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Ignatovia U.B.Deshmukh (Leskeaceae, Bryophyta),
a monospecific genus endemic to Russia,
newly found in Beijing, China with special
references to its complete organelle genomes

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***Ignatovia* U.B.Deshmukh (Leskeaceae, Bryophyta), a monospecific genus endemic to Russia, newly found in Beijing, China with special references to its complete organelle genomes**

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ABSTRACT

The genus *Ignatovia* U.B.Deshmukh comprises the sole species *Ignatovia microphylla* (Ignatov & Ignatova) U.B.Deshmukh, which has been thus far known only from Russia. During our recent expeditions to Shangfangshan National Forest Park in Beijing, China, we encountered an interesting moss that can be assignable to *I. microphylla*, characterized by small leaves, round to oblate and thick-walled lamina cells that are somewhat bulging abaxially, nearly homogeneous thick-walled cells in the cross-section of the stem, a cross-section of the costa without stereids, and triangular inner perichaetial leaves. Molecular phylogenetic analyses based on nrITS1-5.8S-ITS2 and *trnL*-F further support the morphological identification. Our finding represents the first report of *I. microphylla* outside Russia, a new generic record for China. Additionally, we assembled and annotated its organelle genomes. The results showed that the complete chloroplast genome is 124 918 base pairs (bp) in length

KEY WORDS

Beijing,
chloroplast genome,
mitochondrial genome,
mosses,
phylogeny,
new record.

with 29.2% GC content, consisting of 82 protein-coding genes, 37 tRNA genes, and eight rRNA genes. The complete mitogenome is 103 161 bp in length with a GC content of 41.0%, comprising 40 protein-coding genes, 24 tRNA genes, and three rRNA genes. The discovery of *I. microphylla* could lay the foundation for investigating biogeographical patterns and species evolution in further studies.

RÉSUMÉ

Ignatovia (Leskeaceae, Bryophyta), un genre monospécifique endémique de Russie, nouvellement trouvé à Pékin, Chine, avec des références spéciales aux génomes complets de ses organelles.

Le genre *Ignatovia* U.B.Deshmukh comprend la seule espèce *Ignatovia microphylla* (Ignatov & Ignatova) U.B.Deshmukh, qui n'est connue jusqu'à présent qu'en Russie. Au cours de nos récentes expéditions dans le parc forestier national de Shangfangshan à Pékin, en Chine, nous avons rencontré une mousse intéressante qui peut être attribuée à *I. microphylla*, caractérisée par de petites feuilles, des cellules laminaires rondes à oblongues et à parois épaisses, quelque peu bombées abaxialement, des cellules à parois épaisses presque homogènes dans la section transversale de la tige, une section transversale de la nervure sans stéréides, et des feuilles périchétiales internes triangulaires. Les analyses phylogénétiques moléculaires basées sur nrITS1-5.8S-ITS2 et *trnL*-F confirment l'identification morphologique. Notre découverte représente le premier rapport d'*I. microphylla* en dehors de la Russie, un nouveau signalement du genre pour la Chine. En outre, nous avons assemblé et annoté les génomes de ses organelles. Les résultats ont montré que le génome complet du chloroplaste est de 124 918 pb avec 29,2 % de contenu en GC, comprenant 82 gènes codant pour des protéines, 37 gènes d'ARNt et huit gènes d'ARNr. Le mitogénome complet est de 103 161 pb avec une teneur en GC de 41,0 %, comprenant 40 gènes codant pour des protéines, 24 gènes d'ARNt et trois gènes d'ARNr. La découverte d'*I. microphylla* pourrait jeter les bases de l'étude des schémas biogéographiques et de l'évolution des espèces dans le cadre d'études ultérieures.

MOTS CLÉS
Beijing,
génomme chloroplastique,
génomme mitochondrial,
mousses,
phylogénie,
nouveau signalement.

INTRODUCTION

China is the country with the richest diversity of bryophytes in the world, encompassing 3 082 species across 609 genera (Wang *et al.* 2018; Zhu *et al.* 2022). However, our understanding of this diversity remains insufficient in China because many areas remain poorly investigated. Since 2018, eight genera have been added to the Chinese bryoflora, including *Konstantinovia* Bakalin & Fedosov (Bakalin *et al.* 2021a), *Mawenzhangia* Enroth, Shevock & Ignatov (Enroth *et al.* 2018), *Protoharpanthus* Bakalin, Fedosov & D.G.Long (Bakalin *et al.* 2021b), *Ramudaria* D.K.Singh, S.Majumdar, D.Singh & Molinari (Xu *et al.* 2022), *Rheoshevoekia* Ignatov, W.Z.Ma & D.G.Long (Ma *et al.* 2018), *Sinomylia* P.C.Wu, Y.Jia & M.Z.Wang (Wu *et al.* 2018), *Soella* R.L.Zhu, L.Shu, QiongHe & Y.M.Wei (Zhu *et al.* 2018), and *Sphaerocarpos* P.Micheli ex Boehm. (Xiang & Zhu 2019). These studies have significantly enhanced our understanding of bryophyte diversity in China. Despite this, it is important to note that these new records were primarily found in the southern and southwestern regions of China (e.g., Hengduan Mountains, Himalayas), where the unique species diversity attracts considerable attention of numerous bryologists, while little has been known from northern China, especially those urban areas.

During a bryophyte expedition to Shangfangshan National Forest Park in Beijing, northern China, we encountered a diminutive moss resembling *Ignatovia microphylla* Ignatov & Ignatova) U.B.Deshmukh. This moss is characterized by small leaves, typically measuring between 0.15 and 0.25 mm, and a transverse section of the stem composed of nearly homoge-

neous thick-walled cells, without a central strand. Through a review of the literature and phylogenetic analyses based on the ITS and *trnL*-F loci, we confirmed that the moss belongs to *I. microphylla*, a species known only in the Primorsky Territory of Russia (Ishchenko *et al.* 2022; Ignatov *et al.* 2019). This species and genus have not been previously reported outside Russia; thus, its discovery in Beijing represents the first record of this genus in China.

Ignatovia (Leskeaceae) is a replacing name for *Lazarenkoa* Ignatov & Ignatova, a later homonym of the Ascomycetes fungal genus *Lazarenkoa* Zerova (Ignatov *et al.* 2019; Deshmukh 2021). *Ignatovia* is placed in the Leskeaceae Schimp., a morphologically heterogeneous and phylogenetically polyphyletic family (Ignatov *et al.* 2019; Spence 2014; Li *et al.* 2024). Recently, proposals have emerged to broaden the delimitation of Leskeaceae and merge the traditionally recognized family Thuidiaceae with it (Allen 2018; Kučera *et al.* 2021). However, this taxonomic treatment has not yet been widely accepted (Goffinet & Buck 2020; Hodgetts *et al.* 2020; Wang *et al.* 2023; Brinda & Atwood 2025). Conversely, Li *et al.* (2024) have proposed an opposing view advocating for the merging of Leskeaceae with Thuidiaceae. The relationship between Thuidiaceae and Leskeaceae remains a contentious topic for the foreseeable future. Therefore, providing additional molecular data related to Leskeaceae and Thuidiaceae, particularly from organelle genomes, is of significant value for future analyses of their relationships.

The primary objectives of this study are to newly report the occurrence of *Ignatovia* in Beijing, China, and present

TABLE 1. — Sequences used in the present study, including taxa, countries, voucher specimens, and GenBank accession numbers (ITS, and trnL-F). Newly sequenced specimens are set in **boldface**; —, means data missing.

Taxa	Countries	Voucher specimen	ITS	trnL-F
<i>Abietinella abietina</i> (Hedw.) M. Fleisch.	China	HIMC2011232 (HIMC)	JX853713	JX853719
<i>Abietinella hystricosa</i> (Mitt.) Sakurai	China	HIMC201106008 (HIMC)	JX853712	JX853718
<i>Abietinella</i> sp.	China	HIMC1009118 (HIMC)	JX853714	JX853720
<i>Actinothuidium hookeri</i> (Mitt.) Broth.	China	—	KF770664	KF770502
<i>Boulaya mitteni</i> (Broth.) Cardot	Japan	<i>Tanaka 7308</i> (HIRO)	FM161080	AM990347
<i>Bryonoguchia molkenboeri</i> I (Sande Lac.) Z.Iwats. & Inoue	China	—	KF770666	KF770504
<i>Bryonoguchia molkenboeri</i> II	Russia	<i>Ignatov & Ignatova 13-1936</i> (MW)	KX396260	KX396255
<i>Echinophyllum sachalinense</i> I (Lindb.) T.J.O'Brien	Russia	<i>Ignatov et al. 13-1469</i> (MW)	KX396259	KX396255
<i>Echinophyllum sachalinense</i> II	Russia	<i>Ignatov & Ignatova 13-233</i> (MW)	KX396264	KX396250
<i>Elodium paludosum</i> (A. aeger) Austin ex C.F.Parker	China	—	KF770667	KF770505
<i>Haplocladium angustifolium</i> (Hampe & Müll.Hal.) Broth.	China	—	KF770659	KF770497
<i>Haplocladium microphyllum</i> (Sw. ex Hedw.) Müll.Hal.	China	—	KF770660	KF770498
<i>Haplocladium strictulum</i> (Cardot) Reimers	China	—	KF770661	KF770499
<i>Helodium blandovii</i> (F.Weber & D. Mohr) Warnst.	United States	<i>Schofield 108637</i>	AY009803	AY009852
<i>Ignatovia microphylla</i> I (Ignatov & Ignatova) U.B.Deshmukh	Russia	<i>Tumurova VL-1-14</i> (MHA, UUH)	MN850404	MN849424
<i>Ignatovia microphylla</i> II	Russia	<i>Fedosov, Ishchenko & Shkurko s.n.</i> (MW, MHA)	OQ085094	—
<i>Ignatovia microphylla</i> HTC064	China	<i>R. L. Zhu et al. 20200903-51</i> (HSNU, HTC)	PQ814309	PQ821839
<i>Lescuraea mutabilis</i> (Brid.) Lindb. ex I.Hagen	China	—	KF770682	KF770520
<i>Leskea gracilescens</i> I Hedw.	United States	<i>Tan #91502</i> (MHA)	MH558262	MN871403
<i>Leskea gracilescens</i> II	United States	<i>6.X.2013 Ignatov</i> (MHA)	MH558263	MN871404
<i>Leskea gracilescens</i> III	United States	<i>Buck 57814</i> (NY1221900)	MH558264	MN871396
<i>Leskea obtusa</i> I Renault & Cardot	United States	<i>Buck 30103</i> (NY489398)	MH558266	MN871398
<i>Leskea obtusa</i> II	United States	<i>Buck 22206</i> (NY489277)	MH558265	—
<i>Leskea obtusa</i> III	United States	<i>Buck 46377</i> (NY680473)	MH558267	MN871397
<i>Leskea polycarpa</i> I Hedw.	Russia	<i>11.XI.2009 Donskov</i> (MHA)	MH558269	MN871399
<i>Leskea polycarpa</i> II	Russia	<i>Pisarenko #3765</i> (MHA)	MH558272	MN871402
<i>Leskea polycarpa</i> III	Russia	<i>1.VII.2010 Bezgodov #34</i> (MHA)	MH558270	MN871400
<i>Leskea polycarpa</i> IV	Russia	<i>Ignatov #08-355a</i> (MHA)	MH558271	MN871401
<i>Leskea scabrinervis</i> Broth. & Paris	China	—	KF770663	KF770501
<i>Lindbergia serrulata</i> C.Gao, T.Cao & W.H.Wang	China	—	KF770670	KF770508
<i>Lindbergia sinensis</i> (Müll.Hal.) Broth.	China	—	KF770668	KF770506
<i>Myrinia pulvinata</i> (Wahlenb.) Schimp.	Russia	<i>Chernyadyeva</i> (CBFS19991)	MK327351	MK314034
<i>Pelekium minutulum</i> (Hedw.) Touw	Russia	<i>Bezgodov, Ateeva 217</i> (MW)	KX396265	KX396256
<i>Bryochenea vestitissima</i> (Besch.) Touw	Russia	<i>Ignatov 08-35</i> (MW)	KX396261	KX396252
<i>Platylomella lescurii</i> (Sull.) A.L.Andrews	United States	<i>Vanderpoorten s.n.</i> (AV, BG)	AY242371	AY242379
<i>Pseudoleskeopsis zippeli</i> (Dozy & Molk.) Broth.	China	<i>Redfearn 36225</i> (H)	AY568548	AY683603
<i>Raiiella fujisana</i> (Paris) Reimers	China	<i>Wang, M 400</i> (PE)	AY568546	AY683600
<i>Sasaokaea aomoriensis</i> (Paris) Kanda	Japan	<i>Takaki s.n.</i> (S)	JF280974	JF280981
<i>Scorpidium cossonii</i> (Schimp.) Hedenäs	Sweden	<i>Hedenas</i> (S; B61807)	AY625996	AY626013
<i>Thuidium cymbifolium</i> (Dozy & Molk.) Dozy & Molk.	China	<i>He, Q. 061</i> (PE)	AY568542	KF770482
<i>Thuidium thermophilum</i> Czernjad.	Russia	<i>8.VIII.1991 O.A. Chernyagina</i> (LE)	EF368013	EF368012

the complete genomes of its chloroplast and mitochondrion for the first time.

MATERIAL AND METHODS

TAXON SAMPLING

The Chinese specimen of *Ignatovia microphylla* was collected from Shangfangshan National Forest Park in Beijing by Rui-Liang Zhu, Chao Shen and Hao Xu on 3 September 2024. The voucher specimen (*R.L.Zhu et al. 20240903-51*) has been deposited in the herbarium of the East China Normal University (HSNU) and the herbarium of the Hangzhou Normal University (HTC). To determine the phylogenetic position of

this Chinese species, we conducted an analysis utilizing the same two DNA loci employed by Ignatov *et al.* (2019): *trnL-F*, and *nrITS1-5.8S-ITS2*. *Lescuraea mutabilis* (Brid.) Lindb. ex I.Hagen, *Myrinia pulvinata* (Wahlenb.) Schimp. and *Scorpidium cossonii* (Schimp.) Hedenäs were selected as outgroups, while the remaining 37 accessions were downloaded from GenBank. A list of taxa, including collection localities, vouchers, herbarium codes, and GenBank accession numbers, is provided in Table 1.

MORPHOLOGICAL STUDY

The species pictures were taken using a digital camera (Canon M6; Canon, Tokyo, Japan). A Leica stereo zoom scope (Leica EZ4; Leica, Wetzlar, Germany) and an Olympus microscope (Olympus BX51; Olympus, Tokyo, Japan) were used to

examine the specimens, and microscopic images were captured by a digital camera (MOTICAM S6; Motic, Xiamen, China) attached to the microscope.

DNA EXTRACTION, SEQUENCING, ASSEMBLY AND ANNOTATION

The sample preparation, DNA extraction, and sequencing followed protocols used in earlier studies (Huang *et al.* 2019; Xiang *et al.* 2022). We used the GetOrganelle pipeline (Jin *et al.* 2020) for the *de novo* assembly of the nuclear DNA and complete circular organelle genome. The newly generated chloroplast and mitochondrial genome were deposited in GenBank (accession number: PQ821839 and PQ821862, respectively). The genomes were annotated automatically using CPGAVAS2 (Shi *et al.* 2019) and then adjusted using Geneious v.11.1.5 (Kearse *et al.* 2012) based on the *Haplocladium microphyllum* (Sw. ex Hedw.) Müll. Hal. as reference plastome and *Thuidium tamariscinum* (Hedw.) Schimp. as mitochondrial genome. Circular organelle genome maps were drawn using OrganellarGenome DRAW (Lohse *et al.* 2013). The assembled nuclear data were aligned with published data using *Ignatovia microphylla* as reference (nrITS1-5.8S-ITS2 accession number, MN850404) in Geneious version 11.1.5 (Kearse *et al.* 2012) and then annotated and extracted.

PHYLOGENETIC ANALYSES

The *trnL-F*, and nrITS1-5.8S-ITS2 partitions were aligned using MAFFT v7.311 (Katoh & Standley 2013) and ambiguous alignment regions were trimmed using trimAl v1.2 (Capella-Gutiérrez *et al.* 2009). The resulting individual alignments were concatenated in Geneious ver. 11.1.5 (Kearse *et al.* 2012). Phylogenetic analyses were carried out using maximum likelihood (ML) and Bayesian inference (BI) methods in IQtree version 2.0.6 (Minh *et al.* 2020) and MrBayes 3.2.6 (Ronquist *et al.* 2012), respectively. We performed phylogenetic analyses using three different data sets: nuclear ITS, *trnL-F*, and concatenated data set of two loci. Maximum likelihood (ML) analyses were performed in IQtree v2.0.6 (Minh *et al.* 2020) with the sampling repeated 1000 times. The best-fitting substitution model was selected by ModelFinder (Chernomor *et al.* 2016; Kalyaanamoorthy *et al.* 2017) according to the Bayesian Information Criterion (BIC). For BI analyses, each DNA region was also assigned its own substitution model, as determined by the Akaike information criterion (Chernomor *et al.* 2016; Kalyaanamoorthy *et al.* 2017). Two independent analyses consisting of four Markov chain Monte Carlo chains were run for 5 000 000 generations, with one tree sampled for every 1 000 generations. The posterior distribution of trees was summarised by a > 50% majority-rule consensus tree after discarding the first 25% of samples as burn-in. Convergence was assessed by examining the likelihood plots in Tracer version 1.7 (Rambaut *et al.* 2018).

RESULTS

PHYLOGENETIC RESULTS

The aligned 2-loci data set comprised 1 216 characters: nrITS1-5.8S-ITS2 (778 bp), and *trnL-F* (438 bp). Maximum

likelihood (ML) and Bayesian inference (BI) analyses resulted in almost identical trees with strong support for most nodes. The BI topology tree with bootstrap values (BS_{ML} and PP_{BI}) is shown in Fig. 1.

Phylogenetic analyses of the concatenated dataset (Fig. 1A) revealed that the Chinese moss forms a maximum clade with two other accessions of *I. microphylla* from Russia (BS_{ML} = 100; PP_{BI} = 1), including one accession from the holotype voucher specimen. The phylogenetic analyses of ITS alone (Fig. 1B) also placed the Chinese plants nested within the two accessions of *I. microphylla* from Russia (BS_{ML} = 100; PP_{BI} = 1). The phylogenetic analyses of *trnL-F* alone (Fig. 1C) demonstrated that the Chinese plants form a highly supported clade with another accession of *I. microphylla* from the holotype voucher specimen (BS_{ML} = 99; PP_{BI} = 0.97).

ORGANELLE GENOMES

The chloroplast genome of *Ignatovia microphylla* was 124 918 bp in length and possessed a circular DNA molecule with the typical quadripartite structure, consisting of a large single-copy (LSC) region of 86 929 bp, a small single-copy (SSC) region of 18 492 bp, and a pair of inverted repeats (IRs) of 19 500 bp (Fig. 2A). Nucleotide composition was 35.4% A, 35.4% T, 14.5% G, and 14.7% C, with an overall GC content of 29.2%. It contains 127 genes, including 82 protein-coding genes, eight rRNAs, and 37 tRNAs; of these, nine genes (four rRNAs and five tRNAs) are duplicated in the IR regions (Fig. 2A). Among these genes, 19 intron-containing genes were identified, 17 of which contain one intron, while only the genes *clpP* and *ycf3* harbored two introns (Fig. 2A).

The mitogenome of *I. microphylla* assembled as a single circular chromosome of 103 161 bp with 41.0% GC content (Fig. 2B), including coding regions with a total length of 32 355 bp, introns with 32 189 bp, and intergenic spacers with 38 617 bp. We identified 67 genes, including three rRNAs, 24 tRNAs and 40 protein-coding genes (Fig. 2B). There were a total of 27 introns distributed over 16 genes, among which the gene *cox1* had the largest number of introns (four) (Fig. 2B).

NEW RECORD FOR CHINA

Family LESKEACEAE Schimp.
Genus *Ignatovia* U.B.Deshmukh

Ignatovia microphylla (Ignatov & Ignatova)
U.B.Deshmukh
(Fig. 3)

Phytotaxa 497 (2): 173. (Deshmukh 2021). — Type: **Russia** • Primorsky Territory, Partizansk District, Nakhodka City surroundings, foothills of the Lozovyj Range (former Chandolaz), E-facing slope, or rocks in streamlet bed; 43°00'51.1"N, 133°01'13.6"E; 240 m alt.; 21.IX.2015; *O.D. Tumurova VL-1-14* (holotype: MHA; isotype: UUH).

SPECIMEN EXAMINED. — **China** • Beijing City, Fangshan District, Shangfangshan National Forest Park; on wet rock; 39°40'22.99"N,

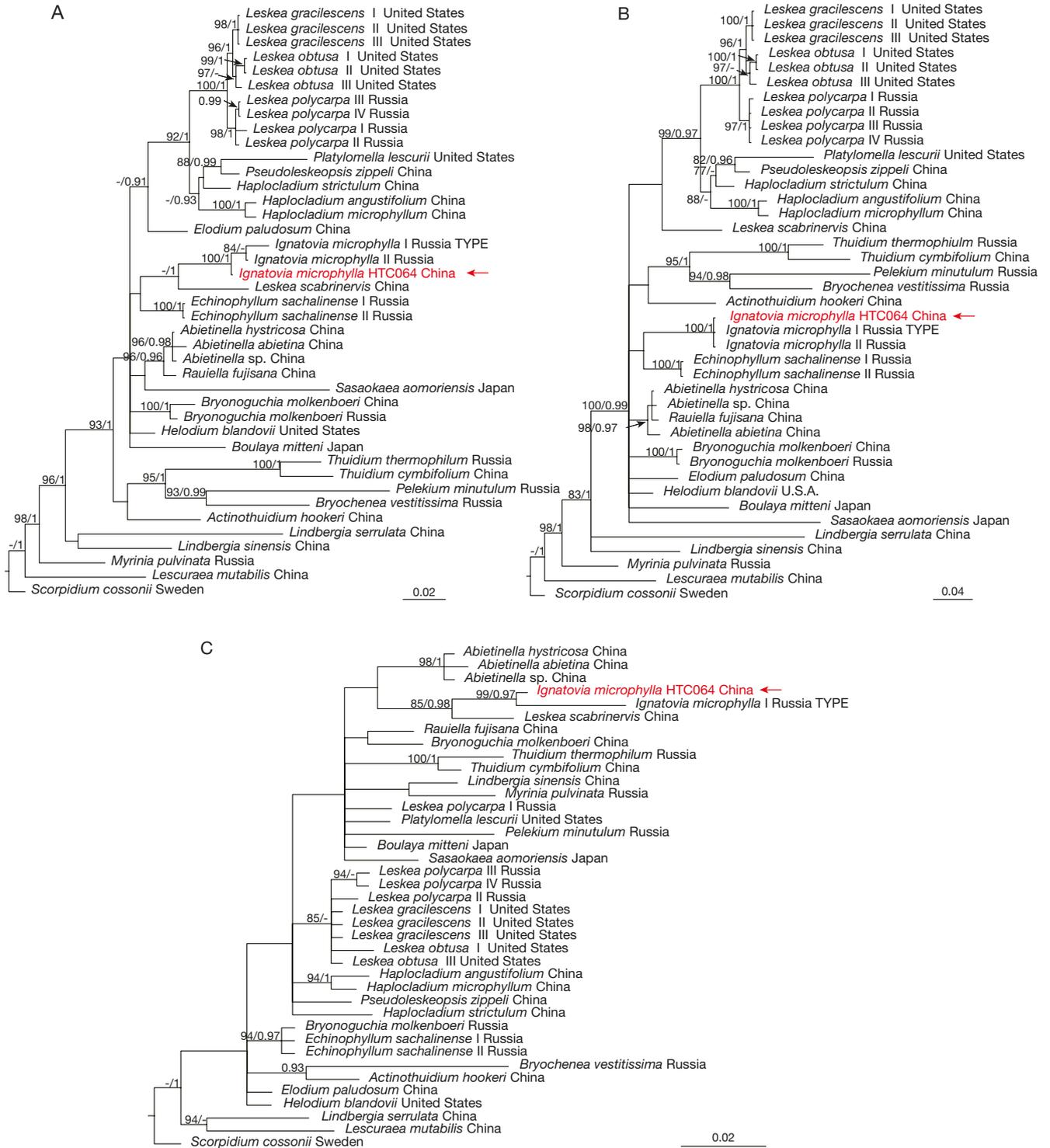


Fig. 1. — Phylogeny tree of Thuidiaceae and Leskeaceae species. The topology derived from the Bayesian tree is shown. **A**, phylogeny tree based on ITS + trnL-F dataset; **B**, phylogeny tree based on ITS dataset; **C**, phylogeny tree based on trnL-F dataset. ML bootstrap values BS ≥ 75 are shown at **left** and Bayesian posterior probabilities values PP ≥ 0.95 at **right**. The newly sequenced Chinese accessions are marked in **arrows**.

115°49'18.23"E; 407 m alt.; 3.IX.2024; R. L. Zhu et al. 20240903-51 (HSNU, HTC).

DISTRIBUTION AND HABITAT. — This species and genus were previously known only from Russia (Ignatov et al. 2019; Ishchenko et al. 2022), the present report represents a new addition to the moss flora

of China. In China, it was collected on wet rock, associated with *Anomodon minor* Lindb.

DESCRIPTION

Plants tiny, green to yellow-green, in prostrate tufts. Stems irregularly branched, up to 1.3 cm long, cross-section of stem

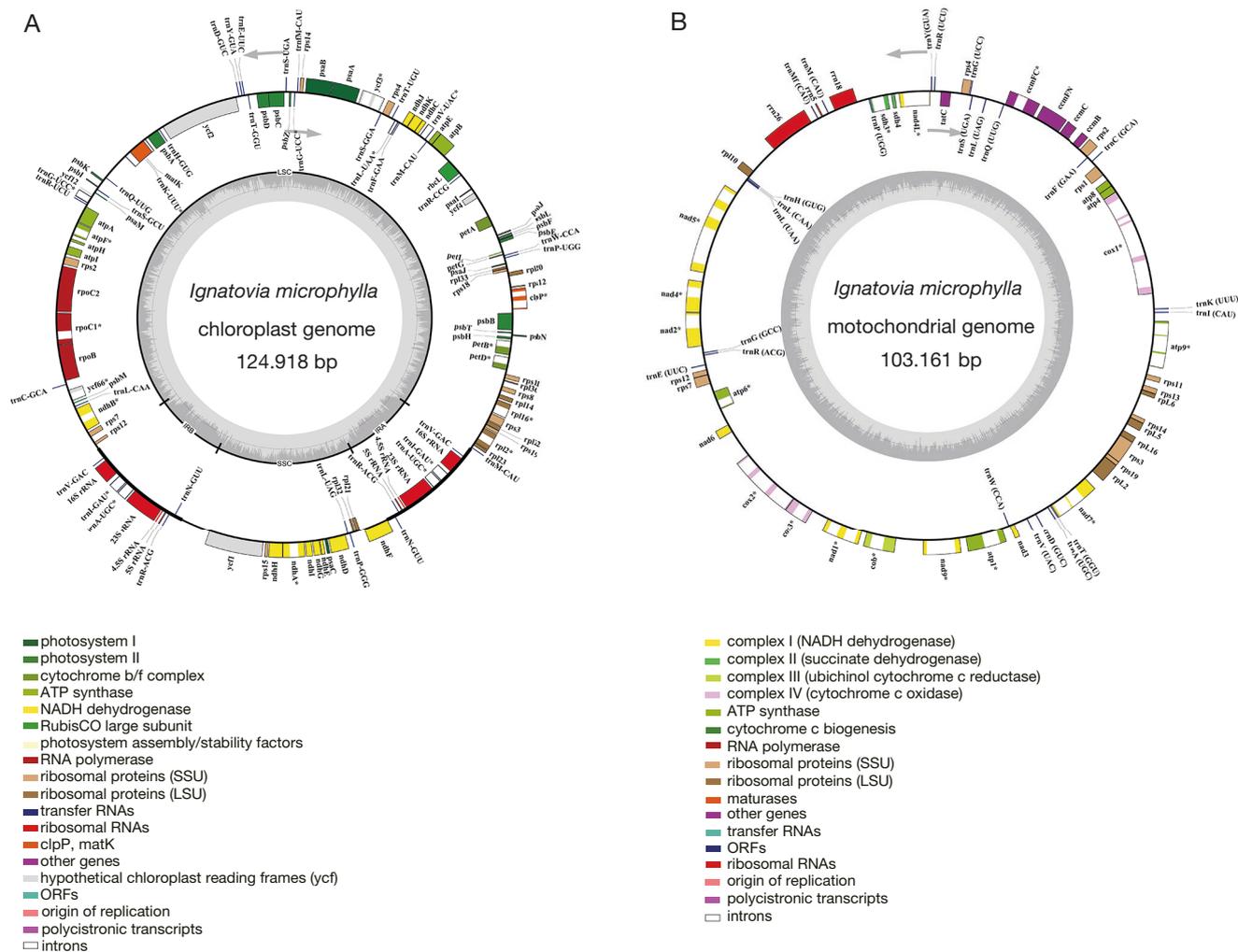


Fig. 2. — Circular genome maps of the plastome (A) and mitogenome (B) of *Ignatovia microphylla* (Ignatov & Ignatova) U.B.Deshmukh. Genes shown on the outside of the circle are transcribed clockwise, whereas those on the inside are transcribed counter-clockwise. The asterisk * indicates intron-containing genes.

oval, diameter *c.* 0.12 mm, composed of nearly homogeneous cells, epidermal cells with slightly thicker walls than cells inwards, without central strand. Paraphyllia absent. Stem leaves appressed when dry, erectopatent when moist, ovate-lanceolate to triangular, 0.25-0.32 × 0.1-0.13 mm, plane; branch leaves shorter, ovate-triangular, 0.15-0.30 × 0.08-0.11 mm, plane. Both stem and branch leaves smooth or only slightly irregularly crenulate near apex. Costa *c.* 40 μm wide at base, occupying 1/3-1/4 the leaf base, ending shortly below the apex or reaching apex, in transverse section with two rows of cells, rarely three, without stereids. Laminal cells unistratose, isodiametric to oblate throughout, 4-8 μm, thick-walled, with low bulgings on dorsal surface, alar cells not differentiated. Autoicous. Both perigonia and perichaetia grows on stem. Perigonial leaves small, ovate-lanceolate, 0.25-0.35 × 0.15-0.17 mm, costa absent. Perichaetial leaves triangular and narrowly acute, 0.5-0.6 × 0.21-0.32 mm, costa robust, extends to the leaf apex. Sporophyte not seen.

DISCUSSION

Ignatovia microphylla is characterized by the following features: 1) small leaves, less than 0.5 mm in length, ovate-lanceolate to narrow-triangular (Fig. 3C); 2) thick-walled laminal cells that are round to oblate and somewhat bulging abaxially (Fig. 3N, O); 3) nearly homogeneous thick-walled cells in the cross-section of the stem (Fig. 3M); 4) a cross-section of the costa devoid of stereids (Fig. 3L); 5) an autoicous sexual condition (Fig. 3F); and 6) inner perichaetial leaves that are triangular (Fig. 3H).

For the sexual condition of *Ignatovia microphylla*, when Ignatov *et al.* (2019) first published this species, they were unable to identify a mother plant with both androecium and gynoecium in the limited material examined. Consequently, the sexual condition was recorded as dioicous with a question mark in the protologue (Ignatov *et al.* 2019). However, in the material collected from China, we successfully identified

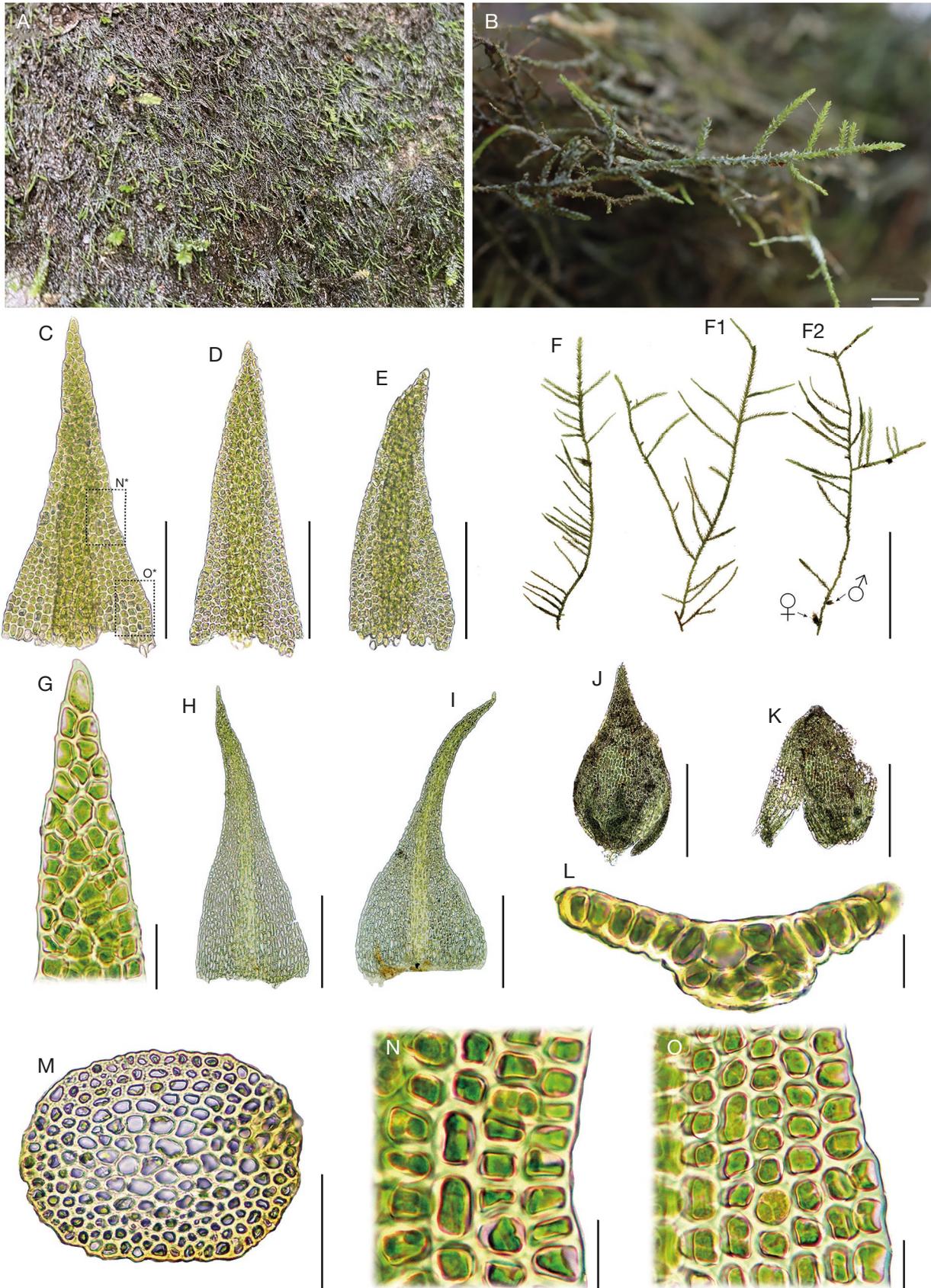


FIG. 3. — *Ignatovia microphylla* (Ignatov & Ignatova) U.B.Deshmukh: **A**, field population on rock; **B**, closer view of plant; **C**, stem leaf; **D**, **E**, branch leaves; **F**, plants; **G**, apex of leaf; **H**, **I**, perichaetial leaves; **J**, **K**, perigonal leaves; **L**, cross section of leaf; **M**, cross section of stem; **N**, middle laminal cells; **O**, basal laminal cells. All from *R.L. Zhu et al. 20240903-51* (HSNU, HTC). Scale bars: A, B, 2 mm; C-E, 100 μ m; F, 5 mm; G, 20 μ m; H-K, 200 μ m; L, N, O, 10 μ m; M, 50 μ m.

such mother plants, which exhibited both androecium and gynoecium on the stem (Fig. 3F). We confirmed that the sexual condition of this species is autoicous.

Ignatovia microphylla shares similarities with *Arvernella microclada* Hugonnot & Hedenäs in terms of their overall plant appearance and leaf shape, as well as the undifferentiated stem cells in transverse sections. However, the costa of *I. microphylla* is robust, terminating shortly below the apex or reaching the apex (Ignatov *et al.* 2019; Fig. 3C-E, G), while it is absent or virtually absent in *A. microclada* (Hugonnot & Hedenäs 2015; Lüth 2019). Additionally, the median leaf laminal cells of *A. microclada* are oblong-rhomboidal, or more rarely, rectangular to short linear-vermicular (Hugonnot & Hedenäs 2015; Lüth 2019), whereas the median laminal cells of *I. microphylla* are isodiametric to oblate (Ignatov *et al.* 2019; Fig. 3N). Furthermore, the inner perichaetial leaves of *A. microclada* are rectangular-oblong and suddenly or progressively acuminate (Hugonnot & Hedenäs 2015), while those of *I. microphylla* are triangular and narrowly acute (Ignatov *et al.* 2019; Fig. 3H, I). *Ignatovia microphylla* is also similar to *Arvernella pisarenkoi* Ignatov & Ignatova and *A. sibirica* Ignatov & Ignatova. However, the costa of both *A. pisarenkoi* and *A. sibirica* is forked, reaching 0.2-0.4 times the leaf length in *A. pisarenkoi* and approximately 0.2 times the leaf length in *A. sibirica* (Ignatov *et al.* 2021; Pisarenko *et al.* 2022). In contrast, the costa of *I. microphylla* is robust, terminating just below the apex or reaching the apex (Ignatov *et al.* 2019; Fig. 3C-E, G).

Ignatovia microphylla also can be confused with *Microamblystegium saxicola* Fedosov, Ignatova & Jan Kučera. However, the costa of *M. saxicola* is single, 0.3-0.7 times the leaf length, and its median laminal cells are rhomboidal or elongate-rhomboidal, smooth (Fedosov *et al.* 2021). In contrast, *I. microphylla* has a robust costa that extends to the leaf apex, and its median laminal cells are isodiametric to oblate, with low bulgings on the dorsal surface (Ignatov *et al.* 2019; Fig. 3N).

Ignatovia microphylla is also similar to *Leskea polycarpa*. However, *L. polycarpa* possesses paraphyllia on its stems and branches (Noguchi 1991; Wu 2001), whereas *I. microphylla* lacks paraphyllia (Ignatov *et al.* 2019). Additionally, the middle laminal cells of *L. polycarpa* are rhomboidal to subrectangular, mostly with a central papilla on the dorsal surface (Noguchi 1991; Wu 2001), while those of *I. microphylla* are isodiametric to oblate, exhibiting low bulgings on the dorsal surface (Ignatov *et al.* 2019; Fig. 3N). Furthermore, *Leskea scabrinervis* Broth. & Paris is also similar to *I. microphylla*, and the differences between the two species have been thoroughly discussed in Ignatov *et al.* (2019).

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