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INTRAFAMILIAL HYBRIDIZATION IN MOSSES? AN ENIGMATIC CASE IN THE GENUS PODPERAEA (HYPNALES, BRYOPHYTA)

ГИБРИДИЗАЦИЯ МЕЖДУ ПРЕДСТАВИТЕЛЯМИ РАЗНЫХ СЕМЕЙСТВ У МХОВ? ЗАГАДОЧНЫЙ СЛУЧАЙ В РОДЕ PODPERAEA (HYPNALES, BRYOPHYTA)

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Abstract

A new species from China, *Podperaea baii*, is described. In addition to morphological differences from the second species of the genus, *P. krylovii* (Amlystegiaceae s.l.), *P. baii* differs in the nrITS1 sequence, which is very similar to that of the genus *Herzogiella* from the phylogenetically distant family Plagiotheciaceae. At the same time, nrITS2 in *P. baii* is much more similar to Amblystegiaceae than Plagiotheciaceae. This case is the first report of the putative remote hybridization in mosses.

Резюме

Из Китая описан новый вид, *Podperaea baii*, который, помимо небольших морфологических отличий от второго вида рода, *P. krylovii* (семейство Amlystegiaceae s.l.), отличается еще последовательностью ITS1, которая соответствует роду *Herzogiella* из филогетически далекого семейства Plagiotheciaceae. При этом последовательность ITS2 у *P. baii з*начительно более сходна с Amblystegiaceae, нежели с Plagiotheciaceae. Данный случай является первым примером возможной отдаленной гибридазации у мхов.

KEYWORDS: Bryophytes, pleurocarpous mosses, Plagiotheciaceae, Amblystegiaceae, *Podperaea*, new species, China, remote hybridization, nrITS

INTRODUCTION

The genus *Podperaea* was established by Iwatsuki & Glime (1984) for one species, originally described as *Campylium krylovii* Podp. The strongly prorate cells and specific ‘compound’ teeth along leaf margin formed by upper end of lower cell and lower end of next upper cell, were found to be quite odd for *Campylium*. Similar teeth are rare in Hypnales, and are well developed, as far as we know, only in *Myurella* and *Platydictya*.

All other species ever placed in the genus *Campylium* (except *C. krylowii*) never have ‘compound’ teeth. This genus in its traditional circumscription included species that are now treated in many genera: *Campylium* s. str*., Campylophyllum, Campyliadelphus, Campylidium*, and in addition some species were transferred to *Amblystegium, Drepanocladus* and *Pseudocampylium* (cf. Hedenäs, 1997; Ochyra et al., 2003; Ignatov et al., 2007; Vanderpoorten & Hedenäs, 2009). None of these genera have sufficient similarity with *Podperaea krylovii*, and none of them have been found related to it in the molecular analysis of Troitsky et al. (2007), the only study where the position of *Podperaea*

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krylowii has been tested by phylogenetic methods.

The placement of the genus remains problematic, which is a common case at the moment for many genera of pleurocarpous mosses. Originally it was referred to Hypnaceae that was a repository for pleurocarps with double costa and complete double alternate peristome and without specific characters that would indicate an affinity to families like Neckeraceae, Sematophyllaceae, Hylocomiaceae, etc. However, the type species of the family Hypnaceae, *Hypnum cupressiforme,* is obviously quite unrelated to *Podperaea* (Troitsky et al., 2007).

Podperaea krylovii was described from the Russian Far East and later found in a number of places in South Siberia, and in Hokkaido, Japan (Iwatsuki & Glime, 1984), in Liaoning Province of China (Ignatov et al., 1996) and then also in Inner Mongolia Autonomous District of China (Zhao et al., 2006; Bai, 2010).

Collections from different parts of Russia studied by us have been fairly homogeneous morphologically, so posed no questions about their species identity. The variation seen in Chinese specimens however was bigger: specimens from Khingan Mts. (ranging from Amurskaya Province of Russia and Heilongkiang Province of China to Inner Mongolia) were found nearly identical to Russian ones, whereas plants from another region, Inner Mongolia, appeared to be different in morphology, so the testing with molecular markers was applied to these specimens.

An unexpected preliminary results have forced us to search additional collections from Inner Mongolia, and new gatherings have confirmed the preliminary observation that the most widespread population in the Inner Mongolia is an undescribed species, *Podperaea baii* (see description below).

MATERIAL AND METHODS

The taxa selection for phylogenetic analysis was done with the focus on genera possibly related to Podperaea according to the results of Troitsky et al. (2007). The subset of taxa used in the previous analyses (Ignatov et al., 2007; Troitsky et al., 2007) was taken. New and already published sequence data used in analysis are given in Appendix 1.

Laboratory protocol was essentially the same as in some of our previous analyses (e.g., Gardiner et al., 2005). The sequences were aligned manually in Bioedit (Hall, 1999). Maximum parsimony analysis and jackknifing for 1000 replications was performed in Nona (Goloboff, 1994) under Winclada shell (Nixon, 1999).

In the present paper only ITS data are analyzed, as this DNA region is the most variable in mosses, and the results of its sequence analyses often correspond to genera and families of many pleurocarpous moss groups in their traditional circumscriptions. Preliminary tests with chrloroplast markers *trn*L-F and *rps*4 have given poor resolution and are not presented here.

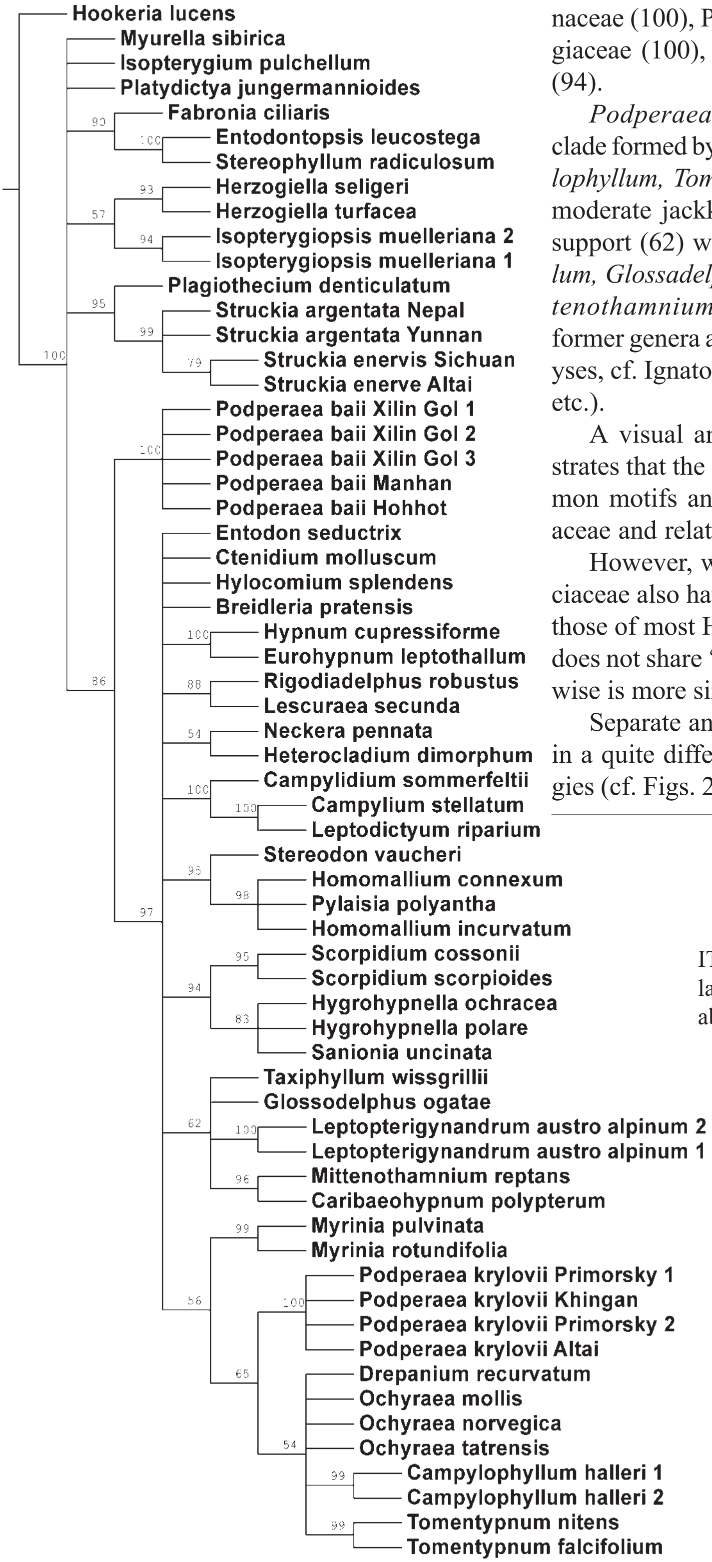
As the prelimirnary study revealed a considerable difference between systematic position that follows from a separate analysis of ITS1 and ITS2, these loci were studied separately. Hereafter within this paper we will call them ITS1 and ITS2 for simplicity, although the former locus includes ITS1, 5.8 RNA gene and a short part of 3'end of ITS2 (38 positions in the alignment (30-37 nucleotides for different species, up to 678 position of the alignment), while ITS2 in a slightly reduced part of this spacer, representing 503 positions closer to 5'-end, i.e. without 38 mentioned positions of the alignment from the 3'-end.

RESULTS

The MP tree based on the ITS1-2 region and rooted on *Hookeria* (Fig. 1) includes basal polytomy of the species classified in Plagiotheciaceae (sensu Pedersen & Hedenäs, 2002; Ignatov et al., 2007, etc.) and also Fabroniaceae and Stereophyllaceae and terminal clade.

Within the basal polytomy, a high jackknife support was obtained for clades formed by species of one genus, e.g., *Herzogiella* (93), *Struckia* (99), and also *Plagiothecium*+ *Struckia* clade was supported (95), as well as Fabroniaceae+ Stereophyllaceae (90).

Terminal clade includes two subclades. The first small subclade is formed by 5 accessions of *Podperaea baii* (jackknife support 100). The second larger subclade (support 97) represents a poorly resolved terminal polytomy of various groups of Hypnales. Within this polytomy, a high support has been received by many families (usually represented by few specimens), e.g., Hyp-



naceae (100), Pseudoleskeaceae (88), Amblystegiaceae (100), Pylaisiaceae (95), Scorpidiaceae (94).

Podperaea krylovii was found within the clade formed by *Ochyraea*, '*Drepanium*', *Campylophyllum, Tomentypnum*. This clade got only a moderate jackknife support, 65. A comparable support (62) was found for a clade of *Taxiphyllum, Glossadelphus, Leptopterigynandrum, Mittenothamnium, Carribaeohypnum* (the three former genera appear in many phylogenetic analyses, cf. Ignatov et al., 2007; Olsson et al., 2009, etc.).

A visual analysis of the alignment demonstrates that the ITS1 of *Podperaea baii* has common motifs and substitutions with Plagiotheciaceae and related families (Fig. 4).

However, within the ITS2, where Plagiotheciaceae also have sequences quite different from those of most Hypnales (Fig. 5), *Podperaea baii* does not share 'plagiothecioid' motifs, but otherwise is more similar to some Amblystegiaceae.

Separate analyses of ITS1 and ITS2 resulted in a quite different strict consensus tree topologies (cf. Figs. 2 and 3). The former one made for

Fig. 1. Jackknife tree based on ITS 1–2 dataset; supports >50% calculated for 1000 replications are shown above branches.

Fig. 2. Strict consensus tree (L=536) based on the analysis of ITS 1 and 5,8S RNA gene sequences (first 678 positions of alignments used, 503 positions deleted). Strict consensus of 20 shortest tree (L=533) found in heuristic analysis by Nona (100000, hold=100, iterations = 1000), CI=0.59, RI=0.79.

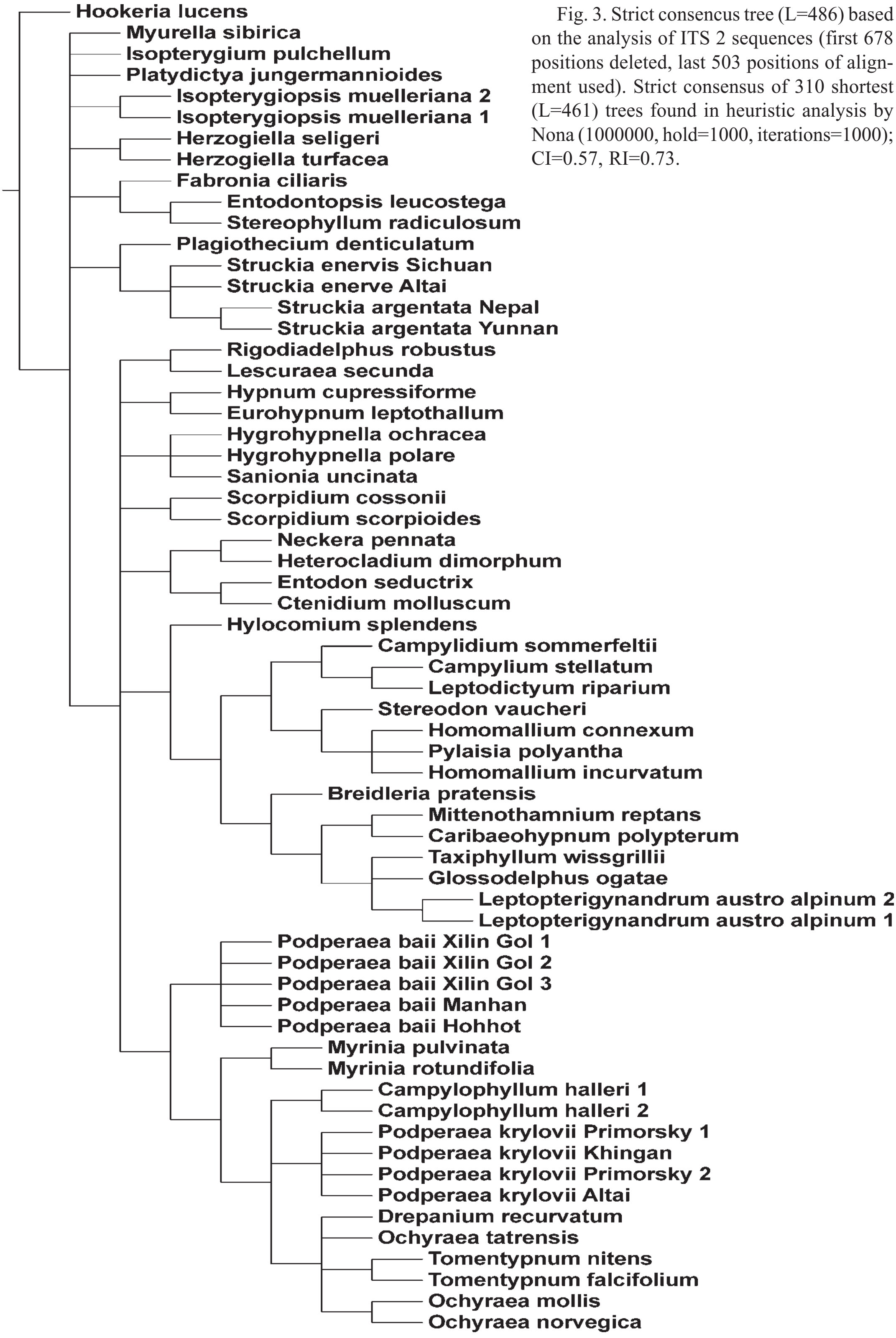


Fig. 3. Strict consencus tree (L=486) based on the analysis of ITS 2 sequences (first 678 positions deleted, last 503 positions of alignment used). Strict consensus of 310 shortest (L=461) trees found in heuristic analysis by Nona (1000000, hold=1000, iterations=1000); CI=0.57, RI=0.73.

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                              100       110        120     130       140       150       160       170      180
                                .|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|....|...
HOMOMALLIUM CONNEXUM            CCTTCG-CCAATCGCCACGCG---CG----------------------------------CGCGGCGT-CGGG-------------TT
HOMOMALLIUM_INCURVATUM          CCTTCG-CCAATCGCCACGCG---CG----------------------------------CGCGGCGT-CGGG-------------TT
PYLAISIA_POLYANTHA              CCTTCG-CCAATCGCCACGCG---CG----------------------------------CGCGGCGT-CGGG-------------TT
STEREODON_VAUCHERI              CCTTCG-C-------CACGCG---CG----------------------------------CGCGGCGT-CGGG-------------TT
HYPNUM_CUPRESSIFORME            CCTTCG-T-------CACGAG---C--------TC-------GCT---------------CGTGGCGC-GGGG-------------CT
EUROHYPNUM_LEPTOTHALLUM         CCTTCG-T-------CACGAG---C--------TC-------GCT---------------CGTGGCGC-GGGG------------CTT
BREIDLERIA PRATENSIS            CCTTCG-T-------CACGA----CGAGC-------------GC----GCTCGCT-----CGGGACGT-CGGG-------------TT
CTENIDIUM_MOLLUSCUM             CCTCCG-T-------CACGA----CGAGC----T--------------------------CGT-GCGT-GGGG-------------TT
NECKERA_PENNATA                 CCT-CG-T-------CACGCG---C--------TC-------------GCG---------CGTGGCGT-CGGG-------------TT
HYLOCOMIUM_SPLENDENS            CCTTCG-T-------CACGT----C--------TC-------------GCGA--------CGTGGCGA-AGGGGGG----------AT
ENTODON_SEDUCTRIX               CCTTCG-T-------CACGAG---CGAGC----TC-------------GCTCGTT-----CGCGGCGT-GGGG-------------TT
MITTENOTHAMNIUM_REPTANS         CCTTCG-T-------CACGAG---C-----------------------AAG-ACT-----CGGGGCGT-GGGG-------------TT
HYGROHYPNELLA_OCHRACEA          CCTTCG-T-------CACGGG---CGAGA-------------------GCT---------CGGGGCGT-CGGG-------------TT
HYGROHYPNELLA_POLARE            CCTTCG-T-------CACGAG---CGAGA-------------------GCT---------CGCGGCGT-CGGG-------------TT
SANIONIA_UNCINATA               CCTTCG-T-------CACGAG-GTCGTGA-------------------CCT---------CGCGGCGT-CGGG-------------TT
SCORPIDIUM_COSSONII             CCTTCG-T-------CACGAG---CGAGA-------------------GCT---------CGGGGCGT-CGGG-------------TT
SCORPIDIUM_SCORPIOIDES          CCTTCG-T-------CACGAG---CGAGA-------------------GCT---------CGGGGCGT-CGGG-------------TT
CARIBAEOHYPNUM_POLYPTERUM       CCTTCG-T-------CGCGAG---C-------TCCG-TCGA-GTC---ACGGACT-----CGGGGCGT-CGGG-------------TT
HETEROCLADIUM_DIMORPHUM         CCTTCG-T-------CACGAG---C-------TTCG-TC---------ACGAACT-----CGCGGCGT-CGGG-------------TT
LESCURAEA_SECUNDA               CCTTCG-T-------CACGAG---C--------T--------------------------CGTGGCGT-CGGG-------------TT
RIGODIADELPHUS_ROBUSTUS         CCTTCG-T-------CACGAG---C-------TTCG-TC---------ACGAACT-----CGGGGCGT-CGGG-------------TT
TAXIPHYLLUM_WISSGRILLII         CCTTCG-T-------CACGAG---C-------TTCG-TC-ACGTC---ACGAACT-----CGGGGCGT-CGGG-------------TT
LEPTOPTERIGYNANDRUM_A-ALPINUM2  CCTTCG-T-------CACGAG---C-------TTCG-TCT-CGTC---ACGAACT-----CGGGACGT-CGGG-------------TT
LEPTOPTERIGYNANDRUM_A-ALPINUM1  CCTTCG-T-------CGCGAG---C-------TTCG-TCC-CGTC---ACGAACT-----CGGGGCGT-CGGG-------------TT
GLOSSODELPHUS_OGATAE            CCTTCG-T-------CACGAG---C-------TTCG-TC-ACGTC---ACGAACT-----CGGGGCGT-CGGG-------------TT
DREPANIUM_RECURVATUM            CCTTCG-T-------CACGAG---CGAGC----TCCCTC---GCGA--GCTCCCT-----CGCGGCGT-CGGG-------------TT
OCHYRAEA_MOLLIS                 CCTTCG-T-------CACGAG---CGAGC----TCCCTC---GCGA--GCTCCCT-----CGCGGCGT-CGGG-------------TT
OCHYRAEA_NORVEGICA              CCTTCG-T-------CACGAG---CGAGC----TCCCTC---GCGA--GCTCCCT-----CGCGGCGT-CGGG-------------TT
OCHYRAEA_TATRENSIS              CCTTCG-T-------CACGAG---CGAGC----TCCCTC---GCGA--GCTCCCT-----CGCGGCGT-CGGG-------------TT
CAMPYLOPHYLLUM_HALLERI_1        CCTTCG-T-------CACGAG---CGAGC----TC-------GCGA--GCTCTCT-----CGCGGCGT-CGGG-------------TT
CAMPYLOPHYLLUM_HALLERI_2        CCTTCG-T-------CACGAG---CGAGC----TC-------GCGA--GCTCTCT-----CGCGGCGT-CGGG-------------TT
MYRINIA_PULVINATA               CCTTCG-T-------CACGCT---CGAGC----TT-------------GCTCT-------CGTGGCGT-CGGG-------------TT
MYRINIA_ROTUNDIFOLIA            CCTTCG-T-------CACGCT---CGAGC----TC-------------GCTCT-------CGTGGCGT-CGGG-------------TT
CAMPYLIUM_STELLATUM             CCTTCG-T-------CACGCG---CGAGCGAGTTC-CTC---GTGG--GCTCCCTCGCGGCGCGGCGT-CGGG--------------T
LEPTODICTYUM_RIPARIUM           CCTTCA-T-------CACG-G---AGAGCGAGTTC-CTC----TGG--GCTCCCTCGCGGCGCGGCGT-CG-G--------------T
CAMPYLIDIUM_SOMMERFELTII        CCCTCG-T-------CACGCG---CGAGCGAG-TCCCTC---GTGG--GCTCCCTCGCGGCGCGGCGT-CGGG--------------T
TOMENTYPNUM_NITENS              CCTTCG-T-------CACGAG---CGAGCGAGCTC--TC---GCGA--GCTCTCT-----CGCGGCGT-CGGG-------------TT
TOMENTYPNUM_FALCIFOLIUM         CCTTCG-T-------CACGAG---CGAGCGAGCTC--TC---GCGA--GCTCTCT-----CGCGGCGT-CGG--------------TT
PODPERAEA_KRYLOVII_PRIMORSKY1   CCTTCGGT-------CGCGCG---CGAGCCCGCTC-------GCGG--GCTCCCT-----CGCGGCGT-CGGG--------------T
PODPERAEA_KRYLOVII_KHINGAN      CYTTCG-T-------CACGCG---CGAGCCCGCTC-------GCGG--GCTCCCT-----CGCGGCGT-CGGG--------------T
PODPERAEA_KRYLOVII_PRIMORSKY2   CCTTCG-T-------CACGCG---CGAGCCCGCTC-------GCGG--GCTCCCT-----CGCGGCGT-CGGG--------------T
PODPERAEA_KRYLOVII_ALTAI        CCTTCG-T-------CACGCG---CGAGCCCGCTC-------GCGG--GCTCCCT-----CGCGGCGT-CGGG--------------T
PODPERAEA_BAII_XILIN_GOL1       TCGAGG-T-------CACGAG---C-------GT--------------CAAAACT-----CGCGGCGT-CGGGGGG-TAA----TCTT
PODPERAEA_BAII_XILIN_GOL2       TCGAGG-T-------CACGAG---C-------GT--------------CAAAACT-----CGCGGCGT-CGGGGGG-TAA----TCTT
PODPERAEA_BAII_XILIN_GOL3       TCGAGG-T-------CACGAG---C-------GT--------------CAAAACT-----CGCGGCGT-CGGGGGG-TAA----TCTT
PODPERAEA_BAII_MANHAN           TCGAGG-T-------CACGAG---C-------GT--------------CAAAACT-----CGCGGCGT-CGGGGGG-TAA----TCTT
PODPERAEA_BAII_HOHHOT           TCGAGG-T-------CACGAG---C-------GT--------------CAAAACT-----CGCGGCGT-CGGGGGG-TAA----TCTT
PLAGIOTHECIUM_DENTICULATUM      CCGAAG-T-------CACGAG---C-------GT--------------CAAACCT-----CGCGGCGT-CGGGGG--TACCCTTTCTT
STRUCKIA_ENERVIS_SICHUAN        CCGATG-T-------CTCGAG---C-------GT--------------CCAAACT-----CGGGGCGT-CGGGGG--TAC----TCTT
STRUCKIA_ARGENTATA_NEPAL        CCGAAG-T-------CTCGAG---C-------GT--------------CAAAACT-----CGGGGCGT-CGGGGG--TAC-----TCT
MYURELLA_SIBIRICA               CCGAGG-T-------CACGAG---C-------GT--------------CAAAACT-----CGTGGCGT-CGGGGGG-TAA-----TTT
HERZOGIELLA_SELIGERI            TCGAGG-C-------CCCGAG---C-------GT--------------CAAAACT-----CGGGGCGT-CGGGGGG-TAA----TCTT
HERZOGIELLA_TURFACEA            TCGAGG-T-------CACGAG---C-------GT--------------CCAAACT-----CGGGGCGT-CGGGGGG-TAA----TCTT
STRUCKIA_ARGENTATA_YUNNAN       CCGAAG-T-------CTCGAG---C-------GT--------------CAAACCT-----CGCGGCGT-CGGGGG--TAC-----TCT
STRUCKIA_ENERVE_ALTAI           CCGATG-T-------CTCGAG---C-------GT--------------CCAAACT-----CGGGGCGT-CGGGGG--TAC-----TCT
ISOPTERYGIOPSIS_MUELLERIANA2    CCGAGG-T-------CACGAG---C-------GT--------------CGCAACT-----CGTGGCGT-CGGGGGG-TAC----TCTT
ISOPTERYGIOPSIS_MUELLERIANA1    CCGAGG-T-------CACGAG---C-------GT--------------CGCAACT-----CGTGGCGT-CGGGGGG-TAC----CCTT
ISOPTERYGIUM_PULCHELLUM         CCGTTG-T-------CACGAG---C-------GT--------------CCAAACT-----CGTGGCGT-CGGGGGG-TAA----TCTT
PLATYDICTYA_JUNGERMANNIOIDES    CCGAGG-T-------CACGAG---C-------TT--------------CAAAACT-----CGTGGCGT-CGGGGGG-TAA----TCTT
ENTODONTOPSIS_LEUCOSTEGA        CCGAGG-T-------CGCGAG---C-----------------------CCGA-CT-----CGCGGCGT-CGGGGG--TCA----CCTT
STEREOPHYLLUM_RADICULOSUM       CCGAGG-T-------CGCGAG---C-----------------------CCGA-CT-----CGCGGCGT-CGGGGG--TCA----TCTT
FABRONIA_CILIARIS               CCGAGA-C-------CGCGAG---C-------TT--------------CAAACCT-----CACGGCGT-CGGGGG--TAA----TCTT
HOOKERIA_LUCENS                 CCGAGG-T-------CACGAGA--C-------TT--------------CCC-GCT-----CGCGGCTTCCGGGGGA-AAA----TC--
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Fig. 4. Part of ITS 1 alignment, showing common substitutions and indels of *Podperaea baii* and Plagiotheciaceae.

ITS1, resolved *Podperaea baii* as sister to *Herzogiella* within the basal grade.

At the same time, strict consensus for ITS2 sequences has found both *Podperaea krylovii* and *P. baii* in one clade, which also includes *Myrinia* and four genera, *Ochyraea*, '*Drepanium*', *Campylophyllum, Tomentypnum,* the same as have been found in the combined analysis of ITS1 and ITS2.

Visual evaluation of sequences demonstrates at once that ITS1 region in *Podperaea baii* has all characteristic motifs of Plagiotheciaceae, which are numerous and readily seen (Fig. 4).

ITS2 in pleurocarpous mosses is less variable compared with ITS1 and rather few characteristic places in the alignment are revealing. Most of them demonstrate the difference between

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                               690       700       710    1080      1090      1100      1110      1120      1130      1140
                               .|....|....|....|....|/ /....|....|....|....|....|....|....|....|....|....|....|....|....|...
HOMOMALLIUM_CONNEXUM           -TC--------------GGTC--CGCGCCCC-TTCATG------------------------------------------GG---GC---ACG
PYLAISIA_POLYANTHA             -TC--------------GGGG--CGTGCCCC-TTCAT-------------------------------------------GG---GGC--ACG
HOMOMALLIUM_INCURVATUM         -TC--------------GGGG--CGCGCCCCCTTCATG------------------------------------------GG---GGC--ACG
STEREODON_VAUCHERI             GTG----------AACCGGGG--CGCGCCCCC------------------------------------------------GC---GGC--GCG
TAXIPHYLLUM_WISSGRILLII        AGC--------------GCG---CGCGCCCCC------------------------------------------------GC---GGC--GCG
LEPTOPTERIGYNANDRUM_A-ALPINUM2 -T---------------GCG---CGCGCCCCC------------------------------------------------GC---GGC--GCG
LEPTOPTERIGYNANDRUM_A-ALPINUM1 -T---------------GCG---CGCGCCCCC------------------------------------------------GC---GGC--GCG
GLOSSODELPHUS_OGATAE           AGT--------------GCG---CGCGCCCCC------------------------------------------------GC---GGC--GCG
ENTODON_SEDUCTRIX              GCC--------------GGG---TCACCGCCCCCC---------------------------------------------GT---GGC--GCG
MITTENOTHAMNIUM_REPTANS        -----------------------CGCGCCCCC------------------------------------------------GC---GGC--GCG
CARIBAEOHYPNUM_POLYPTERUM      GCCCCGCGCG-------GCG---CGCGCCCCC------------------------------------------------GCGGGGGC--GCG
HYPNUM_CUPRESSIFORME           GTTCGCG----------GCGG--CGCGCCC--------------------------------------------------GCGA-GGC--GCG
EUROHYPNUM_LEPTOTHALLUM        GTTCGCG----------GTGG--CGCGCCCC-------------------------------------------------GCGA-GGC--GCG
CTENIDIUM_MOLLUSCUM            GTG--------------GGG---CGCGGCCCC------------------------------------------------GCGG-GGT-CGCG
NECKERA_PENNATA                ACC--------------GGGA--CGCGCCCCC------------------------------------------------GC---GGC--GCG
HETEROCLADIUM_DIMORPHUM        ACC--------------GGG---CGCGCCCCC------------------------------------------------GC---GGC--GCG
HYLOCOMIUM_SPLENDENS           -----------------GGG---CG-GCCCCCC----------------------------------------------------GGC--GCG
BREIDLERIA_PRATENSIS           GCC--------------GGG---CGCGCCCCC------------------------------------------------GC---GGC--GCG
CAMPYLOPHYLLUM_HALLERI_1       ATT----------CATTGGG---CGCGCCCCC------------------------------------------------GC---GGC--GCG
CAMPYLOPHYLLUM_HALLERI_2       ATT----------CATTGGG----GCGCCCCC------------------------------------------------GC---GGC--GCG
DREPANIUM_RECURVATUM           TTT--------------GGG---CGCGCCCCC------------------------------------------------GC---GGC--GC-
CAMPYLIUM_STELLATUM            GTG---------AAATCGGG---CGCGCCACCCCCTCCCGCATGGGTTTGG-----------------------------GC---GGC--GCG
LEPTODICTYUM_RIPARIUM          GTGT-------GAAATCGGG---CGC-CCACCCCCTCCCGCATGGGTTTGG-----------------------------GC---GGC--GCG
HYGROHYPNELLA_OCHRACEA         GTC--------------GGG---CGCGCCCCC------------------------------------------------GT---GGC--GCG
HYGROHYPNELLA_POLARE           GCC--------------GGG---CGCGCCCCC------------------------------------------------GC---GGC--GCG
RIGODIADELPHUS_ROBUSTUS        GCG--------------GCG---CGCGCCCAC------------------------------------------------GC---GGC--GCG
SANIONIA_UNCINATA              GCC--------------GGG---CGCGCCCCC------------------------------------------------GC---GGC--GCG
SCORPIDIUM_COSSONII            GCC--------------GGG---CGCGTCCCC------------------------------------------------GT---GGC--GCG
SCORPIDIUM_SCORPIOIDES         GCC--------------AGG---CGCGTCCCC------------------------------------------------GT---GCC--GCG
CAMPYLIDIUM_SOMMERFELTII       GCC--------------GGG---CGCGCC---------------------------------------------------GC---GGC--GCG
LESCURAEA_SECUNDA              GTG--------------TCG---CGCGCCCCC------------------------------------------------GT---GGC--GCG
OCHYRAEA_MOLLIS                CTT--------------GGG---CGCGCCCCCC-----------------------------------------------GT---GGC--GCG
OCHYRAEA_NORVEGICA             CTT--------------GGG---CGCGCCCCCCC----------------------------------------------GT---GGC--GCG
OCHYRAEA_TATRENSIS             -TT--------------GGG-------------------------------------------------------------------------
TOMENTYPNUM_NITENS             CTT-------------CGGG---CGCGCCCCC------------------------------------------------GC---GGC--GCG
TOMENTYPNUM_FALCIFOLIUM        CTT-------------CGGG---CGCGCCCCC------------------------------------------------GC---GGC--GCG
MYRINIA_PULVINATA              CTT----------------G---CGCGCCCCC------------------------------------------------GC---GGC--GCG
MYRINIA_ROTUNDIFOLIA           CTT----------GATCGGG---CGCGCCCCC------------------------------------------------GC---GGC--GCG
PODPERAEA_KRYLOVII_PRIMORSKY_1 CTT----------GATCGGG---CGCGCCCCC------------------------------------------------GC---GGC--GTG
PODPERAEA_KRYLOVII_KHINGAN     CTT----------GATCGGG---CGCGCCCCC------------------------------------------------GC---GGC--GTG
PODPERAEA_KRYLOVII_PRIMORSKY_2 CTT----------GATCGGG---CGCGCCCCC------------------------------------------------GC---GGC--GTG
PODPERAEA_KRYLOVII_ALTAI       CTT----------GATCGGG---CGCGCCCCC------------------------------------------------GC---GGC--GTG
PODPERAEA_BAII_HELAN_1         CTT-------GTGAATCGGG---CGCGCCCCCC-----------------------------------------------GC---GGC--GCG
PODPERAEA_BAII_HELAN_2         CTT-------GTGAATCGGG---CGCGCCCCCC-----------------------------------------------GC---GGC--GCG
PODPERAEA_BAII_HELAN_3         CTT-------GTGAATCGGG-------------------------------------------------------------------------
PODPERAEA_BAII_MANHAN          CTT-------GTGAATCGGG---CGCGCCCCCC-----------------------------------------------GC---GGC--GCG
PODPERAEA_BAII_HOHHOT          CTT-------GTGAATCGGG---CGCGCCCCCC-----------------------------------------------GC---GGC--GCG
PLAGIOTHECIUM_DENTICULATUM     A----------------GCG---C--GTCCCCC------------------TTGGCGCTCC-TTCGGGA--GCGCG-AA-GT---GGC--GTG
STRUCKIA_ENERVIS_SICHUAN       G----------------GCG---C--GTCCCC-------------------TTGGCGCTCC-TTCGGGA--GTGCG-AA-GT---GGC--GTG
STRUCKIA_ARGENTATA_NEPAL       G----------------GCG---C--GTCCCC-------------------TTGGCGCTCC-TTCGGGA--GTGCG-AA-GT---GGC--GTG
MYURELLA_SIBIRICA              A----------------GCG---C-CGC-----------------------TTGCGGCTCT-TC-GGGA--GCGCG-AA-GT---GGC--GTG
HERZOGIELLA_SELIGERI           A----------------GCG---C--GCCCCC-------------------TTGGCGCTCC-TTCGGGA--GCGCG-AA-GG---AGC--GTG
HERZOGIELLA_TURFACEA           A----------------GCG---C--GCCCCC-------------------TTGGCGCTCC-TTCGGGA--GCGCG-AA-GG---AGC--GTG
STRUCKIA_ARGENTATA_YUNNAN      G----------------GCG---C--GTCCCC-------------------TTGGCGCTCC-TTCGGGA--GTGCG-AA-GT---GGC--GTG
STRUCKIA_ENERVE_ALTAI          G----------------GCG---C--GTCCCC-------------------TTGGCGCTCC-TTCGGGA--GTGCG-AA-GT---GGC--GTG
ISOPTERYGIOPSIS_MUELLERIANA_2  G----------------GCG---C--GCCCCCC------------------TTGGCGCTCC-TTCGGGA--GCGCG-AATGGATGGGC--GTG
ISOPTERYGIOPSIS_MUELLERIANA_1  C----------------GCG---CGCGCCCCC-------------------TTGGCGCTCC-TCCGGGA--GCGCG-AA-CG---GGC--GTG
ISOPTERYGIUM_PULCHELLUM        A----------------GCG---C--GCCCCC-------------------TTGGCGCTCC-TTCGGGA--GCGCG-AA-GC---GGC--GTG
PLATYDICTYA_JUNGERMANNIOIDES   A----------------GCG---C---CCCC--------------------TTGGCGCTCC-TTCGGGA--GCGCGAAA-GG---GGC--GAG
ENTODONTOPSIS_LEUCOSTEGA       G----------------GCG---C---CTCC--------------------TCGGCGCTCCCTTCGGGG-CGCGTC-CAGGG---GGC--GAG
STEREOPHYLLUM_RADICULOSUM      A----------------GCG---C---CTCC--------------------TCGGCGCTCCCTTCGGGG-CGCGTC-GA-GG---GGC--GAA
FABRONIA_CILIARIS              A----------------GCG---C---CCCC--------------------TCGGCGCTCCCTTCGGGA-CGCGCC-AA-GG---GGC--GAG
HOOKERIA_LUCENS                A----------------GCG---C---CCCC--------------------TTGGCGCTC--TCCGGGATCGCGCG-AA-G----GGCGCGTG
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Fig. 5. Part of ITS 2 alignment, showing absence of common substitutions and indels of *Podperaea baii* and Plagiotheciaceae.

Plagiotheciaceae+Stereophyllaceae+Fabroniaceae+Hookeriaceae and the rest of group represented in the analysis. However none of them indicate the relationship of *P. baii* with Plagiotheciaceae, but instead show that it belongs to that subclade of the termnial polytomy in Fig. 1 where *Podperaea krylovii, Campylophyllum, Ochyraea, Myrinia* and *Tomentypnum* occur.

When the first sequence of *P. baii* was analyzed, the possible contamination was suspected. Thus the DNA was cloned and re-sequenced and also re-extracted from sporophyte tissue of the same collection. An additional collections from Inner Mongolia were also looked for, including a special field trip in 2011, and two of new collections of *P. baii*, from geographically different

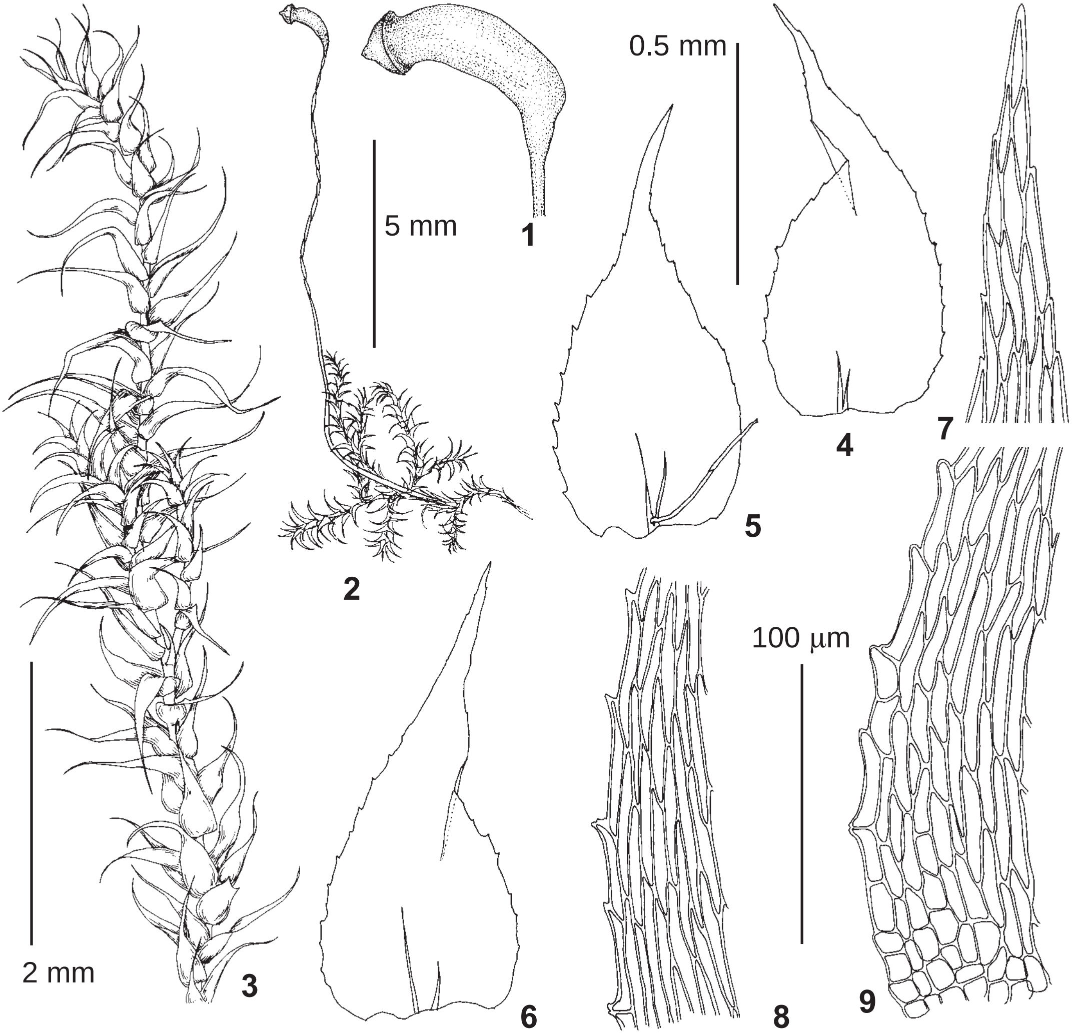

Fig. 6. *Podperaea baii* (Hedw.) Müll. Hal. (from isotype: China, Inner Mongolia, Xilin Gol, Bai X.-L. 058141, MHA): 1 – capsule; 2-3 – habit; 4-6 – leaves; 7 – upper laminal cells; 8 – mid-leaf cells; 9 – basal laminal cells. Scale bars: 5 mm for 2; 2 mm for 1, 3; 0.5 mm for 4-6; 100 µm for 7-9.

areas within Inner Mongolia Autonomous District of China have given the same ITS sequence: “plagiothecioid” ITS1 and “non-plagiothecioid” ITS2.

DISCUSSION

The ITS and especieally ITS1 of Plagiotheciaceae–Stereophyllaceae–Fabroniaceae group has many specific motifs (Fig. 4), also shared with Hookeriaceae. The mentioned families are characterized by expanded insertions, as well as substitutions in a fairly conservative places (Fig. 4).

Peculiar motifs of Plagiotheciaceae in ITS2 are not so many, but nevertheless some expanded indels differ this family (and some above mentioned related families) from the rest of Hypnales (Fig. 5). However none of them are found in *P. baii*, in contrast with ITS1 were the ‘plagiothecioid specificity’ is totally shared by *P. baii*.

ITS2 of *P. baii* differs somewhat also from *P. krylovii*, although strict consensus tree in the maximum parsimony analysis resolves them within one clade, together with marginal groups of Amblystegiaceae (*Camylophyllum, Tomentypnum, Drepanium,* and *Myrinia*).

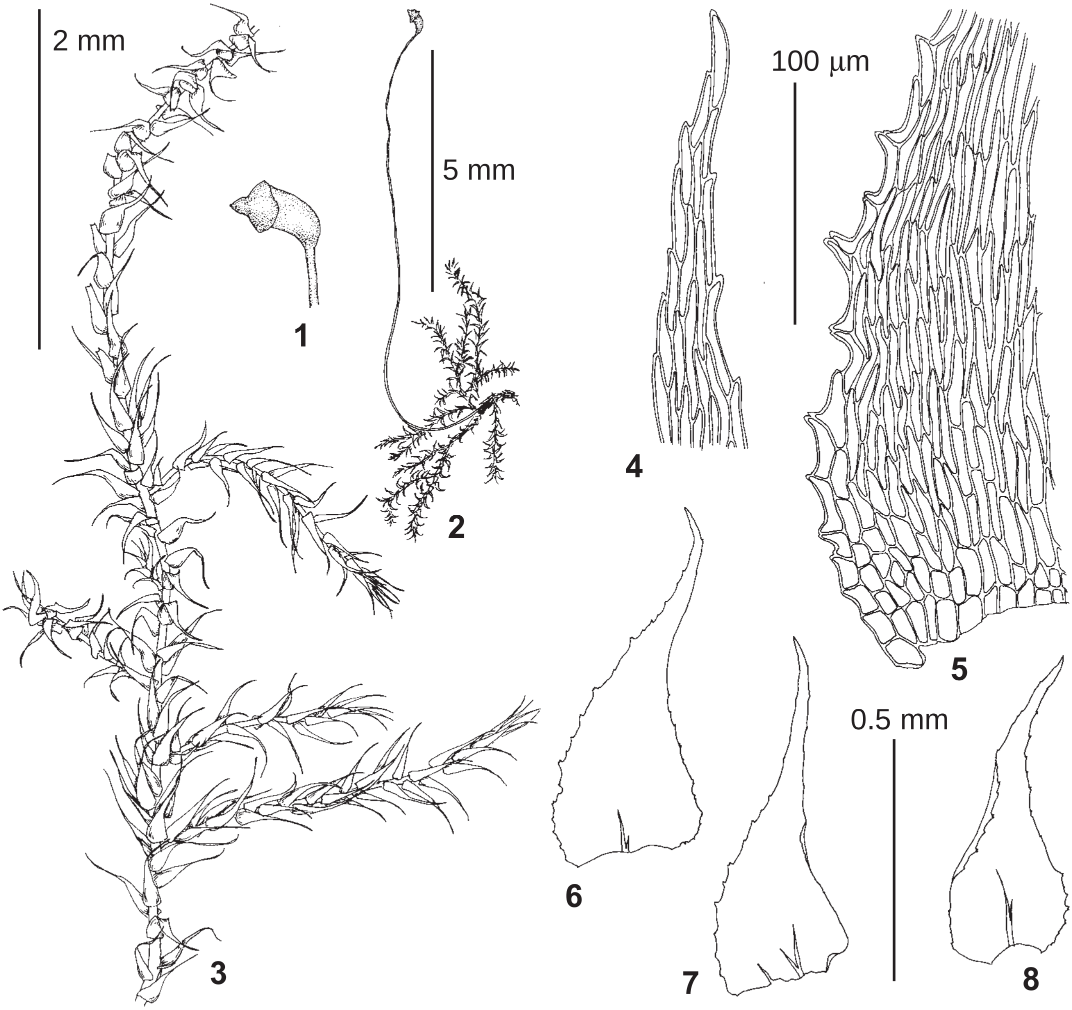

Fig. 7. *Podperaea krylovii* (Podp.) Müll. Hal. (from China, Inner Mongolia, Khingan Mts., Bai X.-L. 04095, MHA): 1 – capsule; 2-3 – habit; 4 – upper laminal cells; 5 – mid-leaf and basal laminal cells; 6-8 – leaves. Scale bars: 5 mm for 2; 2 mm for 1, 3; 0.5 mm for 6-8; 100 μm for 4-5.

Morphological differences between Plagiotheciaceae and 'Hypnales without Plagiotheciaceae and related families' include a number of characters and many of them are highly diagnostic. However, the genus *Herzogiella* does not belong to the 'core Plagiotheciaceae', so the most unique characters of the family, e.g., axillary position of rhizoides, 'lack of pseudopraphyllia' (cf. Ignatov & Hedenäs, 2007), axillary 3-4-celled gemmae, and lack of regular pinnate branching are not the case of this genus. Other characters, like pale peristome and a tendency to a complanate branching being common in Plagiotheciaceae, are known in a many other pleurocarpous groups. Molecular phylogenetic studies however always resolved *Herzogiella* in Plagiotheciaceae, excepting a likely misplaced in the genus *H. adscendens* (Lindb.) Z. Iwats. & W.B. Schofield.

Although the morphological circumscription of *Herzogiella* is rather indefinite, this genus is distinct from *Podperaea* in having only simple marginal teeth, while teeth in the latter are 'compound'. The presence of such teeth in *Podperaea baii* is the main reason for its placement in this genus.

Podperaea baii Ignatov sp. nov.

A Podperaea krylovii plantis robusioribus, foliis longioribus et latioribus, cellulis latoiribus, glabris, sporiis magnis, et ITS sequentia valde differt.

Holotype: China, Inner Mongolia (NE, desert area), Xilin Gol, Hun shan de ka, 21.VIII.2005, coll. Bai X.-L. # 058141(holotype MHA, isotype HIMC).

Ethymology: the species is named in honor of Prof. Bai Xue-liang, an eminent bryologist, who published moss flora of Inner Mongolia in China and collected this moss species.

Plants small, in loose, light green mats. Stem prostrate, to 1 cm long, with weak central strand, without hyalodermis, irregularly to rather regularly pinnately branched. Proximal branch leaves lanceolate to ovate, sitting around branch primordia on stem. Leaves ovate-lanceolate, gradually more or less longly acuminate, 0.7-0.95×0.35-0.45 mm, serrate all around by simple and partly 'compound' teeth; 'compound' teeth rather perpendicular to leaf margin, and more or less acute; costa double or forked, short and weak, or sometimes one of branches of forked costa extends to 0.5 the leaf length; laminal cells 30-70×6-7 μm; basal cells quadrate to short rectangular, 7-11 μm wide, forming small indistinctly delimited group. Autoicous. Perichaetial leaves somewhat larger than stem leaves, with single costa reaching up half-leaf, serrulate, smooth. Setae to 15 mm. Capsules ca. 1.3 mm long, arcuate and strongly contracted below the mouth when dry; operculum conic; annulus separated by fragments; peristome double, complete, with long cilia. Spores 17-18 μm.

Specimens examined: CHINA, INNER MONGOLIA: Xilin Gol, Bai X.-L. #058141 (HIMC, MHA); Manhan Shan, Ignatov #11-1 (MHA); Hohhot, Kou Jin #110(7) (HIMC, MHA).

We did not see specimens from Helan Shan, alt. 1900 m, HQ269, but according to illustrations in Bai (2010) and Zhao et al. (2006) it .

Distinction. *Podperaea baii* is a somewhat larger plant than *P. krylovii*, it has broader laminal cells without prorate upper angles; 'compound teeth' are 'more acute' as cells forming a tooth join each other up to the tooth apex, whereas in *P. krylovii* cells forming a tooth are more or less divergent distally, at least at short distance (cf. Figs. 6 & 7). In addition, spores in *P. baii* are larger than in *P. krylovii*, 17-18 μm versus 10-12 μm.

* * *

Remote hybridization is well-known in flowering plants, where widespread artificial and occasionally natural intrageneric hybrids are known (*Triticum*×*Secale* = *Triticale*; *Hordem*× *Elymus* = *Hordelymus; Sorbus*×*Cotoneaster* = *Sorbocotoneaster*, etc.). These and similar cases however include different genera that belong to the same subfamily, and thus represent a hybridization of only a moderately divergent groups.

Much more remote hybridization is known in orchids, where two or more not very closely related genera may produce stable hybrids: *Cattleya × Laelia = Laeliocattleya; Cattleya × Sophronitis = Sophrocattleya; Cattleya× Laelia× Sophronitis = Sophrolaeliocattleya; Cochlioda ×Miltonia×Odontoglossum =Vuylstekeara.*

In mosses, intrageneric hybrids were found or produced artificially for *Funaria*×*Physcomitium, Physcomitrium*×*Physcomitrella, Weissia*×*Astomum* (the latter genus is often treated within *Weissia*), *Ditrichum*×*Pleuridium* (see review of Anderson, 1980). Some *Physcomitrium*×*Physcomitrella* hybrids produce tetrads with 2 of 4 spores viable. According to Wettstein (1924) they have only maternal chromosomes, thus not further reproducing hybrid organisms.

Some of the recent phylogenetic studies, with construction of haplotype network by two independent markers illustrate the possible hybridization in the genus *Sciuro-hypnum* (Draper & Hedenäs, 2009).

The case of *Podperaea baii* likely represents a rare event. ITS is the most variable of DNA regions which are widely used in moss phylogenetics, but not that variable to be useless for phylogeny reconstruction. The large trees that were based on, among others, ITS data, provided many helpful results on the relationships of pleurcarpous mosses (Gardiner et al., 2005; Ignatov et al., 2007; Huttunen et al., 2012).

However the case of *Podperaea baii* might be important for understanding of a strong incongruence between topology of molecular trees and morphology, like for example, the case of *Pinnatella homaliadelphoides* Enroth, S. Olsson, S. He, Shevock & D. Quandt (Enroth et al., 2009).

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Appendix 1. Studied specimen data and GenBank accessions numbers.

A. ***Newly obtained sequences***

Species	Specimen	GenBank assession
Entodon seductrix	U.S.A., New Jersey, Tan #92-129 (MHA)	JN896314
Herzogiella turfacea	Russia, Kunashir, Ignatov #06-1262 (MW)	JN896315
Homomallium incurvatum	Russia, Altai, coll. Ignatov 0/1714 (MHA)	JQ247725
Homomallium connexum	Russia, Primorsky Territory, Ignatov #07-572 (MHA)	JN896316
Hookeria lucens (Hedw.) Sm.	U.S.A., California, Ignatov 89-1 (MHA)	JN896317
Isopterygiopsis muelleriana (Schimp.) Z. Iwats. 2	Russia, Primorsky Territory, Ignatov #07-296 (MHA)	JN896318
Mittenothamnium reptans	Honduras, Allen # 12298 (MHA)	JN896320
Ochyraea tatrensis Váňa	Czechoslovakia, coll. Váňa s. n. 30.VIII.1987 (MHA)	JQ247724

Podperaea baii Xilin Gol 1 (gametophyte)	China, Inner Mongolia, Xilin Gol, Bai X.-L. 058141 (HIMC, MHA)	JN896321
Podperaea baii Xilin Gol 2 (clone 1 from gametophyte)	China, Inner Mongolia, Xilin Gol, Bai X.-L. 058141 (HIMC, MHA)	JN896322
Podperaea baii Xilin Gol 3 (sporophyte)	China, Inner Mongolia, Xilin Gol, Bai X.-L. 058141 (HIMC, MHA)	JN896323
Podperaea baii Hohhot	China, Inner Mongolia, Hohhot Kou Jin #110(7) (HIMC, MHA)	JN896324
Podperaea baii Manhan	China, Inner Mongolia, Manhan Shan Ignatov #11-1 (MHA)	JN896325
Podperaea krylovii Altai	Russia, Altai, Ignatov #1/10 (MHA)	JN896326
Podperaea krylovii Khingan	China, Inner Mongolia, Great Khingan Mt., Bai Xue-liang 04095 (MHA)	JN896327
Podperaea krylovii Primorsky 1	Russian Far East, Primorsky Territory Ignatov #08-308 (MHA)	JN896328
Podperaea krylovii Primorsky 2	Russia, Primorsky Territory, Ignatov #07-220 (MHA)	JN896329
Stereodon fauriei	Russia, Khabarosk Territory, Ignatov, #97-216 (MHA)	JN896313

B. ***Previous sequences used in the present analysis***

ITS from previous studies (specimen data in Ignatov et al., 2007 or else); if ITS1 and ITS2 have different accessions they are given with / ; the only accesions means both ITS1&2, unless otherwise is specially marked.

Breidleria pratense (J. Koch ex Spruce) Loeske AY693659; *Calliergonella cuspidata* (Hedw.) Loeske AF168145;*Campylidium sommerfeltii* (Myr.) Ochyra AY693654; *Campylium stellatum* (Hedw.) C. Jens. AF168151; *Campylophyllum halleri* (Sw. ex Hedw.) M. Fleisch. (1) AF168134; *Campylophyllum halleri* (Sw. ex Hedw.) M. Fleisch(2) AY693655; *Caribaeohypnum polypterum* (Mitt.) Ando & Higuchi AY009799; *Ctenidium molluscum* (Hedw.) Mitt. AF230989 / AF403632; *Drepanium (Hypnum) recurvatum* (Lindb. & Arnell) G. Roth AY693660; *Entodontopsis leucostega* (Brid.) W. R. Buck & R. R. Ireland AY999175; *Eurohypnum leptothallum* (Müll. Hal.) Ando AY695733 / AY695786; *Fabronia ciliaris* (Brid.) Brid. AY528883; *Glossadelphus ogatae* Broth. & Yas. AY999169; *Herzogiella seligeri* (Brid.) Z. Iwats. AY999174; *Heterocladium dimorphum* (Brid.) Bruch & al. AY695757 / AY695771; *Hygrohypnella ochracea* (Wils.) Ignatov & Ignatova AF168138; *Hygrohypnella polaris* (Lindb.) Ignatov & Ignatova AY695735; *Hylocomium splendens* (Hedw.) Bruch et al. AJ288336 / AJ270021; *Hypnum cupressiforme* Hedw. AY528888 / AF403607; *Isopterygiopsis muelleriana* (Schimp.) Z. Iwats. 1 AY528882; *Isopterygiopsis pulchella* (Hedw.) Z. Iwats. AY695751 / AY695770; *Leptodictyum riparium* (Hedw.) Warnst. AF168163; *Leptopterigynandrum austro-alpinum* Müll. Hal. (1) AY693656; *Leptopterigynandrum austro-alpinum* Müll. Hal. (2) AF516163 / AF516158; *Lescuraea secunda* Arnell AF516164 / AF516150; *Myrinia pulvinata* (Wahlenb.) Schimp. AY528886 / AY528887; *Myrinia rotundifolia* (Arnell) Broth. AY528898; *Myurella sibirica* AJ288415 / AJ277227; *Neckera pennata* Hedw. AY009809; *Ochyraea norvegica* (Bruch & al.) Ignatov & Ignatova AY695753 / AY695789; *Ochyraea mollis* (Hedw.) Ignatov AY999178; *Plagiothecium denticulatum* (Hedw.) Bruch & al. AY528892 / AY528893; *Platydictya jungermannioides* (Brid.) H. A. Crum AF168162; *Pylaisia polyantha* (Hedw.) Schimp. AY528881; *Rhytidiopsis robusta* (Hook.) Broth. AJ288331 / AJ288545; *Sanionia uncinata* (Hedw.) Loeske AF168148; *Scorpidium scorpioides* (Hedw.) Limpr. AY009790; *Scorpidium cossonii* AY625996; *Struckia argentata* Yunnan DQ836734; *Struckia argentata* Nepal Q836733; *Struckia enervis* Sichuan DQ836736 / DQ836737; *Struckia enervis* Altai DQ836735; *Stereodon (Hypnum) vaucheri* (Lesq.) Lindb. ex Broth. AY695762 / AY695791; *Stereophyllum radiculosum* (Hook.) Mitt. AY999176; *Taxiphyllum wissgrillii* (Garov.) Wijk & Marg. AY999168; *Tomentypnum falcifolium* (Renauld ex Nichols) Tuom. AF168136; *Tomentypnum nitens* (Hedw.) Loeske AF168161.