

The genus *Herbertus* is widely considered to be taxonomically 'difficult', largely because the plants have remarkably few clear-cut characters which can be used to distinguish species. In addition, plants are very rarely fertile and no sporophytes have ever been found on *Herbertus* in Europe. Thus almost all described differences are in leaf features, and some of these are very hard to quantify clearly, for example shape and orientation of the lobes. DNA barcoding is a modern technique which it has been claimed is especially useful in character-poor groups like *Herbertus*. At the Royal Botanic Garden, Edinburgh we have been testing this approach on British liverworts (Long *et al.*, 2007), and for David Bell's MSc project the genus *Herbertus* was selected as a pilot study, because of taxonomic uncertainties around the Scottish

and Norwegian *Herbertus borealis*. Because of this Norwegian connection, we chose to include all four European species: (1) *Herbertus aduncus* (Dicks.) Gray subsp. *hutchinsiae* (Gottsche) R.M. Schust. reported from Scotland, England, Wales, Ireland and Norway; (2) *Herbertus stramineus* (Dumort.) Trevis. from Scotland, England, Wales, Norway, Faeroe Islands and Iceland; (3) *Herbertus sendtneri* (Nees) Lindb. from the Austrian and German Alps; and (4) *Herbertus borealis* Crundw., described in 1970 from Scotland and Norway (Crundwell, 1970). We, along with several other bryologists, collected *Herbertus* in Ireland, England, Wales, Scotland and Norway and very recently Austria, and were also given material by other people, including *Herbertus* samples from China, the Himalaya and North America to test links or even synonymy which had been suggested previously.

European *Herbertus* and the 'Viking prongwort'

H. hutchinsiae. John Birks

David Bell & David Long review the difficult liverwort genus *Herbertus*, discussing how DNA barcoding is helping to resolve some of the issues, and has led to the discovery of a fifth European species. A key for identification of the five European species is provided.

History of the genus *Herbertus*

1. *Herbertus* in Europe

In the early 19th century, most leafy liverworts, including those now in *Herbertus*, were placed in the portmanteau genus *Jungermannia*, largely following the concepts of Hooker (1816) in his influential *British Jungermanniae*. His thinking was guided by the Linnaean tradition of primarily using sporophyte characters to classify mosses and liverworts, in this case the remarkably simple, uniform sporophytes of leafy liverworts: ‘the plants that form the genus *Jungermannia*, however numerous, cannot be divided into other genera by means of characters taken merely from the fructification’ (Hooker, 1816). However, Hooker’s concepts became superseded both in Britain and Europe as gametophyte characters were increasingly brought in to define smaller genera. Samuel Frederick Gray (1766–1828) in his *Natural Arrangement of British Plants* (Gray, 1821) was the first in Britain to break away, describing numerous new generic segregates, including *Herbertus*. This name, according to Müller (1951–1954), commemorates the British nobleman Thomas Herbert (*ca* 1656–1733), the 8th Earl of Pembroke and 5th Earl of Montgomery. Herbert was not a botanist, but was one of the patrons of the celebrated early Italian botanist Pier Antonio Micheli (1679–1737), and one of his plates (Micheli, 1729, tab. 27) is dedicated to Herbert.

Gray’s names, however, were largely ignored both in Britain and Europe, partly through Hooker’s influence, the lack of communication of Gray’s work abroad and also because Gray used the masculine gender for his new genera, rather than the traditional feminine. This was considered improper – according to Dumortier ‘these are the names of men and not of plants’ (Evans, 1917). In Europe, bryologists such as

Raddi (1818), Dumortier (1822) and Corda (1828) were steadily describing new segregates of *Jungermannia* and these gained gradual acceptance. The last two authors were ignorant of Gray’s work and one of Dumortier’s new genera was *Schisma*, synonymous with Gray’s *Herbertus*. *Schisma* gained acceptance and survived for half a century, although it was briefly replaced by *Sendtnera* Endl. which also included *Mastigophora*. Carruthers (1865) argued for resurrection of Gray’s genera (which had nomenclatural priority) and Lindberg (1874, 1875) was the first to agree, simply changing the gender of *Herbertus* to *Herberta* to replace *Schisma*. Lindberg’s spelling *Herberta* survived for a century until nomenclatural conflict with a flowering plant genus *Herbertia* Sweet was pointed out, and following Florschütz & Grolle (1975), Gray’s original spelling *Herbertus* was reinstated.

2. *Herbertus* in Britain and Ireland

The first localized and dated collections of a *Herbertus* in Europe were made by the Scottish surgeon/botanist Archibald Menzies (1754–1842) on Ben Nevis and Ben Lomond in Scotland in 1778. These were annotated ‘*Jungermannia juniperina*’ by Menzies and later identified as *Herbertus hutchinsiae*, and are preserved in Menzies’ herbarium (E, BM). Nine years later, Menzies, as surgeon on the *Prince of Wales*, explored the northern Pacific and collected *Herbertus* in British Columbia ‘NW America’ in 1787. However, the first description of a European *Herbertus* was not until 1793 by the Scottish botanist and nurseryman James Dickson (1738–1822) as *Jungermannia adunca*, described supposedly from the Scottish Highlands ‘in *alpibus Scotiis*’, but without locality, date or collector (Dickson, 1793). The Scottish plants may have been those of Menzies or his own

material now lost, but as later expertly detected by Proskauer (1962) Dickson definitely included in his description and illustration sporophyte-bearing plants which could only have come from Canada (Long, 1979). Proskauer correctly fixed the type of *Jungermannia adunca* with a Menzies collection from British Columbia. For almost 170 years up to 1962 it had been wrongly thought that *J. adunca* originated from Scotland.

Not all authorities accepted the name *Jungermannia adunca*, for example Smith & Sowerby (1812) and Hooker (1816) considered it to be a synonym of *J. juniperina* Sw. [now *Herbertus juniperoideus* (Sw.) Grolle] from the West Indies. Soon after 1800, *Herbertus* was collected from several new localities, such as Ben Lawers by William Hooker in 1808 (BM) and near Bantry in Ireland in 1810 by Miss Ellen Hutchins (BM). These were both identified by Hooker as *J. juniperina*, although in reality they represented two different undescribed species. Others such as Dumortier (1822) retained the name *adunca* for British plants, though he placed it in his 'new' genus *Schisma*. Nine years later, Dumortier (1831) described a second species from Scotland, *Schisma stramineum* Dumort., under another vague citation '*in alpibus Scotiae*'. This is possibly based on Hooker's Ben Lawers material. Very few botanists accepted this name either, and so it was that the epithet *straminea* remained effectively 'lost' until Proskauer (1962) showed that it applied to the plant which many had simply called *Herberta adunca* before that.

In 1862, Carl Moritz Gottsche, from Altona in Germany, decided that Miss Hutchins' Irish plants represented a taxon different from '*adunca*'. He therefore, in Rabenhorst's *Exsiccatae* (Hepaticae Europaeae), distributed material under a new name *Sendtnera adunca* (Dicks.) Gottsche var. *hutchinsiae* Gottsche. Although his new variety commemorated Miss Hutchins, he

did not distribute her Bantry material (probably due to insufficient quantity available) but rather specimens from Killarney collected by the English botanist Benjamin Carrington. Not until Evans (1917) was *Herberta hutchinsiae* (Gottsche) A. Evans elevated to species rank, though Schuster (1966) preferred to keep it as a subspecies of *Herberta adunca* (subsp. *hutchinsiae*). Ellen Hutchins (1785–1815) lived at Ballylickey near Bantry in County Cork and due to her fragile health took up field botany and embarked on compiling a catalogue of plants of the district (Bevan, 1984; Mitchell, 1999; Hutchins, 2003). She corresponded with Dawson Turner in England who encouraged her studies and in return she supplied him with specimens, including her *Herbertus* and others such as *Jungermannia* (now *Jubula*) *hutchinsiae*. These eventually came to Turner's son-in-law William Hooker, who doubtless distributed her liverwort duplicates to others such as Gottsche.

Well into the 20th century, many authors, notably Macvicar (1912), continued to recognize *Herberta adunca* as the only species in Britain and Ireland, although Macvicar segregated some mountain plants from Perthshire and Shetland as *H. adunca* var. *alpina*, now regarded as a stunted form of *Herbertus stramineus* (Damsholt, 2002). Müller (1951–1954) went to the other extreme and recognized three species from Britain: *Herberta hutchinsiae*, from Ireland, Wales, England and Scotland, *H. adunca* (syn. *H. straminea*) from Wales and Scotland, and a third species, the North American *Herberta tenuis* A. Evans from Loch Assynt in Scotland and Cwm Glas in Wales. Soon after, Jones (1958) considered that these plants were not *H. tenuis* but '*merely slender forms of H. hutchinsiae*'. However, Jones also mentioned that '*an as yet undescribed species of Herberta has recently been found on Beinn Eighe in Scotland*'.

This undescribed species was *Herbertus borealis* Crundw., described (Crundwell, 1970) from material collected by Derek Ratcliffe on Beinn Eighe in August 1958, although it had been first collected there by Charles Howie and Charles Jenner 90 years earlier in 1868 (BM, E). Ten years after he collected *Herbertus borealis*, Derek Ratcliffe was on Shetland where he collected for the first time in 1968 what is now known to be a fourth British *Herbertus*, *H. norenus*, as described by Bell *et al.* (2012) and below. More recently this was re-collected on the Mainland of Shetland by Maren Flagmeier on the BBS field meeting in July 2008 which contributed significantly to its discovery as a new species. Others who have collected the Shetland plant include Jean Paton, as well as Sandy Payne and Sheila Gear on Foula. The present authors visited Ronas Hill in October 2009 and found quite extensive populations of *H. norenus*.

3. *Herbertus* in the rest of Europe

Outside the British Isles, *Herbertus* is a rare genus in Europe, known only from Norway, the Faeroe Islands, Iceland, Germany and Austria. In Norway, the first collection made was in Rogaland, at Andresaeen waterfall at the head of Lysefjord by B. Kaalaas in 1885. This was reported by Jørgensen (1934) as *H. hutchinsiae*, then by Crundwell (1970) and Damsholt (2002) as *H. borealis*; in fact it is neither of these but represents the new species *H. norenus*. In September 2008, DGL visited Lysefjord with Hans Blom, Gordon Rothero and David Rycroft, and collected *H. norenus* at five sites, enabling morphological and ecological comparisons with *H. borealis* to be made. *H. hutchinsiae* is surprisingly rare in Norway and was first collected also in Rogaland by Sigfrid Arnell and Ole Martensson in May 1949 (Crundwell, 1970). *H. stramineus* is more widespread in

Norway and also extends to the Faeroes and Iceland (Damsholt, 2002).

In central Europe, the discovery of *Herbertus* was at an unknown date prior to 1838, when Dr Otto Sendtner (1814–1859), Professor of Botany in Munich, discovered a *Herbertus* in the Ober-Inntal near Innsbruck. This was described by Nees von Esenbeck (1838) as *Schisma sendtneri* Nees, now known as *Herbertus sendtneri* (Nees) Lindb., although in the past also known as *Schisma sauteriana* Huebener & Genth and even wrongly synonymized under *Herbertus stramineus* (von Dalla Torre & von Sarnthein, 1900–1913). It is a rare species in Europe, known only from the Austrian Alps (Müller, 1951–1954; von Dalla Torre & von Sarnthein, 1900–1913), except for a single record from Germany, where it was discovered in north-west Thuringia in 1854 by Hugo von Möhl, but is now extinct (Meinunger & Köckinger, 2002). In BM, two early collections of *H. sendtneri* labelled ‘Switzerland’ exist in the Stephani herbarium but are of doubtful provenance as they appear never to have been published or accepted as a Swiss species.

DNA barcoding of European *Herbertus*

The DNA barcoding work, along with a morphological re-assessment, was undertaken as part of an MSc study and the results have now been published (Bell *et al.*, 2012). The principle of DNA barcoding is to establish a central reference database using a standard set of molecular markers as a tool for discriminating among species (Hebert *et al.*, 2003). We used four different markers, three from chloroplast DNA and one from nuclear DNA. To our surprise, the DNA barcoding analyses clearly indicated that there are five distinct species of *Herbertus* in Europe, not four as previously recognized. These correspond to

H. sendtneri, *H. stramineus*, *H. hutchinsiae*, *H. borealis* and a previously overlooked new species. Our suspicions (based on field observations on Beinn Eighe and at Lysefjord in Norway) that Scottish and Norwegian populations of *H. borealis* might be different, were confirmed, with the Lysefjord samples constituting the new species now formally described as *H. norenius* (Bell *et al.*, 2012). What was even more unexpected, however, was that a specimen of *Herbertus* collected by Maren Flagmeier on Ronas Hill on the BBS Shetland meeting in July 2008, turned out to be the same as the Norwegian species. In fact several other bryologists had collected the new species on Shetland and had found it difficult to identify. Hence we now have five European species, each with clear morphological differences (see below). In order to test the correct rank and name for two of these species, we had included

(a) samples of *H. aduncus* subsp. *aduncus* and subsp. *tenuis* from North America, and concluded that *H. hutchinsiae* was best treated as a species in its own right, and (b) samples of *H. cf. delavayi* from the Sino-Himalaya, which indicated that the previous treatment of *H. borealis* as a synonym of *H. delavayi* Steph. (Feldberg & Heinrichs, 2005) could not be confirmed.

Key to European *Herbertus*

Below we present a key to the European species of *Herbertus*, with the most useful morphological characters for identification summarized in Table 1. A brief note on each species, their distribution and ecology is also presented. As a newly described species (Bell *et al.*, 2012) *H. norenius* is treated in greater detail than the other species which have been more thoroughly described in the past.

- 1 Lateral leaves erect, strongly asymmetrical and postically secund, 1.5–2.2 times longer than broad; dorsal lobes ca 1.5 times wider than ventral lobes; slime papillae on single- or multicellular appendages to halfway up margin of lamina 2
 - Lateral leaves erecto-patent, weakly to strongly asymmetrical and postically secund, 2–3.5 times longer than broad; dorsal lobes not significantly different in size from ventral lobes; slime papillae sessile on margin at base of lamina (rarely on single-celled teeth) 3
- 2 Flagella abundant, mostly in pairs; lateral leaves 1.4–1.8 mm long, 1.5–2.2 times longer than broad; lobes 2–3(–4) times longer than broad; slime papillae on 1- to 2-celled stalks (rarely sessile) on margins towards base of lamina 1. *H. borealis*
 - Flagella infrequent, solitary; lateral leaves 0.8–1.2 mm long, to 1.5 times longer than broad; lobes 1.5–2 times longer than broad; slime papillae on coarse multicellular appendages on margins to halfway up leaf lamina 2. *H. sendtneri*
- 3 Lateral leaves symmetrical to weakly asymmetrical; lateral leaves 0.8–1.6 mm long, 2–2.5 times longer than broad; lobes 2–3 times longer than broad 3. *H. stramineus*
 - Lateral leaves asymmetrical; lateral leaves 1.4–2.2 mm long, 2.5–3.5 times longer than broad; lobes 3–5 times longer than broad 4

- 4 Lobes of lateral leaves irregularly squarrose, dorsal lobe ±straight to weakly falcate, ventral lobe falcate; lobes 3.5–5 times longer than broad, divergent; lateral leaves 1.4–2.0 mm long; reddish pigmentation usually present **4. *H. hutchinsiae***
- Lobes of lateral leaves not squarrose, dorsal and ventral lobe equally and regularly falcate; lobes 3–4 times longer than broad, sub-parallel (to weakly divergent); lateral leaves 1.5–2.2 mm long; reddish pigmentation absent **5. *H. norenius***

1. *H. borealis* Crundw. (Figs 1a, 2, 3)

A robust species growing in large, orange-brown mats to 1 m² or more. Shoots grow to 20 cm long with closely overlapping leaves neatly pointed to one side and abundant flagella. The 2 mm long leaves are strongly asymmetrical with a dorsally inflated lamina and dorsal lobes ca 1.5 times broader than the ventral lobes. Slime papillae are sessile or held on short (1- to 2-celled) appendages at the base of the lamina.

The only other European *Herbertus* with broader dorsal than ventral lobes is *H. sendtneri*, but in this species the lobes are much shorter than in *H. borealis*. The strongly asymmetrical leaves and abundant flagella distinguish *H. borealis* from the other western European species and the leaves pointing neatly to one side make confusion with *H. hutchinsiae* and *H. stramineus* unlikely in the field. The shoots of *H. norenius* have a similarly neat appearance, but in this species the leaves are less asymmetrical and both lobes are of similar width.

Habitat. A plant of northern hepatic heath, growing amongst heather on quartzite scree, with associates such as *Racomitrium lanuginosum*, *Pleurozia purpurea* and *Cladonia* spp. (90–)400–550 m.

Distribution. A Scottish endemic, known from a single locality (Beinn Eighe, Wester Ross), where it is locally abundant on the plateau.

2. *H. sendtneri* (Nees) Lindb. (Figs 1b, 4, 5)

Growing in loose, green to golden-brown turfs. Shoots to 20 cm with overlapping leaves pointed

to one side and infrequent solitary flagella. Leaves are short (to 1.2 mm) and strongly asymmetrical with broadly triangular lobes, the dorsal lobe being around 1.5 times wider than the ventral lobe. Slime papillae can often be found on coarse multicellular appendages on the lower half of the lamina.

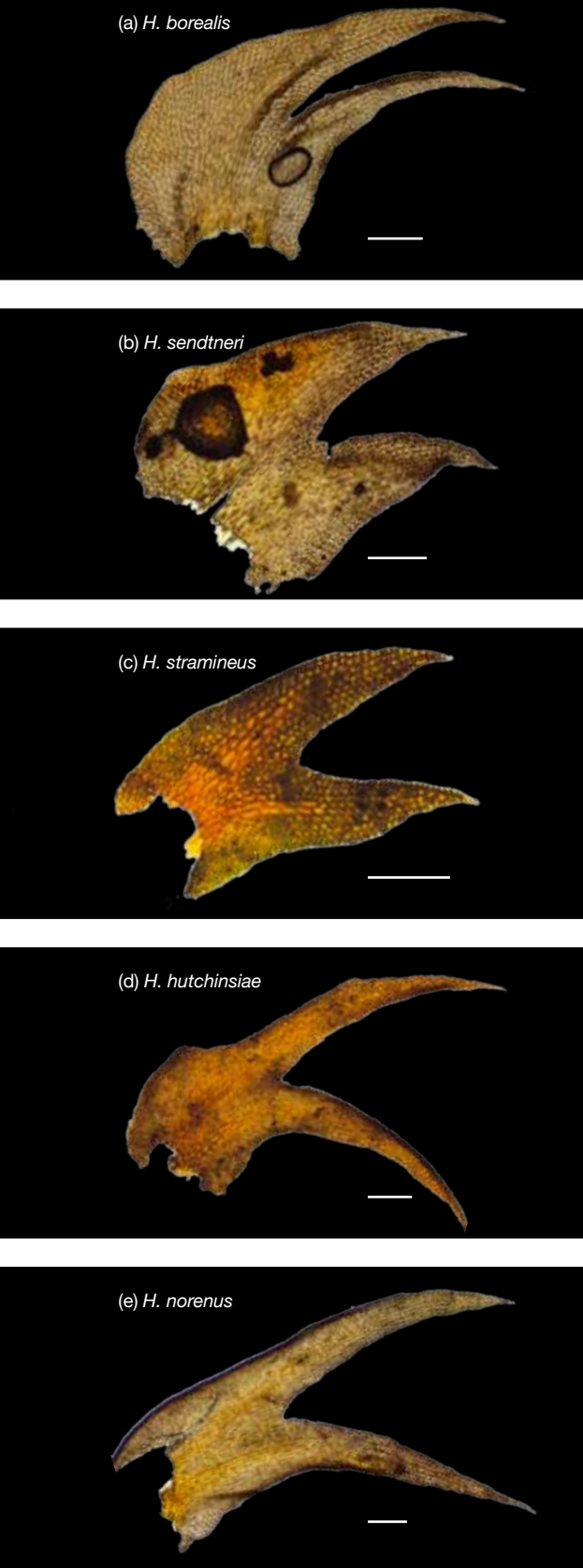
As the only species of *Herbertus* known from central Europe, *H. sendtneri* is unlikely to be confused with any other species. The short asymmetrical leaves with broadly triangular lobes and dorsal lobe 1.5 times wider than ventral lobe are distinctive. *H. borealis* also has asymmetrical leaves with the dorsal lobe 1.5 times wider than the ventral lobe, but the lobes of *H. borealis* are longer and narrower and the plants more robust with abundant paired flagella.

Habitat. Grows in shady rock crevices in block scree at high elevations. 1,600–2,900 m.

Distribution. In Europe, known from only one region of the Austrian Alps and previously one site in Germany from which it is now believed to be extinct. Also reported from Asia (Bhutan, China) and North America (British Columbia, Alaska). We consider that reports from the Azores and South America should be re-assessed as those populations show some striking morphological and molecular differences with European and Sino-Himalayan material.

3. *H. stramineus* (Dumort.) Trevis. (Figs 1c, 6, 7)

Typically growing in small, brown to blackish tufts. Stems to around 10 cm long have erect to spreading leaves and infrequent solitary flagella.



< Fig. 1. Typical lateral leaves of the five species of *Herbertus* in Europe. (a) *H. borealis* (v.-c. 105) (D. Bell 14); (b) *H. sendtneri*, Austria (J. Heinrichs 4378); (c) *H. stramineus* (v.-c. 49) (D. Bell 7); (d) *H. hutchinsiae* (v.-c. 98) (D. Bell 22); (e) *H. norenius*, Norway (D.G. Long 38081 – holotype). Bars, 200 μ m.

The leaves are only weakly asymmetrical, to 1.6 mm long and occasionally develop additional lobes.

The smallest *Herbertus* species in western Europe, *H. stramineus* is only likely to be confused with *H. hutchinsiae* from which it differs in having more symmetrical leaves with relatively shorter, broader lobes, and never having the reddish pigmentation normally visible in *H. hutchinsiae*.

Habitat. Calcareous mossy turf on north-facing rock ledges. 20–1,180 m.

Distribution. North-west Wales, Lake District, Scottish Highlands to Orkney and Shetland, south-west Norway, Faeroes, Iceland. Also reported from North America (Alaska).

4. *H. hutchinsiae* (Gottsche) A. Evans (Figs 1d, 8, 9)

Syn. *H. aduncus* (Dicks.) Gray subsp. *hutchinsiae* (Gottsche) R.M. Schust.

Typically growing in orange to red (or more rarely green) mats or tufts. Shoots to 20 cm long have spreading leaves with squarrose lobes and solitary flagella. The 2 mm long leaves are asymmetrical with an inflated dorsal lamina and divergent lanceolate lobes.

H. hutchinsiae is distinctive in its shaggy appearance (due to the squarrose leaf lobes) and the often striking reddish pigmentation which is absent from the other European species.

Habitat. Amongst boulder scree at the base of north-facing cliffs and beneath *Calluna* in hepatic heaths. Also occasional on rocks and



△ Fig. 2, 3. *H. borealis* (2) and its habitat (3) at Beinn Eighe (v.-c. 105). D.G. Long

△ Figs 4, 5. *H. sendtneri* (4) and its habitat (5) at Rosskogel in the Austrian Alps. G.P. Rothero (3), D.G. Long (4)

turfy hummocks in woodland. From close to sea level to 1,040 m.

Distribution. The most widespread European *Herbertus* species, from the west coast of Ireland, north-west Wales, Lake District, western Scottish Highlands through to Orkney and south-west Norway. European endemic.

5. *H. norenius* D.G.Long, D.Bell & H.H.Blom (Figs 1e, 10–13)

Syn. *H. borealis sensu* Damsholt (2002), *non* Crundw.

Plants erect to semi-prostrate, growing in dense, green to golden-brown tufts. Shoots (4–)6–10 cm long, 2–3 mm wide, decurved at tip; flagella few to many, usually solitary. Leaves imbricate, erecto-patent, asymmetrical,

with postically secund, but not squarrose lobes. Lateral leaves 1.5–2.2 mm long, 2.5–3 times longer than wide, half to two-thirds bifid; lamina inflated dorsally, 0.5–0.8 mm wide; slime papillae sessile on margin at base. Lobes of lateral leaves lanceolate, slightly curved to falcate, 3–4 times longer than wide, divergent to sub-parallel, dorsal and ventral more or less equal in width, tips acute, terminating in 3–8 uniseriate cells. Vitta indistinctly defined, bifurcating one-third to three-fifths up lamina, extending halfway into lobes. Marginal cells 12–23 × 17–29 μm, vitta cells 12–20 × 41–87 μm. Underleaves similar to lateral leaves, but symmetrical, lobes divergent to sub-parallel, narrowly lanceolate with acute tips.

Dioicous; reproductive organs not seen, but male plants reported from Norway by Crundwell (1970).

H. norenius is a distinctive new species showing some similarities to *H. borealis* (with which it was formerly confused), but in some respects

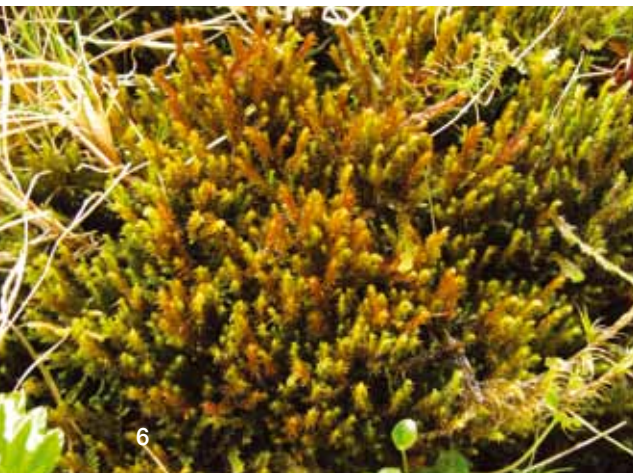
it is more similar to *H. hutchinsiae*. From *H. borealis* it differs in usually having fewer flagella which are normally solitary; its leaves and leaf lobes are proportionately longer and leaves are less asymmetrical; the dorsal and ventral lobes are approximately equal in width, sub-parallel to weakly divergent and the slime papillae are sessile on the margins at the base of the leaf lamina. It differs from *H. hutchinsiae* in its leaves which are not irregularly squarrose but are regularly secund more or less in one direction; its leaf lobes which are proportionately slightly shorter and broader

(3–4 times as long as broad) and which are sub-parallel to only weakly divergent.

Ecology. *H. norenius* displays some markedly different ecology in Norway and Scotland (Figs. 12–13), the most profound being the occurrence in sheltered north-facing wooded ravines at low elevation (3–216 m) in the Lysefjord

▽ Fig. 6, 7. *H. stramineus* (6) and its habitat (7) at Piers Gill (v.-c. 70). D.G. Long (6); D. Bell (7)

▽ Figs 8, 9. *H. hutchinsiae*, Beinn Eighe (v.-c. 105) (8) and its habitat (9) at Twelve Bens (v.-c. H16). D. Bell (8); D.G. Long (9)



sites, whereas in Shetland where no tree cover exists the plant grows on exposed north-facing hillsides at between 177 and 342 m altitude. The habitat at the long-known Norwegian locality (Andresbrekka or Andresaeen) was described in some detail by Crundwell (1970) under '*H. borealis*', and from observations made by DGL and colleagues in 2008 at a number of sites on Lysefjord this is typical of the Norwegian sites. All are in wooded *Betula/Sorbus aucuparia* ravines, where it grows on rock and cliff ledges, rock slabs and large boulders in at least partial shade. Common associates are the vascular plants *Hymenophyllum wilsonii* and *Calluna vulgaris*, and

the bryophytes *Breutelia chrysocoma*, *Sphagnum denticulatum*, *Pleurozia purpurea*, *Scapania ornithopodioides*, *Racomitrium lanuginosum* and several others listed by Crundwell (1970).

The Shetland sites are also north-facing, but are consistently much more exposed with limited shelter only from relatively small boulders and dwarf shrubs, including *Calluna vulgaris*, *Empetrum* sp., *Vaccinium myrtillus* and *V. vitis-idaea*. The plants are often embedded in a mixed turf with other bryophytes and some vascular plants, such as *Luzula sylvatica* (Foula), *Trichophorum caespitosum*, *Carex binervis* and *Potentilla erecta*. Nevertheless, a number of the

Table 1. Morphological character differences among European *Herbertus* species

Character	1. <i>H. borealis</i>	2. <i>H. sendmeri</i>	3. <i>H. stramineus</i>	4. <i>H. hutchinsiae</i>	5. <i>H. noreus</i>
Leaf orientation	Erect, strongly postically secund	Erect, weakly postically secund	Erecto-patent, weakly postically ecund	Erecto-patent, postically secund	Erecto-patent, postically secund
Lobe orientation	Plane	Plane	Plane, rarely weakly squarrose	Strongly & irregularly squarrose	More or less plane
Flagella	Many, mostly in pairs	Few, solitary	Few, solitary	Few to many, solitary, rarely in pairs	Few to many, usually solitary
Leaf length (mm)	1.4–2.0	0.8–1.2	0.8–1.6 (–1.8)	1.4–2.0	1.5–2.2
Leaf length/width ratio	1.5–2.2	1–1.5	2–2.5	2.5–3.5	2.5–3
Lobe length/width ratio	2–3(–4)	1.5–2	2–3	3.5–5	3–4
Dorsal/ventral lobe width ratio	ca 1.5	ca 1.5	ca 1	ca 1	ca 1
Lobe separation	Parallel	Sub-parallel	Divergent to sub-parallel	Divergent	Sub-parallel to weakly divergent
Dorsal lobe shape	Ovate-lanceolate, falcate	Broadly triangular, curved	Broadly lanceolate, weakly falcate	Lanceolate, weakly falcate	Lanceolate, falcate
Ventral lobe shape	Lanceolate, falcate	Broadly triangular, curved	Broadly lanceolate, straight	Lanceolate, falcate	Lanceolate, falcate
Slime papillae	On 1- to 2-celled stalks towards base of lamina (rarely sessile)	On coarse, multi-cellular appendages, to halfway up lamina	Sessile at base of lamina	Sessile at base of lamina (rarely on single-celled teeth)	Sessile at base of lamina



bryophyte associates on Shetland are shared with some of the Norwegian sites, such as *Pleurozia purpurea*, *Racomitrium lanuginosum*, *Rhytidiadelphus loreus*, *Diplophyllum albicans*, *Scapania gracilis*, *Plagiothecium undulatum* and *Scapania ornithopodioides*, whereas the rarer oceanic liverworts *Mastigophora woodsii* and *Plagiobhila carringtonii* are unknown in the Norwegian localities.

Distribution. south-west Norway (five localities) and Shetland Islands of Scotland (two localities).

Etymology. The specific epithet reflects the unique distribution of this new species which echoes part of the former range of the Vikings in Norway and the Shetland Islands; the name derives from the ‘Norrøn’ language and culture of the Vikings; an additional inspiration is the uppermost curved tips of the shoots which are reminiscent of the curved bows of the historic Viking longships. The proposed vernacular English name is therefore ‘Viking prongwort’.

△ Figs 10–13. *H. norenius* at Lysefjord, Norway (10) and habitat (11), and at Ronas Hill (v.-c. 112) (12) and habitat (13). D.G. Long

Glossary of terms used in key and descriptions

<i>bifid</i>	divided into two lobes
<i>decurved</i>	broadly curved downwards or backwards
<i>dorsal</i>	upper (surface)
<i>erecto-patent</i>	spreading at an angle of 40°–70°
<i>fulcate</i>	curved to one side (like a sickle)
<i>imbricate</i>	overlapping
<i>lamina</i>	main body of leaf below the lobe division
<i>lanceolate</i>	narrowing gradually from the base
<i>postically secund</i>	angled downwards or backwards to below the lower surface
<i>sessile</i>	without a stalk
<i>slime papillae</i>	mucilage-secreting cells
<i>squarrose</i>	spreading at an angle of more than 90°
<i>sub-parallel</i>	just off parallel
<i>uniseriate</i>	cells arranged in a single row
<i>ventral</i>	lower (surface)
<i>vitta</i>	band of elongate cells

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