

BRYOPHYTES OF ST HELENA, SOUTH ATLANTIC OCEAN. 3.
SAINTHELENIA, A NEW GENUS OF BRACHYTHECIACEAE (BRYOPHYTA)

МОХООБРАЗНЫЕ ОСТРОВА СВЯТОЙ ЕЛЕНЫ, АТЛАНТИЧЕСКИЙ
ОКЕАН. 3. SAINTHELENIA, НОВЫЙ РОД МХОВ (BRACHYTHECIACEAE)

M.S. IGNATOV¹, M.J. WIGGINTON², O.I. KUZNETZOVA³ & S. HUTTUNEN⁴

М.С. ИГНАТОВ¹, М.Д. ВИГГИНТОН², О.И. КУЗНЕЦОВА³, С. ХУТТУНЕН⁴

Abstract

Brachythecium athrocladum (Mitt.) Paris, an endemic species of St Helena Island, South Atlantic Ocean, is re-studied by morphology and molecular markers, nr ITS region and chloroplastic trnL-F. Molecular markers independently indicate the position of the species in Brachytheciaceae subfamily Helicodontoideae, especially close to the genera *Helicodontium* and *Clasmatodon*. Common characters of the plants from St Helena with these genera are discussed. Resulting from these studies, the new genus *Sainthelenia* Ignatov & M. Wigginton is described, with a single species, confined in its distribution to this island.

Резюме

Brachythecium athrocladum (Mitt.) Paris, эндемик острова Святой Елены в южной части Атлантического океана, изучен в отношении как его морфологии, так и последовательностей ядерной (ITS) и хлоропластной ДНК (trnL-F). Оба молекулярных маркера независимо указывают на положение в подсемействе Helicodontoideae, и наиболее близко к родам *Helicodontium* и *Clasmatodon*. Обсуждается морфологическое сходство этих родов с растениями с острова Святой Елены. В качестве таксономического решения предложено выделение данного эндемичного для острова вида в род *Sainthelenia* Ignatov & Wigginton.

KEYWORDS: mosses, Brachytheciaceae, *Sainthelenia*, taxonomy, molecular phylogenetics, ITS, trnL-F

INTRODUCTION

The bryophyte collections of W.J. Burchell, made on St Helena, South Atlantic Ocean, between 1805 and 1810 during his residence on the island, include a small pleurocarpous moss that Mitten later described as having “*the habit of Homalothecium sericeum, but more rigid, and with a capsule exactly corresponding to that of the section Brachythecium*”. He noted that very little of this plant was gathered and that only one capsule was seen by Burchell, who marked [the specimen] *Hypnum athrocladum* B., the name under which Mitten

(1875) published it in Sect. *Brachythecium*. Paris (1900) later validated its placement in *Brachythecium*.

Brotherus (1925) in “Pflanzenfamilien...” overlooked this species, and as this publication is still the only one that includes a worldwide classification of the genus *Brachythecium*, its position within the genus remained unclear.

The only other known collections of this interesting species were made two hundred years later, in 2005, by one of the authors (MJW). *Brachythecium athrocladum* looks quite odd com-

¹ – Main Botanical Garden of Russian Academy of Sciences, Botanicheskaya, 4, Moscow 127276 Russia – Россия 27276 Москва, Ботаническая, 4, Главный ботанический сад им. Н.В.Цицина РАН; misha_ignatov@list.ru

² – 36 Big Green, Warmington, Peterborough PE8 6TU, U.K.; e-mail: m.wigginton868@btinternet.com

³ – A.N.Belozersky' Research Institute of Physico-Chemical Biology, Moscow State University, Moscow 119991 Russia – НИИ Физико-химической биологии им. А.Н. Белозерского, МГУ, Москва 119991 e-mail: kuznetsova_oi@mail.ru

⁴ – Laboratory of Genetics, Department of Biology, FI-20014 University of Turku, Finland; e-mail: shuttu@utu.fi

pared with the other known species of the genus, and in order to clarify its taxonomic position, we carried out a morphological and molecular study, in particular with molecular markers that have proved to be useful for Brachytheciaceae taxonomy (e.g. Huttunen & Ignatov, 2004; Ignatov & Huttunen, 2002), as well as for other mosses and also many other groups of eukaryots.

METHODS

The most variable loci in moss DNA, nr ITS and chloroplastic trnL-F, were studied. The protocols of PCR and sequencing was standard (as described, for example, in Gardiner et al., 2005), and the program Nona with the Winclada shell was used for parsimony analyses (Nixon, 1999 a,b; Goloboff, 1994). The extracts from the sets of molecular data on the Brachytheciaceae already used in the analysis of Huttunen & Ignatov (2004), Huttunen et al. (2007) and Huttunen et al. (2008) were utilized as 'testing chips' to evaluate the relationships of this enigmatic species.

RESULTS

Molecular analysis of ITS and trnL-F are shown in the Fig. 1.

Despite the rather low variation in the trnL-F sequences, the strict consensus tree resolved '*Brachythecium athrocladum*' in Brachytheciaceae subfamily Helicodontioideae, and in the group especially rich in monospecific genera, many of which have a restricted distribution in oceanic regions. The statistical support of the clades of the trnL-F tree was, however, very low.

The ITS analysis gave almost the same topology, though slightly differed due to a somewhat different species set (this was determined by the availability of data). The high jack-knife support was found for some clades, including 92 for the Helicodontioideae clade, thus supporting the '*Brachythecium athrocladum*' position within this subfamily, and not in the Brachythecioideae. The group of '*Brachythecium athrocladum*' plus *Helicodontium* and *Clasmatodon* has only a very low support (53), and this clade was included in a broader clade with *Homalotheciella*, *Remyella*, *Aerolindigia*, '*Rhynchostegiella durieui*' and '*Oxyrrhynchium pumilum*'. The two latter taxa are shown in inverted commas due to their distant position from the core taxa of their respective genera (cf. Huttunen et al., 2007; Alojin et al., submitted).

DISCUSSION

The position of '*Brachythecium athrocladum*' in the clade of Helicodontioideae and especially within the 'oceanic-epiphytic' group may look somewhat unexpected. Species of *Clasmatodon*, *Helicodontium*, *Homalotheciella* and *Remyella* are epiphytes with erect capsules and usually strongly modified peristomes, and often with relatively short leaves and laminal cells. However, the group also includes '*Rhynchostegiella durieui*' which is characterized by its inclined capsule having the 'perfect peristome' that is commonly fully developed in epigeic and epilithic species. *Rhynchostegiella durieui* grows mostly on rocks (Hedenäs, 1992), and has a geographical range including islands of the North Atlantic (Azores, Canaries, Madeira) and the Mediterranean Sea, and also mountains in the oceanic regions of Atlantic Europe and North Africa.

Similarly, '*Brachythecium athrocladum*' grows on rocks and tree bases, i.e. is not a 'true epiphyte', and also has an at least somewhat inclined capsule which, however, has a slightly reduced peristome, with basal membrane of only 1/4 endostome length, narrow and narrowly perforated segments, and no ciliae. The exostome teeth are striolate below, and hygroscopic movements are xerocastique (i.e. the teeth close the mouth when wet, and open when dry). Thus the degree of exostome reduction is similar to that in *Helicodontium capillare*, a widespread South and Central American species which, however, has a symmetrical capsule and a xerocastique exostome that is usually pale in colour.

The common morphological characters of members of the oceanic-epiphytic clade are unknown. Most of the representatives of the clade, including *Homalotheciella*, *Clasmatodon*, *Remyella* and *Aerolindigia*, have characters usually associated with epiphytic habitats: a variously reduced peristome, erect perichaetial leaves and large spores. The extent of peristome reduction (or modification) is, however, very different – from moderate reduction in *Helicodontium* to 'complete' peristome development in '*Rhynchostegiella durieui*', as described above. At the same time, *Helicodontium* has short and thick-walled laminal cells, whereas in '*Rhynchostegiella durieui*' they are fairly long. '*Brachythecium*

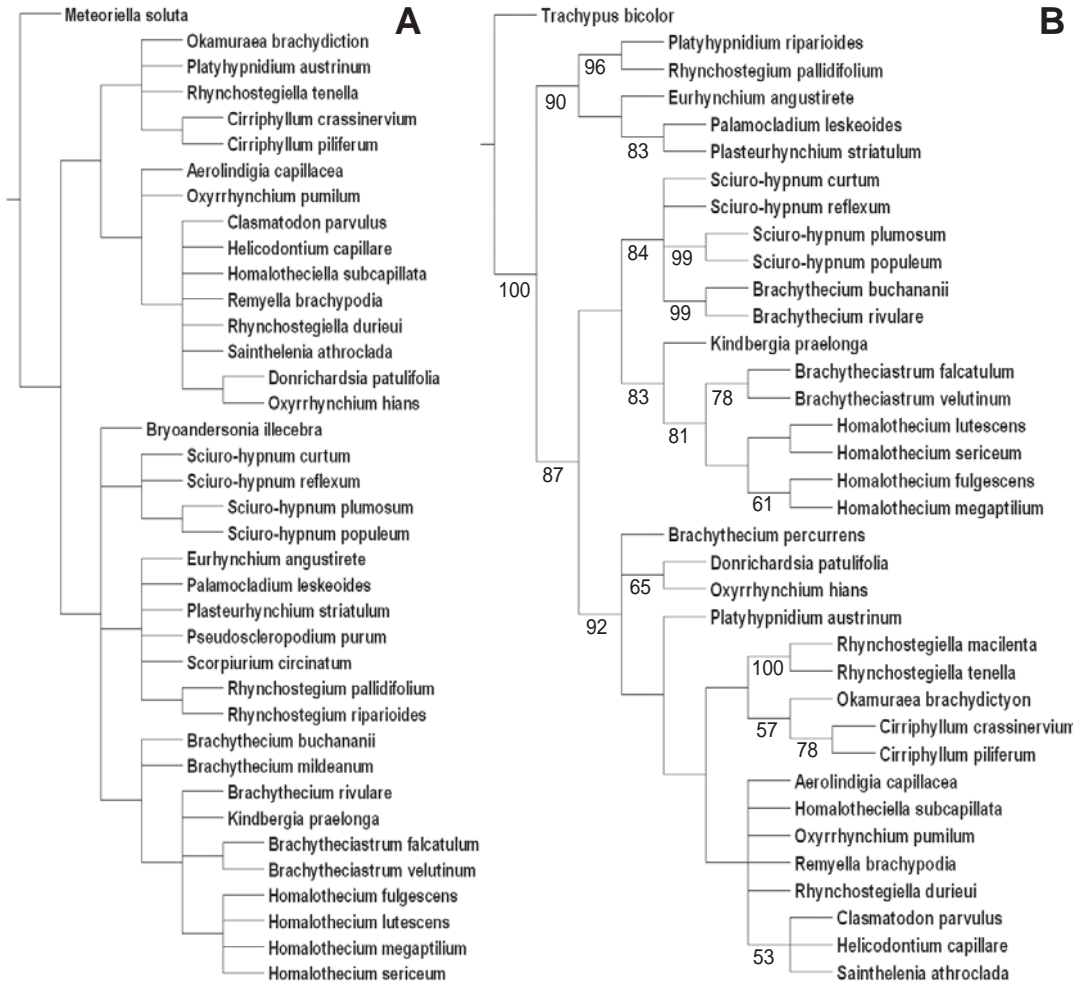


Fig. 1. A: Strict consensus tree of 1143 shortest trees (L=128) found in parsimony ratchet analysis of *trnL-F* sequences (L=350; RI=1; CI=0); B: Strict consensus tree of 73 shortest trees (L=482) found in parsimony ratchet analysis of ITS sequences (L=1975; RI=1; CI=0); jackknife values calculated for 1000 replications are shown below branches.

athrocladum’ would not be easy to confuse with the latter species, as it has habit of ‘typical *Rhynchostegiella*’, with leaves from lanceolate-triangular base very longly acuminate, with length to width ratio >3.5:1, laminal cells usually >15:1, and also it is dioicous. *Clasmatodon* and *Helicodontium* have dull plants with leaves composed of short cells, strongly reflexing in wet state so they for a long time were classified in Fabroniaceae or Myriniaceae. Blunt ovate leaves make *Helicodontium* quite distinct from ‘*Brachythecium athrocladum*’, although in peristome structure, wide distribution in South America and by

ITS data they are similar and can be assumed as a closest relatives.

Although our molecular phylogenetic analysis indicates closely related genera, it does not link ‘*Brachythecium athrocladum*’ to any particular genus. Among the Helicodontioideae there are a few other genera, with just one or two species, whose DNA has not yet been studied because they are known only from old collections. African *Schimperella* and South American *Mandoniella* are also in urgent need of molecular study. However, both these genera have smooth setae which, in addition to other characters, makes their rela-

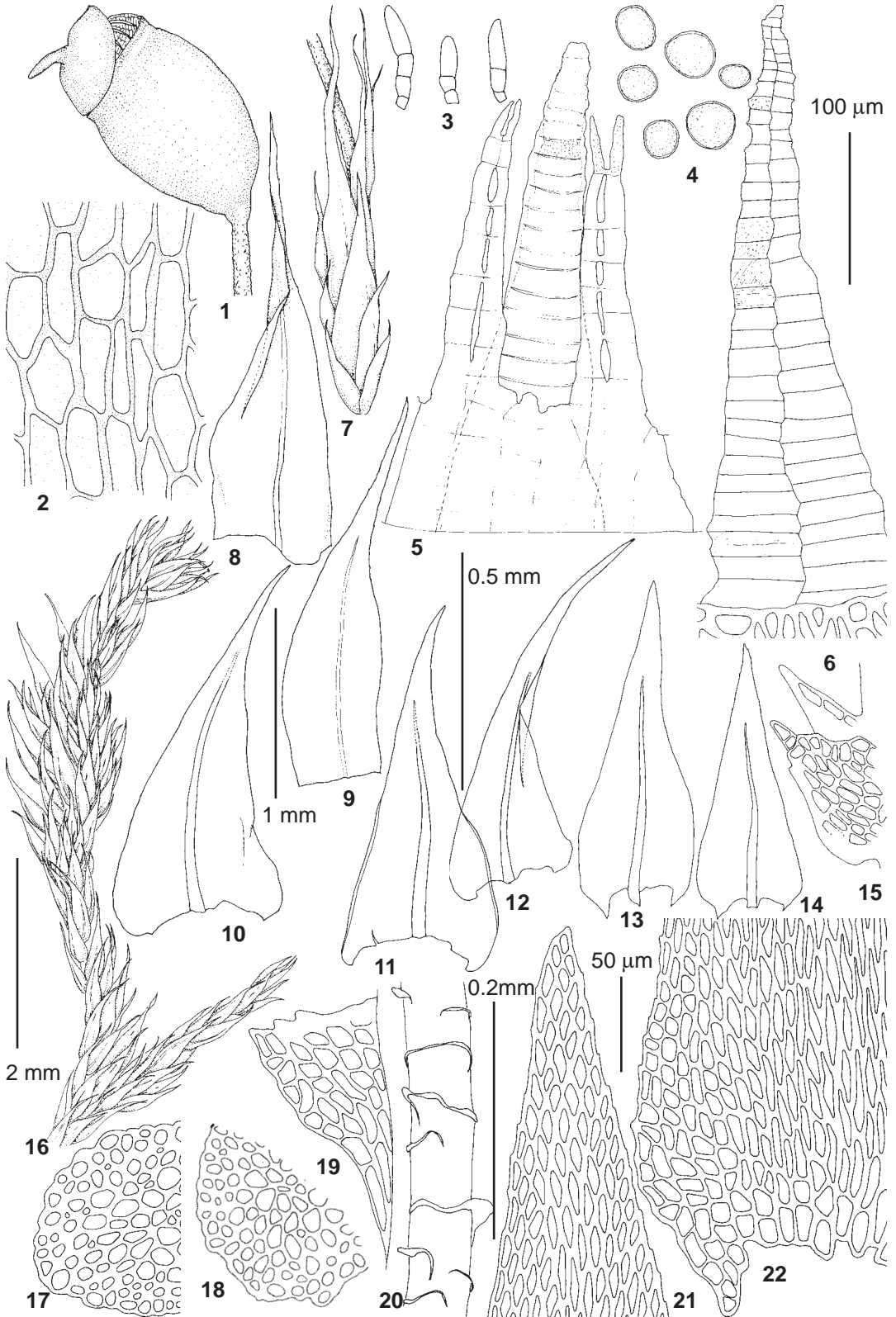


Fig. 2. *Sainthelenia athroclada* (Mitt.) Ignatov & M. Wigginton (from St Helena, 1-9 & 13-22 from Wigginton 05/513; 10-12 from Wigginton 05/165D, MHA): 1 – capsule with partly separated operculum (dry); 2 – exothecium; 3 – axillary hairs; 4 – spores; 5 – part of endostome and exostome from inside; 6 – exostome tooth from outside; 7 – perichaetium; 8-9 – perichaetial leaves; 10-11, 13 – stem leaves; 12, 14 – branch leaves; 15 – pseudoparaphyllia around branch primordium; 16 – habit; 17-18 – stem transverse section; 19 – leaf decurrency; 20 – stem with detached leaves, showing lines of their attachment to stem; 21 – upper laminal cell; 22 – lower laminal cells. Scale bars: 2 mm for 7, 16; 1 mm for 1, 8-9; 0.5 mm for 10-14; 0.2 mm for 20; 100 μ m for 4-6; 50 μ m for 2-3, 13, 17-19, 21-22.

tion to '*Brachythecium athrocladum*' unlikely.

The above facts left no better choice than the segregation of '*Brachythecium athrocladum*' to a new monospecific genus that is described below.

Sainthelenia Ignatov & M. Wigginton, gen nov.

Genus *Helicodontio* et *Clasmatodonti* proximum, sed capsula inclinata, peristomio madefacto inflexo, et cellulis foliorum longioribus differt.

Typus: *Hypnum athrocladum* Mitt.

The genus is close to *Helicodontium* and *Clasmatodon*, but differs in its inclined to horizontal capsule, xerocastique peristome and long laminal cells.

Sainthelenia athroclada (Mitt.) Ignatov & M. Wigginton, comb. nov.

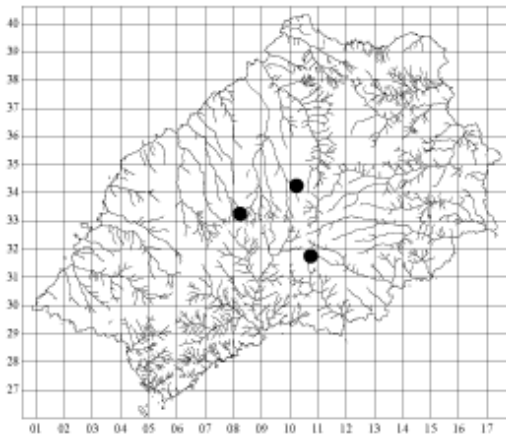
Hypnum athrocladum Mitt., in J.C. Melliss, *St. Helena*: 365. 1875; *Brachythecium athrocladum* (Mitt.) Paris, *Index bryologicus*, Suppl. 1. 1900. (holotype: *Burchell* 223-5, NY; isotype, BM).

Plants small, in dense mats, golden-yellow, glossy. Stems creeping, to 10 mm long, with small central stand and 2-layer cortex, densely pinnate-

ly branched; branches to 4 mm long, densely terete foliated; axillary hairs 30–55 μ m; pseudoparaphyllia triangular, small; rhizoids weakly papillose, abundant where stem attached to substrate. Leaves dimorphic. Stem leaves appressed when dry, spreading when moist, straight, 0.7–1.1 mm long, 0.25–0.4 mm wide, cordate-triangular below and from about mid-leaf tapered to lanceolate acumen, widest at about leaf insertion, rounded to insertion, conspicuously decurrent; weakly concave; margin often narrowly recurved below, otherwise flat, serrulate all around (sometimes weakly so above); costa 25–30 μ m near base, rather stout, reaching 0.6–0.7 of leaf length, ending without spine; mid-leaf cells 25–55 \times 5–7 μ m, thick-walled, basal cells shorter in 2–3 rows, to 8–13 \times 7–10 μ m, in leaf corners small cells numerous, forming extensive group to 10 cells wide and more than 15 long, indistinctly delimited from laminal cells. Branch leaves 0.55–0.8 mm, narrower and usually lanceolate, less broadened near base and less conspicuously decurrent, cells shorter, but otherwise similar to stem leaf cells. Autoicous. Perichaetial leaves reflexed, larger than stem leaves, innermost to 2.5 mm long and 0.6 mm wide, from ovate base moderately abruptly contracted to lanceolate acumen; costa thin but conspicuous, reaching the base of acumen. Seta dark-brown, to 5 mm long, strongly papillose. Capsule 1.0–1.3 mm long (without operculum), inclined to horizontal, elliptic, slightly curved, especially at back; operculum shortly rostrate. Peristome xerocastique; exostome teeth to 0.4 mm long, red-brown, striolate below and papillose above; endostome to 0.3 mm long, basal membrane about 1/3 of endostome height, segments narrow, narrowly perforated; cilia absent. Spores 20–34 μ m, variable in size within one capsule. Calyptra unknown.

Sainthelenia is known only from St Helena. The Burchell locality is not known, but in 2005 it was found at three sites (Fig 3) during a target-

Fig. 3. Distribution of *Sainthelenia athroclada* on St Helena.



ed search for this species, namely at Wash House Gut (467 m alt.), near Hutts Gate (620 m alt.) and below Casons (640 m alt.). Although the species is likely to occur elsewhere on the island, the fact that it was found in only three places might suggest the species is rare and local.

Sainthelenia grows on rocks and trunk bases. At the roadside near Hutts Gate it occurred in a pure extensive mat on the base of a large thorn tree, *Erythrina caffra* (Fig. 14). At Casons, it grew on a *Cupressus macrocarpa* trunk. Both *Erythrina caffra* and *Cupressus macrocarpa* were introductions to the island in the 19th century, and thus the original habitat might be rock, on which the species was found at the third site, Wash House Gut (dry rock face near waterfall). It is also possible that *Sainthelenia* may once have grown on large native trees at middle elevations on the island, but which were destroyed during the massive deforestation that occurred from the 16th century onwards.

Specimens examined:

1. Unknown location and habitat, 1805-1810, *Burchell* 223-5 (BM, isotype).

2. Below Casons: on trunk of large *Cupressus macrocarpa*, with *Cheilolejeunea ascensionis* and *Leucolejeunea xanthocarpa*, 640 m alt., 15°58'S 5°43'W, 23 October 2005, *Wigginton* 05/165D.

3. Near Hutts Gate: on roots and lower trunk of old thorn tree *Erythrina caffra* by the Alarm Forest road, N of Hutts Gate, 620 m alt., 15°57'S 5°42'W, 7 November 2005, *Wigginton* 05/513.

4. Wash House Gut: on vertical surface of dry rock, close to and on N side of waterfall, 467 m alt., 15°58'S 5°42'W, 11 November 2005, *Wigginton* 05/574.

Mature sporophytes were found to be fairly frequent in October–November 2005 in the populations near Casons and Hutts Gate, and sparse in the Wash House Gut population. In the Burchell collection, despite the statement in Mitten (1875) that only a single capsule is known, one capsule is present in the NY specimen (according to W.R. Buck, letter of 8 Jan 2009) and one in the BM specimen. The holotype, designated by Thiers (1992) is in NY, the isotype in BM.

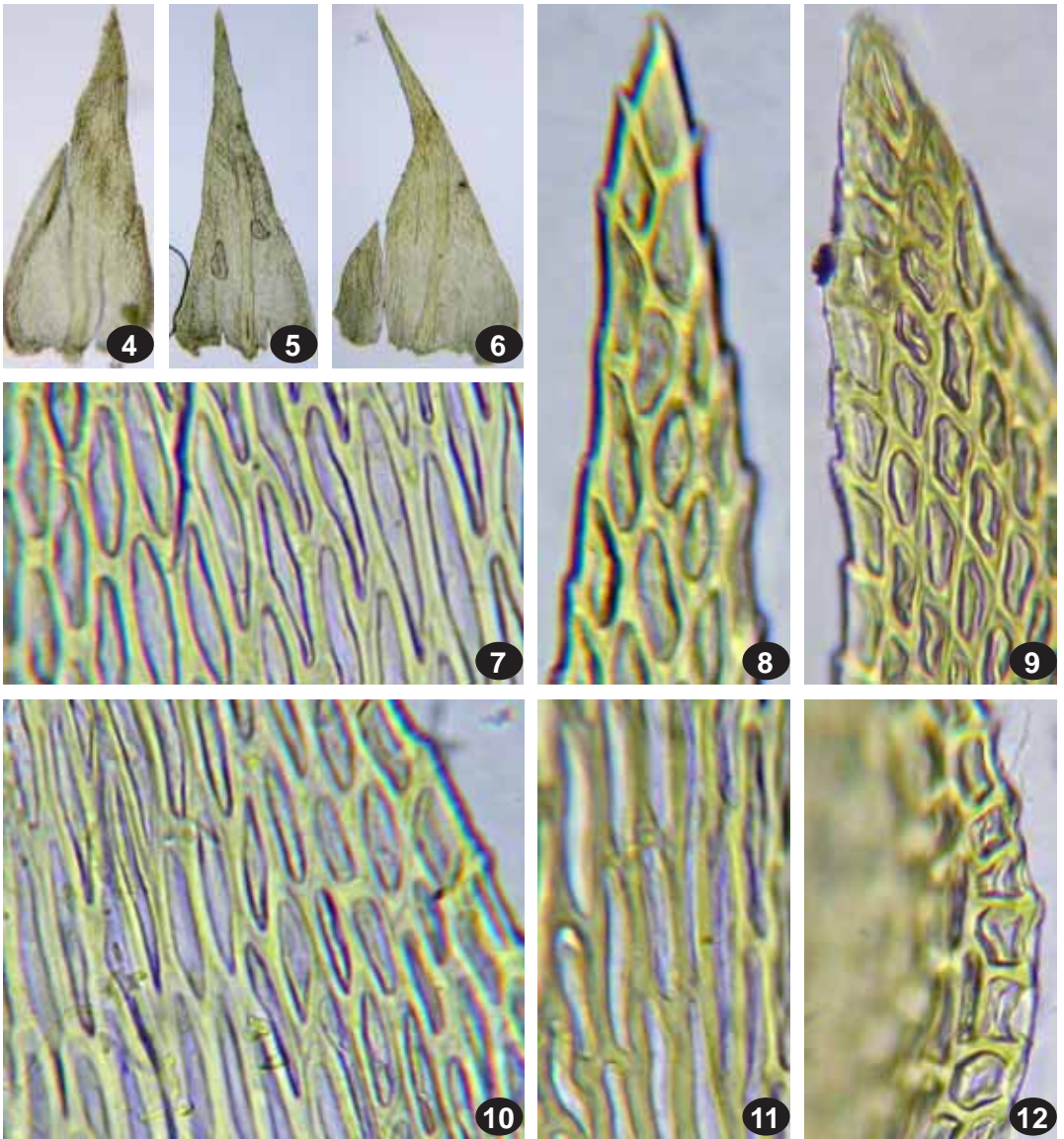
ACKNOWLEDGEMENTS

The support of the British Government's Overseas Territories Environmental Programme for the 2005 bryological survey of St Helena is acknowledged. MJW would also like to thank staff at the

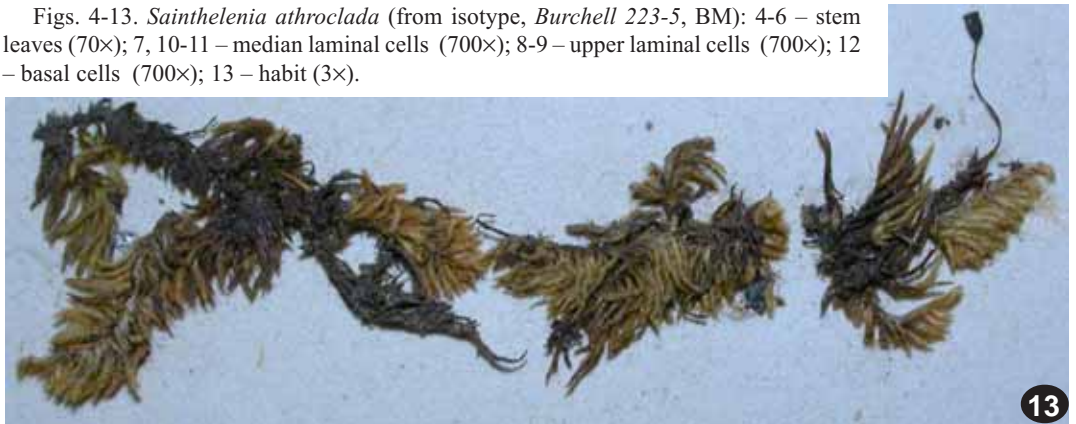
Department of Agriculture and Forestry Conservation & Wildlife Section, St Helena for permission to collect bryophytes on the island, and to Rebecca Cairns-Wicks and the St Helena National Trust for logistical support and help in many ways. We are indebted to Tom Blockeel for the Latin diagnosis, to Bill Buck for information on the NYBG specimen, and to Elena Ignatova for line drawings for the paper. The work of MI and OK was partly supported by RFBR 06-04-49493, 07-04-00013, 09-04-01324 and HIII-1275.2008.4.

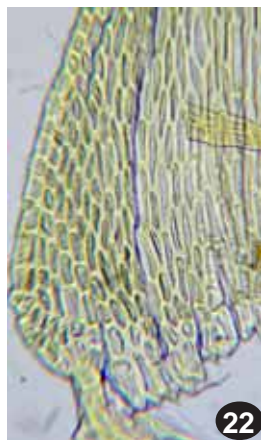
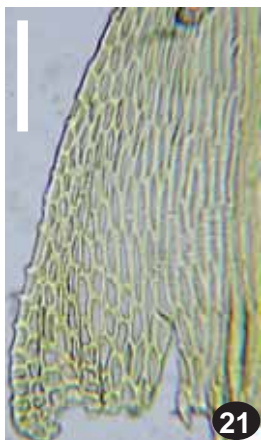
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Figs. 4-13. *Sainthelenia athroclada* (from isotype, *Burchell* 223-5, BM): 4-6 – stem leaves (70×); 7, 10-11 – median laminal cells (700×); 8-9 – upper laminal cells (700×); 12 – basal cells (700×); 13 – habit (3×).





Figs. 14-23. *Sainthelena athroclada* (21-22 - from isotype, *Burchell 223-5*, BM; 14-20,23 from *Wigginton 05/513*): 14 – habitat; 15-16, 23 – habit (2×,7×,10×); 21-22 – lower part of leaves (300×); 17 & 19 – somewhat immature operculate capsules, dry (13×); 18 – operculum (30×); 20 – opened capsule, wet (20×).

Table 1. Specimen data and Genbank accession numbers
Species

	trnL-F	ITS1	ITS2	Voucher specimen for sequences
<i>Aeolindigia capillacea</i> (Hornch.) Menzel	AY044072	DQ200118	AF395634	Ecuador, Norris & Bolivar 92175 (H)
<i>Brachytheciasastrum falcattulum</i> (Broth.) Ignatov & Huttunen	AF397774	DQ336897	AF403662	Russia, Altai, Ignatov 0/1680 (MHA)
<i>Brachytheciasastrum velutinum</i> (Hedw.) Ignatov & Huttunen	AF397832	EU567476	AF403667	Finland, Huttunen 23 Aug. 1988 (H)
<i>Brachythecium buchananii</i> (Hook.) Jaeger	AF397792	DQ200075	AF403595	China, Koponen et al. 53972 (H)
<i>Brachythecium mildeanum</i> (Schimp.) Schimp.	-	GQ246846	GQ246846	Russia, Tatarstan, Ignatov & Ignatova 18.VIII.2003 (MHA)
<i>Brachythecium mildeanum</i> (Schimp.) Schimp.	AY184777	-	-	Russia, Ignatov 20 May 1999 (MHA)
<i>Brachythecium percurrrens</i> Hedenäs	-	AY737469	AY737469	Madeira, Hedenäs MA91-295 (S)
<i>Brachythecium rivulare</i> Bruch et al.	AF397866	DQ200076	AF403651	Finland, Parnela, 19 May 1996 (H)
<i>Brachythecium rutabulum</i> (Hedw.) Bruch et al.	-	DQ200078	AF403644	Finland, Huttunen 1415 (H)
<i>Bryandersonia illecebra</i> (Hedwig) H. Robinson	AF397819	-	-	U.S.A. Bowers 22214 (H)
<i>Cirriphyllum crassinervium</i> (Tayl.) Loeske & M.Fleisch.	-	AY848960	AY848960	Frahm, 29 Jul 1999
<i>Cirriphyllum crassinervium</i> (Tayl.) Loeske & M.Fleisch.	AF397868	-	-	Russia, Ignatov, 23. Aug. 1999 (MHA)
<i>Cirriphyllum piliferum</i> (Hedwig) Grout	AF397799	DQ200081	AF403608	Finland, Koponen & Huttunen 1324 (H)
<i>Clasmatodon parvulus</i> (Hampe) Sull.	AF397813	DQ200082	AF403614	U.S.A.Redfearn & Allen, 23 Apr 1992 (H)
<i>Donrichardia patulifolia</i> (Card. & Ther.) Ignatov & Huttunen	AF397850	DQ336913	DQ336913	China, Koponen et al., 53920 (H)
<i>Eurhynchium angustirete</i> (Broth.) T.Kop.	AF397825	DQ200086	AF403621	Russia, Ignatov, 3 July 1998 (MHA)
<i>Helicodontium capillare</i> (Hedw.) Jaeg.	AF397855	DQ200087	DQ336905	Colombia, Churchill et al. 4 May 1990 (H)
<i>Homalotheciella subcapillata</i> (Hedw.) Broth.	AF397860	DQ200088	AF403658	USA, Allen & Redfearn, 29 Mar 1995 (H)
<i>Homalothecium fulgescens</i> (Mitt.) Lawt.	AF397877	EF558542	AF403637	British Colombia, Streimann 43136 (H)
<i>Homalothecium lutescens</i> (Hedw.) Robinson	-	EF617559	EF617559	Denmark, Hedenäs 20 Apr 2005 (S)
<i>Homalothecium lutescens</i> (Hedw.) Robinson	AF397827	-	-	Czech Rep., Vána & Enroth, 30 Apr. 1999 (H)
<i>Homalothecium megaptilium</i> (Sull.) Robinson	-	EF617568	EF617568	U.S.A., Washington, Schofield 119346 (UCB)
<i>Homalothecium megaptilium</i> (Sull.) Robinson	AF397842	-	-	U.S.A., Newton 5206 (H)
<i>Homalothecium sericeum</i> (Hedw.) B.S.G.	AF397805	DQ336906	AF403587	Finland, Koponen & Huttunen 1322 (H)
<i>Kindbergia praelonga</i> (Hedw.) Ochyra	-	AY654610	AY654610	Belgium, Goffinet 3840
<i>Kindbergia praelonga</i> (Hedw.) Ochyra	AY184795	-	-	Colombia, Churschill et al., 13418 (BONN)
<i>Meteoriella soluta</i> (Mitt.) S. Okamura	AF397808	-	-	China, Koponen et al. 49610 (H)
<i>Okamuraea brachydiction</i> (Card.) Nog.	AY184789	DQ200090	AF503537	China, Koponen et al. 48969 (H)
<i>Oxyrrhynchium hians</i> (Hedw.) Warnst.	AF397815	DQ336908	AF403603	China, Koponen et al. 53740 (H)
<i>Oxyrrhynchium pumilum</i> (Wilson) Schimp.	AY184790	DQ336909	DQ336909	Abkhazia, Ignatov, 8 Aug. 1987 (MHA)

Table 1. Specimen data and Genbank accession numbers (continued)
Species

	trnL-F	ITS1	ITS2	Voucher specimen for sequences
<i>Palamocladium leskeoides</i> (Hook.) Britt.	AF397791	DQ200093	AF403596	China, Koponen et al. 52596 (H)
<i>Plasteurhynchium striatulum</i> (Spruce) M.Fleisch.	-	AY737454	AY737454	Vanderpoorten s.n (LG)
<i>Plasteurhynchium striatulum</i> (Spruce) M.Fleisch.	AY184792	-	-	Abkhazia, Ignatov, 1 Aug 1987 (MHA)
<i>Platyhypnidium austrinum</i> (Hook. et Wils.) M.Fleisch.	AY184791	DQ200095	AY166449	Australia, Streimann 49544 (H)
<i>Pseudoscleropodium purum</i> (Hedw.) Fleisch	AF397797	-	-	Czech Rep., Vana & J. Enroth (H)
<i>Remyella brachypodia</i> (Fleisch.) Ignatov & Huttunen	AF397854	DQ336920	AF403600	Papua New Guinea, Koponen 33007 (H)
<i>Rhynchostegiella durieui</i> (Mont.) P. Allorge & Perss.	DQ208213	DQ200104	DQ200975	Azores, Hedenäs 28 Sept 2000 (S)
<i>Rhynchostegiella macilenta</i> (Ren. & Card.) Card.	AF397781	DQ200105	AF403570	Madeira, Hedenäs B4503 (S)
<i>Rhynchostegiella tenella</i> (Dicks.) Limpr.	AY044070	DQ200107	AF395633	Abkhazia, Ignatov, 2 Aug. 1987 (MHA)
<i>Rhynchostegium pallidifolium</i> (Mitt.) Jaeg.	AF397807	DQ200110	AF403618	China, Koponen et al. 51301 (H)
<i>Rhynchostegium riparioides</i> (Hedw.) Cardot	DQ208207	DQ200100	DQ200970	Abkhazia, Ignatov, 8 Aug. 1987 (MHA)
<i>Sainthelenia athroclada</i> (Mitt.) Ignatov & M. Wigginton	GQ254300	GQ246862	GQ246862	St Helena, Wigginton 05/513 (MHA)
<i>Sciuro-hypnum curtum</i> (Lindb.) Ignatov	-	EU715329	EU715329	Russia, Ignatov&Ignatova 18 Aug 2003 (MHA)
<i>Sciuro-hypnum curtum</i> (Lindb.) Ignatov	AF397784	-	-	Finland, Huttunen 1439 (H)
<i>Sciuro-hypnum plumosum</i> (Hedw.) Ignatov & Huttunen	-	AY737457	AY737457	U.S.A., Vanderpoorten 5042 (LG)
<i>Sciuro-hypnum plumosum</i> (Hedw.) Ignatov & Huttunen	AF397814	-	-	China, Koponen et al. 56777 (H)
<i>Sciuro-hypnum populeum</i> (Hedw.) Ignatov & Huttunen	AF397873	DQ200114	AF403640	Finland, Pykälä 7029 (H)
<i>Sciuro-hypnum reflexum</i> (Stärke) Ignatov & Huttunen	-	EU715353	EU715353	Russia, Ignatov&Ignatova 19 Aug 2001 (MHA)
<i>Sciuro-hypnum reflexum</i> (Stärke) Ignatov & Huttunen	AF397858	-	-	Finland, Huttunen 1195 (H)
<i>Scorpiurium circinnatum</i> (Brid.) Fleisch. & Loeske	AF397834	-	-	Abkhazia, Ignatov, 8 Aug. 1987 (MHA)
<i>Trachypus bicolor</i> Reinw. & Hornsch.	-	DQ200118	AF395624	China, Koponen et al. 50721 (H)