

A FURTHER RANGE EXTENSION FOR *REDFEARNIA* (BRYOPHYTA,
AMBLYSTEGiaceae), WITH NEW DATA ON ITS PHYLOGENETIC POSITION
О РАСШИРЕНИИ АРЕАЛА РОДА *REDFEARNIA* (BRYOPHYTA, AMBLYSTEGiaceae)
И НОВЫХ ДАННЫХ О ЕГО ФИЛОГЕНЕТИЧЕСКОМ ПОЛОЖЕНИИ

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Abstract

Redfearnia bairi is reported from southern Siberia, Russia, from the Altai Mountains in the Altai Republic and from the West Sayan foothills in Khakassia. Its previously suggested enigmatic origin as a putative intrafamilial hybrid is supported. Molecular phylogenetic analysis of a wider set of pleurocarps confirmed the similarity of its nuclear ITS1 to *Herzogiella* (Plagiotheciaceae), while ITS2 is similar to *Campylophyllum*, *Platyhypnum*, *Drepanium*, *Podperaea*, and *Tomentypnum*, which form a basal grade within the Amblystegiaceae. Affinity to the latter group of genera is found in separate analyses of plastid *atpB-rbcL*, *trnG* and *trnS-trnF*, and of mitochondrial *nad5*. IGS sequences that are situated in the genome after ITS2 also support affinity to the Amblystegiaceae. Thus, the only evidence for foreign genes with affinity to the *Herzogiella* come from nuclear ITS1. However, this evidence is very clear and confirmed from plants from five localities separated from each other by hundreds or thousands of kilometers. Possible explanations for this inconsistency are discussed. Morphological distinctions between the Asian and American species of *Redfearnia* are reviewed.

Резюме

Приводятся находки *Redfearnia bairi* из России – с юга Сибири в горах Алтая (Республика Алтай) и в предгорьях Западного Саяна (Хакасия). Подтверждено ранее высказанное предположение о происхождении рода *Redfearnia* в результате гибридизации между представителями разных семейств. Молекулярно-филогенетический анализ расширенной выборки бокоплодных мхов подтвердил сходство ядерного маркера ITS1 *Redfearnia* с этим маркером рода *Herzogiella* (Plagiotheciaceae), тогда как его ITS2 свидетельствует о родстве с родами *Campylophyllum*, *Platyhypnum*, *Drepanium*, *Podperaea* и *Tomentypnum*, образующими в филогенетическом древе базальную группу к семейству Amblystegiaceae. Сходство *Redfearnia* с этой группой родов было выявлено и при независимом анализе пластидных маркеров *atpB-rbcL*, *trnG* и *trnS-trnF*, а также митохондриального *nad5*. Несколько полученных последовательностей IGS, расположенного в геноме после ITS2, сходны с последним маркером в том, что они показывают родство *Redfearnia* с семейством Amblystegiaceae. Таким образом, единственное свидетельство родства этого рода с *Herzogiella* происходит от ядерного маркера ITS1. Тем не менее, ITS1, полученный из растений из пяти популяций, разделенных друг от друга сотнями и тысячами километров, показывает очень четкую картину. Обсуждаются возможные объяснения этого несоответствия данных по ITS1 и остальным изученным маркерам. Приведены морфологические отличия между азиатскими и американскими популяциями рода *Redfearnia*.

KEYWORDS: mosses, hybridization, disjunctions, Plagiotheciaceae, *Herzogiella*, *Redfearnia*, *Podperaea*, taxonomy, ITS, molecular phylogenetics

INTRODUCTION

Molecular phylogenetic studies in recent decades have given new insights into phylogenetic relationships in many groups of living beings. The traditional classification of well-defined groups has usually been supported, while molecular studies of difficult taxa with questionable placement have often yielded unexpected

results, which have often been corroborated by closer morphological studies. This has been especially true for groups with a deficiency of morphological characters, such as mosses, and especially pleurocarpous mosses (Vanderpoorten *et al.*, 2002; Ignatov *et al.*, 2007; Goffinet *et al.*, 2009; Huttunen *et al.*, 2012, 2013; Kučera *et al.*, 2019).

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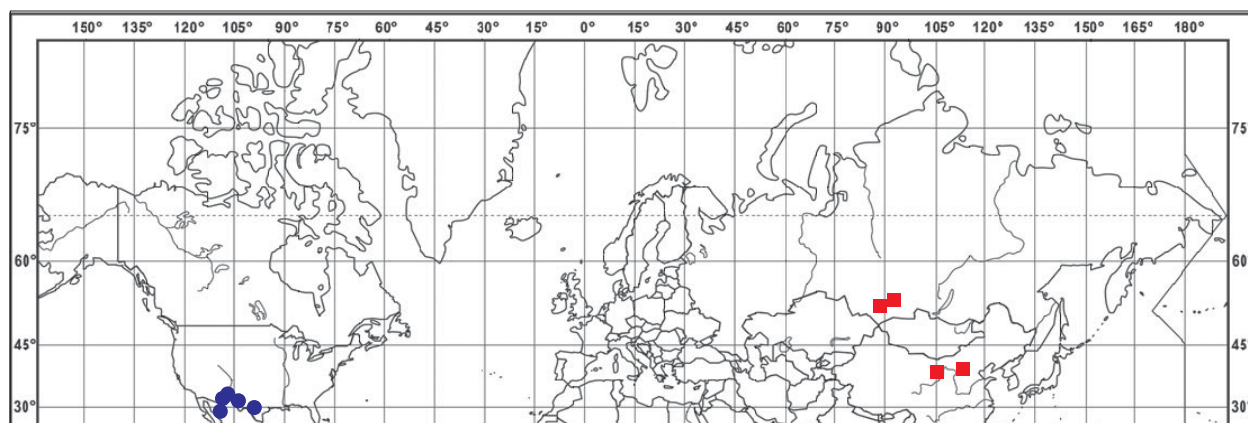


Fig. 1. Distribution of *Redfearnia homomallifolia* (Redf.) J.T. Wynns (blue circles) and *R. baii* (red squares).

However, not all molecular phylogenetic studies yield unequivocal results. One such case is the genus *Redfearnia* J.T. Wynns. Wynns (2020) erected this genus for the rare North American species *Pseudotaxiphyllum homomallifolium* (Redf.) Ireland, which he found to be very different from other species of the genus *Pseudotaxiphyllum* Z. Iwats. in terms of nuclear ITS sequences; however, he failed to place it in any family. Wynns also found that *P. homomallifolium* has very similar ITS sequence as *Podperaea baii* Ignatov, described from Inner Mongolia, China (Ignatov & Milyutina, 2011), which he also transferred to *Redfearnia*.

Thus, *Redfearnia baii* (Ignatov) J.T. Wynns is an enigmatic moss with a putative intrafamilial hybrid origin: its ITS1 sequence is very similar to *Herzogiella turfacea* (Lindb.) Z. Iwats. belonging to the Plagiotheciaceae (Ignatov & Milyutina, 2011), while ITS2 has nothing to do with that family. Plants from Inner Mongolia were previously referred to *Podperaea krylovii* (Podp.) Z. Iwats. & Glime (Zhao *et al.*, 2006; Bai, 2010) on the basis of morphological similarity, and later Ignatov & Milyutina (2011) found a certain similarity in the ITS2 sequences of Inner Mongolian plants to species of Ambystegiaceae, including *P. krylovii*. The link was not as obvious as the

similarity of ITS1 to *Herzogiella* Broth., but was most similar to a group of genera in a basal grade of the Amblystegiaceae, including *Campylophyllum* (Schimp.) M. Fleisch., *Drepanium* (Schimp.) Lange & C.E.O. Jensen, *Myrinia* Schimp., *Platyhypnum* Loeske, and *Tomentypnum* Loeske (Ignatov *et al.*, 2007; Huttunen *et al.*, 2012).

The original conclusion of Ignatov & Milyutina (2011) was that *Podperaea baii* is an extremely strange moss with an “impossible” combination of ITS1 and ITS2. However, as its distribution was thought to be confined only to one province of China, this case remained not much further studied, also due to a paucity of collections and ambiguous results found in preliminary analyses of small sets of *trnL*-F and *rps4* sequences.

Shortly afterward, the species was collected in South Siberia in two mountain areas, in Altai and in the West Sayans (east of Altai), thus its Asian distribution appeared to exceed 2200 km (unpublished). In addition, Wynns (2020) found that the North American moss known as *Pseudotaxiphyllum homomallifolium*, occurring 10000–12000 km from Asian populations of *Podperaea baii*, is very similar to that species in terms of ITS. Wynns thus placed these two species in the newly established genus

Table 1. Primers for PCR used in this study, and programs for DNA regions.

Region	Primer		F/R	Reference	Program
IGS	26dR2	GAGATGAATCCTTTGCAGACG	F	Wicke <i>et al.</i> , 2011	94°C 3' (initial denaturation); 30 cycles: 94°C 20", 62°C 20", 72°C 40"; 72 5'
	5S(r)R2	GAGTTCTGATGGGATCYGGTG	R	Wicke <i>et al.</i> , 2011	
ITS	ITS1	TCCGTAGGTGAACCTGCGG	F	White <i>et al.</i> , 1990	94°C 3' (initial denaturation); 58°C 30"; 72°C 1'; 32 cycles: 94°C 30", 58°C 30", 72°C 1'; 72°C 5'
	ITSB	GATATGCTTAAACTCAGCGGG	R	Sahin <i>et al.</i> , 2007	
<i>trnS-trnF</i>	trnSf	TACCGA GGGTTCGAA TC	F	Souza-Chies <i>et al.</i> , 1997	80°C 5' (initial denaturation); 30 cycles: 95°C 1', 56°C 1', 62°C 50'; Ramp 0,3 C/s, 62°C 4'; 94°C 30", 58°C 30", 72°C 1'; 62°C–5'
	F	ATT TGAACCTGGTGACACGAG	R	Taberlet <i>et al.</i> , 1991	
<i>trnG</i>	trnGF1	ACCCGCATCGTT AGCTTG	F	Pacak & Szweykowska -Kulińska, 2000	95°C 5' (initial denaturation); 35 cycles: 95°C 30", 56°C 30", 72°C 90"; 72°C 8'
	trnGR	GCGGGTATAGTTTAGTGG	R		
<i>atpB-rbcL</i>	atpB1	ACATCKARTACKGGACCA ATA A	F	Chiang <i>et al.</i> , 1998	95°C 3' (initial denaturation); 28 cycles: 95°C 30", 48°C 1', 72°C 2'; 72°C 3'
	rbcL1	AACACCAGCTTTTRAATCCAA	R	Chiang <i>et al.</i> , 1998	
<i>nad5</i>	Nad5F4	GAAGGAGTAGGTCTCGCTTCA	F	Beckert <i>et al.</i> , 1999	94°C 3' (initial denaturation); 30 cycles: 94°C 20", 48°C 30", 72°C 1'; 72°C 5'
	Nad5R3	AAA ACGCCTGCTGTTACCAT	R	Beckert <i>et al.</i> , 1999	

Table 2. Specimens used in the molecular phylogenetic analysis, their isolate numbers and GenBank accession numbers.

Species	Isolate	Voucher	trnS-F	ITS	nad5	atpB	trnG	IGS
<i>Podperaea krylovii</i>	IM141 [653]	Russia, Primorsky, Ignatov 08-308, MHA	MZ333189	JN896328	MZ333174	MZ333206	MZ333183	
<i>Podperaea krylovii</i>	IM69 [651]	China, Inner Mongolia, Bai 04095, MHA		JN896327		MZ333207		MZ333167
<i>Podperaea krylovii</i>	OK420	Russia, Amur, Bezgodov, MHA	MZ333191		MZ333176		MZ333184	MZ333168
<i>Podperaea krylovii</i>	IM19 [650]	Russia, Altai, Ignatov 1/10, MHA		JN896326				
<i>Podperaea krylovii</i>	IM192 [652]	Russia, Primorsky, Ignatov 07-220, MHA	MZ333190	JN896329	MZ333175	MZ333205	MZ333182	
<i>Redfearnia baii</i>	IM238	China, Inner Mongolia, Hohhot Koi Jin, MHA	MZ333193	JN896324	MZ333178			MZ333170
<i>Redfearnia baii</i>	IM237	China, Inner Mongolia, Manchuan Ignatov 24-10-2008, MHA		JN896325				
<i>Redfearnia baii</i>	IM82 [649]	China, Inner Mongolia, Bai X.-L. 058141, MHA	MZ333194	JN896321	MZ333179	MZ333201	MZ333188	MZ333171
<i>Redfearnia baii</i>	IM142 [649]	China, Inner Mongolia, Bai X.-L. 058141, MHA	MZ333192	JN896323	MZ333177	MZ333200	MZ333185	MZ333169
<i>Redfearnia baii</i>	OK2862	Russia, Khakasia, Abakan, Ignatov & Spirina, 11-5015, MHA	MZ333195	MZ269419	MZ333180	MZ333199	MZ333186	
<i>Redfearnia baii</i>	OK2862a	Russia, Khakasia, Abakan, Ignatov & Spirina, 11-5040, MHA			MZ333181			
<i>Redfearnia baii</i>	OK549	Russia, Altai, Chulyshman, Ignatov & Ignatova, MHA	MZ333196	MZ269418		MZ333202	MZ333187	
<i>Amblystegium serpens</i>	OK2668	Russia, Murmansk, Kozhin M-M-717, MW9078005				MZ333197		
<i>Campylophyllopsis sommerfeltii</i>	IM169	Russia, Kuril Islands, Ignatov #06-1901, MHA				MZ333198		
<i>Herzogiella perrobusta</i>	OK2631	Russia, Kuril Islands, Ignatov #06-1470, MHA9035906		MZ269420				
<i>Herzogiella perrobusta</i>	OK2633	Russia, Primorsky Territory, Ignatov et al. #13-1796, MHA9035893		MZ269421				
<i>Herzogiella turfacea</i>	IM162	Russia, Kuril Islands, Ignatov #06-1262, MW				MZ333203		MZ333172
<i>Herzogiella turfacea</i>	IM335	Russia, Vologda, Ignatov & Ignatova 11 Aug 2001, MHA				MZ333204		MZ333173
<i>Herzogiella turfacea</i>	OK2630	Russia, Karelia, Maksimova #K-03/69, MHA9035889		MZ269422				

Redfearnia. Further elucidation of the phylogenetic position of this genus is the aim of this report, along with new data on its distribution and ecology in Asia.

MATERIAL AND METHODS

Redfearnia specimens from the previous study were supplemented with new collections from Russia (Fig. 1), from the Altai Mountains and from the Abakan River basin in the foothills of the West Sayans. Some additional specimens of the genus *Herzogiella* that showed a similarity to *Redfearnia* in terms of ITS1 were also sequenced.

In addition to nuclear ITS, we sequenced mitochondrial *nad5* and plastid *trnG* and *trnS-trnF*. These regions have been widely used in recent molecular studies of pleurocarps, so their sequences are well represented in GenBank for many pleurocarpous moss families (Olsson *et al.*, 2009a, 2009b, 2010, 2011; Stech & Quandt, 2014; Wynns & Lange, 2014; Kučera *et al.*, 2019; Ignatov *et al.*, 2019a).

A few nuclear ribosomal IGS sequences were also obtained for *Redfearnia bairi* and the two species closest to it, *Herzogiella turfacea* and *Podperaea krylovii*. This marker is more variable than ITS, but also more difficult to amplify, align and analyse, although in some cases it obviously improves the phylogenetic resolution (Ignatova *et al.*, 2017, 2020). Although it can not be used for an expanded data set of pleurocarpous mosses, a comparison between three genera (in this case *Redfearnia*, *Herzogiella* and *Podperaea*) can easily be performed.

Molecular phylogenetic studies

The laboratory protocol was essentially the same as in Gardiner *et al.* (2005). Primers used for amplification are shown in Table 1.

Datasets

BLAST searches of plastid and mitochondrial sequences from *Redfearnia bairi* were carried out in GenBank, and the 300 most similar results were used for subsequent analyses. Redundant sequences were removed. Final plastid data sets included 96 sequences of *atpB-rbcL*, 117 of *trnG*, and 77 of *trnS-trnF*, as well as 201 sequences of mitochondrial *nad5*. Data on newly sequenced samples are in Table 2.

We tried to include as many groups of Hypnales as possible, especially for families that have leaves with poorly developed costae. In many cases one species was represented by more than one specimen, especially for the Plagiotheciaceae and the Amblystegiaceae, families that according to Ignatov & Milyutina (2011) and preliminary tests were most likely related to *Redfearnia*.

Sequences were aligned using MAFFT v. 7.402 (Kato & Standley, 2013) with standard settings.

For ITS we used the alignment from Kučera *et al.* (2019), supplemented by *Redfearnia*, *Podperaea*, and some additional Plagiotheciaceae.

Bayesian analyses were performed in MrBayes v. 3.2.6 (Ronquist *et al.*, 2012), using four rounds, six Markov

chains, 20,000,000 generations, and the GTR+G model of nucleotide sequence evolution. The chain temperature was set at 0.02 in all analyses. Convergence of each analysis was evaluated using Tracer v. 1.4.1 (Rambaut & Drummond, 2007). Consensus trees were calculated after omitting the first 25% of trees as a burn-in. Analyses were performed on the Cipres Science Gateway (<http://www.phylo.org/portal2>) on XSEDE (Miller *et al.*, 2010).

RESULTS

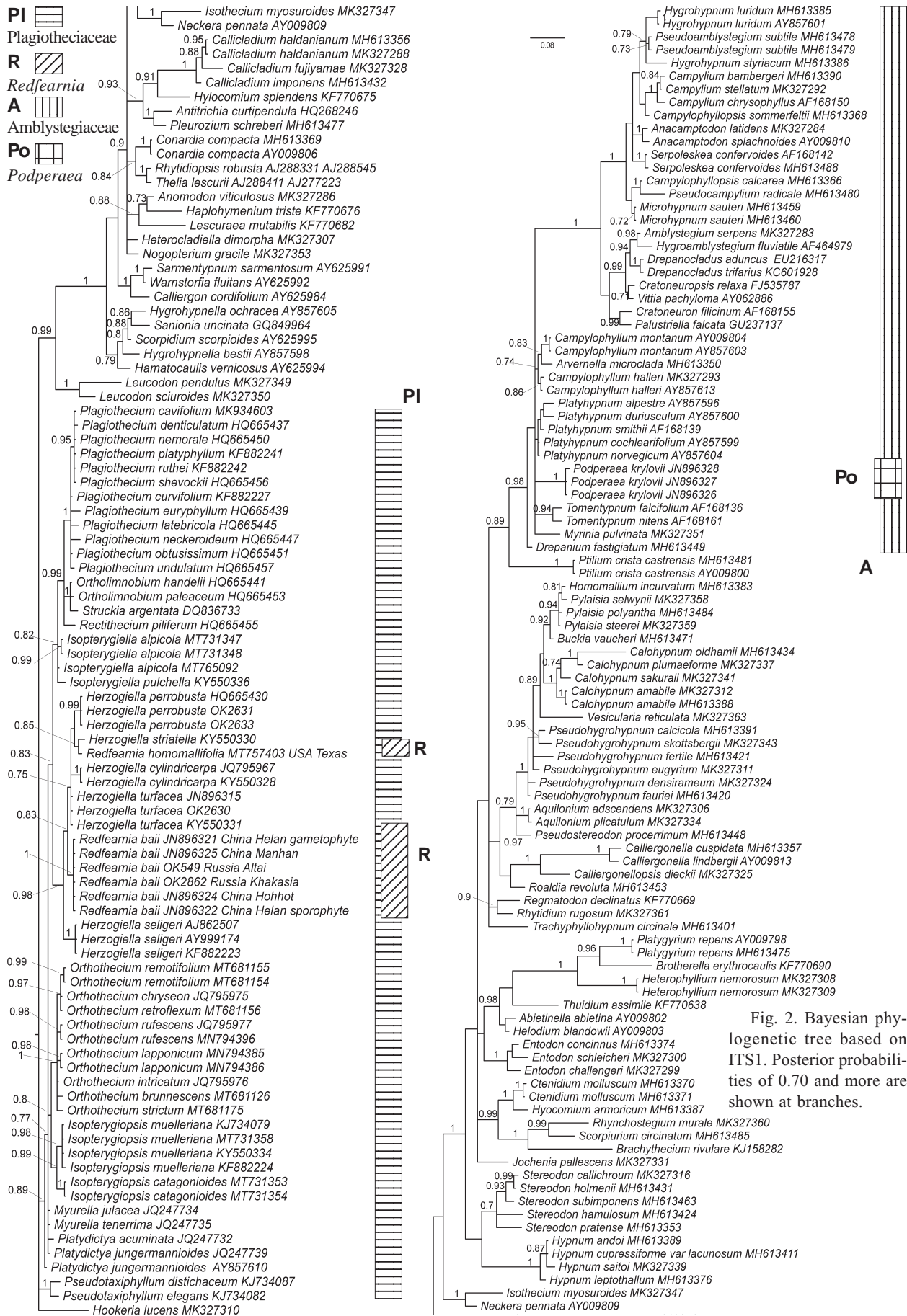
ITS1 tree (Fig. 2). *Redfearnia* was resolved in a *Herzogiella* clade (PP=0.98) that was sister to a *Plagiothecium* Schimp.+*Struckia* Müll. Hal.+*Ortholimnobia* Dixon+*Rectithecium* Hedenäs & Huttunen +*Isopterygiella* Ignatov & Ignatova clade (PP=0.82), and their mutual clade is weakly supported (PP=0.82). All representatives of Plagiotheciaceae in this analysis formed a basal grade. Within the *Herzogiella*+*Redfearnia* clade, *H. seligeri* (Brid.) Z. Iwats. was sister to the rest of the group; then *Redfearnia bairi* formed a clade (PP=1.0) sister to the other species of *Herzogiella* plus *Redfearnia homomallifolia*. The latter species formed a poorly-supported subclade with *H. striatella* (Brid.) Z. Iwats. within the terminal clade. *Podperaea krylovii* was resolved in a basal grade of Amblystegiaceae (PP=0.98) with *Arvernella* Hugonot & Hedenäs, *Campylophyllum*, *Drepanium*, *Myrinia*, *Platyhypnum* p.p., and *Tomentypnum*.

ITS2 tree (Fig. 3). Similar to ITS1, the tree included a basal grade of Plagiotheciaceae, but *Redfearnia* was absent there. Both *Redfearnia* and *Podperaea* were resolved in a grade that included *Arvernella*, *Campylophyllum*, *Platyhypnum* p.p., and *Tomentypnum*. This grade subtended a polytomy of many groups of mosses terminated by a clade of Pylaisiaceae. The genera *Myrinia*, *Drepanium*, and some species of *Platyhypnum* were scattered in the polytomy. The species that formed a basal grade of Amblystegiaceae in ITS1 were not all resolved together, nor did they fall in the Amblystegiaceae.

trnG tree (Fig. 4). This plastid marker resolved most species in a polytomy of five clades. The Plagiotheciaceae and Amblystegiaceae were found in different clades, which included representatives of other families as well. *Redfearnia* and *Podperaea* formed a clade with low support, while their own clades had maximal posterior probabilities. This *Redfearnia*+*Podperaea* clade fell in a basal grade of Amblystegiaceae, which also included *Scorpidium* and *Sanionia* of the Scorpidiaceae.

trnS-trnF tree (Fig. 5). This tree showed a pattern similar to *trnG*: most species were resolved in a polytomy of six clades. One of these clades included only Plagiotheciaceae, and another only Amblystegiaceae s.str. plus *Redfearnia* and *Podperaea*.

atpB-rbcL tree (Fig. 6). The tree was poorly resolved, somewhat resembling the ITS2 tree. The Amblystegiaceae clade included both *Podperaea* and *Redfearnia*, however, it was not supported. Core Plagiotheciaceae (*Plagiothecium* and also *Herzogiella*), Scorpidiaceae and part



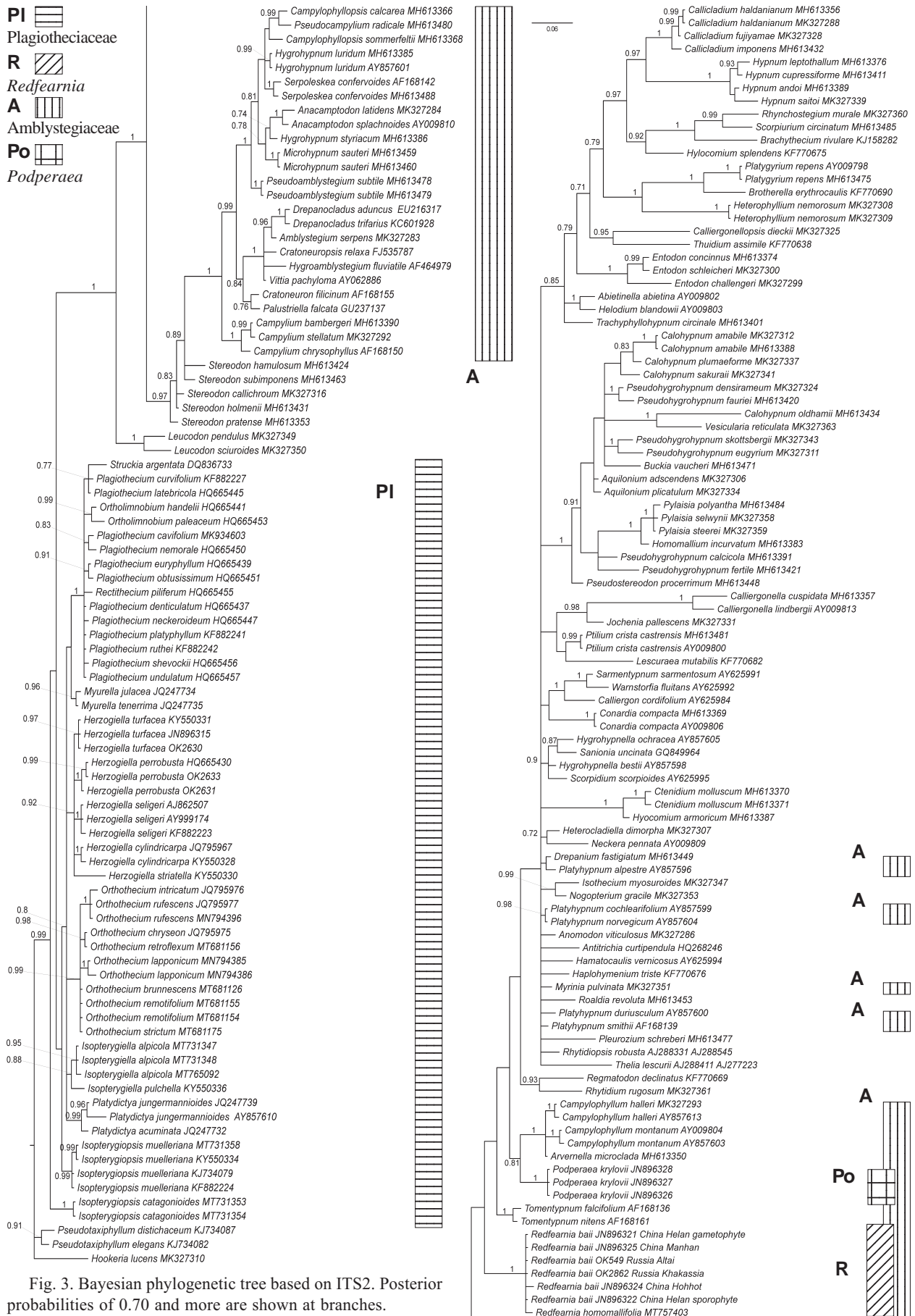
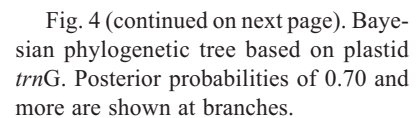


Fig. 3. Bayesian phylogenetic tree based on ITS2. Posterior probabilities of 0.70 and more are shown at branches.



ITS differences between *Redfearnia bairi* and *R. homomallifolia* included four substitutions and one insertion (of 3 nt) in ITS1, and two substitutions and one insertion (of 1 nt) in ITS2. At the same time, the differences between *Redfearnia bairi* and *Herzogiella turfacea* included three substitutions and no insertions in ITS1, and 35 substitutions and 6 indels (of 1, 9, 8, 1, 4, and 24

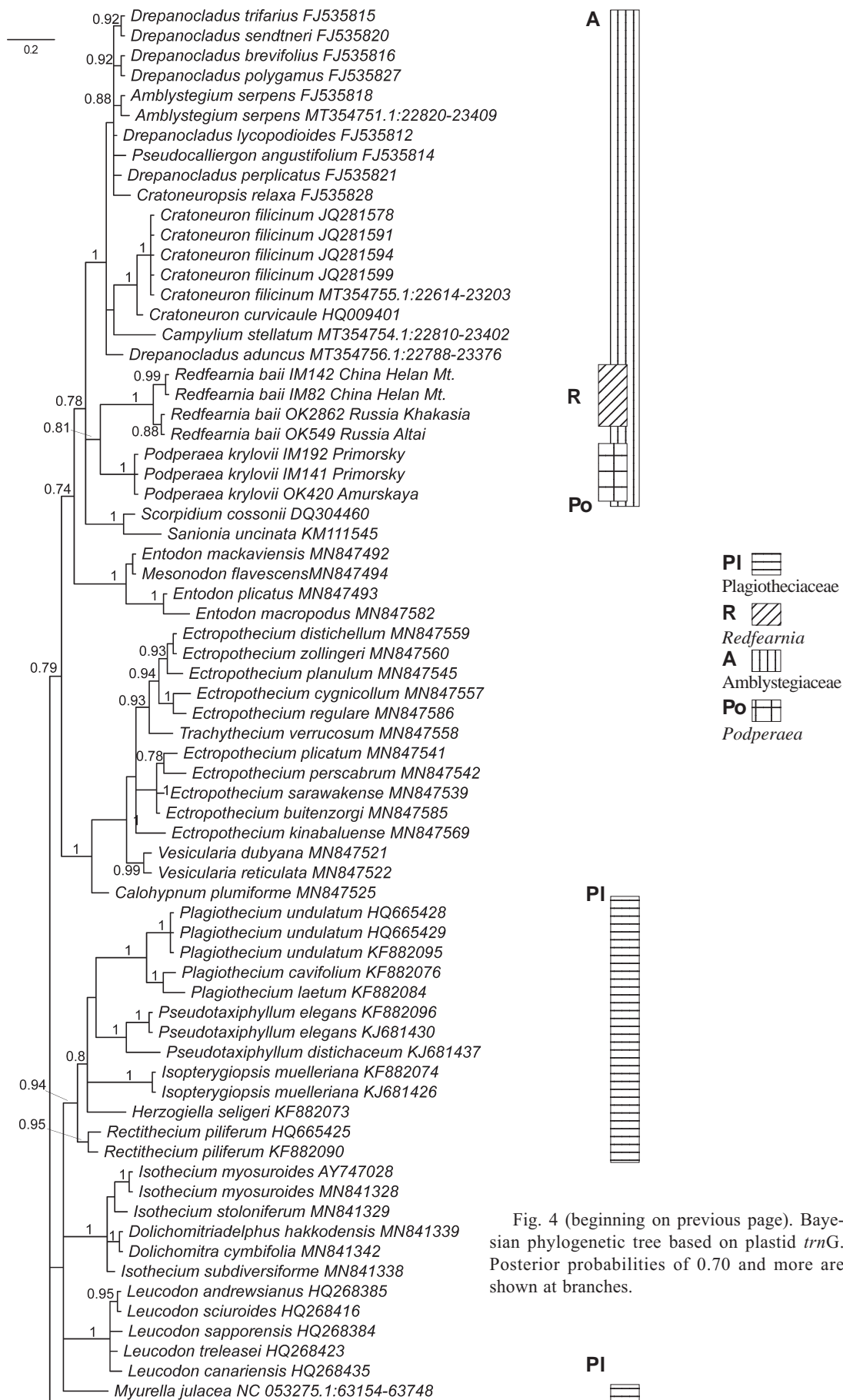


Fig. 4 (beginning on previous page). Bayesian phylogenetic tree based on plastid *trnG*. Posterior probabilities of 0.70 and more are shown at branches.

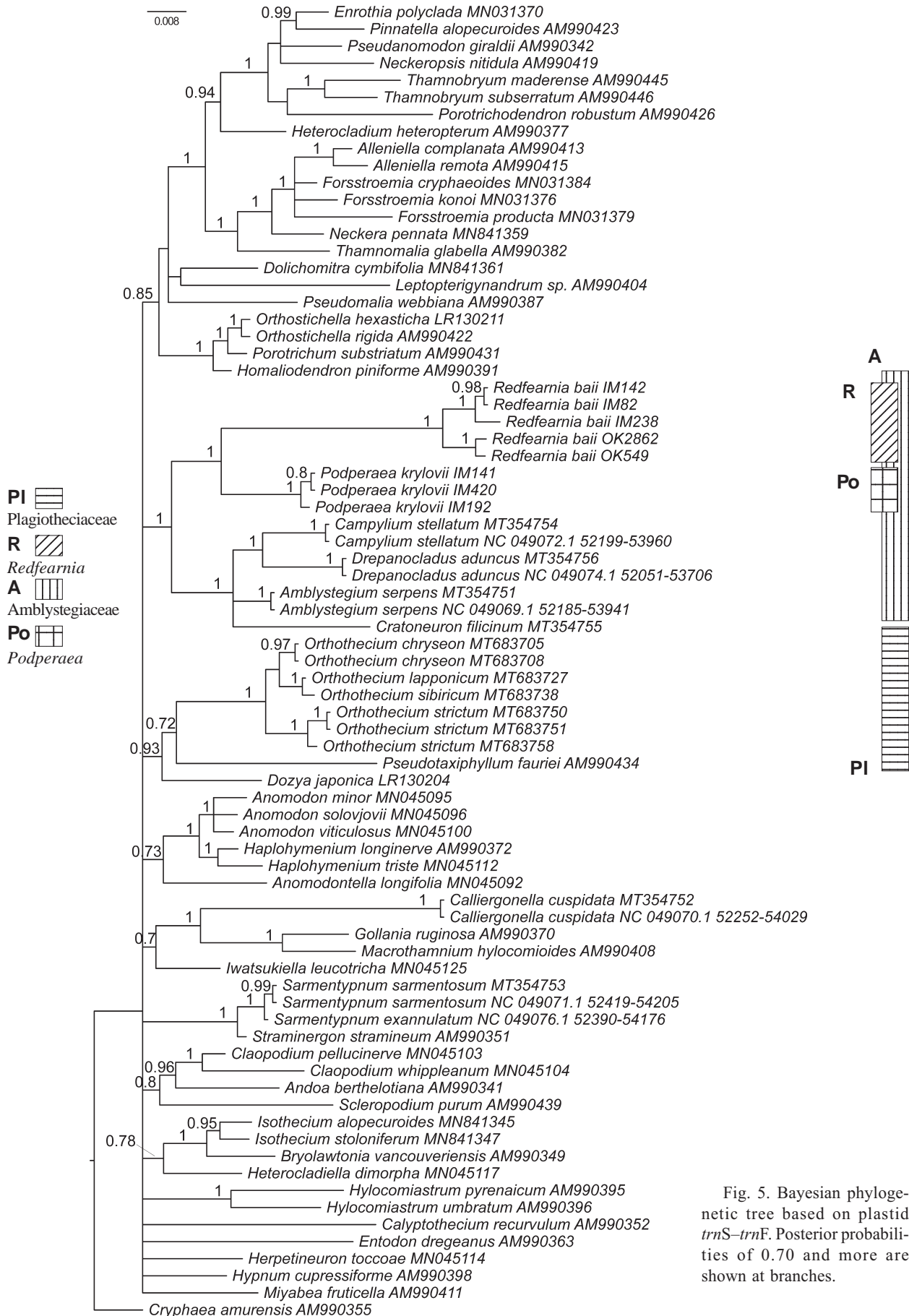
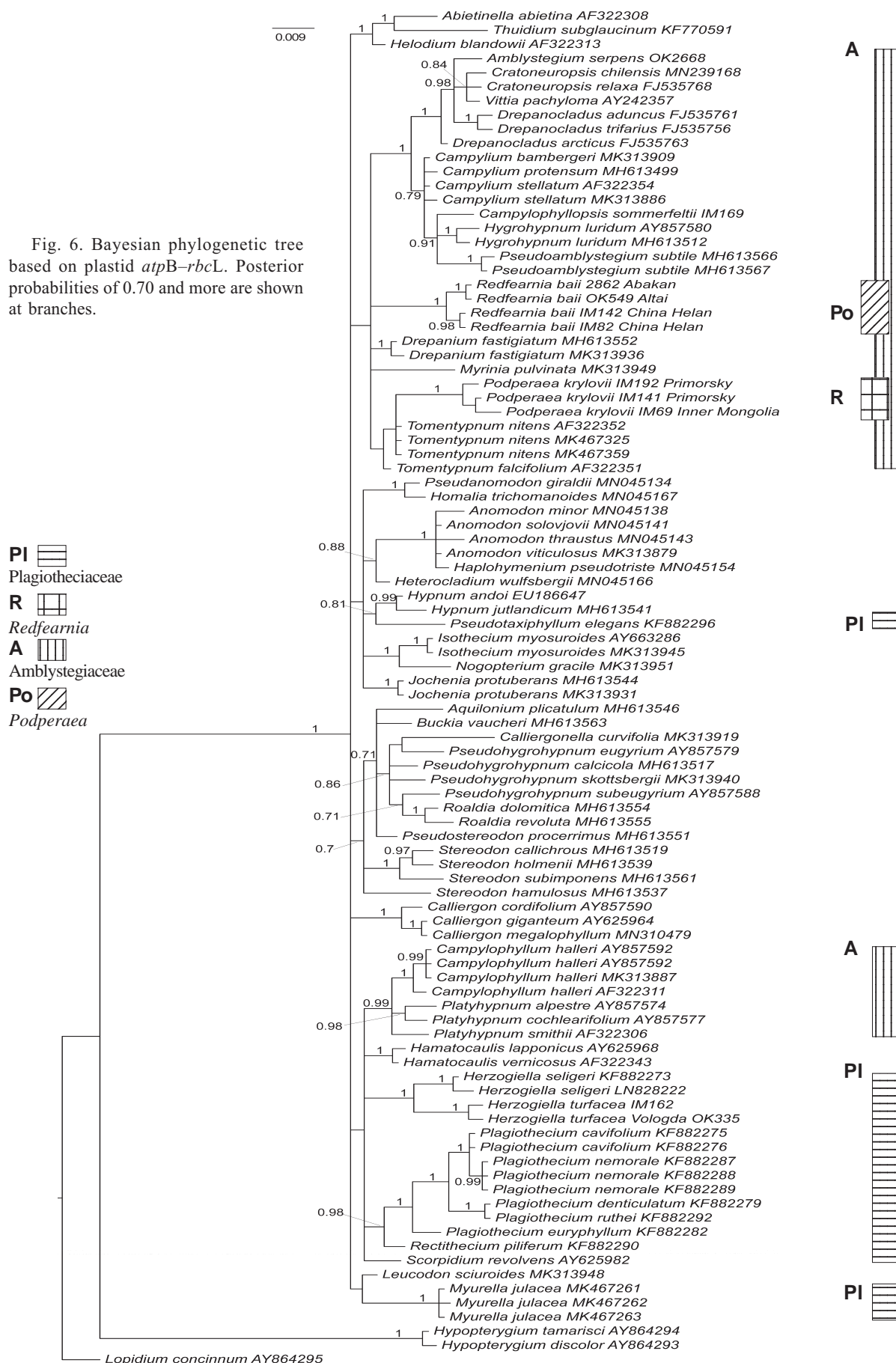
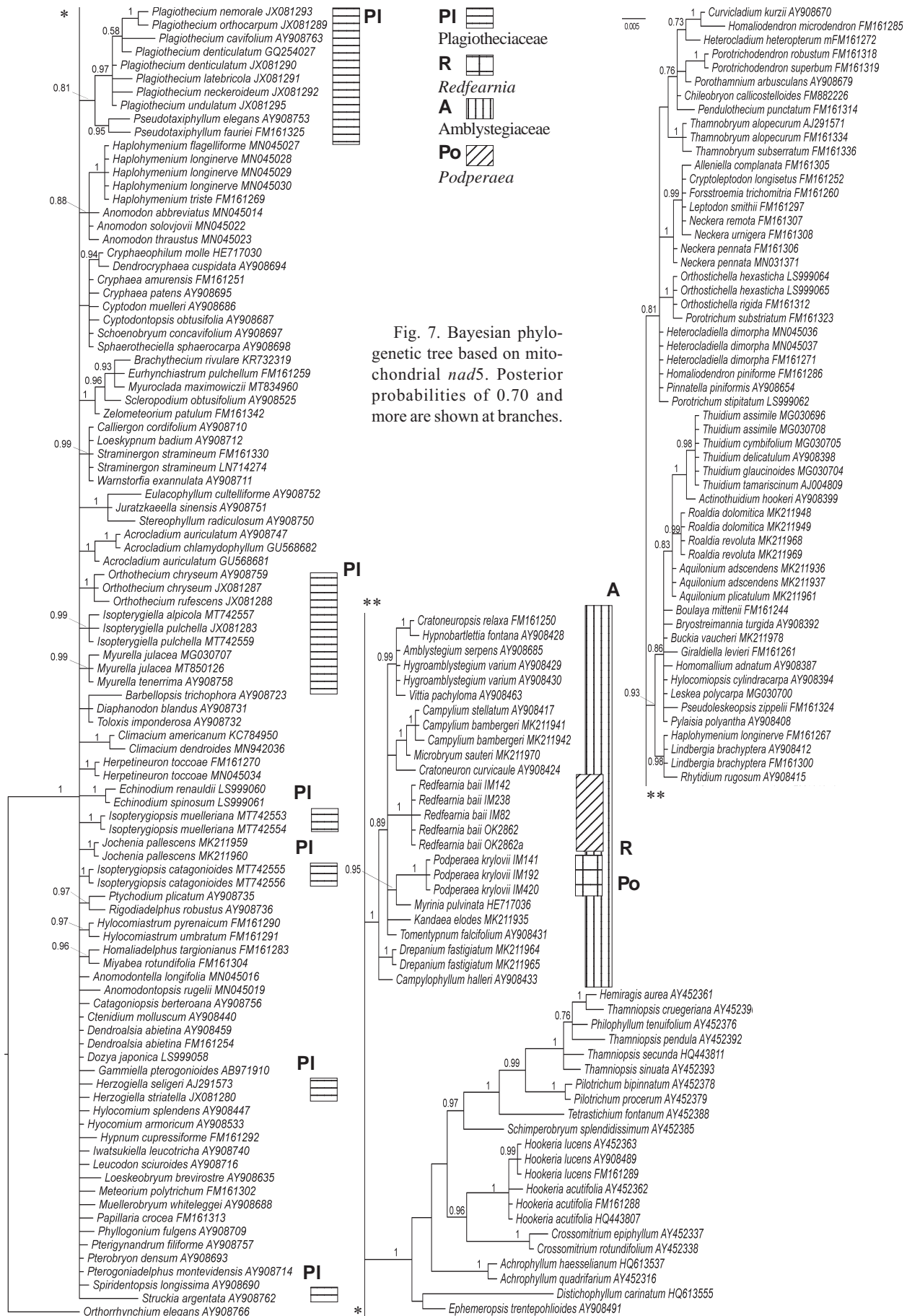


Fig. 5. Bayesian phylogenetic tree based on plastid *trnS-trnF*. Posterior probabilities of 0.70 and more are shown at branches.

Fig. 6. Bayesian phylogenetic tree based on plastid *atpB-rbcL*. Posterior probabilities of 0.70 and more are shown at branches.





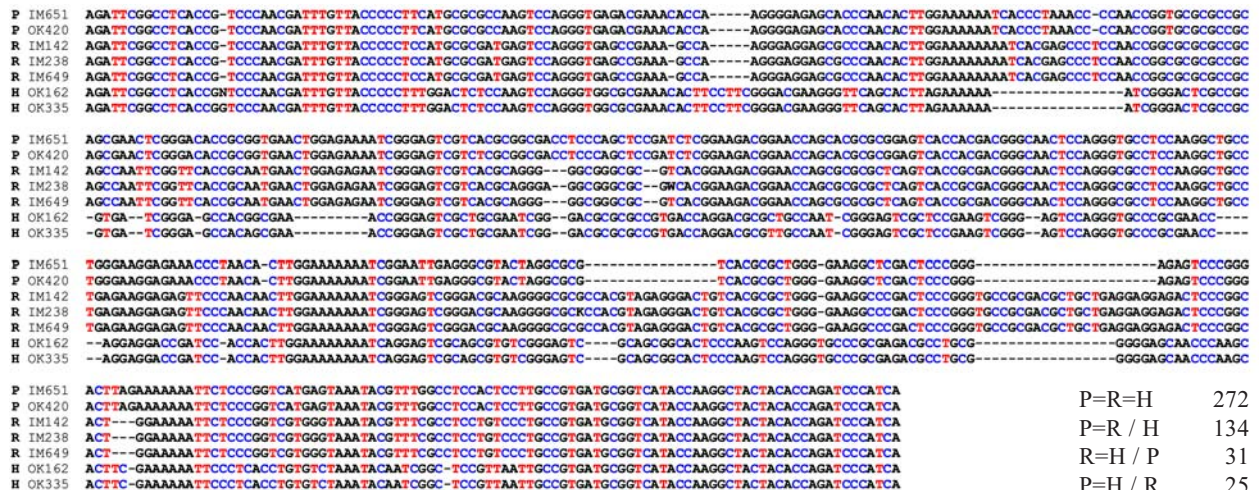


Fig. 8. Part of IGS alignment of (P) *Podperaea krylowii*, (R) *Redfearnia baii*, and (H) *Herzogiella turfacea*, and statistics on similarities of sequences, showing number of positions with six variants, where = means identical sequences, / different sequences, ? positions ignored due to polymorphism.

nt) in ITS2. The differences between *Redfearnia baii* and *Podperaea krylowii* included 48 substitutions and 11 indels (of 3, 3, 4, 1, 3, 5, 3, 1, 3, 2, and 1 nt) in ITS1, and 18 substitutions and 6 indels (of 1, 2, 1, 18, 1, and 1 nt) in ITS2.

DISCUSSION

The new results support previously obtained ones, showing that the nuclear ITS1 sequence of *Redfearnia* is similar to *Herzogiella*, whereas three plastid regions, one mitochondrial region, and nuclear ITS2 are similar to basal Amblystegiaceae (*Arvernella*, *Campylophyllum*, *Drepanium*, *Myrinia*, *Platyhypnum* p.p., and *Tomentypnum*).

Ignatov & Milyutina (2011) explained this case as a rare intrafamilial hybridization event, which resulted in a narrowly distributed species. However, it is now clear that the group includes two broadly disjunct species, one in northern China and southern Asian Russia, and one in northern Mexico and the southwestern U.S.A. (Fig. 1). Such a disjunction implies a Tertiary or at least early Quaternary age of the genus, resembling a number of disjunctions classified as Arcto-Tertiary (Schofield & Crum, 1972; Schofield, 1980). This huge disjunction also suggests a possible alternative explanation, i.e. that *Redfearnia* is a relict, a remnant of an ancient group which existed before bifurcation into lineages represented in the modern flora by the Amblystegiaceae and the Plagiotheciaceae. However, the latter hypothesis is unlikely. An early-diverging position of the Plagiotheciaceae in the phylogenetic trees of the Hypnales has been found in many studies, some with ITS included (Ignatov *et al.*, 2007; Huttunen *et al.*, 2012, 2013), but also in some based only on organellar markers (Cox *et al.*, 2010) or on a large dataset of plastid markers (Tsubota *et al.*, 2004). These analyses also resolved the Amblystegiaceae in a more derived position. Liu *et al.* (2019) used a rather small sampling of pleurocarps in their phylogenetic analysis

based on big data, but the Plagiotheciaceae were found in a basal position in all separate analyses of plastid, mitochondrial, and nuclear regions (Liu *et al.*, 2019; supplementary materials). Albeit with a limited sampling of pleurocarps, the results of Bell *et al.* (2020) also support a basal position of the Plagiotheciaceae.

It is difficult to imagine that in *Redfearnia* five of the DNA regions studied here, representing the nuclear, plastid and mitochondrial genomes, evolved from an ancestor towards the Amblystegiaceae state, while only ITS1 retained a plesiomorphic state. Also, the number of substitutions in ITS1 is almost equal, on one hand, between the two species of *Redfearnia*, and on the other hand, between *Redfearnia baii* and *Herzogiella turfacea*. This limited variation does not suggest the great age that an ancestor of such well-differentiated families would have.

In the present analysis some plastid trees do not resolve the Plagiotheciaceae as monophyletic, or if they do, as in *trnS-trnF* (Fig. 5), or almost do (with one exception), in *trnG* (Fig. 4), then the Plagiotheciaceae clade is not the basal one. However, the sampling for this study did not address the whole phylogeny of pleurocarpous mosses, being focused on *Redfearnia*. A lack of key pleurocarpous groups in these analyses therefore results in incomplete phylogenetic reconstruction. A more comprehensive selection of taxa for plastid *rbcl* (Tsubota *et al.*, 2004) resolved the Plagiotheciaceae near the base of pleurocarpous moss phylogenetic tree, similar to that shown in Figs. 2–3, as did trees from other studies that included ITS (Ignatov *et al.*, 2007; Huttunen *et al.*, 2012, 2013; Kučera *et al.*, 2019).

Therefore, the conclusion from the previous study (Ignatov & Milyutina, 2011) about a putative hybrid origin for *Redfearnia* remains the most probable, although additional study using complete genomes and karyological evidence undoubtedly will bring more clarity to this interesting case.

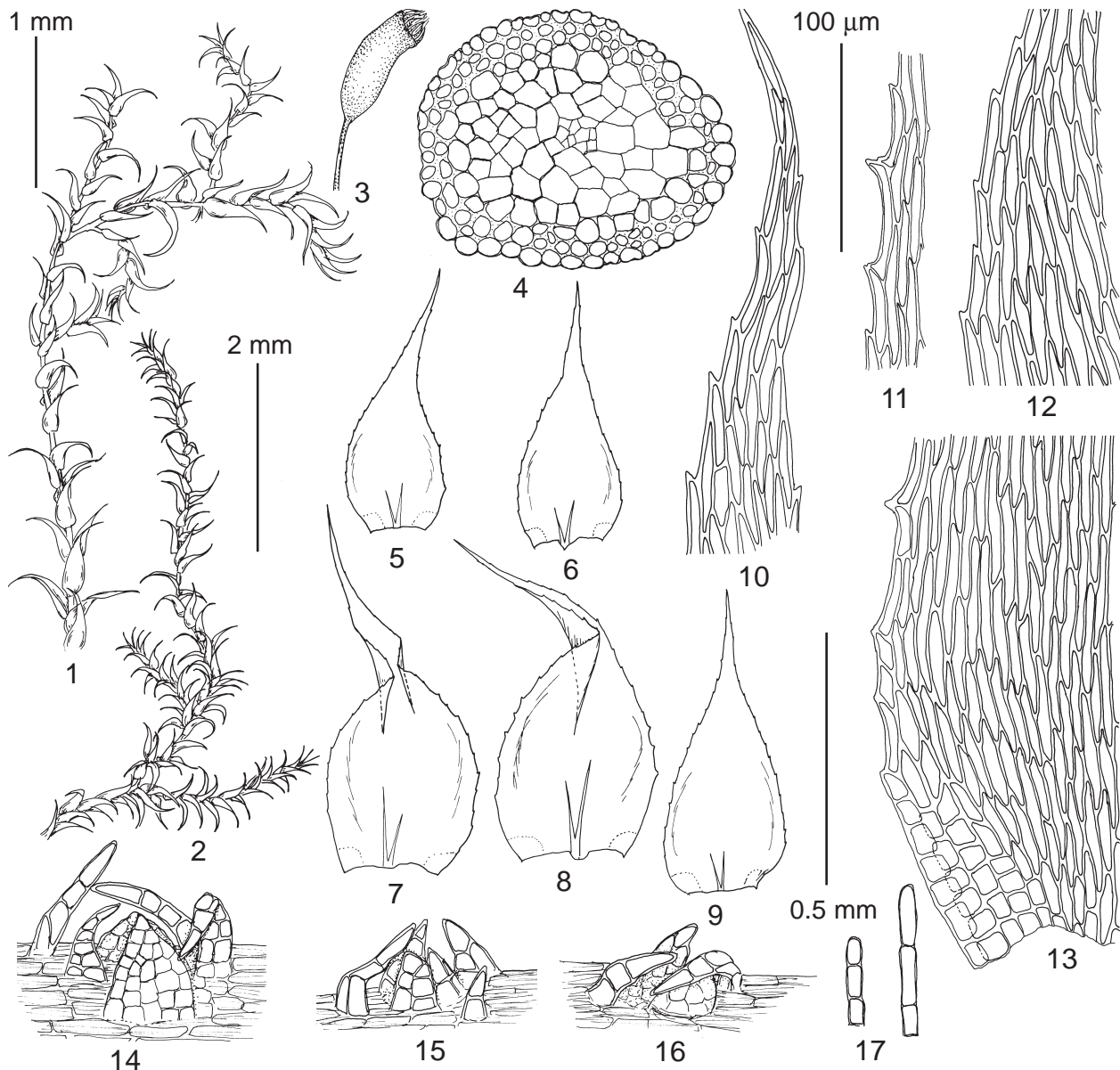


Fig. 9. *Redfearnia baii* (from: Russia, Khakassia, Ignatov & Spirina 11-5015, MHA9020702): 1–2: habit, dry; 3: capsule; 4: stem transverse section; 5–6: branch leaves; 7–9: stem leaves; 10: upper leaf cells; 11, 12: median leaf cells; 13: basal leaf cells; 14–16: branch primordia; 17: axillary hairs. Scale bars: 2 mm for 2, 3; 1 mm for 1; 0.5 mm for 5–9; 100 μ m for 4, 10–17.

Recent studies using high-tech methods have considerably expanded our understanding of interspecific, intersectional and sometimes intergeneric hybridization in mosses (Ignatov *et al.*, 2019b; Sawangproh & Cronberg, 2021), including extremely unexpected evidence of how easily they can acquire foreign DNA (Hedenäs *et al.*, 2021). In this context, the *Redfearnia* case provides an illustration of how a unique hybridization event retains long-lasting detectability after millions of years.

TAXONOMY

Although we did not study *Redfearnia homomallifolia*, published descriptions and illustrations (Redfearn, 1973; Ireland, 1994, 2014; Ireland & Buck, 2009; Wynns, 2020) allow us to provide a comparison of the two species of the genus.

Redfearnia J.T.Wynns, Bryologist 123: 641. 2020.

Type species: *Redfearnia homomallifolia* (Redf.) J.T.Wynns.

Plants moderately small, in loose or compact mats, green or light green, glossy. Stems prostrate, irregularly to rather regularly pinnately branched, loosely to densely, terete or subcomplanate-foliate; branches flexuose or curved, terete, hyalodermis developed but sometimes incomplete, central strand weak; paraphyllia absent; proximal branch leaves surrounding branch primordia on stem lanceolate to ovate; axillary hairs 3-celled; rhizoids just below leaf insertion. Leaves from an erect base gradually reflexed to squarrose or erect-spreading, straight and homomallous to upturned-homomallous, ovate-lanceo-

Table 3. Differential characters of two species of the genus *Redfearnia*.

Character/Species	<i>R. baii</i>	<i>R. homomallifolia</i>
Foliage	terete	terete to subcomplanate
Leaves	from erect base reflexed to squarrose	erect-spreading, homomallous to upturned -homomallous
Leaf shape	ovate-lanceolate, \pm abruptly acuminate	lanceolate to ovate-lanceolate, gradually tapered to apex
Leaf size, mm	0.7–0.95 \times 0.35–0.45	0.8–1.2 \times 0.3–0.5
Laminal cells, μ m	30–70 \times 6–7	60–120 \times 5–9
Spores, μ m	17–18	9–16

late, gradually or more or less abruptly tapered to the apex, gradually rounded to the base, not decurrent; margins plane, serrate all around by acute simple teeth and partly by ‘compound’ teeth, the ‘compound’ teeth rather perpendicular to the leaf margin, formed by projections of two cells; costa double or forked shortly above the base, short and weak, or occasionally with one branch extending to 0.5 the leaf length; laminal cells linear, rather thin-walled, smooth; alar cells quadrate to short rectangular, forming a small, indistinctly delimited group, leaf margins above alars with elongate hyaline cells. Autoicous. Perichaetial leaves somewhat larger than the stem leaves, with a single costa reaching midleaf, margin serrulate, laminal cells smooth. Setae long. Capsules inclined to horizontal, asymmetric, arcuate, strongly contracted below the mouth when dry and empty; operculum conic to shortly rostrate; annulus separated by fragments; peristome double, complete, with long cilia. Spores 9–18 μ m.

We refer *Redfearnia* to the Amblystegiaceae, because: (1) it belongs to this family in all but one of the single-marker trees (Figs. 3–7); (2) it has proximal branch leaves occurring around dormant buds, whereas in the Plagiotheciaceae branch primordia remain for a long time leafless or ‘naked’ [we avoid the term ‘pseudoparaphyllia,’ which is applied to non-homologous structures (Spirina *et al.*, 2020)]; and (3) costa extending to mid-leaf in perichaetial leaves, whereas in the Plagiotheciaceae costa in perichaetial leaves is absent or thin and indistinct. We failed to find in *Redfearnia* any morphological features that would suggest its placement in Plagiotheciaceae rather than in Amblystegiaceae.

The differences between *Redfearnia baii* and *Podperaea krylovii* were discussed and illustrated by Ignatov & Milyutina (2011): (1) laminal cells are smooth in *Redfearnia* vs. distinctly prorate in *Podperaea*; (2) simple teeth at the leaf margin prevail, while double teeth are few in *Redfearnia* vs. double teeth prevail in *Podperaea*; (3) the capsule is long when mature in *Redfearnia* vs. short in *Podperaea*.

The genus includes two species; their distinctions are listed in Table 3. The main differences seem to be the foliage pattern, leaf shape, and degree of leaf margin serration. In habit *Redfearnia homomallifolia* is most similar to *Herzogiella turfacea*, whereas *P. baii* is easily confused with *Campylophyllopsis sommerfeltii* (Myrin) Ochyra.

1. *Redfearnia homomallifolia* (Redf.) J.T.Wynns, Bryologist 123: 641. 2020. — *Isopterygium homomallifolium* Redf., Bryologist 76(3): 440–442. 1973. — *Pseudotaxiphyllum homomallifolium* (Redf.) Ireland, Caldasia 16(79): 267. 1991.

Described from USA, Texas (see type information in Wynns, 2020).

Illustrations and descriptions: Redfearn (1973); Ireland (1994); Ireland & Buck (2009); Ireland (2014); Wynns (2020).

Distribution and Ecology: USA: Arizona (Cochise, Navajo, and Santa Cruz counties), New Mexico (Doña Ana County), Texas (Kimble County); Mexico: Sonora. At 1400–2000 m elev., on rocks and under rock ledges.

2. *Redfearnia baii* (Ignatov) J.T.Wynns, Bryologist 123: 641. 2020. — *Podperaea baii* Ignatov, Arctoa 20: 115. 2011. Fig. 9.

Described from China, Inner Mongolia (see type information in Ignatov & Milyutina, 2011).

Illustrations and descriptions: Zhao *et al.* (2006); Bai (2010); Ignatov & Milyutina (2011).

Distribution and Ecology: At present *Redfearnia baii* is known from five areas (specimens are listed in Table 1), three in China and two in Russia.

1. China, Inner Mongolia, Manchian Mts. (Figs. 10A–C). The range is elevated ca. 500 m above the nearby lowland. Its slopes are under reforestation with *Picea crassifolia* Kom. The foothills have *Pinus* and xeric shrub vegetation, at ca. 1800 m becoming hemiboreal *Betula* forest with *Lonicera*, *Sambucus*, *Convallaria*, *Pyrola*, *Trientalis*, *Pulmonaria*, *Vicia*, *Moehringia*, etc.; *Redfearnia baii* grows on a soil bank along a trail with *Tortula subulata* Hedw., *Encalypta* cf. *rhaptocharpa* Schwägr., *Fissidens* cf. *bryoides* Hedw., and *Amblystegium*. It was collected in May with very young sporophytes.

2. China, Inner Mongolia, Helan Mts. We did not see specimens from Helan Shan, alt. 1900 m, cited as #HQ269 in Zhao *et al.* (2006), but according to the illustrations in Bai (2010) and Zhao *et al.* (2006), it is this species. The most common type of pine forest at this elevation, where collection was likely done, is shown in Fig. 10 D–E. For more about the forest of this area see Bai *et al.* (2011).

3. China, Inner Mongolia, Hohhot, on lawn near university, ca. 1100 m.

4. Russia, Khakassia, Abakan River, ca. 550 m; *R. baii* was collected in a flood valley with *Populus* stands,



Fig. 10. Areas where *Redfearnia bairi* was collected. A–C: China, Manhan Mts., *Betula* (+planted *Pinus* and *Picea*) forest on slope, *R. bairi* grows on soil bank (C), near trail with *Tortula subulata* and *Encalypta* cf. *rhaptocarpa*, 1800 m elev.; D–E: China, Helan Mts., *Pinus tabulaeformis* stands with *Prunus* and *Juniperus*, ca. 1900 m elev.; I–J: Russia, Khakassia, Abakan River; *R. bairi* was collected in flood valley with *Populus* stands, on fallen logs, and on soil bank at base of slope to the valley, in shade of trees.

on rocks and on a soil bank at the base of a slope of the valley, in shade of trees (Fig. 10F–G).

5. Russia, Altai, Chulyshman valley, ca. 550 m., steppe slope with scattered shrubs and rock outcrops; *Redfearnia bairi* grows on soil near rocks, and often close to shrub trunks, especially those that provide deep shade under their canopies (Fig. 11); *Rhododendron ledebourii* Pojark., *Caragana arborescens* Lam., and *Lonicera microphylla* Willd. ex Schult. are the most common shrub species, where we collected *Redfearnia bairi* in this area.

The common feature of all these areas is that they are rather xeric and therefore poor in bryophytes. Mosses are scattered and occur as scanty patches, and since these places are well exposed to sun, they often look depauper-

ate and non-attractive for bryophyte collectors. It seems likely that *Redfearnia bairi* (and maybe *R. homomallifolia* as well) will be found in many more localities after intentional search, which these plants deserve.

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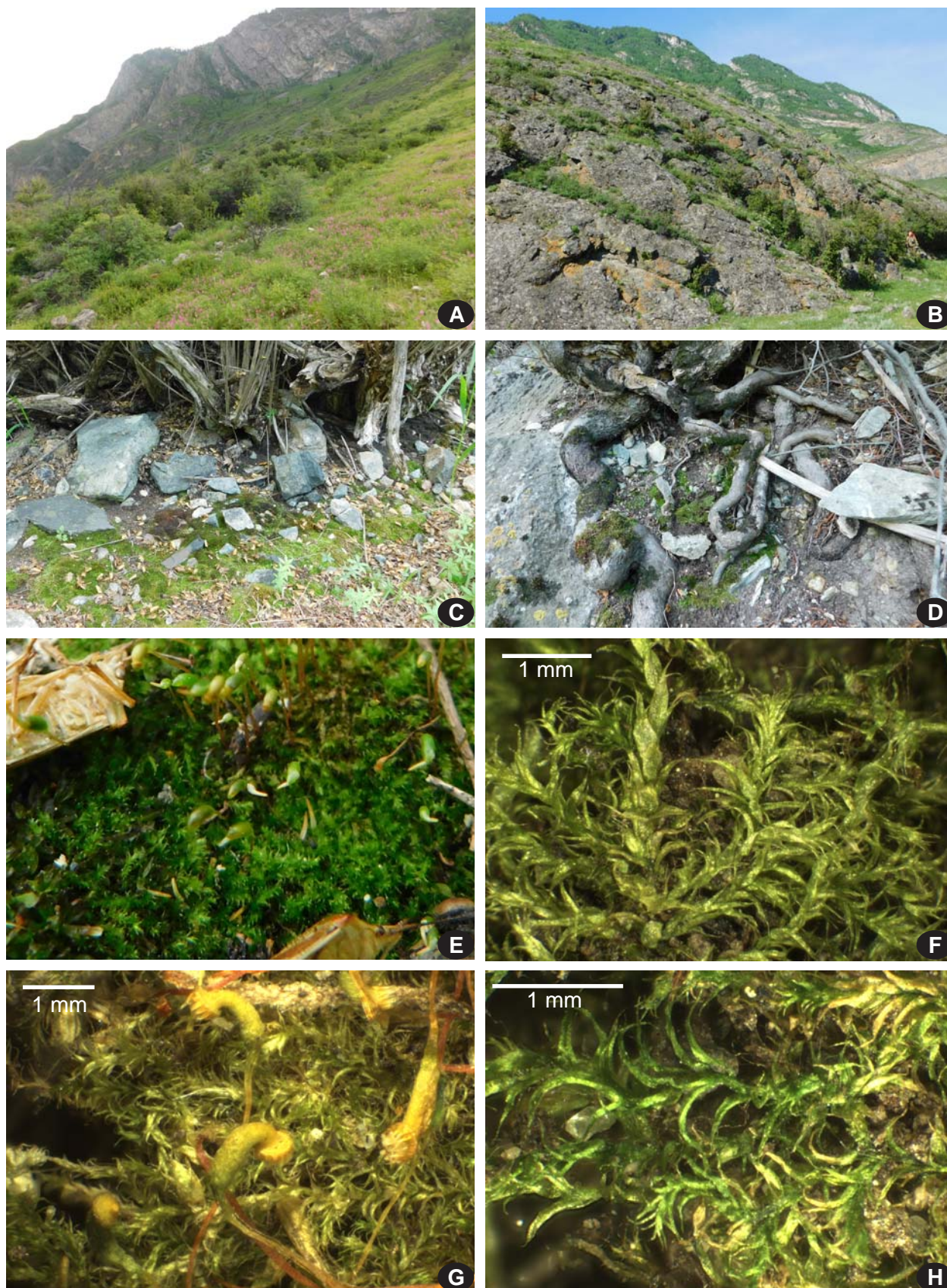


Fig. 11. Areas where *Redfearnia baii* was collected in Altai Mountains, slopes to Chulyshman River valley. A–B: general type of environments; C–D: populations under canopy of *Lonicera* (C) and *Rhododendron* (D); E: close up of “C”; F–H: herbarium specimens from Altai, photographed under stereomicroscope.

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