellowish, or brownish. In intermediately mineral-rich to relatively poor fen habitats. [pH 4.1-6.0 (n = 45) ; Vitt & Hamilton (1975)]. Occurs in boreal and subarctic North America, north of the southernmost ice-limit during the Pleistocene glaciations, in NE China, and the Lake Baikal area in Russia.

This species is very similar to *Tomentypnum nitens* in most characters. Vitt & Hamilton (1975) compared these two taxa in detail and found that they can be separated by means of the characters that are given in the key and in Fig. 41. Chinese populations of *Tomentypnum falcifolium* deviate from North American ones, especially in having less strongly curved leaves, thus being somewhat intermediate between *T. nitens* and North American *T. falcifolium* (Vitt. et al. 1990).

Drepanocladus (Müll. Hal.) G. Roth

Autoicous, synoicous, or dioicous. Plants branched ± in one plane, never with red colours. Stem leaves falcate, straight or squarrose, almost plane or concave, sometimes strongly concave and sub-clasping, not plicate, broadly

ovate, ovate, triangular, or cordate, gradually or suddenly narrowed to acumen, the latter sometimes distinctly furrowed, apex obtuse, acuminate, or longly acuminate ; costa short and double, or single and ending in upper leaf to excurrent ; margin entire, sub-entire, or finely denticulate ; median lamina cells linear or shortly linear, mostly with square to shortly narrowed cell ends, smooth, sometimes bistratose (S American species) ; alar cells shortly to longly rectangular, inflated, thin-walled and hyaline or yellowish and incrassate, in usually distinctly delimited, transversely triangular group which reaches from leaf margin to leaf costa, or alar group separated from costa by a ± large portion of not inflated basal cells, non-decurrent or sometimes decurrent (N American species) ; rhizoid initials never present in leaves. Paraphyllia absent. Axillary hairs well developed and abundant, with 1-3-celled, hyaline upper part. Rhizoids mostly slightly branched, smooth, red-brown, inserted on stem at or just below insertion of leaf costa. Stem with central strand and usually a well developed cortex of incrassate cells. Inner perichaetial leaves straight and erect, ovate or lanceolate-ovate, plicate. Capsule cylindrical, ± horizontal ; annulus separating. Peristome well developed ; outer layer of exostome cross-striolate in lower part.

Key to the species of Drepanocladus

Note ! : In *Drepanocladus*, the ratios between the sizes of different cells or organs should be based on measurements in 8-10 adjacent stem leaves. In all cases, the total size range should be searched for. For the median lamina cells measurements should be made on both sides of the costa, also in curved leaves. Leaf length is measured from the insertion of the costa to the leaf apex. The median values of these ranges (i.e., mid-point values of the measured ranges) are then used for the calculations of the ratios.

1. Dioicous. Leaves falcate-secund to sometimes entirely ± straight and erect (plant habit "*Drepanocladus*-like" ; Figs 42-46) ; leaf acumen in straight-leafed plants plane or at most slightly furrowed. **2**

-. Autoicous. Leaves from ± straight and erect bases usually with leaf acumina ± spreading, or squarrose (plant habit "*Campylium*-like" ; Fig. 9, p. 20) ; leaf acumen furrowed. **6**

2. Stem leaf costa excurrent or longly so, rarely ending a few cells below leaf apex ; one or both leaf margins often partly finely denticulate. . . . . .**2. *D. longifolius***

-. Stem leaf costa ending well below leaf apex ; leaf margin entire, or occasionally very finely denticulate. **3**

3. Ratio "median leaf lamina cell length (µm) / leaf length (mm)" between 37.6-45.6. Stem leaves 1.1-2.1 mm long and 0.5-0.7 mm wide ; alar groups quadrate or rectangular, not reaching costa (Fig. 46, p. 80). (Rare arctic species, not yet found in Europe). . . . . .**5. *D. latinervis***

-. Ratio "median leaf lamina cell length (µm) / leaf length (mm)" between 17.9-36.5 (in *D. aduncus* rarely up to 38.2). Stem leaves 0.9-5.2 mm long and 0.4-1.6 mm wide ; alar groups variously developed (Figs 42, 44, 45). (Widespread species, also occurring in arctic areas). **4**

4. Alar groups transversely triangular, reaching costa or almost so (Fig. 42). Stem leaves variously straight or falcate-secund, the latter especially in small plants growing under relatively dry conditions. . . . . **1. *D. aduncus***

-. Alar groups quadrate or shortly transversely triangular, not reaching costa (Figs 44, 45). Stem leaves mostly falcate-secund or strongly so, rarely weakly so or almost straight, the latter occasionally in submerged plants. **5**

5. Ratio "median leaf lamina cell length (µm) / leaf length (mm)" between 23.3-36.5. Ratio "median lamina cell width (µm) / leaf length (mm)" between 1.9-5.9. (In intermediately mineral-rich to mineral-rich habitats). . . . . **3. *D. sordidus***

-. Ratio "median leaf lamina cell length (µm) / leaf length (mm)" between 17.9-24.4. Ratio "median lamina cell width (µm) / leaf length (mm)" between 1.5-4.2. (In strongly calcareous habitats). . . . . **4. *D. sendtneri***

6. Stem leaf insertion shallowly curved to almost straight ; leaf base when moist concave, erect to ± spreading, acumen gradually differentiated from basal leaf and frequently more spreading than leaf base, straight or falcate ; costa double and extending 30-50 % way up leaf or single and extending 40-65 % way up, leaves 0.6-1.0 (-1.1) mm wide. (Temperate and arctic species). . . . . **6. *D. polygamus***

-. Stem leaf insertion usually deeply U-shaped ; leaf base when moist concave or strongly concave, erect and sub-clasping, acumen usually sharply differentiated from basal leaf and (erect), patent, spreading or squarrose ; costa double and extending < 25 % way up leaf, or if single extending < 45 % way up ; leaves 0.6-1.5 mm wide. (Arctic species). **7. *D. arcticus***

1. Drepanocladus aduncus (Hedw.) Warnst. (Figs 15, p. 28 ; 42)

***Drepanocladus aduncus* var. *pseudofluitans* (Sanio) Glow. ; *Drepanocladus aquaticus* (Schimp.) Warnst. ; *Drepanocladus kneiffii* (Schimp.) Warnst. ; *Drepanocladus polycarpus* (Voit) Warnst. ; *Drepanocladus simplicissimus* Warnst. ; *Drepanocladus stagnatus* Żarnowiec; *Drepanocladus* sp. of Hedenäs (1993a)**

Dioicous. Stem leaves ovate-lanceolate, ovate, triangular-ovate, rounded-triangular, or broadly ovate, gradually narrowed to (obtuse), acute, or shortly to longly acuminate apex, erect-patent to ± spreading, straight, slightly falcate, or especially in small plants growing under relatively dry conditions more strongly falcate, in submerged specimens leaves often somewhat distantly inserted, acumen in straight-leafed plants plane or at most slightly furrowed ; costa weak or rather strong, 31.5-90.0 (-105.0) µm wide near base, ending in mid-leaf or above, but well below leaf apex ; margin entire or almost so ; median lamina cells (14.0-) 14.5-188.0 (-263.0) µm long ; alar groups transversely triangular and reaching from leaf margin ± to costa, consisting

of inflated and thin-walled cells, sometimes with a few rows of undifferentiated basal cells between alar group and costa. - Plants medium-sized, sometimes large, pinnately or irregularly pinnately branched, green, yellow-green, or brownish green. This species is found in ± nutrient-rich wetland habitats, such as ditches, eutrophic fens, lake or sea shores, sometimes in swampy forests or submerged in lakes or smaller waters. [pH 4.3-9.6 (n = 102) ; EC 38-1 600 mS/m (n = 26) (in lakes 1-53 mS/m ; n = 13) ; Ca 0.9-88,8 mg/l (n = 29) ; IR 0.26-0.97 (n = 29)]. *Drepanocladus aduncus* is widely distributed throughout the temperate to sub-polar zones of both hemispheres, and occurs in scattered localities in mountains of tropical and subtropical areas.

Hedenäs (1996) showed that the quantitative characters that were earlier employed for separating taxa within the *D. aduncus* complex are size-dependent. Small plants with short leaf cells and weak costae (and frequently falcate leaves) were earlier called *D. polycarpus*, intermediate plants *D. aduncus*, and large plants, with long cells and strong costae *D. aquaticus*. Specimens with acute or sometimes obtuse leaf apices were named *D. simplicissimus*, but because specimens of the latter have sometimes got 'normal' *D. aduncus* leaves in some parts of the stems, and *D. simplicissimus* leaves in other parts, it seems likely that the *simplicissimus* phenotypes are environmentally induced. A different opinion was recently expressed by Żarnowiec (2001), who separated plants of different sizes into different species, but neither providing other evidence than size-dependent characters for their recognition nor explaining why their size-limits were put as they were.

The species most likely to be confused with *D. aduncus* is *D. polygamus*, and the differences between these species are discussed under the latter. *Drepanocladus aduncus* is also frequently confused with *Warnstorfia* species, but the latter frequently get red colours when growing in exposed habitats whereas *D. aduncus* never gets red. In *Warnstorfia* species the shoots

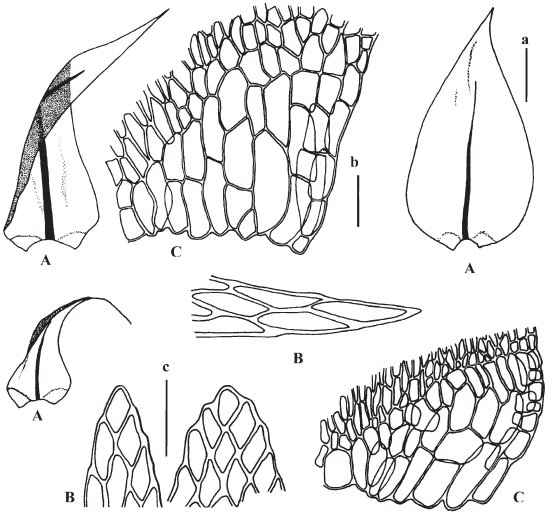
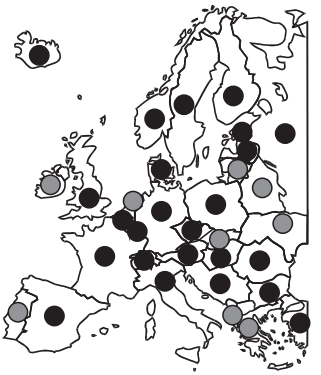


Fig. 42. *Drepanocladus aduncus*. A : Stem leaves. B : Leaf apices. C : Alar cells. Scales : a : 0.5 mm, A. b : 25 µm, B. c : 50 µm, C.



are radially branched (in sparsely branched specimens this may be difficult to see ; distichously branched in *Drepanocladus*), and the margins are mostly distinctly denticulate in at least some parts of the leaves (most distinct just above the alar groups and / or near the leaf apex ; entire in *D. aduncus*). When several leaves are checked, rhizoid initials can almost invariably be found near the apex of at least some leaves of most *Warnstorfia* species (very rare only in *W. trichophylla*), whereas leaf-borne initials are never found in *Drepanocladus*. Finally the very different ontogeny of the alar cells in these two genera is a safe separating character for the very few specimens that may remain when the just mentioned differentiating characters are not sufficient (see Fig. 19, p. 35). Another species that is sometimes confused with *D. aduncus* is *Leptodictyum riparium* (Hedw.) Warnst. (*Amblystegium riparium* (Hedw.) Schimp. ; *Amblystegium vacillans* Sull. ; *Leptodictyum sipho* (P. Beauv.) Broth.). *Leptodictyum riparium* differs from *D. aduncus* by its frequently complanate foliation, especially in the branches, something which does not occur in *D. aduncus*. The alar cells are more indistinctly delimited from the surrounding cells in *L. riparium* than in *D. aduncus*, and the first species is autoicous whereas the latter is dioicous. Finally, the upper part of the axillary hairs in *L. riparium* is 2-7-celled, whereas in *D. aduncus* it is 1-2 (-3)-celled. Because axillary hairs of these two species are frequent and easy to see when the leaves are removed in the uppermost portion of the shoot, this character is very useful for their separation.

2. Drepanocladus longifolius (Mitt.) Par. (Figs 14B, p. 28 ; 43)

***Drepanocladus capillifolius* (Warnst.) Warnst. ; *Drepanocladus crassicostatus* Janssens**

Dioicous. Stem leaves ovate to triangular or broadly rounded triangular, gradually narrowed to longly acuminate apex, erect-patent to patent, falcate or rarely almost straight ; costa strong, 80.0-193.0 µm wide near base, excurrent or longly so, rarely ending a few cells below leaf apex ; margin entire or frequently finely denticulate on one or both sides ; median lamina cells 10.0-183.0 µm long ; alar groups transversely triangular and mostly reaching from leaf margin 2/3-4/5 of distance to costa, consisting of inflated and thin-walled to incrassate cells. - Plants medium-sized to large, pinnately or more irregularly branched, green, yellow-green, or brownish. The species is found in ± mineral- and ± nutrient-rich habitats, submerged in lakes and pools, ox-bow lakes, in water-filled kettle holes, sometimes in periodically dry pools, in small and usually slowly flowing brooks, sometimes in connection with springs, and in

periodically wet depressions in meadows. [pH 5.8-8.7 (n = 74) ; EC 1-236 ms / m (n = 34) ; Ca 1.6-70,6 mg/l (n = 34) ; IR 0.54-0.96 (n = 34)]. *Drepanocladus longifolius* is widely distributed in the northern temperate to sub-polar zones, and occurs also throughout the South American Andes, south to Patagonia and the Falkland Islands, in Australia, and in Kerguelen.

Drepanocladus longifolius differs from all other *Drepanocladus* species in Europe and North America by its excurrent leaf costa, and because of this it could hardly be confused with any other wetland species included in this overview except *Warnstorfia trichophylla*, another species that frequently grows submerged, or possibly with specimens of the much smaller *Campyliadelphus elodes* with long costae (see the note after the latter). *Warnstorfia trichophylla* has, however, more strongly denticulate leaf margins than *D. longifolius*, it frequently becomes red when emergent, and the axillary hairs consist of 2-7, early brown upper cells (1-2, hyaline cells in *D. longifolius*).

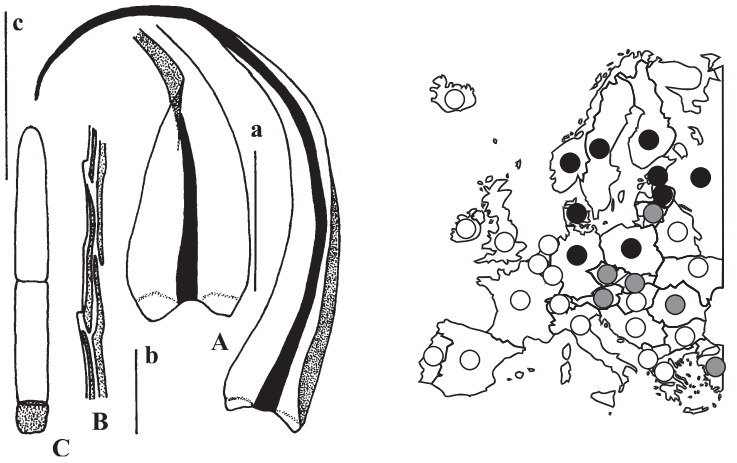


Fig. 43. *Drepanocladus longifolius*. A : Stem leaves. B : Leaf margin in lower half of leaf. C : Axillary hair. Scales : a : 1 mm, A. b : 50 µm, B. c : 60 µm, C.

In Patagonia and subtropical to tropical mountain areas of South America, another *Drepanocladus* species with excurrent leaf costae occurs in similar habitats as *D. longifolius*, the rare *D. perplicatus* (Dusén) G. Roth (syn. *Sciaromium lacustre* Herzog & P. W. Richards, *Richardsiopsis lacustris* (Herzog & P. W. Richards) Ochyra). This species can be separated from *D. longifolius* by means of the following key.

1. Ratio "median leaf lamina cell length (µm) / leaf length (mm)" between 16.5-23.9 (25.5). Leaf lamina throughout unistratose ; margin sometimes finely denticulate ; alar groups relatively large, extending from leaf margin 2/3-4/5 of distance to leaf middle at insertion. . . . . ***D. longifolius***

-. Ratio "median leaf lamina cell length (µm) / leaf length (mm)" between 25.5-34.5. Leaf lamina partly bistratose, especially in upper leaf and near margin ; margin entire ; alar groups small, extending from leaf margin 1/6-1/2 of distance to leaf middle at insertion. . . . . ***D. perplicatus***

3. Drepanocladus sordidus (Müll. Hal.) Hedenäs (Fig. 44)

***Drepanocladus tenuinervis T.* J. Kop.**

Dioicous. Stem leaves ovate, broadly ovate, or triangular-ovate, gradually narrowed to acuminate apex, strongly falcate-secund, rarely only weakly so ; costa weak or mostly rather strong, 42.0-120.0 (-147.0) µm wide near base, ending in lower or upper acumen (rarely forked or double in arctic areas) ; margin entire or occasionally very finely denticulate ; median lamina cells 12.5-213.0 (-250.0) µm long ; alar groups small, transversely triangular or quadrate, extending from leaf margin 40-55 % of distance to leaf middle at insertion, consisting of inflated and thin-walled to incrassate cells, separated from costa by a ± large portion of not inflated linear or shortly linear basal cells. - Plants medium-sized, sometimes large or small, pinnately or irregularly pinnately branched, green or brownish green. In Fennoscandia this species seems to be most frequently growing submerged in lakes, pools, and ox-bow lakes, usually in mesotrophic or eutrophic ones. However, recently it has been realised that it grows also in terrestrial wetland habitats, but how common it is in these in Fennoscandia or elsewhere in Europe and North America is not known at present. [pH 6.1-8.1 (n = 118) ; EC 1-24 mS/m (n = 45) ; Ca 1.1-41,9 mg/l (n = 45) ; IR 0.54-0.95 (n = 45)]. *Drepanocladus sordidus* is widely distributed in the temperate and arctic zones of Eurasia and North America, and occurs also in the subtropical and tropical mountains of South and Central America.

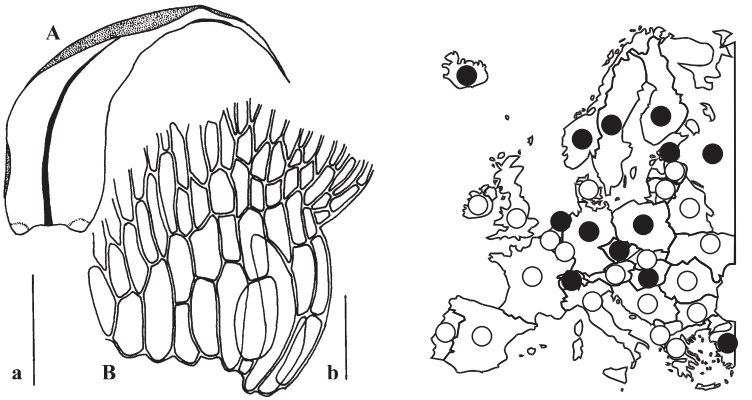


Fig. 44. *Drepanocladus sordidus*. A : Stem leaf. B : Alar cells. Scales : a : 1 mm, A. b : 50 µm, B.

Drepanocladus sordidus and *D. sendtneri* have for some time been considered to be distinct species in Fennoscandia. However, the characters that were used to separate the two, such as leaf costa length and width, and appearance of the alar groups, are too variable to allow certain identification of the two. However, as shown by Hedenäs (1998) the two species differ in the ratio between the median lamina cell length and the leaf length, and to some degree in the ratio between the median lamina cell width and the leaf length. Specimens with low values of the first ratio, *D. sendtneri*, do not occur in America, and grow in strongly calcareous habitats, whereas specimens with higher values of this ratio, *D. sordidus*, occur throughout Eurasia and in large parts of America, and grow in intermediately mineral-rich habitats. Possibly, specimens of *D. sendtneri* could sometimes have a slightly higher ratio than given in the key above, but I have so far not found any method to establish this with certainty. For the differences between *D. sordidus* and *D. latinervis*, see the notes after the latter.

In Australia and New Zealand *D. sordidus* is replaced by *D. brachiatus* (Mitt.) Dix. The latter is autoicous, has a "median leaf lamina cell length (µm) / leaf length (mm)" ratio of 21.2-35.3, and a relatively weak leaf costa (3 (-4)-stratose, ratio "costa width (µm) / leaf length (mm)" between 16.5-26.2 ; *D. sordidus* has a (3-) 4-5-stratose costa, and a ratio between 13.5-49.4).

4. Drepanocladus sendtneri (Schimp. ex H. Müll.) Warnst. (Fig. 45)

***Drepanocladus wilsonii* (Schimp.) Loeske**

Dioicous. Stem leaves ovate or triangular-ovate, gradually narrowed to acuminate apex, ± strongly falcate-secund, rarely only weakly so ; costa weak or mostly rather strong, 44.0-105.0 µm wide near base, ending in lower or upper acumen ; margin entire or occasionally very finely denticulate ; median lamina cells (10.5-) 11.0-133.0 µm long ; alar groups small, transversely triangular or quadrate, extending from leaf margin 40-55 % of distance to leaf middle at insertion, alar cells inflated and thin-walled to strongly incrassate, separated

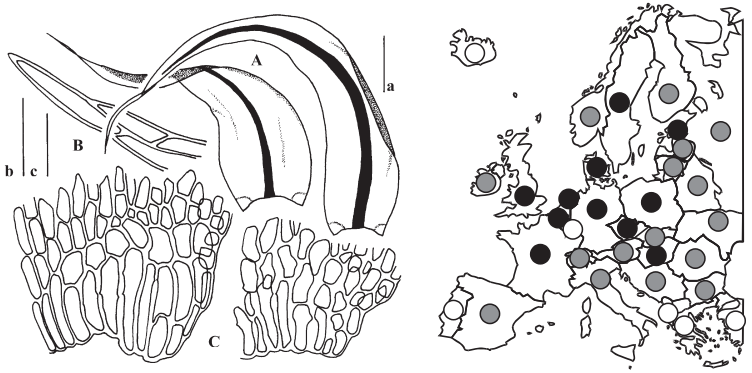


Fig. 45. *Drepanocladus sendtneri*. A : Stem leaves. B : Leaf apex. C : Alar cells. Scales : a : 0.5 mm, A. b : 25 µm, B. c : 50 µm, C.

from costa by a ± large portion of not inflated linear or shortly linear basal cells. - Plants medium-sized, sometimes large or small, pinnately or irregularly pinnately branched, green or brownish green. This species grows in strongly calcareous wetlands, such as periodically dry depressions in alvar and in calcareous fens. [pH 5.9-7.8 (n = 31) ; EC 140-960 mS/m (n = 19) ; Ca 22.7-219,0 mg/l (n = 9) ; IR 0.57-0.96 (n = 9)]. *Drepanocladus sendtneri* is widely distributed in Eurasia and occurs also in Africa. In Europe it seems to be rare or absent in the more northern areas, whereas it is more common in Central Europe.

Drepanocladus sendtneri is most often confused with *D. sordidus*, and the differences between these two species are given after the latter.

5. Drepanocladus latinervis Warnst. (Fig. 46)

Dioicous. Stem leaves ovate or broadly ovate, gradually narrowed to acuminate apex, ± strongly falcate-secund ; costa relatively weak, 37.5-75.0 µm wide near base, ending around mid-leaf or in lower acumen ; margin entire or very finely and obtusely denticulate ; median lamina cells 15.0-158.0 µm long ; alar groups small, transversely triangular, transversely rectangular, or quadrate, extending from leaf margin 30-60 % of distance to leaf middle at insertion, alar cells inflated and incrassate or slightly so, separated from costa by a ± large portion of not inflated linear or shortly linear basal cells. - Plants small, sparsely and irregularly pinnately branched, youngest shoot portions yellow-green, otherwise yellow-brown or brown. This species appears to grow in calcareous wetlands in the Arctic. *Drepanocladus latinervis* is widely distributed, but seemingly rare in arctic areas of Asia and North America, but is so far unknown from Europe. However, like other widespread Arctic taxa, it can be expected to occur also in northernmost Europe.

Drepanocladus latinervis is most similar to *D. sordidus*, which reaches into the arctic areas. Both have relatively small alar groups, and the two can be safely separated only on the basis of the ratio "median leaf lamina cell length (µm) / leaf length (mm)", which is much larger in *D. latinervis* than in any other *Drepanocladus* species with falcate leaves, between 37.6-45.6. *Drepanocladus latinervis* is a small species, with stem leaves 1.1-2.1 mm long and 0.5-0.7 mm wide, but because *D. sordidus* is frequently also small in arctic areas, difference in plant size is not sufficient for their separation.

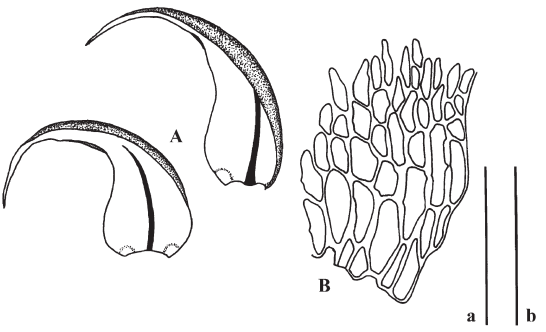
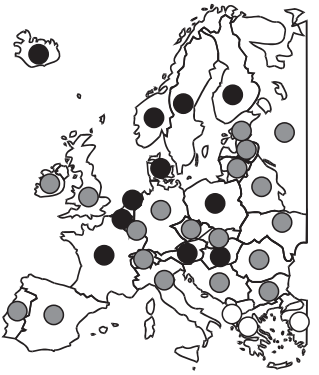


Fig. 46. *Drepanocladus latinervis*. A : Stem leaves. B : Alar cells. Scales : a : 1 mm, A. b : 50 µm, B.

6. Drepanocladus polygamus (Schimp.) Hedenäs (Fig. 47)

***Campyliadelphus polygamus* (Schimp.) Kanda ; *Campylium polygamum* (Schimp.) C. E. O. Jensen ; *Campylium polygamum* var. *fluitans* Grout**

Autoicous. Stem leaves ovate, broadly ovate or rounded-triangular, mostly distinctly narrowed at insertion, gradually narrowed to acuminate apex, acumen not or hardly differentiated from basal leaf, leaf insertion shallowly U-shaped to almost straight, leaves concave, erect-patent to spreading, sometimes basal leaf portion slightly more erect than rest of leaf, straight or falcate, in acumen channelled, when dry somewhat twisted ; costa either double and extending 30-50 % way up leaf, or single or branched and extending 40-65 %, 31.5-73.5 µm wide near base ; margin entire or slightly sinuose ; median lamina cells (26.5-) 40.0-130.0 (-136.5) µm long ; alar groups large, transversely triangular and extending 65-100 % of distance from leaf margin to leaf middle at insertion, ± well delimited, consisting of inflated and thin-walled or slightly incrassate cells. - Plants medium-sized, irregularly and sparsely to more or less pinnately branched, green, yellow-green, or green-brown. This species is found in ± nutrient-rich wetland habitats, such as ditches, eutrophic fens, lake or sea shores, sometimes in swampy forests, or submerged in lakes or smaller waters. [pH 5.5-7.9 (n = 40) ; EC 63-1 600 mS/m (n = 17) (in lakes 2-11 mS/m ; n = 14) ; Ca 1.1-175,0 mg/l (n = 23) ; IR 0.48-0.96 (n = 23)]. *Drepanocladus polygamus* is widely distributed throughout the temperate to sub-polar zones of both hemispheres, and occurs in scattered localities in mountains of tropical and subtropical areas.



Some specimens of *Drepanocladus polygamus* are very similar to *D. aduncus*. However, *D. polygamus* is aut-oicous, whereas *D. aduncus* is dioicous. Mostly at least parts of the shoots in *D. polygamus* remind about species of *Campylium*, such as *C. stellatum*, with the ± spreading leaves

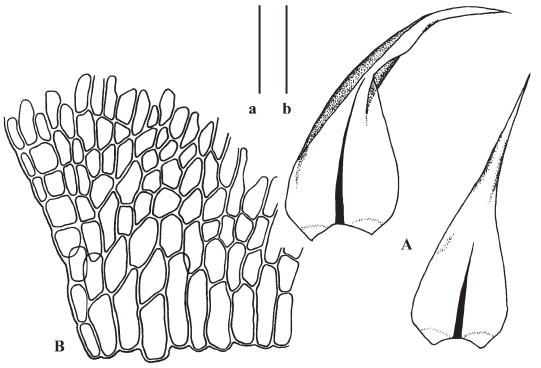


Fig. 47. *Drepanocladus polygamus*. A : Stem leaves. B : Alar cells. Scales : a : 1 mm, A. b : 50 µm, B.

having a furrowed acumen. In *D. aduncus* the leaf acumen is more or less flat in straight-leafed specimens, which are the ones likely to be confused with *D. polygamus*, and the leaves are not spreading in a *Campylium*-like fashion (cf. Fig. 15, p. 28).

The differences between *Drepanocladus polygamus*, *D. arcticus*, and *Campylium stellatum* are given after *D. arcticus*, whereas differences between *D. polygamus* and *Campyliadelphus chrysophyllus* are discussed after the latter.

In North America, *D. cardotii* (Thér.) Hedenäs is known from a single collection. This species has 1.0-1.4 mm long stem leaves that are narrowly decurrent 25-75 % of the distance to the leaf below.

7. Drepanocladus arcticus (R. S. Williams) Hedenäs (Fig. 48)

***Campylium arcticum* (R. S. Williams) Broth. ; *Campylium stellatum* var. *arcticum* (R. S. Williams) L. I. Savicz-Ljubitskaya ; *Chrysohypnum arcticum* R. S. Williams**

Autoicous. Stem leaves ovate, broadly ovate, or triangular-ovate, only weakly or sometimes not at all narrowed at insertion, but may seem to be so due to broadly inflexed basal leaf corners when the leaves are torn off, suddenly or gradually narrowed to acumen, acumen (1.0-) 1.2-2.3 times as long as basal leaf, leaf insertion usually deeply U-shaped, leaves from concave or strongly concave, erect and sub-clasping base with erect, patent, or spreading, channelled or strongly channelled acumen, when dry slightly twisted ; costa short and double, reaching at most ca. 25 % way up leaf, sometimes indistinct or rarely in an occasional leaf single and reaching up to 40-45 % way up leaf ; margin entire, or near apex sometimes slightly sinuose ; median lamina cells (31.5-) 44.0-117.5 (-136.5) µm long ; alar groups large, transversely triangular and extending 62-100 % of distance from leaf margin to leaf middle at insertion, well delimited from lamina cells further up but sometimes confluent with basal lamina cells, consisting of inflated, thin-walled to incrassate or strongly incrassate cells. - Plants medium-sized to large, irregularly and often sparsely branched, green, yellow-green, yellowish, or brownish. This species rarely grows very far from the sea, and is found in association with lagoons, salt water pools, shore meadows, fens, or in asso-

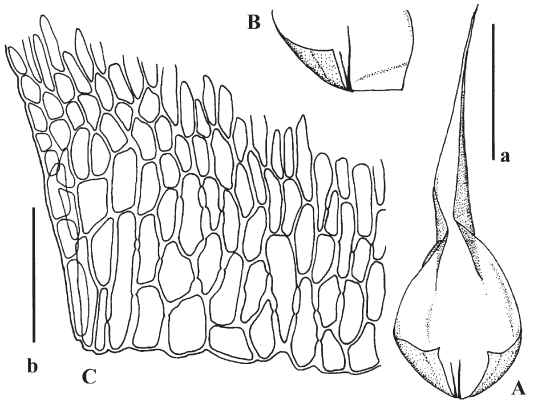


Fig. 48. *Drepanocladus arcticus*.
A : Stem leaf.
B : Leaf base.
C : Alar cells.
Scales : a : 1 mm,
A, B. b : 50 µm, C.

ciation with bird cliffs, in mineral- and more or less nutrient-rich habitats. *Drepanocladus arcticus* is known from scattered localities in the high arctic regions of Canada, Alaska, and Greenland in North America, and from scattered localities along the arctic coast of Eurasia. It is relatively frequent on Svalbard.

Drepanocladus arcticus has frequently been confused with *D. polygamus* and *Campylium stellatum*, both of which can also be found in arctic areas. The three can be separated by means of the characters in the following table.

Characters differentiating *Drepanocladus arcticus* from *D. polygamus* and *Campylium stellatum* (after Hedenäs 1997c).

Character	*D. arcticus*	*D. polygamus*	*C. stellatum*
Sexual condition	Autoicous	Autoicous	Dioicous
Leaf insertion	Strongly U-shaped	Slightly to moderately curved	Slightly to moderately curved
Leaf base	Strongly concave	Slightly concave	Slightly to moderately concave
Leaf acumen	Often markedly more spreading than basal leaf	Rarely markedly more spreading than basal leaf	Often markedly more spreading than basal leaf
Leaf length (mm)	(1.0-) 1.7-3.6	(1.3-) 1.7-3.5	1.7-2.8
Leaf width (mm)	0.6-1.5	0.6-1.0 (-1.1)	0.7-1.2
Leaf costa	Double and short	Double and short or single and long	Double and short
Alar groups	Transversely triangular	Transversely triangular	Ovate or rectangular, along basal leaf margin
Extending from leaf margin c.	62-100 % of distance from leaf margin to leaf middle at insertion	67-100 % of distance from leaf margin to leaf middle at insertion	28-33 % of distance from leaf margin to leaf middle at insertion

***Pseudocalliergon* (Limpr.) Loeske**

Dioicous. Plants branched ± in one plane, never with red colours. Stem leaves ± concave, ovate-lanceolate to broadly ovate, at apex gradually to rather suddenly narrowed to shortly or longly acuminate point, or broadly rounded or suddenly narrowed to apiculate point, falcate or straight and then mostly imbricate, not plicate ; margin plane, entire or distinctly denticulate ; costa long and single or short and double ; median lamina cells linear, smooth or, in some specimens of *P. angustifolium*, partly prorate ; alar cells in approximately transversely triangular group or sometimes, in *P. trifarium*, in single transverse basal row, inflated or slightly inflated, thin-walled or mostly incrassate to strongly so, indistinctly delimited from surrounding cells, supra-alar cells in one or several rows along leaf margin above alar cells, sometimes indistinct or apparently lacking, indistinctly delimited from surrounding

cells ; rhizoid initials never present in leaves. Paraphyllia absent. Axillary hairs well developed and abundant, with 1-2 (-3) upper, early yellowish or brownish cells, apical cell usually comparatively long. Rhizoids rare, smooth, red-brown, inserted on stem at or just below leaf insertion. Stem with central strand and a usually well developed cortex of incrassate cells. Inner perichaetial leaves straight and erect, plicate ; margin not or indistinctly bordered at shoulder, smooth or partly denticulate below, more strongly denti-culate or with single teeth at shoulder ; vaginula with paraphyses. Seta tall ; capsule cylindrical, curved, horizontal or inclined ; annulus separating. Exostome well developed, outside cross-striolate in lower part. Endostome well developed or with somewhat narrow processes. - Plants often with golden, metallic gloss when dry (rare in *P. trifarium*).

Key to the species of Pseudocalliergon

1. Stem leaves gradually or ± suddenly narrowed to shortly or longly acuminate apex, normally falcate or strongly falcate. . . . . **.2**
-. Stem leaves suddenly narrowed to apiculate point or leaf apex broadly rounded, ± straight. . . . . **.4**
2. Southern or mountainous species, rarely reaching the Arctic. Stem leaves long and longly and sometimes narrowly acuminate (Figs 49, 50) ; costa single and ending in leaf acumen, 3-5 (-6)-stratose and (31.5-) 38.5-90.0 (-100.0) µm wide near base.. . . . . **.3**
-. Arctic species. Stem leaves comparatively short and more shortly acuminate (Fig. 51) ; costa single and ending just above mid-leaf or in lower acumen (sometimes branched), or double, when single 2-3-stratose and 21.0-53.0 µm wide near base.. . . . . **3. *P. brevifolium***
3. Medium-sized, not turgid species distributed in mountains and parts of the northern boreal zone. Stem leaves narrow in basal half (Fig. 49A), (0.45-) 0.56-1.12 (-1.23) mm wide ; margin partly denticulate or finely denticulate. Upper lamina cells frequently dorsally prorate (Eurasia and North America). . . . . **.1. *P. angustifolium***
-. Usually robust, somewhat turgid, southern species, reaching north to approximately the middle boreal zone. Stem leaves broad in basal half (Fig. 50A), (0.68-) 0.90-1,68 mm wide ; margin entire or sometimes partly finely denticulate. Upper lamina cells always smooth (Europe and westernmost Asia).. . . . . **.2. *P. lycopodioides***
4. Stem leaves apiculate. . . . . **4. *P. turgescens***
-. Stem leaves with broadly rounded apex. . . . . **5. *P. trifarium***

1. Pseudocalliergon angustifolium Hedenäs (Figs 16B, p. 32 ; 49)

***Drepanocladus lycopodioides* var. *abbreviatus* W. Mönkemeyer**

Dioicous. Stem leaves erect-patent or spreading, falcate, ovate-lanceolate to rather broadly ovate and gradually narrowed to longly acuminate apex, concave, acumen channelled or almost tubular, (0.45-) 0.56-1.12 (-1.23) mm

wide ; margin denticulate or finely so, often partly entire ; costa single and ending in acumen, (31.5-) 38.5-70.0 (-73.5) µm wide near base, 3-5-stratose ; median lamina cells (28.0-) 31.5-87.5 (-110.0) µm long, scattered upper cells frequently abaxially and distally prorate ; alar cells rectangular, rarely quadrate, not or usually slightly inflated, thin-walled or incrassate and then ± porose and with yellow walls when mature, in approximately transversely triangular or indistinct group, indistinctly delimited from surrounding cells, supra-alar cells quadrate or shortly rectangular, in 1-7 rows of cells (up to 5 (-9) cells long) along leaf margin above alar cells, indistinctly delimited from surrounding cells. [Sporophyte unknown]. - Plants medium-sized, not turgid, slightly or irregularly pinnately branched, green, yellow-brown, or brownish yellow, when dry with golden metallic gloss in spots. Grows in fens or shallow, wet depressions on ± calcareous ground, in the mountains often close to late snow-bed vegetation, from the lowlands to the low-alpine region of the mountains. [pH 6.0-7.3 (n = 12) ; EC 22-88 mS/m (n = 12) ; Ca 2.3-12,2 mg/l (n = 8) ; IR 0.43-0.71 (n = 8)]. The species is known from scattered localities in northern Europe, northern Asia, and western North America, in boreal, mountainous, and arctic areas.

Pseudocalliergon angustifolium is frequently confused with *Warnstorfia fluitans* and *Drepanocladus sendtneri*. These three species have similar leaf shapes and have relatively small and / or indistinctly delimited alar groups. *Pseudocalliergon angustifolium* and *D. sendtneri* have similarly shaped and commonly incrassate alar cells, and are dioicous. Contrary to *W. fluitans*, these two species are usually found in calcareous habitats. *Warnstorfia fluitans* is separated from the other two by being autoicous, by the frequent occurrence of rhizoid initials or rhizoids on the stem and branch leaf laminae (especially near the leaf apices), and by its more strongly inflated alar cells that form groups which reach or almost reach the costa (the latter is not the case in the other two species). *Drepanocladus sendtneri* has often a stronger

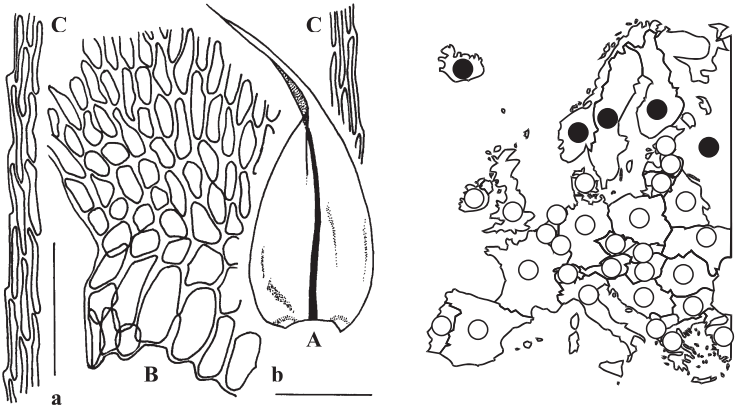


Fig. 49. *Pseudocalliergon angustifolium*. A : Stem leaf. B : Alar cells. C : Leaf margin in mid-leaf. Scales : a : 1 mm, A. b : 50 µm, B, C.

costa and more sharply delimited alar groups than *P. angustifolium*. *Pseudocalliergon angustifolium* differs from both the other species in the frequently occurring golden gloss in dry plants, in the early yellowish upper parts of the axillary hairs (frequently with a markedly elongate apical cell), and in the often distally prorate cells in the upper back of the stem and branch leaf lamina. The differences between *P. angustifolium, P. lycopodioides* and *P. brevifolium* are discussed under the latter two.

2. Pseudocalliergon lycopodioides (Brid.) Hedenäs (Figs 18B, p. 33 ; 50)

***Drepanocladus lycopodioides* (Brid.) Warnst. ; *Scorpidium lycopodioides* (Brid.) H. K. G. Paul**

Dioicous. Stem leaves erect-patent or spreading, falcate or strongly falcate, ovate to very broadly ovate and ± gradually narrowed to longly acuminate apex, concave, acumen channelled or almost tubular, (0.68-) 0.90-1.68 mm wide ; margin entire or partly finely denticulate ; costa single and ending in acumen, (37.0-) 42.0-90.0 (-100.0) µm wide near base, 3-5 (-6)-stratose ; median lamina cells (27.0-) 31.5-166.0 µm long, smooth ; alar cells rectangular or shortly rectangular, inflated, slightly or strongly incrassate, somewhat porose and with yellow walls when mature, in approximately transversely triangular group (rarely apparently undifferentiated), indistinctly delimited from surrounding cells, supra-alar cells shortly rectangular, quadrate, or transversely rectangular, in one or a few rows of cells (up to ca. 8 cells long) along leaf margin above alar cells, indistinctly delimited from surrounding cells. Capsule horizontal or almost so ; endostome well developed. - Plants robust and somewhat turgid, slightly or irregularly pinnately branched, green, brown-green, or yellow-brown, when dry with golden metallic gloss in parts. Grows mainly in small, strongly calcareous wetland habitats, in shallow depressions on flat limestone rocks, on sea and lake shores, and in man-made hollows and ditches. Nowadays the species seems to occur less

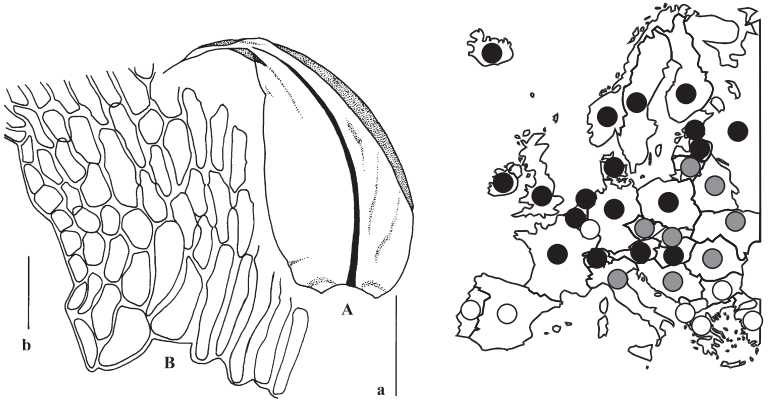


Fig. 50. *Pseudocalliergon lycopodioides*. A : Stem leaf. B : Alar cells. Scales : a : 1 mm, A. b : 50 µm, B.

often in habitats of the agricultural landscape than in earlier times. [pH 6.0-8.2 (n = 49) ; EC 48-960 mS/m (n = 32) ; Ca 25.8-218,0 mg/l (n = 17) ; IR 0.67-0.97 (n = 17)]. This species is widespread in more or less calcareous areas of Europe, barely reaching east of the Ural Mts.

Pseudocalliergon lycopodioides is usually recognised by its large size, its broad and concave, falcate stem leaves and by its indistinctly delimited alar groups. *Pseudocalliergon angustifolium* has narrower leaves ((0.45-) 0.56-1.12 (-1.23) vs. (0.68-) 0.90-1.68 mm wide), more distinctly denticulate leaf margins, and has frequently got dorsally prorate upper lamina cells. For the differences between *P. lycopodioides* and *P. brevifolium*, see the notes after the latter.

3. Pseudocalliergon brevifolium (Lindb.) Hedenäs (Fig. 51)

***Drepanocladus brevifolius* (Lindb.) Warnst. ; *Drepanocladus latifolius* (Lindb. & H. W. Arnell) Warnst. ; *Drepanocladus lycopodioides* var. *brevifolius* (Lindb.) W. Mönkemeyer ; *Scorpidium brevifolium* (Lindb.) H. K. G. Paul**

Dioicous. Stem leaves erect-patent to patent, falcate or strongly falcate, ovate to very broadly ovate and gradually or ± suddenly narrowed to acuminate or longly acuminate apex, concave, acumen channelled or almost tubular, (0.44-) 0.60-1.08 mm wide ; margin entire or sometimes partly very finely denticulate ; costa either single, extending 60-75 % way up leaf, 21.0-53.0 µm wide near base and 2-3-stratose, or costa double and extending 30-40 (-50) % way up leaf ; median lamina cells (17.5-) 22.0-79.0 (-87.0) µm long, smooth ; alar cells rectangular or longly rectangular, inflated, slightly or strongly incrassate, partly porose and with yellow walls when mature, in approximately transversely triangular group, indistinctly delimited from surrounding cells, supra-alar cells rectangular or quadrate (rarely transversely rectangular), in three to several rows of cells (up to ca. 10 cells long) along leaf margin above alar cells, indistinctly delimited from surrounding cells. Capsule almost horizontal ; endostome well developed. - Plants medium-sized, often somewhat turgid, usually slightly and irregularly branched, green, brown-green, or yel-

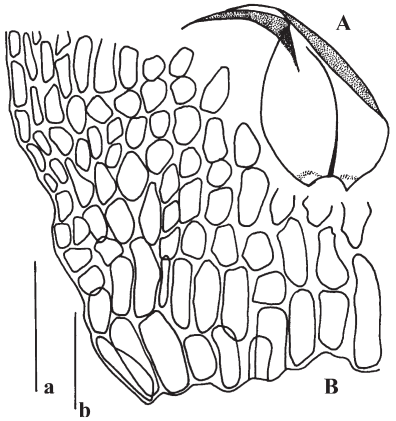


Fig. 51. *Pseudocalliergon brevifolium*. A : Stem leaf. B : Alar cells. Scales : a : 1 mm, A. b : 50 µm, B.

low-brown, often with golden gloss when dry. Found in calcium-rich wetland habitats in arctic areas, in rich fens, on moist excavated soil, and in percolation areas. This species is known from arctic parts of Europe, Asia, North America, and Greenland. Subfossil, interstadial remains of this species are known from northernmost Sweden (Hedenäs 1992d).

Pseudocalliergon brevifolium has the most shortly acuminate leaves of the three *Pseudocalliergon species* with acuminate leaves. The other northern species of the genus, *P. angustifolium*, is easily separated from *P. brevifolium* by its more longly and more narrowly acuminate leaves (see Figs. 49 and 51), its normally single and stronger costa, and by its more strongly denticulate leaf margins. *Pseudocalliergon brevifolium* is often distinctly turgid, this not being the case in *P. angustifolium*. *Pseudocalliergon lycopodioides* differs from *P. brevifolium*, i. a., in its wider, more longly acuminate stem leaves (see Figs. 50 and 51) and in its usually single and stronger costa.

4. Pseudocalliergon turgescens (T. Jensen) Loeske (Fig. 52A-C)

***Calliergon turgescens* (T. Jensen) Kindb. ; *Scorpidium turgescens* (T. Jensen) Loeske**

Dioicous. Stem leaves imbricate or sometimes ± spreading, straight, ovate or broadly ovate, upwards suddenly narrowed to short apiculus, strongly concave, (0.84-) 1.52-2.88 mm long, (0.67-) 0.80-1.46 mm wide ; margin entire or partly very finely denticulate ; costa mostly double and extending 20-40 % way up leaf, in scattered leaves single and extending 60-65 % way up leaf ; median lamina cells (18.0-) 21.0-107.0 (-117.0) µm long, smooth ; alar cells quadrate or rectangular, slightly inflated, incrassate or strongly so, slightly porose and with yellow walls when mature, in approximately transversely triangular group, indistinctly delimited from surrounding cells, supra-alar cells transversely rectangular, quadrate or shortly rectangular, in four to several rows of cells (up to ca. 15 cells long) along leaf margin above alar cells, indistinctly delimited from surrounding cells and sometimes impossible

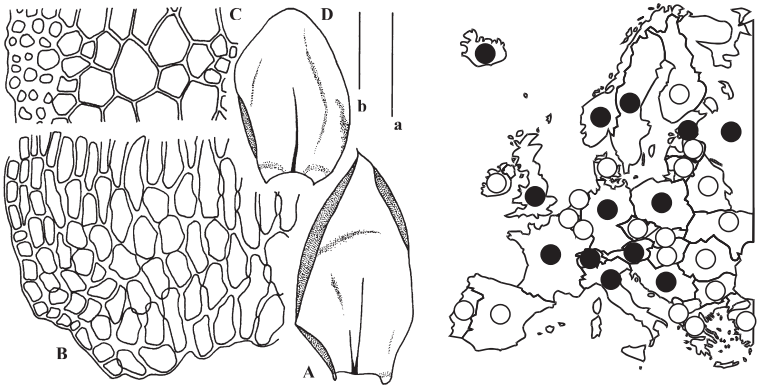


Fig. 52. *Pseudocalliergon turgescens* (A-C) and *P. trifarium* (D). A, D : Stem leaves. B : Alar cells. C : Partial transverse section of stem. Scales : a : 1 mm, A, D. b : 50 µm, B, C.

to delimit from both alar cells and lamina cells further up. Capsule horizontal to inclined ; endostome well developed, or sometimes with relatively narrow processes. - Plants robust, rarely medium-sized, turgid, slightly and irregularly branched, green, brown-green, or yellow-brown, often with golden gloss when dry. Grows in calcareous wetland habitats, often temporarily dry, such as small fens, small depressions (often on flat limestone rocks), along rills, or on rocks flushed with calcium-rich water, more rarely submerged in small lakes or pools, in the mountains and in treeless lowland areas. [pH 5.9-8.6 (n = 21) ; EC 187-885 mS/m (n = 26) ; Ca 15.4-137,0 mg/l (n = 10) ; IR 0.74-0.97 (n = 10)]. Distributed in northern, western, and central Europe, northern and central Asia, North and South America, and Greenland.

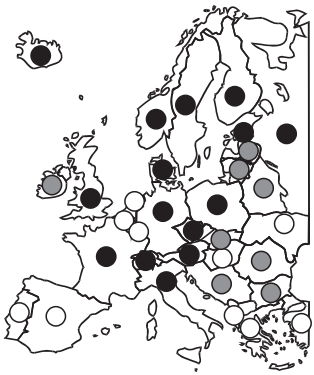
Pseudocalliergon turgescens is easily known by its rather robust and usually weakly branched shoots, with straight, imbricate, or sometimes slightly spreading, broad, apiculate, and strongly concave leaves. Except in shaded habitats, it has usually got yellow or yellow-brown colours. The species is often propagated vegetatively by means of easily detached shoot apices. *Pseudocalliergon turgescens* is often confused with *Scorpidium scorpioides*, especially with phenotypes of the latter having straight leaves. However, besides differences in colour the two are separated by the numerous small and incrassate alar cells that form indistinctly delimited alar groups, and the complete lack of a stem hyalodermis in *P. turgescens*, versus the few, inflated and thin-walled alar cells in sharply delimited groups, and the presence of at least a partial hyalodermis in *S. scorpioides*.

5. Pseudocalliergon trifarium (F. Weber & D. Mohr) Loeske (Fig. 52D)

***Calliergon trifarium* (F. Weber & D. Mohr) Kindb. ; *Scorpidium trifarium* (F. Weber & D. Mohr) H. K. G. Paul**

Dioicous. Stem leaves imbricate or, more rarely, ± spreading, straight, broadly or very broadly ovate with broadly rounded apex, concave or strongly so, 1.08-2.24 mm long, 0.80-1.68 mm wide ; margin entire or almost so ; costa single and extending 60-90 (-95) % way up leaf, 33.0-69.0 µm wide near base ; median lamina cells (30.5-) 33.0-104.0 (-107.0) µm long, smooth ; alar cells longly rectangular, inflated, incrassate or strongly incrassate, somewhat porose and with yellow walls when mature, in single transverse row or, more commonly, in approximately transversely triangular group, indistinctly delimited from surrounding cells, supra-alar cells quadrate to rectangular, in four to several rows of cells (up to ca. 10 cells long) along leaf margin above alar cells, indistinctly delimited from surrounding cells and sometimes impossible to delimit from both alar cells and lamina cells further up. Capsule horizontal to inclined ; endostome well developed, or often with relatively narrow processes. - Plants medium-sized, rarely almost robust, slightly turgid, unbranched or slightly and irregularly branched, green, brown-green, yellowish, or yellow-brown. This species is found in base-rich and usually deep fens, often as single shoots among other species (especially *Scorpidium scorpioides*). It occurs from the sea level to the alpine region. [pH 5.6-8.1 (n = 79) ; EC

27-555 mS/m (n = 63) (in lakes 4 mS/m ; n = 2) ; Ca 4.2-75,8 mg/l (n = 28) ; IR 0.47-0.97 (n = 28)]. Distributed in northern, western, and central Europe, northern Asia, North and South America, and Greenland.



Pseudocalliergon trifarium is easily known by its unbranched or almost unbranched shoots with straight and imbricate or more rarely ± spreading, concave and broadly or very broadly ovate leaves with broadly rounded apices. Sometimes the shoots in *P. trifarium* can be divided into segments which probably correspond to growth seasons. In the lower part of each segment, the leaves are smaller and more strongly imbricate than in the upper part of the same segment. The transition between the differently sized leaves is gradual within each segment, whereas the transition between segments is sudden.

Sanionia (Hedw.) Loeske

Autoicous. Plants branched ± in one plane, never with red colours. Stem leaves with rounded-triangular to broadly ovate base, lanceolate, circinate, falcate, or almost straight, ± smooth to strongly plicate ; margin very finely to strongly denticulate above, finely denticulate or entire below ; costa single, ending in acumen ; median lamina cells linear, some cells near leaf apex sometimes dorsally with prorate distal ends ; alar cells few or numerous, hyaline, inflated and thin-walled, in transversely triangular or ± isodiametric group, not or hardly decurrent ; rhizoid initials never present in leaves. Paraphyllia absent. Axillary hairs abundant, well developed, with 1-8 upper hyaline cells. Rhizoids reddish brown, smooth, slightly branched, inserted at or just below leaf costa insertion. Stem with central strand, a well developed cortex of incrassate cells, and a hyalodermis. Inner perichaetial leaves straight and erect, plicate, some lamina cells in acumen sometimes with prorate distal ends ; margin in upper part finely to strongly denticulate or dentate ; vaginula with paraphyses. Capsule cylindrical or shortly cylindrical, curved and horizontal to straight and erect ; annulus separating. Peristome well developed or reduced ; outer layer of exostome cross-striolate in lower part.

Key to the species of Sanionia

1. Stem leaves longly to very longly acuminate, above with finely denticulate to denticulate margins. Inflated alar cells in transversely triangular group ; transition to supra-alar cells sudden ; supra-alar cells quadrate to rectangular and mostly chlorophyllose. Small or large species, stem leaves

0.30-1.45 mm wide. Endostome well developed or reduced, perforated only along mid-line of processes. Inner perichaetial leaves gradually narrowed to longly acuminate apex, with margins finely denticulate to denticulate above. **2**

-. Stem leaves acuminate to longly acuminate, above with denticulate to strongly denticulate margins. Inflated alar cells in ± isodiametric group ; transition to supra-alar cells usually gradual ; supra-alar cells mostly rectangular, sometimes longly rectangular, and often ± echlorophyllose (These features of the alar and supra-alar cells often give the impression of a longitudinally ovate group of 'alar' cells along the basal leaf margin). Large species, stem leaves 0.48-1.70 mm wide. Endostome reduced, irregularly perforated in all parts. Inner perichaetial leaves ± suddenly narrowed to acute or shortly acuminate apex, with margins strongly denti-culate to dentate above. . . . . **4. *S. georgico-uncinata***

2. Supra-alar cells of stem leaves thin-walled or slightly incrassate, eporose, usually forming a group equal in size to or smaller than alar cell group. Stem leaf costa (study cross-section in lower leaf) mostly in the bottom of a shallow, in transverse section wide-angled fold (or not in a fold). Smaller species (stem leaves 0.30-1.05 mm wide), usually ± pinnately branched. Endostome in recently dehisced capsules pale, brownish to yellowish, or strongly yellow ; basal membrane 36-45 % or 25-33 % of total endostome height ; cilia well developed or rudimentary. **3**

-. Supra-alar cells of stem leaves slightly or strongly incrassate, porose, forming a group equal in size to or larger than alar cell group. Stem leaf costa mostly in the bottom of a deep, in transverse section narrow-angled fold. Larger species (stem leaves 0.62-1.45 mm wide), usually slightly and irregularly branched. Endostome in recently dehisced capsules strongly yellow ; basal membrane 20-30 % of total endostome height ; cilia rudimentary. . . . . **3. *S. orthothecioides***

3. Endostome in recently dehisced capsules pale, brownish to yellowish ; basal membrane 36-45 % of total endostome height ; cilia well developed. Capsules horizontal or occasionally erect to inclined. . . . **1. *S. uncinata***

-. Endostome in recently dehisced capsules strongly yellow ; basal membrane 25-33 % of total endostome height ; cilia rudimentary. Capsules erect to slightly inclined. . . . . **2. *S. symmetrica***

1. Sanionia uncinata (Hedw.) Loeske (Figs 11, p. 23 ; 53)

Drepanocladus contiguus **(Hüb.) Loeske ;** ***Drepanocladus subjulaceus*** **(Schimp.) Roiv. ;** ***Drepanocladus uncinatus*** **(Hedw.) Warnst. ;** ***Hypnum moseri*** **Kindb. ;** ***Hypnum uncinatum*** **var.** ***subestriatum*** **Kindb.**

Autoicous. Stem leaves circinate or falcate, rarely ± straight, from rounded-triangular or ovate base lanceolate, apex longly or very longly acuminate, 0.35-1.05 mm wide, plicate or strongly so, rarely smooth ; margin plane or rarely partly recurved above, denticulate or finely denticulate above ; costa mostly in the bottom of a shallow, wide-angled fold (or not in a fold) ; median

lamina cells 28.0-110.0 µm long, cells near leaf apex occasionally with distal ends prorate on back ; alar cells in transversely triangular group, transition to supra-alar cells sudden, supra-alar cells quadrate to rectangular and mostly chlorophyllose, thin-walled or slightly incrassate, eporose, usually forming a group equal in size to or smaller than alar cell group. Inner perichaetial leaves gradually narrowed to longly acuminate apex, with margins finely denticulate to denticulate above. Capsule horizontal, rarely erect to inclined ; exothecial cells just below capsule mouth in 1-3 rows of ± isodia-metric cells ; exostome well developed, marginal border of tooth widened at zone of transition in pattern of tooth outside ; endostome well developed, in recently dehisced capsules pale, brownish to yellowish, basal membrane constituting 36-45 % of total endostome height, processes perforated only along mid-line, cilia well developed. - Plants slender to medium-sized, usually ± pinnately branched, when viewed from back of shoot often typically "combed", with leaves pointing stiffly, obliquely forwards-outwards (Fig. 11, p. 23), green or yellowish green. This species is found from the sea level to high up in the alpine region, both in forests and in more open habitats, on rocks, logs, stumps, trees, soil, or sometimes (especially in northern areas) in mires. [pH 4.3-7.8 (n = 14) ; EC 83-169 mS/m (n = 3)]. It is widely distributed in temperate to sub-polar areas all over the world, and occurs also at higher altitudes in many subtropical and tropical areas.

Sanionia uncinata is usually easily separated from the other species of the genus by its well developed peristome, its usually curved and horizontal capsules and from all except *S. symmetrica* by the structure of the alar and supra-alar cells. It is usually somewhat smaller and more regularly pinnately branched than *S. orthothecioides* and *S. georgico-uncinata*. From *S. georgico-uncinata* it is also distinguished by its much more longly acuminate inner perichaetial leaves.

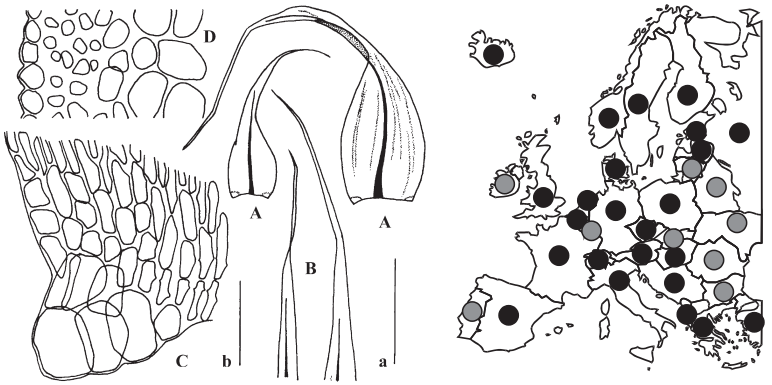


Fig. 53. *Sanionia uncinata*. A : Stem leaves from different plants. B : Apices of inner perichaetial leaves. C : Alar and supra-alar cells. D : Partial transverse section of stem. Scales : a : 1 mm, A, B. b : 50 µm, C, D.

2. Sanionia symmetrica (Renauld & Cardot) J. A. Wheldon

***Hypnum uncinatum* subsp. *symmetricum* Renauld & Cardot**

Autoicous. Stem leaves circinate or falcate, from rounded-triangular base lanceolate, apex longly or very longly acuminate, 0.30-1.05 mm wide, plicate or strongly so ; margin plane or often narrowly recurved approximately in mid-leaf, denticulate or finely denticulate above ; costa mostly in the bottom of a shallow, wide-angled fold (or not in a fold) ; median lamina cells 33.5-115.5 µm long, cells near leaf apex occasionally with distal ends prorate on back ; alar cells in transversely triangular group, transition to supra-alar cells sudden, supra-alar cells quadrate to rectangular and mostly chlorophyllose, thin-walled or slightly incrassate, eporose, usually forming a group equal in size to or smaller than alar cell group. Inner perichaetial leaves gradually narrowed to longly acuminate apex, with margins finely denticulate to denticulate above. Capsule erect or slightly inclined ; exothecial cells just below capsule mouth in 2-4 rows of ± isodiametric cells ; exostome specialised, teeth long and narrow, with border not widened at zone of transition in pattern of tooth outside ; endostome specialised, in recently dehisced capsules strongly yellow, basal membrane constituting 25-33 % of total endostome height, processes perforated only along mid-line, cilia rudimentary. - Plants medium-sized, usually ± pinnately branched, green or yellow-green, in moist and wet habitats in forests (usually deciduous), on shores of lakes and rivers, and in swamps, on logs, stumps, tree and shrub bases, or on the ground. This is mainly a lowland species. It is a western North American endemic that is only known from British Columbia, Idaho, Oregon, and Washington.

The gametophyte of *S. symmetrica* is impossible to separate with certainty from that of *S. uncinata*. However, the specialised peristome of *S. symmetrica* is very different from that of *S. uncinata*. Occasional specimens of *S. uncinata* may have more or less straight and erect capsules, but in these the capsules are somewhat wider than in *S. symmetrica* and the peristome is well developed. *Sanionia symmetrica* differs from *S. orthothecioides* and *S. georgico-uncinata* in its smaller size, in being more regularly pinnately branched, and in the structure of the alar and supra-alar cells. *Sanionia georgico-uncinata* has in addition got acute or much more shortly acuminate inner perichaetial leaves than *S. symmetrica*.

3. Sanionia orthothecioides (Lindb.) Loeske (Fig. 54)

***Drepanocladus orthothecioides* (Lindb.) G. Roth ; *Drepanocladus uncinatus* var. *majus* (C. E. O. Jensen) Amann**

Autoicous. Stem leaves falcate or strongly falcate, more rarely straight or almost so, from ovate-triangular to broadly ovate base lanceolate, apex longly or very longly acuminate, 0.62-1.45 mm wide, slightly or usually strongly plicate ; margin mostly partly or entirely recurved (most distinct in ventral leaves), sometimes incurved in lower part, finely denticulate or almost entire above ; costa mostly in the bottom of a deep narrow-angled fold ; median lamina cells 28.0-90.0 µm long, cells near leaf apex smooth ; alar cells in

transversely triangular group, transition to supra-alar cells sudden, supra-alar cells quadrate or shortly rectangular, slightly or strongly incrassate, porose, forming a group as large as to much larger than alar cell group. Inner perichaetial leaves gradually narrowed to longly acuminate apex, with margins finely denticulate to denticulate above. Capsule erect or inclined ; exothecial cells just below capsule mouth in 3-7 rows of isodiametric or transversely rectangular cells ; exostome specialised, teeth long and narrow, with border not widened at zone of transition in pattern of tooth outside ; endostome specialised, in recently dehisced capsules strongly yellow, basal membrane constituting 20-30 % of total endostome height, processes perforated only along mid-line, cilia rudimentary. - Plants medium-sized to robust, mostly unbranched or sparsely and irregularly branched, rarely ± pinnately branched, green or yellow-green. It grows mainly in coastal areas and is rarely found in the inland, usually in open habitats, in rock crevices or meadows, often in sea shore meadows. The species is distributed along the coasts of the northern tempe-rate to arctic zones of Eurasia and northern North America.

Sanionia symmetrica is easily separated from *S. uncinata* and *S. georgico-uncinata* because of its reduced and strongly yellow endostome. From these two species as well as from *S. symmetrica* it differs by its numerous (3-7 as compared with 1-4) rows of isodiametric or transversely rectangular cells below the capsule mouth, and by the structure of its alar and supra-alar cells. The leaf margin is usually recurved in *S. orthothecioides*, more rarely so in the other three *Sanionia* species. The costa is usually situated in the bottom of a deep fold in the lower part of the leaves in *S. orthothecioides*, which is rare in the other three species.

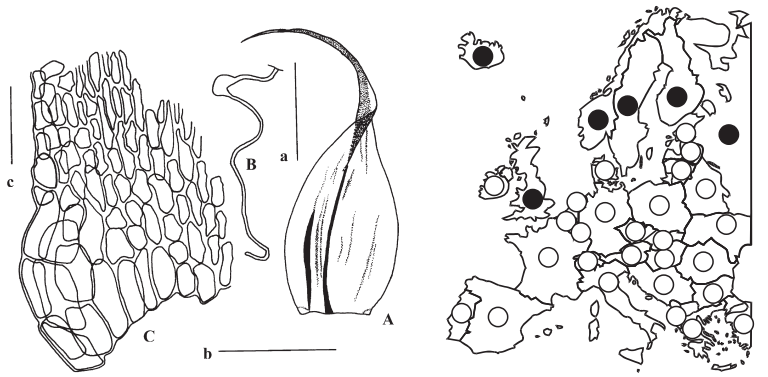
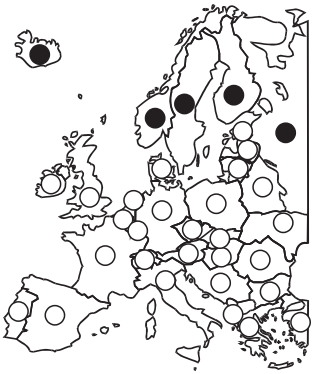


Fig. 54. *Sanionia orthothecioides*. A : Stem leaf. B : Transverse section in lower 1/4 of stem leaf. C : Alar and supra-alar cells. Scales : a : 1 mm, A. b : 300 µm, B. c : 50 µm, C.

4. Sanionia georgico-uncinata (Müll. Hal.) Ochyra & Hedenäs (Fig. 55)

***Sanionia nivalis* Hedenäs**

Autoicous. Stem leaves falcate or strongly falcate, rarely straight or almost so, from ovate-triangular to broadly ovate base lanceolate, apex acuminate to longly so, 0.48-1.70 mm wide, smooth or plicate, rarely strongly plicate ; margin plane or sometimes partly recurved in upper part, usually strongly denticulate above ; costa mostly in the bottom of a shallow, wide-angled fold (or not in a fold) ; median lamina cells (17.5-) 24.0-105.0 (-122.0) µm long, cells near leaf apex occasionally with distal ends prorate on back ; alar cells in ± isodiametric group, transition to supra-alar cells gradual (alar and supra-alar cells together often forming a ± homogeneous ovate basal marginal group), supra-alar cells rectangular or longly rectangular, thin-walled and eporose, mostly ± echlorophyllose, forming a group as large as to much larger than alar cell group. Inner perichaetial leaves ± suddenly narrowed to acute or shortly acuminate apex, with margins strongly denticulate to dentate above. Capsule ± erect ; exothecial cells just below capsule mouth in (1-) 2-3 rows of ± isodiametric cells ; exostome specialised, teeth narrow in upper part, with border not widened at zone of transition in pattern of tooth outside ; endostome specialised, in recently dehisced capsules hyaline or slightly yellowish, basal membrane constituting 17-33 % of total endostome height, processes and basal membrane with one or both cell wall layers strongly perforated all over, cilia rudimentary or absent. - Plants medium-sized to robust, mostly unbranched or sparsely and irregularly branched, rarely ± pinnately branched, green or yellow-green. Occurs in the lowlands in sub-polar areas, in mountains of the northern temperate zone mainly in the middle and high-alpine regions (rarely at lower altitudes), in large



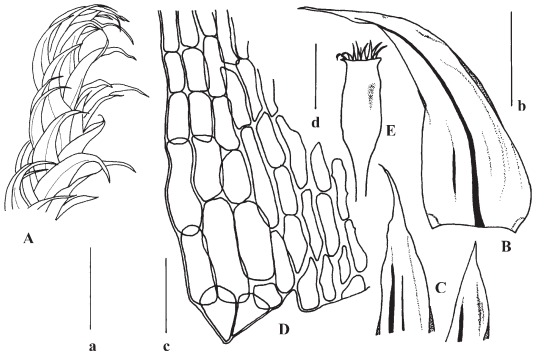


Fig. 55. *Sanionia georgico-uncinata*. A : Shoot apex. B : Stem leaf. C : Apices of inner perichaetial leaves. D : Alar cells (with supra-alar cells above along margin). E : Capsule (dry). Scales : a : 2 mm, A. b : 1 mm, B, C. c : 50 µm, D. d : 1 mm, E.

late snow-beds and on the shores of glacier-fed brooks. Known from northern North America, northern Europe, and Antarctic to sub-Antarctic areas.

Sanionia georgico-uncinata is easily separated from the other three *Sanionia* species by its reduced and irregularly perforate endostome, its acute to shortly acuminate inner perichaetial leaves with strongly denticulate or dentate upper margins (the other three species have longly acuminate inner perichaetial leaves with finely denticulate or denticulate upper margins), and by the structure of the alar and supra-alar cells. In addition, the stem leaves of *S. georgico-uncinata* are more shortly acuminate and have more strongly denticulate margins that in the three other species.

Campyliadelphus (Kindb.) R. S. Chopra

Dioicous. Plants branched ± in one plane, never with red colours. Stem leaves either rounded-triangular to broadly ovate, or triangular to lanceolate, gradually or suddenly narrowed to ± long acumen, apex acuminate, from almost erect to spreading base straight or falcate, sometimes with recurved acumen, acumen channelled, not plicate ; margin entire or denticulate ; costa mostly single and long, ending in mid-leaf to excurrent, occasionally shorter and double ; median lamina cells rectangular to linear, smooth ; alar cells relatively small, mostly numerous, forming a distinct but sometimes not sharply delimited, quadrate, ovate, broadly ovate, or transversely triangular group, reaching from leaf margin 25-65 % of distance to leaf middle at insertion, narrowly decurrent ; rhizoid initials never present in leaves. Paraphyllia absent. Axillary hairs frequent, with 1-4 upper hyaline cells. Rhizoids red-brown, smooth or warty-papillose, inserted at or just below leaf costa insertion. Stem with central strand and a well developed cortex of small and incrassate cells. Inner perichaetial leaves straight and erect, plicate, lamina cells smooth ; margin entire throughout, or in acumen and at shoulder denticulate or (at shoulder) with single teeth ; vaginula with paraphyses. Capsule cylindrical or shortly so, curved and horizontal ; annulus separating. Peristome well developed ; outer layer of exostome cross-striolate in lower part.

Species of *Campyliadelphus* are sometimes confused with species of *Campylium*, *Campylophyllum*, and *Ctenidium*. The differences between these four genera are discussed under *Campylium*.

Key to the species of Campyliadelphus

1. Stem leaves rounded-triangular, ovate, or broadly ovate, relatively short and broad, 0.9-1.5 (-1.8) x 0.4-0.7 mm, acumen mostly recurved in at least parts of shoots ; margin entire or partly sinuose to very weakly and ± obtusely denticulate ; costa ending (40-) 50-80 % way up leaf, occasionally shorter and double, 23.0-46.0 (-52.5) µm wide near base. Spores 8.5-14.5 µm. . . . . **1. *C. chrysophyllus***

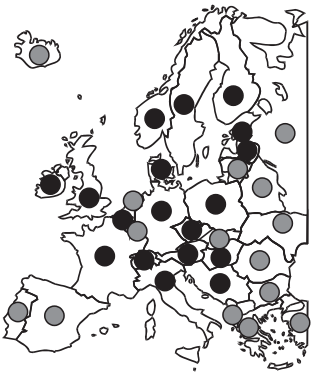
-. Stem leaves triangular, narrowly triangular, triangular-ovate, or lanceo-

late, relatively long and narrow, 1.0-2.4 x 0.2-0.6 mm, leaves sometimes curved, but acumen not recurved ; margin partly or entirely denticulate to finely denticulate, most distinct above alar groups and near leaf apex ; costa ending 50-100 % way up leaf, sometimes excurrent, 29.0-60.0 µm wide near base. Spores 15.0-20.5 µm. . . . . **2. *C. elodes***

1. Campyliadelphus chrysophyllus (Brid.) Kanda (Fig. 56A, B)

***Campylium chrysophyllum* (Brid.) Lange ; *Kurohimehypnum ctenidioides* Sak.**

Dioicous. Stem leaves almost erect to spreading, often with acumen curved more strongly outwards than basal leaf, straight, falcate, or recurved, 0.9-1.5 (-1.8) mm long, 0.4-0.7 mm wide, rounded-triangular, ovate, or broadly ovate, gradually or ± suddenly narrowed to acumen, apex acuminate, concave, in acumen furrowed, acumen when distinct constituting 42-65 % of leaf length ; margin partly entire, partly sinuose or weakly and often obtusely denticulate ; costa single, long, ending (40-) 50-80 % way up leaf, occasionally shorter and double, single costae 23.0-46.0 (-52.5) µm wide near base ; median lamina cells (17.0-) 19.0-73.5 µm long ; alar cells differentiated, basal alar cells shortly rectangular to shortly linear, slightly inflated, widest cells 10.5-17.5 (-21.0) µm wide, incrassate or slightly so, upper alar cells transversely rectangular, quadrate, or rectangular, smaller than lower cells, group distinctly or indistinctly delimited, quadrate, ovate, or broadly ovate, extending from leaf margin 1/3-2/3 of distance to leaf middle at insertion, narrowly decurrent, half way down to next leaf or shorter. Spores 8.5-14.5 µm. - Plants small, irregularly to pinnately branched, green, yellowish, or brownish. Found from the sea level to high up in the mountains, but rarely above the tree limit, on rocks and soil, frequently temporarily wet, in calcareous or



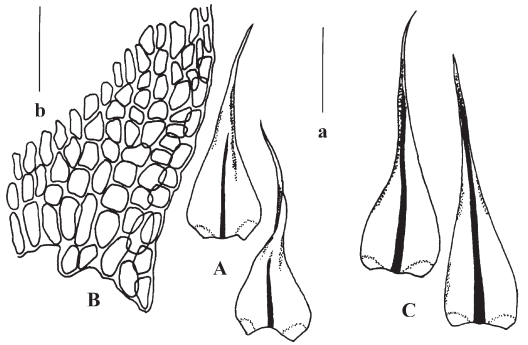


Fig. 56. *Campyliadelphus chrysophyllus* (A, B) and *C. elodes* (C). A, C : Stem leaves. B : Alar cells. Scales : a : 1 mm, A, C. b : 50 µm, B.

otherwise mineral-rich habitats. [pH 5.0-7.8 (n = 60) ; EC 265 mS/m (n = 1) ; Ca 51,7 mg/l (n = 1) ; IR 0.94 (n = 1)]. Widely distributed in Eurasia, northern Africa, North, Central, and northern South America.

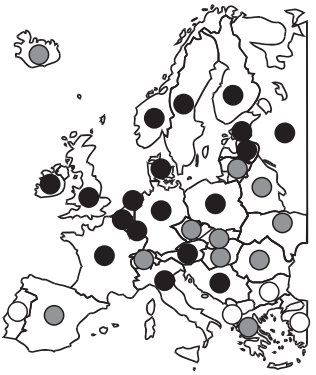
Campyliadelphus chrysophyllus may be confused with *C. elodes*, but has somewhat broader and shorter leaves, a somewhat weaker costa, and smaller spores. In *C. elodes* the leaf margins are in addition often more clearly denticulate than in *C. chrysophyllus*. *Drepanocladus polygamus* differs from *C. chrysophyllus* by being autoicous rather than dioicous, by its larger size (stem leaves (1.3-) 1.7-3.5 vs. 0.9-1.5 (-1.8) mm long), and by having wider alar cells (widest cells 17.0-31.5 vs. 10.5-17.5 (-21.0) µm wide). The differences between *C. chrysophyllus*, *Ctenidium molluscum*, and *Campylium stellatum* are discussed under the latter.

In E Asia *C. chrysophyllus* could be confused with *C. glaucocarpoides* (Salm.) Hedenäs (*Campylium glaucocarpoides* (Salm.) Broth.). The latter species is slightly larger than *C. chrysophyllus*, and has erect-spreading to almost spreading, rounded-cordate stem leaves with a relatively short acumen (25-35 % of leaf length, 42-65 % in *C. chrysophyllus*), and larger, broadly ovate to almost quadrate alar groups that extend from the leaf margin ca. 3/4 of the distance to the leaf middle at the leaf insertion (1/3-2/3 in *C. chrysophyllus*). The leaf costa is 44.0-52.5 µm wide near its base (23.0-46.0 (-52.5) µm in *C. chrysophyllus*). *Campyliadelphus glaucocarpoides* may represent an extreme phenotype of *C. chrysophyllus*, but further studies of more material are needed to evaluate this.

2. Campyliadelphus elodes (Lindb.) Kanda (Fig. 56C)

***Campylium elodes* (Lindb.) Kindb.**

Dioicous. Stem leaves from erect to spreading base almost straight to falcate-secund, 1.0-2.4 mm long, 0.2-0,6 mm wide, triangular, narrowly triangular, triangular-ovate, or lanceolate, gradually or suddenly narrowed to acumen, apex narrowly acuminate, slightly concave, acumen when distinct constituting ca. 50 % of leaf length ; margin entire or partly finely denticulate, often distinctly denticulate for a short distance above alar groups ; costa single, long, ending 50-100 % way up leaf or sometimes excurrent, 29.0-60.0 µm wide near base ; median lamina cells 17.5-82.0 µm long ; alar cells shortly transversely rectangular, quadrate, or rectangular, occasionally longly rectangular at insertion, widest cells 13.0-19.0 µm wide, incrassate or slightly so, forming a distinct, but not sharply delimited, square or transversely triangular group that reaches from leaf margin 1/2-2/3 (-4/5) of distance to leaf middle at insertion, decurrent 1/3-2/3 of distance to leaf



below. Spores 15.0-20.5 µm. - Plants small to almost medium-sized, irregularly to pinnately branched, green, yellow-green, or often brownish. Grows mainly in the lowlands, in more or less calcareous habitats, in swampy forest, along brook and lake shores, and in shallow fens, often in habitats that dry out for longer or shorter periods. [pH 6.1-8.1 (n = 46) ; EC 220-622 mS/m (n = 28) ; Ca 40.6-72,2 mg/l (n = 10) ; IR 0.74-0.95 (n = 10)]. This species is known from Europe and has in addition been reported from Himalaya.

Campyliadelphus elodes could be confused with *C. chrysophyllus*, and the differences between these species are mentioned after the latter.

Campylium (Sull.) Mitt.

Autoicous or dioicous. Plants branched ± in one plane, never with red colours. Stem leaves from cordate, cordate-ovate, ovate, or rounded-triangular base gradually or suddenly narrowed to short or long acumen, apex acuminate or long-acuminate, from subsheathing erect or erect-spreading basal portion with straight and erect or more or less spreading upper part, occasionally homomallous to distinctly falcate-secund, in acumen distinctly channelled or occasionally almost tubular, not plicate ; margin entire or slightly sinuose ; costa short and weak, double or single, extending < 40 (-50) % way up leaf ; median lamina cells linear, rarely shortly so, smooth ; lower alar cells partly inflated and large, rectangular or shortly so (rarely quadrate), hyaline (when old sometimes brown), upper alar cells slightly inflated, rectangular, quadrate, or sometimes transversely rectangular, upper cells constituting 25-50 % of alar group, alar cells forming a distinct, (quadrate), broadly ovate, ovate, or rectangular group along basal leaf margin, reaching from leaf margin 15-60 % of distance to leaf middle at insertion, not or hardly decurrent ; rhizoid initials never present in leaves. Paraphyllia absent or sometimes present. Axillary hairs frequent, with 1-4 hyaline upper cells. Rhizoids red-brown, smooth or lowly warty-papillose, inserted at or just below leaf costa insertion. Stem with central strand and a well developed cortex of small and incrassate cells. Inner perichaetial leaves straight and erect, acumen sometimes slightly flexuose, plicate or slightly so, lamina cells smooth ; margin entire or at shoulder weakly denticulate, occasionally with scattered, irregular teeth ; vaginula with paraphyses. Capsule cylindrical, curved and horizontal or rarely inclined ; annulus separating. Peristome well developed ; outer layer of exostome cross-striolate in lower part.

Species of *Campylium* are sometimes confused with *Amblystegium radicale*, *Ctenidium molluscum*, *Drepanocladus arcticus*, *D. polygamus*, or species of *Campyliadelphus* and *Campylophyllum*. *Ctenidium molluscum* and the *Drepanocladus* species are discussed under *Campylium stellatum*, whereas the other taxa can be separated by the following auxiliary key.

1. Plants small (stem leaves 0.4-1.0 mm long). Stem leaf costa short and double, often ending in a spine on back ; scattered upper lamina cells usually distally prorate on dorsal side, at least in some branch leaves. Seta short, 8-22 mm long. . . . . ***Campylophyllum*** (e. g., *C. calcareum* (Crundw. & Nyh.) Hedenäs (not in N America) and *C. halleri* (Hedw.) Fleisch. mainly on calcareous rocks ; *C. hispidulum* (Brid.) Hedenäs (not in Europe) and *C. sommerfeltii* (Myr.) Hedenäs on soil, tree bases, and rotten wood, sometimes in swampy forest).

-. Plants usually medium-sized or large (stem leaves 0.9-3.6 mm long). Stem leaf costa short or long, double or single, not ending in a spine ; upper lamina cells smooth. Seta often tall, 12-45 mm long. . . . . **.2**

2. Stem leaves not decurrent ; costa short and double. . . . . ***Campylium***

-. Stem leaves decurrent ; costa mostly long and single. . . . . **.3**

3. Largest cells in lower half of alar group mostly 18.0-25.0 µm wide. Paraphyllia often present, narrowly lanceolate to ovate-lanceolate. Endostome cilia nodose.. . . . . ***.Amblystegium radicale***

(*Amblystegium radicale* (P. Beauv.) Schimp. (*Amblystegium saxatile* Schimp. ; *Campylium radicale* (P. Beauv.) Grout) grows in ± mineral- and ± nutrient-rich wetland habitats, both without tree cover and in swampy forests).

-. Largest cells in lower half of alar group mostly 10.5-19.0 µm. Paraphyllia absent. Endostome cilia nodose or partly appendiculate. . ***Campyliadelphus***

Key to the species of *Campylium*

1. Autoicous. Stem leaves from sub-sheathing base erect or spreading ; leaf base broadly cordate-ovate, cordate-ovate, ovate or narrowly ovate ; acumen when differentiated constituting at most 33 % of leaf length.. . . . **.2**

-. Dioicous. Stem leaves spreading or ± squarrose from sub-sheathing, erect to erect-spreading base ; leaf base cordate or rounded-triangular ; acumen when differentiated constituting 33-77 % of leaf length.. . . . . **.3**

2. Stem leaves slightly concave, 1.8-2.4 mm long, from ± broadly cordate-ovate base gradually narrowed to longly acuminate apex, acumen not differentiated from rest of leaf. . . . . **1. *C. laxifolium***

-. Stem leaves concave or strongly concave, 2.1-4.6 mm long, from ovate or narrowly ovate base ± suddenly or more gradually narrowed to straight or slightly flexuose acumen, acumen frequently clearly differentiated and then constituting 18-33 % of leaf length. . . . . **.2. *C. longicuspis***

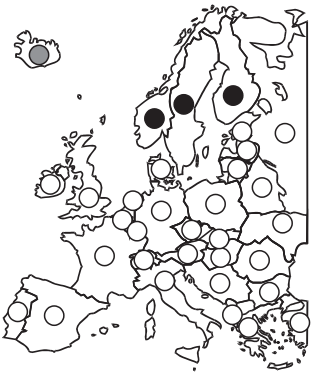
3. Plants usually erect, irregularly or sometimes irregularly pinnately branched. Stem leaves 1.7-2.8 mm long, 0.7-1.2 mm wide, acumen when differentiated constituting 40-65 % (in Arctic plants rarely 33-40 %) of leaf length. Paraphyllia always lacking. . . . . **.3. *C. stellatum***

-. Plants usually creeping, irregularly pinnately branched. Stem leaves 1.0-2.3 mm long, 0.4-1.0 mm wide, acumen when differentiated constituting 55-77 % of leaf length. Paraphyllia sometimes present. **4. *C. protensum***

1. Campylium laxifolium Engelmark & Hedenäs (Fig. 57)

Autoicous. Stem leaves from slightly clasping base erect or slightly spreading, straight, 1.8-2.4 mm long, 0.6-0.9 mm wide, from ± broadly cordate-ovate base gradually narrowed to long-acuminate apex, slightly concave, acumen not clearly differentiated from rest of leaf ; margin entire or nearly so ; costa double, extending 25-50 % way up leaf ; median lamina cells 35.0-91.0 (-105.0) µm long ; alar cells differentiated, quadrate or shortly rectangular in upper part of group, shortly rectangular or rectangular and somewhat inflated in lower portion, widest cells 20.0-27.5 µm wide, forming a quadrate, rectangular, or ovate group along basal leaf margin, not or hardly decurrent. Rhizoids unbranched to strongly branched, smooth. Paraphyllia absent. Spores (12.5-) 14.0-21.0 µm. - Plants medium-sized, erect or creeping, ± irregularly branched, golden brown or golden yellow. Grows in the lowlands and in the mountains, in intermediately mineral-rich and slightly nutrient-enriched, often spring-influenced fens. Known from northern Europe, Greenland, and Alaska, but because it was described only in 1992 its geographical distribution is still incompletely known.

This species differs from *C. stellatum* and *C. protensum* in being autoicous and in having erect or less distinctly spreading leaves than the latter two. Its leaves are also more ovate than in the other two species, and are gradually narrowed towards the leaf apex, never with a distinctly differentiated acumen. From *C. longicuspis* it differs in having more weakly concave leaves, a slightly smaller size (stem leaves 1.8-2.4 vs. 2.1-4.6 mm long) and more broadly ovate leaves without a differentiated acumen. In *C. longicuspis* a short acumen, 18-33 % of leaf length, is frequently differentiated. *Drepanocladus polygamus*, which is also autoicous, differs in having more triangular leaves and transversely triangular alar groups.



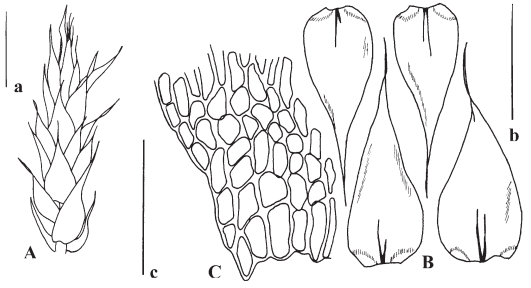


Fig. 57. *Campylium laxifolium*. A : Shoot apex. B : Stem leaves. C : Alar cells. Scales : a : 2 mm, A. b : 1 mm, B. c : 100 µm, C.

2. Campylium longicuspis (Lindb. & H. W. Arnell) Hedenäs (Fig. 58)

***Amblystegium longicuspis* Lindb. & H. W. Arnell ; *Drepanocladus longicuspis* (Lindb. & H. W. Arnell) Broth.**

Autoicous. Stem leaves from sub-sheathing base ± erect to patent, straight or slightly homomallous, 2.1-4.6 mm long, 0.6-1.0 mm wide, ovate or narrowly ovate, ± suddenly or more gradually narrowed to long, straight or slightly flexuose acumen, apex narrowly acuminate, concave or strongly concave, acumen channelled, acumen when distinct constituting 18-33 % of leaf length ; margin entire or very indistinctly denticulate in upper part ; costa double or occasionally in single leaves single or branched, weak, extending 35-40 (-50) % way up leaf ; median lamina cells 38.5-94.5 (-102.0) µm long ; alar cells differentiated, quadrate or shortly rectangular in upper group, rectangular and inflated in lower portion, widest cells 26.5-29.5 µm wide, forming a rectangular or broadly ovate group along basal leaf margin, not or hardly decurrent. Rhizoids not or slightly branched, smooth. Paraphyllia absent. Spores 10.5-14.0 or 19.0-24.0 µm, finely papillose (smaller ones ca. 50 times as abundant as large ones, and probably not functional). - Plants medium-sized, erect or creeping, almost unbranched or irregularly branched, glossy to golden brown. From the few known finds this species appears to grow mainly in relatively mineral-rich fens. The known distribution includes arctic Europe, arctic and central Asia, and Greenland (leg. F. J. A. Daniels ; C. Schmidt, unpubl.).

This species is easily separated from *C. stellatum* by ovate or narrowly ovate, rather than cordate or rounded-triangular stem leaves with a shorter leaf acumen (18-33 vs. 40-65 or in the Arctic rarely 33-40 % of leaf length) and by its autoicous rather than dioicous sexual condition. The differences between *C. longicuspis* and *C. laxifolium* are discussed under the latter.

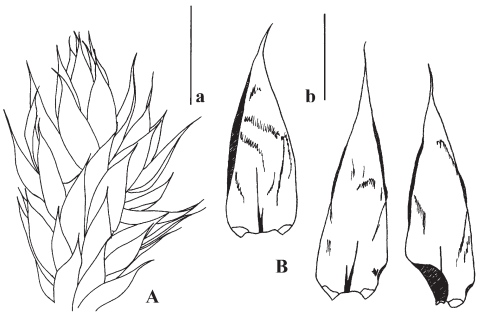


Fig. 58. *Campylium longicuspis*. A : Shoot apex. B : Stem leaves. Scales : a : 2 mm, A. b : 1 mm, B.

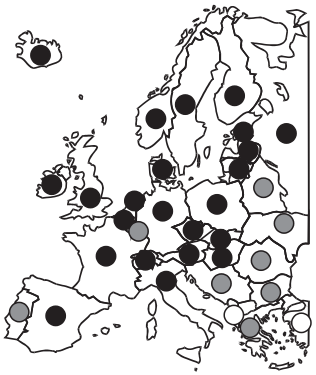
3. Campylium stellatum (Hedw.) C. E. O. Jensen (Fig. 59)

***Campyliadelphus stellatus* (Hedw.) Kanda**

Dioicous ; occasionally with dwarf males. Stem leaves from sub-sheathing, erect or erect-patent basal portion with (erect or) more or less patent to spreading and ± squarrose upper part, occasionally homomallous to distinctly falcate-secund, 1.7-2.8 mm long, 0.7-1.2 mm wide, cordate or rounded-trian-

gular, gradually or suddenly narrowed to long acumen, apex longly acuminate, concave, acumen distinctly channelled or occasionally almost tubular, acumen when distinct constituting 33-65 % of leaf length ; margin entire or slightly sinuose ; costa short and weak, double or single, extending 20-35 % way up leaf ; median lamina cells (29.5-) 33.5-94.5 µm long ; alar cells differentiated, upper cells rectangular, quadrate, or sometimes transversely rectangular, slightly inflated, lower alar cells rectangular or shortly so (quadrate), inflated and hyaline (when old sometimes brown), widest cells 17.0-29.5 µm wide, forming an ovate or rectangular group along basal leaf margin, not or hardly decurrent. Rhizoids slightly to strongly branched, smooth. Paraphyllia absent. Spores 11.0-17.0 µm. - Plants medium-sized, usually erect, irregularly or sometimes irregularly pinnately branched, green, yellowish, or brownish. Occurs from the sea level to the alpine region, in intermediately mineral-rich or mineral-rich fens, on lake and river shores. [pH 5.4-8.2 (n = 229) ; EC 18-644 mS/m (n = 142) ; Ca 2.6-74,1 mg/l (n = 45) ; IR 0.33-0.97 (n = 45)]. Widely distributed in Eurasia, North America, northern South America, northern and eastern Africa, Australia, and New Zealand.

Plants with a relatively short acumen, 33-40 % of leaf length, are occasionally found in the Arctic. When seen from above in the field, shoots of *Campylium stellatum* often look like small stars. The species is closely related to *C. protensum*, from which it differs in its more erect habit, its slightly larger size, and its relatively shorter leaf acumen. Paraphyllia were never observed in *C. stellatum*, whereas scattered plants of *C. protensum* have a few paraphyllia. To the south of and below the forest limit, *C. stellatum* occurs mainly in wetlands without dense tree cover, whereas *C. protensum* is more frequent in swampy forests.



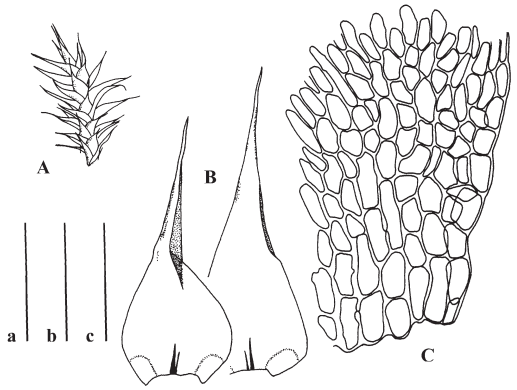


Fig. 59. *Campylium stellatum*. A : Shoot apex. B : Stem leaves. C : Alar cells. Scales : a : 2 mm, A. b : 1 mm, B. c : 100 µm, C.

Campylium stellatum is sometimes confused with species belonging to other genera. The differences between *C. stellatum*, *Drepanocladus arcticus*, and *D. polygamus* are discussed under *D. arcticus*. *Campyliadelphus chrysophyllus* is smaller than *C. stellatum* (stem leaves 0.9-1.5 (-1.8) vs. 1.7-2.8 mm long), and has mostly got a single, long costa in at least some leaves. Its widest alar cells are 10.5-17.5 (-21.0) µm wide, whereas those of *C. stellatum* are 17.0-29.5 µm wide. Both *C. stellatum* and *C. chrysophyllus* are occasionally confused with some phenotypes of *Ctenidium molluscum* (Hedw.) Mitt. However, *Ctenidium molluscum* is always easy to separate from these two species because of its distally prorate cells of the dorsal leaf lamina.

4. Campylium protensum (Brid.) Kindb. (Fig. 60)

***Campyliadelphus protensus* (Brid.) Kanda ; *Campylium polymorphum* (Hedw.) Pilous ; *Campylium stellatum* var. *protensum* (Brid.) Bryhn**

Dioicous. Stem leaves from sub-sheathing, erect or erect-patent basal part with patent to spreading and ± squarrose upper portion, occasionally slightly homomallous, 1.0-2.3 mm long, 0.4-1.0 mm wide, cordate or rounded-triangular, gradually or more often suddenly narrowed to long acumen, apex ± longly acuminate, concave, acumen furrowed, acumen when distinct constituting 55-77 % of leaf length ; margin entire or almost so ; costa short and weak, double or single, extending 10-25 % way up leaf, occasionally single and extending ca. 35 % way up leaf ; median lamina cells (25.0-) 27.5-77.5 (-88.0) µm long ; alar cells differentiated, upper cells rectangular or quadrate, slightly inflated, lower cells rectangular or shortly so (quadrate), inflated and hyaline, widest cells 19.0-29.5 µm wide, forming an ovate or rectangular group along basal leaf margin, not or hardly decurrent. Rhizoids strongly or moderately strongly branched (occasionally almost unbranched) and sometimes forming a dense tomentum, smooth or lowly warty-papillose. Paraphyllia sometimes present, uniseriate, narrowly triangular, or ovate. Spores

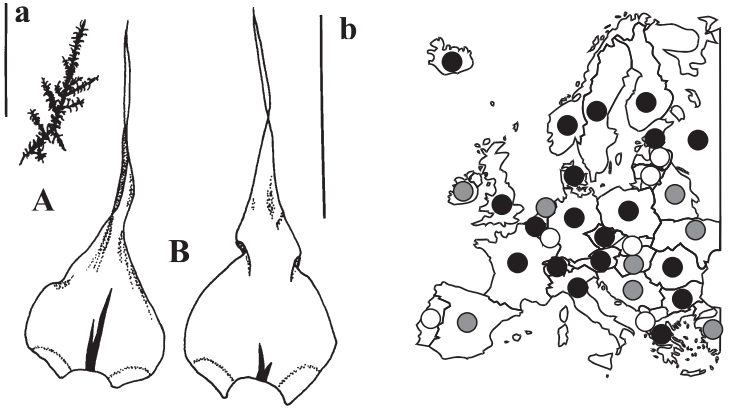


Fig. 60. *Campylium protensum*. A : Habit. B : Stem leaves. Scales : a : 2 cm, A. b : 1 mm, B.

12.5-16.0 µm. - Plants small or medium-sized, usually creeping, irregularly pinnately branched, green or sometimes yellowish green to yellow. From the sea level to the alpine region, in mineral-richer wetland habitats, in the lowlands usually found in swampy forests, higher up sometimes in more open habitats, such as lake and stream shores. [pH 6.2-8.0 (n = 17) ; EC 71-672 mS/m (n = 15) ; Ca 9.0-76,2 mg/l (n = 11) ; IR 0.71-0.97 (n = 11)]. Widespread in Eurasia and North America.

Campylium protensum is recognised by its creeping, relatively small and irregularly pinnate shoots with long or very long, narrow, and spreading leaf acumina. For the differences between this species and *Campylium stellatum*, see the notes after the latter species.

Calliergonella Loeske

Dioicous. Plants branched ± in one plane, never with red colours. Stem leaves ± concave, complanate or sometimes imbricate, either straight and ± oblong-ovate with rounded or apiculate apex, or falcate and from ovate or oblong-ovate base gradually narrowed to acuminate or shortly acuminate apex, not plicate ; costa short and double, thin, rarely absent ; margin often somewhat incurved near leaf apex, entire or near leaf apex finely denticulate ; median lamina cells linear and slightly flexuose, alar cells numerous, strongly inflated, hyaline, in well delimited group, hardly or distinctly decurrent ; rhizoid initials never present in leaves. Pseudoparaphyllia broad, with broadly square or rounded, often irregular apex. Paraphyllia absent. Axillary hairs well developed and usually abundant, with hyaline, 1-6-celled upper part. Rhizoids smooth, red-brown, slightly branched, inserted at or just below leaf costa insertion. Stem with central strand, a well developed cortex of several layers of incrassate cells, and a well developed hyalodermis. Inner perichaetial leaves straight and erect, plicate ; margin entire or partly finely denticulate above ; vaginula with paraphyses. Seta tall ; capsule broadly cylindrical, usually swollen when mature, when dry deeply longitudinally furrowed, curved and ± horizontal ; annulus separating. Peristome well developed ; outer layer of exostome cross-striolate in lower part.

Key to the species of Calliergonella

1. Leaves ± falcate, from ovate or oblong-ovate base gradually narrowed to acuminate or shortly acuminate apex. . . . . **1. *C. lindbergii***

-. Leaves straight, varying around oblong-ovate and suddenly narrowed to rounded or apiculate apex. . . . . **2. *C. cuspidata***

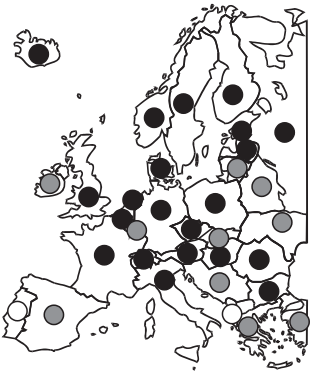
1. Calliergonella lindbergii (Mitt.) Hedenäs (Fig. 61)

***Hypnum arcuatum* Lindb. ; *Hypnum lindbergii* Mitt.**

Dioicous. Stem leaves falcate, erect-spreading, often ± complanate at least in their basal part, ovate or ovate-oblong, gradually narrowed to acu-

minate or shortly acuminate apex, concave ; margin finely denticulate in upper 10-20 %, entire below ; costa short, double or occasionally single, reaching up to 30 % way up leaf ; median lamina cells 52.5-115.0 (-145.0) µm long ; alar cells differentiated, numerous, rectangular, strongly inflated, hyaline, forming well delimited square or shortly transversely triangular group, not or hardly decurrent. Inner perichaetial leaves gradually narrowed to shortly or longly acuminate apex. Pseudoparaphyllia broad, with broadly square or rounded, often irregular apex. Spores 12.0-15.5 µm. - Plants medium-sized or large, irregularly or irregularly pinnately branched, green, pale green, yellowish, or brownish. Grows on sandy or loamy soil in moist or wet and usually rather nutrient-rich habitats, in moist or wet meadows, in ditches, on roadsides, and on brook, river or lake shores. [pH 6.1-7.9 (n = 10) ; EC 106-162 mS/m (n = 2)]. Widely distributed in Eurasia and North America, and known from a few localities in Brazil.

Calliergonella lindbergii is characterised by mostly distinctly falcate leaves that are often somewhat complanate in their basal part, the short, double, costa, the well delimited alar groups consisting of strongly inflated, hyaline cells, and the well developed hyalodermis of the stem. This species is sometimes confused with *Breidleria pratensis*, but in the latter the alar groups are much smaller and more indistinct than in *C. lindbergii* (Figs 61B and 63B). In addition, the pseudoparaphyllia are broad in *C. lindbergii*, narrowly triangular or lanceolate in B. *pratensis* (Figs 61C and 63C). In the field *C. lindbergii* is sometimes confused with species of *Warnstorfia* and *Drepanocladus* with falcate leaves, but such species have long single leaf costae and their foliation is not complanate.



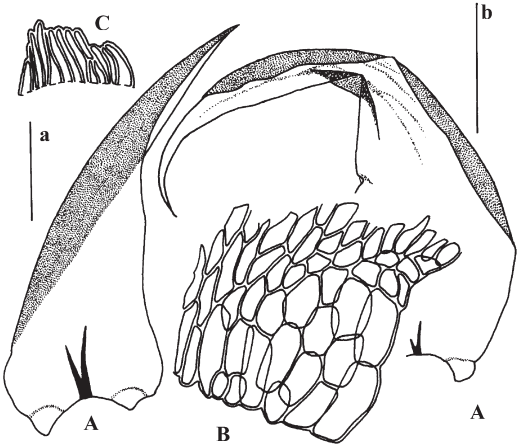
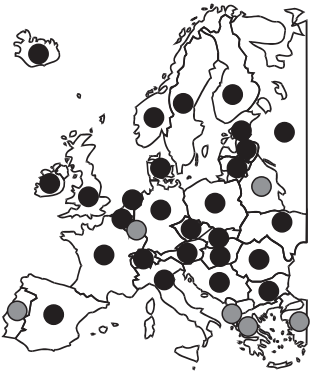


Fig. 61. *Calliergonella lindbergii*. A : Stem leaves. B : Alar cells. C : Pseudo-paraphyllium. Scales : a : 0.5 mm, A. b : 100 µm, B, C.

2. Calliergonella cuspidata (Hedw.) Loeske (Fig. 62)

***Acrocladium cuspidatum* (Hedw.) Lindb. ; *Calliergon cuspidatum* (Hedw.) Lindb.**

Dioicous. Stem leaves straight, erect-spreading, or usually imbricate, often ± complanate, varying around oblong-ovate, suddenly narrowed to rounded, acute, or apiculate apex, concave ; margin ± entire throughout ; costa short, double or occasionally single, reaching at most 20 % way up leaf, rarely absent ; median lamina cells 42.0-122.0 (-140.0) µm long ; alar cells differentiated, numerous, shortly to longly rectangular, strongly inflated, hyaline, forming well delimited quadrate, shortly rectangular, or shortly transversely triangular group, decurrent. Inner perichaetial leaves gradually narrowed to shortly or longly acuminate apex. Pseudoparaphyllia broad, with broadly square or rounded, often irregular apex. Spores 14.0-21.0 µm. - Plants medium-sized or large, usually pinnately branched and often flattened, stem and branch apices frequently stiff from tightly inrolled leaves, green, yellow-green, or brownish. Found in wet or moist and usually nutrient-rich habitats, in fens, ditches, and on brook, river or lake shores. [pH 4.6-8.6 (n = 180) ; EC 16-910 mS/m (n = 64) ; Ca 7.9-121,0 mg/l (n = 41) ; IR 0.44-0.95 (n = 41)]. The geographical distribution includes Eurasia, North and South America, Macaronesia, northern and north-eastern Africa, New Zealand, and Australia.



Calliergonella cuspidata is usually easily recognised by its oblong-ovate, obtuse or apiculate leaves with a short, double costa, distinctly delimited alar cell groups consisting of strongly inflated and hyaline cells, and a stem with a distinct hyalodermis. The shoots are frequently strongly flattened, as if someone has pressed them hard between two fingers.

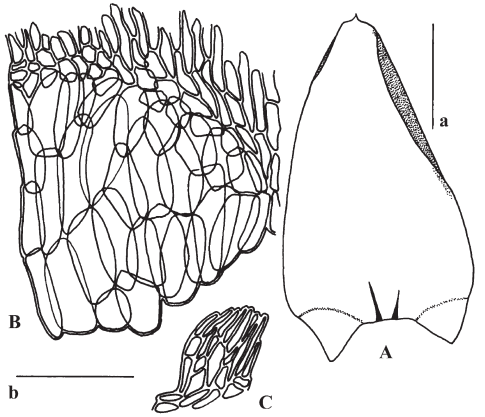


Fig. 62. *Calliergonella cuspidata*. A : Stem leaf. B : Alar cells. C : Pseudoparaphyllium. Scales : a : 0.5 mm, A. b : 100 µm, B, C.

Breidleria Loeske

Dioicous, sometimes with dwarf male plants growing on old leaves. Plants branched ± in one plane, never with red colours. Stem leaves concave, complanate, ± falcate, from ovate or ovate-oblong base gradually narrowed to shortly acuminate apex, not plicate ; costa short and double, thin, rarely absent ; margin finely or strongly denticulate in upper (10-) 25-60 % of leaf ; median lamina cells linear, slightly flexuose ; alar cells few, somewhat inflated, in small and indistinct group, not or hardly decurrent ; rhizoid initials never present in leaves. Pseudoparaphyllia narrowly triangular or lanceolate. Paraphyllia absent. Axillary hairs well developed and usually abundant, with hyaline, 1-7-celled upper part. Rhizoids smooth, red-brown, slightly branched, inserted at or just below leaf costa insertion. Stem with central strand, a well developed cortex of incrassate cells and a well developed hyalodermis. Inner perichaetial leaves straight and erect, plicate ; margin denticulate or dentate above ; vaginula with paraphyses. Seta tall ; capsule cylindrical (not swollen), when dry smooth or almost so, curved and ± horizontal ; annulus separating. Peristome well developed ; outer layer of exostome cross-striolate in lower part.

1. *Breidleria pratensis* (Koch ex Spruce) Loeske (Fig. 63)

***Hypnum pratense* Koch ex Spruce**

Dioicous. Stem leaves complanate, ± falcate, ovate or oblong-ovate, gradually narrowed to shortly acuminate apex, concave ; margin finely or strongly denticulate in upper (10-) 25-35 % of leaf, entire below ; costa short and double, thin, rarely absent ; median lamina cells 42.0-112.0 µm long ; alar cells few, somewhat inflated, forming a small and indistinct group, not or hardly decurrent. Pseudoparaphyllia narrowly triangular or lanceolate. Spores 10.5-13.5 (-16.0) µm. - Medium-sized or almost robust, usually sparsely and irregularly branched plants, green or yellow-green. In more or less calcareous areas, on moist soil, in rich fens (also tree-covered), or on moist rocks. Widespread in Eurasia and North America.

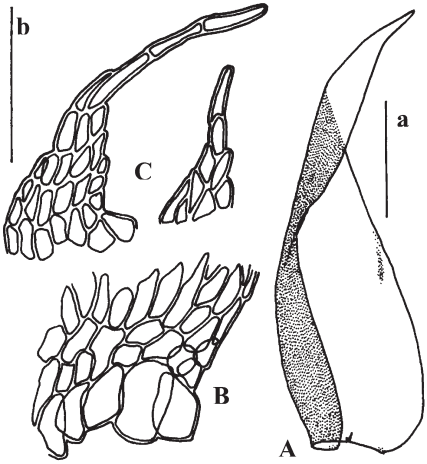
For the differences between this species and *Calliergonella lindbergii*, see the note after the latter.

In Japan and Korea *Breidleria pratensis* could be confused with B. *erectiuscula* (Sull. & Lesq.) Hedenäs (*Hypnum erectiusculum* Sull. & Lesq. ; *Plagiothecium homaliaceum* Besch.), which grows on rocks or tree bases. These two *Breidleria* species can be separated by the characters in the following key.

1. Male plants similar to female plants in size. Stem leaf margin denticulate in upper 25-35 %. . . . . ***B. pratensis***

-. With dwarf male plants. Stem leaf margin denticulate in upper 35-60 %. . . . . ***B. erectiuscula***

The African species reported as *Breidleria africana* P. Varde actually belongs to the genus *Plagiothecium*.



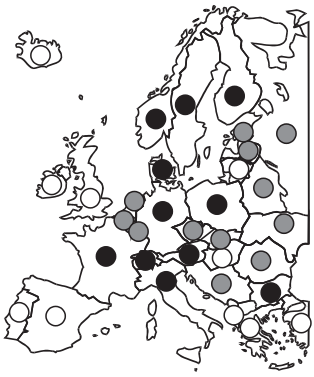


Fig. 63. *Breidleria pratensis*. A : Stem leaf. B : Alar cells. C : Pseudoparaphyllia. Scales : a : 0.5 mm, A. b : 100 µm, B, C.

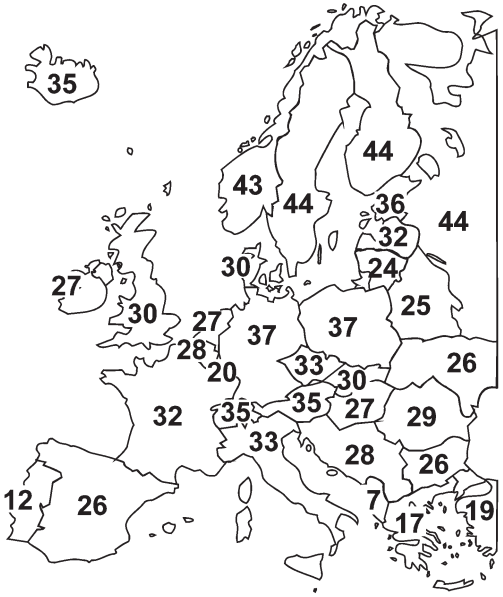


Fig. 64. Number of species per European country or region. The map summarizes the information in the maps of the individual species. The species diversity within the treated group increases from south to north.

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Index to the species

Accepted names of treated Amblystegiaceae species are in bold. Figures in bold refer to species descriptions, figures in italics refer to pages with figures, and underlined figures refer to European distribution maps. All species of the treated genera are included in Table 1 (p. 11), and reference to this table or to the keys are not included below.

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The European species of the *Calliergon-Scorpidium-Drepanocladus* complex, including some related or similar species

Lars Hedenäs

Illustration : a portion of a *Scorpidium cossoni* shoot arrangement by M. Vust and N. Müller, based on drawing by L. Hedenäs.

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