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.

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 значительно более сходна с Amblystegiaceae, нежели с Plagiotheciaceae. Данный случай является первым примером возможной отдаленной гибридизации 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. krylovii) 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 krylowii* 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 Heilongjiang 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 result has 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 chloroplast markers trnL-F and rps4 have given poor resolution and are not presented here.

As the preliminary 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 & Hedénäs, 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-
A putative intrafamilial hybridization in Podperaea

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, Carribaeohyphnum (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 baiii 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 baiii 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 consensus 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.
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 krylovi* and *P. baii* in one clade, which also includes *Myrmina* and four genera, *Ochyrea*, ‘*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
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

![Fig. 5. Part of ITS 2 alignment, showing absence of common substitutions and indels of Podperaea baii and Plagiotheciaceae.](image-url)

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 terminal polytomy in Fig. 1 where *Podperaea krylovii*, *Campylophyllum*, *Ochyraea*, *Myrina* and *Tomentypnum* occur.
areas within Inner Mongolia Autonomous District of China have given the same ITS sequence: “plagiothecioid” ITS1 and “non-plagiothecioid” ITS2.

**DISCUSSION**

The ITS and especially 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 Myrina*).
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.

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

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; Hordeum×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 × Physcomitrium, 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).
ACKNOWLEDGEMENTS

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LITERATURE CITED


ENTODON SEDUCTRIX
Species Specimen GenBank accession

Species

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 (Hedd.) Sm.

Russia, Primorsky Territory, Ignatov #07-296 (MHA)

JN896318

Isopterygiopsis muelleriana

U.S.A., California, Ignatov 89-1 (MHA)

JN896317

(Schimp.) Z. Iwats. 2

Czechoslovakia, coll. Váňa s. n. 30.VIII.1987 (MHA)

JQ247724

Mittenothamnium reptans

Honduras, Allen # 12298 (MHA)

JN896320

Ochyraea tatrensis Váňa

Appendix 1. Studied specimen data and GenBank accessions numbers.

A. Newly obtained sequences
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 accessions 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;
- *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 leptothal- lum* (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.) AJ288336 / AJ270021;
- *Hypnum cupressiforme* Hedw. AY528888 / AF403607;
- *Isopterygiopsis muelleriana* (Schimp.) Z. Iwats. 1 AY528882;
- *Leptodictya jungermannioides* (Brid.) H. A. Crum AF168181;
- *Myrinia pulvinata* (Wahlenb.) Schimp. AY528886 / AY528887;
- *Myurella sibirica* Broth. AY528898;
- *Neckera pennata* Hedw. AY009809;
- *Ochyraea norvegica* (Bruch & al.) Ignatov & Ignatova AY695753 / AY695789;
- *Plagiothecium denticulatum* (Hedw.) Bruch & al. AJ288336 / AJ270021;
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- *Podperaea baii* Xilin Gol 3 (clone 1 from gametophyte) China, Inner Mongolia, XiLin Gol, Bai X.-L. 058141 (HIMC, MHA) JN896323
- *Podperaea baii* Xilin Gol 3 (sporophyte) China, Inner Mongolia, Hohhot Kou Jin #1107 (HIMC, MHA) JN896324
- *Podperaea baii* Manhan China, Inner Mongolia, Manhan Shan Ignatov #11-1 (MHA) JN896325
- *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
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- *Stereodon fauriei* Russia, Khabarosk Territory, Ignatov, #97-216 (MHA) JN896313
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- *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;
- *Lescuracia secunda* Arnell AF516164 / AF516150;
- *Myrinia pulvinata* (Wahlenb.) Schimp. AY528886 / AY528887;
- *Myurrella sibirica* Broth. AY528898;
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