Arctoa (2024) **33:** *1–8*
doi: 10.15298/arctoa.33.01

ONCE AGAIN ON THE GENUS *ANOECTANGIUM* (POTTIACEAE, BRYOPHYTA) IN RUSSIA

ЕЩЕ ОДНА ПОПЫТКА ТАКСОНОМИЧЕСКОЙ РЕВИЗИИ РОДА *ANOECTANGIUM* (POTTIACEAE, BRYOPHYTA) В РОССИИ

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Abstract

An integrative taxonomic study based on a combined molecular and morphological analyses resulted in recognition of three species in the genus *Anoectangium* in Russia: *A. aestivum*, *A. laetevirens,* and *A. stracheyanum*. According to the obtained results, *A. laetevirens* is a rare East Asian species forming a sister clade to all other studied taxa of the genus. It occurs in Russia only in the Far Eastern mainland and in the Kuril Islands. *Anoectangium stracheyanum* is the most widespread species of the genus in the country, being known in eastern part of Asian Russia, eastwards from Baikal Lake, ranging from its southern border to the cold region of Yakutia. The clade of *A. stracheyanum* has two moderately supported subclades composed of northern and southern populations, which, however, are morphologically subidentical, differing only in a slightly longer leaves in plants of the southern clade. The occurrence of *Anoectangium aestivum* is confirmed in Russia in the Caucasus, Kola Peninsula, and the Baikal Lake area. Both *A. stracheyanum* and *A. aestivum* form supported clades, but an occasional occurrense of the DNA motifs of *A. stracheyanum* in some samples of *A. aestivum* may indicate a certain introgression. *Anoectangium handelii* was previously reported from Russia, but DNA barcoding found all so-called specimens belonging to depauperate plants of *Gymnostomum, Hymenostylium,* or *Molendoa*.

Резюме

Интегративное таксономическое исследование, основанное на комбинированном анализе морфологических и молекулярных данных, выявило, что род *Anoectangium* представлен в России тремя видами: *A. aestivum*, *A. laetevirens* и *A. stracheyanum*. Согласно полученным результатам, *A. laetevirens,* редкий восточноазиатский вид, образует кладу, сестринскую всем остальным видам рода. Он встречается в России только в материковой части юга Дальнего Востока и на Курильских островах. *Anoectangium stracheyanum* является самым широко распространенным видом рода в России, он известен в ее азиатской части восточнее озера Байкал, от южных границ до восточной Якутии. Клада *A. stracheyanum* образована двумя умеренно поддержанными кладами, одна из которых включает северные, а вторая – южные популяции, однако морфологически они практически не различаются, за исключением того, что растения южных популяций имеют немного более длинные листья. *Anoectangium aestivum* подтвержден в России на Кавказе, Кольском полуострове и в одном местонахождении в районе озера Байкал. Как *A. stracheyanum*, так и *A. aestivum* образуют хорошо поддержанные клады, однако в последовательностях ДНК некоторых образцов *A. aestivum* присутствуют отдельные мотивы, характерные для *A. stracheyanum*, что может свидетельствовать о редких случаях интрогрессии. *Anoectangium handelii* приводился ранее для России, однако баркодинг ДНК показал, что все так определенные образцы представляют собой сильно угнетенные растения из родов *Gymnostomum, Hymenostylium* или *Molendoa.*

KEYWORDS: mosses, *Anoectangium laetevirens*, Pottiaceae, taxonomy, Russia, phytogeography, nrITS, *trn*V-*trn*M

INTRODUCTION

Anoectangium Schwägr. is a subcosmopolitan genus of the family Pottiaceae. It is rather small; Zander (1993) accepts in it 47 species, while the recent taxonomic revisions of this genus for large territories include fewer: three species in South America (Cano & Jiménez, 2013), three in North America (Zander & Eckel, 2007), three in Europe including Macaronesia (Hodgetts *et al*., 2020), three in Japan (Noguchi & Iwatzuki, 1989), and five in China (Li *et al*., 2001).

Saviz-Lyubitskaya & Smirnova (1970) accepted in Russia three species of *Anoectangium*: *A. aestivum*

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(Hedw.) Mitt., *A. thomsonii* Mitt. (incl. *A. amurense* Broth.), and *A. contortum* Broth. Subsequent publications considered *A. contortum* not different from *A. thomsonii* and accepted for Russia two species, *A. aestivum* and *A. thomsonii* (Ignatov & Afonina, 1992; Ignatov *et al*., 2006).

Saito (1975) recognized in Japan three species: *A. aestivum*, *A. stracheyanum* Mitt., and *A. thomsonii*. The two latter species have been described from Himalayas by Mitten (1869), on the same page but with an insufficient and controversial explanation of their distinctions. Mitten (1869) noted that *A. stracheyanum* has lanceolate leaves vs. ovate-lanceolate in *A. thomsonii*, and that *A. stracheyanum* is smaller than *A. compactum* Schwägr. (=*A. aestivum*), whereas *A. thomsonii* is slightly larger than *A. compactum*. Saito (1975) relied on the leaf shape, finding that the two species differ by the presence of constriction above the leaf base in *A. stracheyanum*, which is lacking in *A. thomsonii*. Using this distinction, Zander & Eckel (2007) accepted *A. stracheyanum* for the North America, and then the name *A. stracheyanum* was accepted for all *Anoectangium* specimens in Asian Russia by Ignatova (2009), and its presence in South America was confirmed by Cano & Jiménez (2013).

However, later Cherdantseva *et al*. (2018) returned the name *A. thomsonii* instead of *A. stracheyanum* without explanation, and Fedosov *et al*. (2022) followed this concept, referring to Sollman *et al*. (2020), which, however, is not fully consistent with the subsequent approach to the genus by Sollman (2023). At the same time, Zander (2019) re-lectotypified *A. stracheyanum,* discussed its taxonomy and also concluded that the lectotype of *A. thomsonii* designated by Li & Iwatsuki (1997) is merely a large form of *A. aestivum* and therefore put it into the synonymy of the latter speceis.

Trying to stabilize the nomenclature for the Russian members of the genus *Anoectangium*, we applied a molecular barcoding approach, which often helps to solve taxonomic problems in the deficit of morphological features or in case of their too broad variation, hampering an unequivocal conclusion.

MATERIAL AND METHODS

This study is mainly adressed the species of *Anoectangium* occurring in Russia. It does not include *A. handelii,* which has been previously reported from Russia. Zander (2019) suggested to exclude it from this genus based on the type study, which belongs to *Molendoa antiqua* R. H. Zander. Also, Russian specimens reported as *A. handelii* appeared to be various taxa of *Gymnostomum*, *Hymenostylium* or *Molendoa*.

Molecular stidies

We sequenced nuclear ITS, the most useful region for species level taxonomy in mosses, as it is most copiosely represented in GenBank, and one plastid region, *trn*M–*trn*V, since *rps*4, judging from the GenBank data, does not help to differentiate *A. stracheyanum* and *A. aestivum* s.str.

DNA extraction was done with the Qiagene Extractor. Amplification used primers L and B for ITS (White, 1990) and primers for *trn*M–*trn*V region followed Werner *et al*. (2009). The sequencing protocols were essentially the same as in our previous studies (Gardiner *et al.,* 2005).

Obtained sequences were aligned using MAFFT v. 7.487, E-INS-i strategy (Katoh & Standley, 2013). Accession numbers and voucher data are in Appendix 1.

Molecular analysis. Preliminary tests demonstrated similar topology of trees based on nuclear and plastid markers, so the further analysis was undertaken for concatenated dataset.

Maximum likelyhood analysis was performed at W-IQ-TREE server (Trifinopoulos *et al*., 2016), 1000 replications and otherwise default parameter, 1000 replications. Substitution models were selected by the server: ITS1: K3P+I; 5.8S RNA gene K2P; ITS2: HKY+F+G4; *trn*M-CAU gene: HKY+F+G4; *trn*M–*trn*V intergenic spacer: K3Pu+F; *trn*V-UAC gene: HKY+F+I.

Morphological studies included specimens from MW, MHA, LE, VLA, IRK, and specimen data from H and S used for previous studies of Ignatova (2009).

RESULTS

The Bayesian phylogenetic tree is shown in Fig. 1. The genus *Anoectangium* is resolved monophyletic and maximally supported, being a sister to *Gymnostomum aeruginosum*-clade (PP=1, BS=100), forming together the moderately supported clade (PP=95, BS=89).

The *Anoectangium* clade includes two maximally supported clades. The first clade includes three specimens from the Russian Far East (one form mainland, two from Kuril Islands), and one specimen from southern Japan, representing the same species. In Figs. 1–2 and in the text hereafter it is called *A. laetevirens* Besch. & Card., by the reason explained in the Discussion section.

The second clade includes all other studied specimens. It has the paraphyletic grade of specimens from tropical regions: South America, Canary Island, and Himalayan region; they are named here as *A.* cf. *stracheyanum, A.* cf. *aestivum*, and specimen from Canary Islands is from GenBank, where it was deposited as *A. angustifolium* Mitt. These specimens will be outside the main focus of the paper. Two supported clades are nested in the paraphyletic grade: one includes most specimens of *A. stracheyanum* from temperate Asia (PP=0.95, BS=95) and the second is formed of *A. aestivum* from temperate regions of Europe, Asia and North America (PP=1, BS=99).

The clade of *A. stracheyanum* includes two subclades, northern and southern, shown in Figs 1 & 2 in light-blue and dark blue colors. The former is low supported (PP=0.78, BS=74), while the support of the latter is rather high (PP=0.98, BS=95). Morphologically they are subidenical, though the southern clade has a slightly larger leaves (Fig. 2). Plants of the *A. aestivum*-clade are very variable in the leaf shape (Fig. 2).

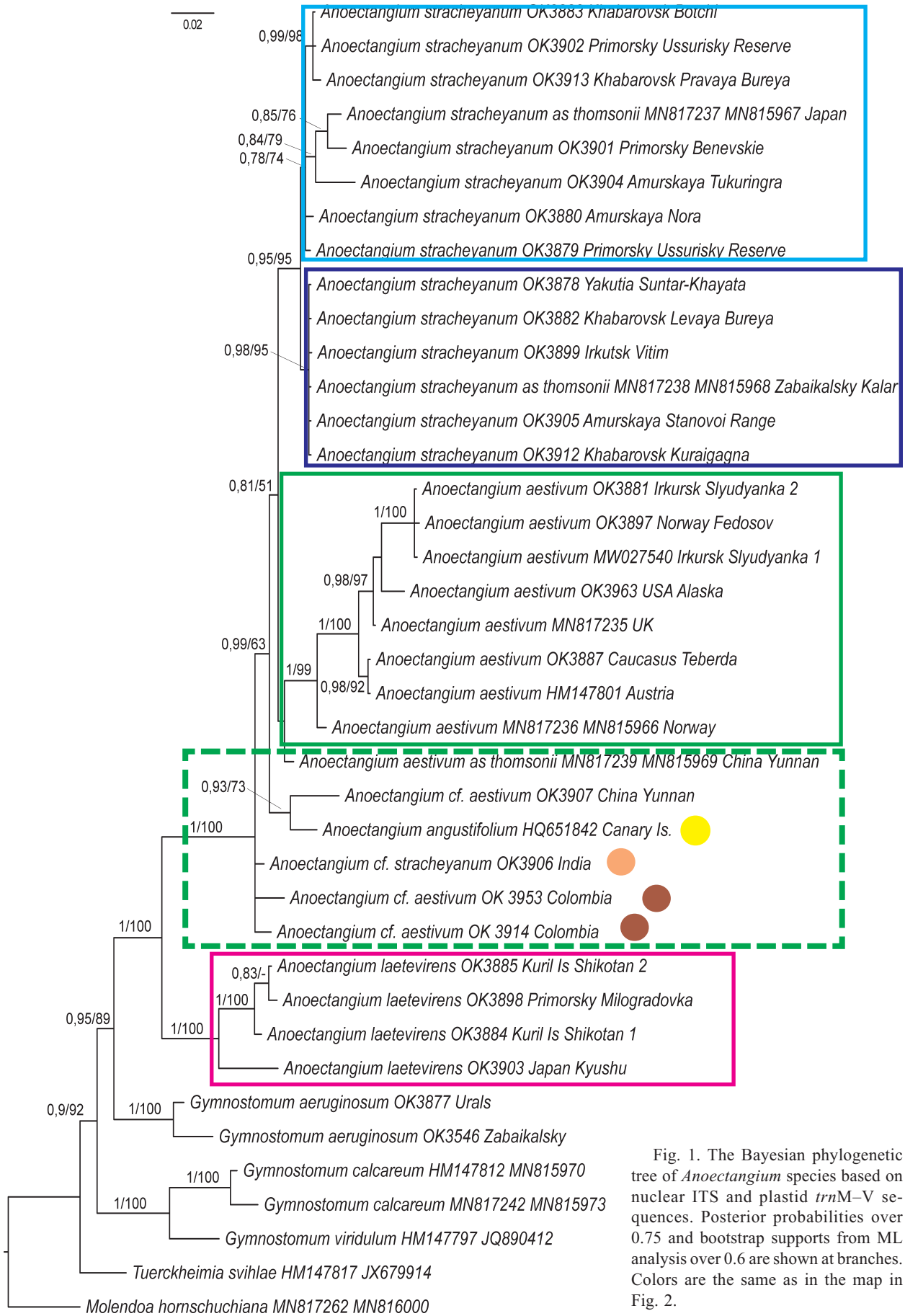

Fig. 1. The Bayesian phylogenetic tree of *Anoectangium* species based on nuclear ITS and plastid *trn*M–V sequences. Posterior probabilities over 0.75 and bootstrap supports from ML analysis over 0.6 are shown at branches. Colors are the same as in the map in Fig. 2.

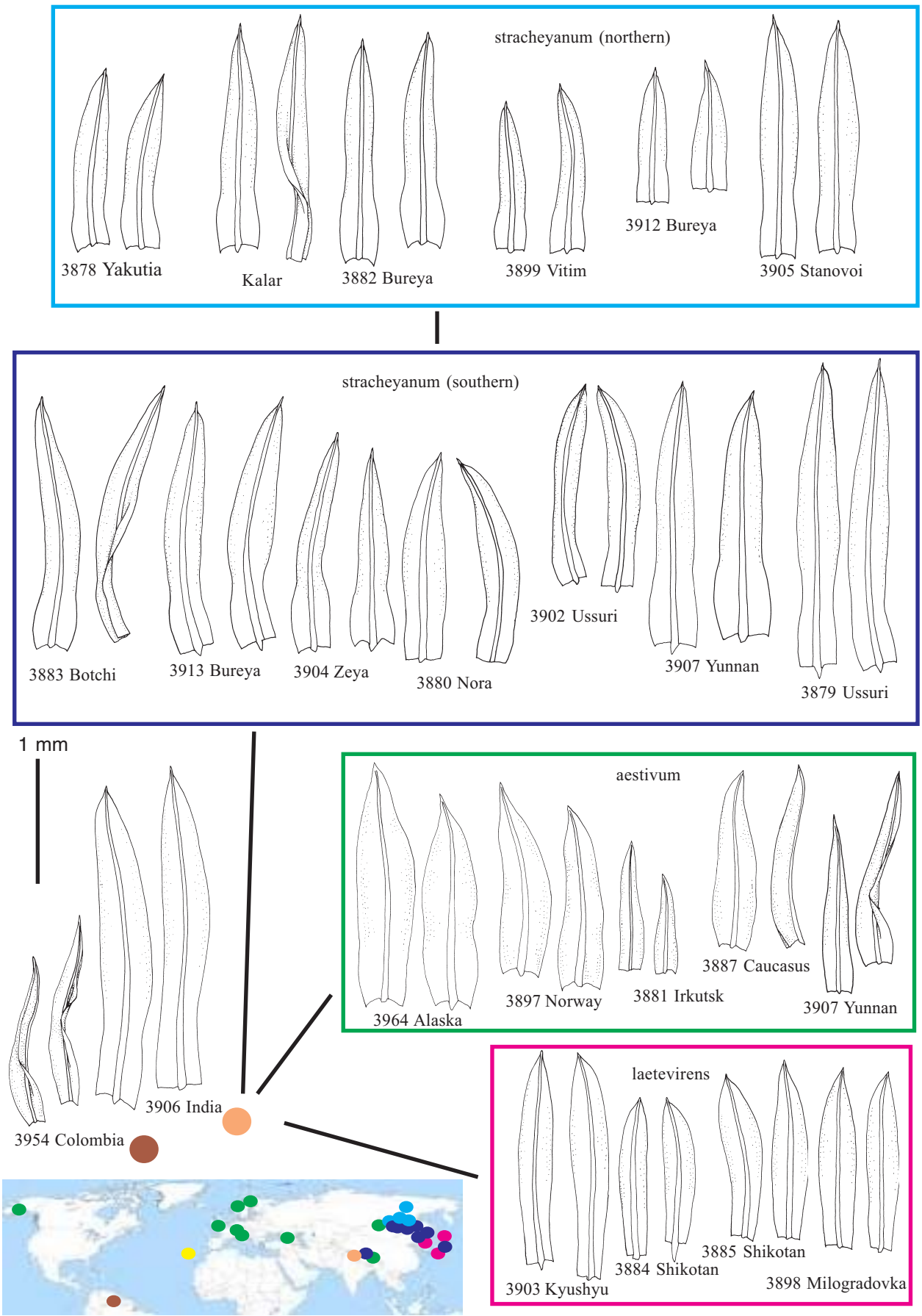

Fig. 2. Leaf shape and size of *Anoectangium* specimens from clades shown in Fig. 1, and their distribution. Scale bar 1 mm for all.

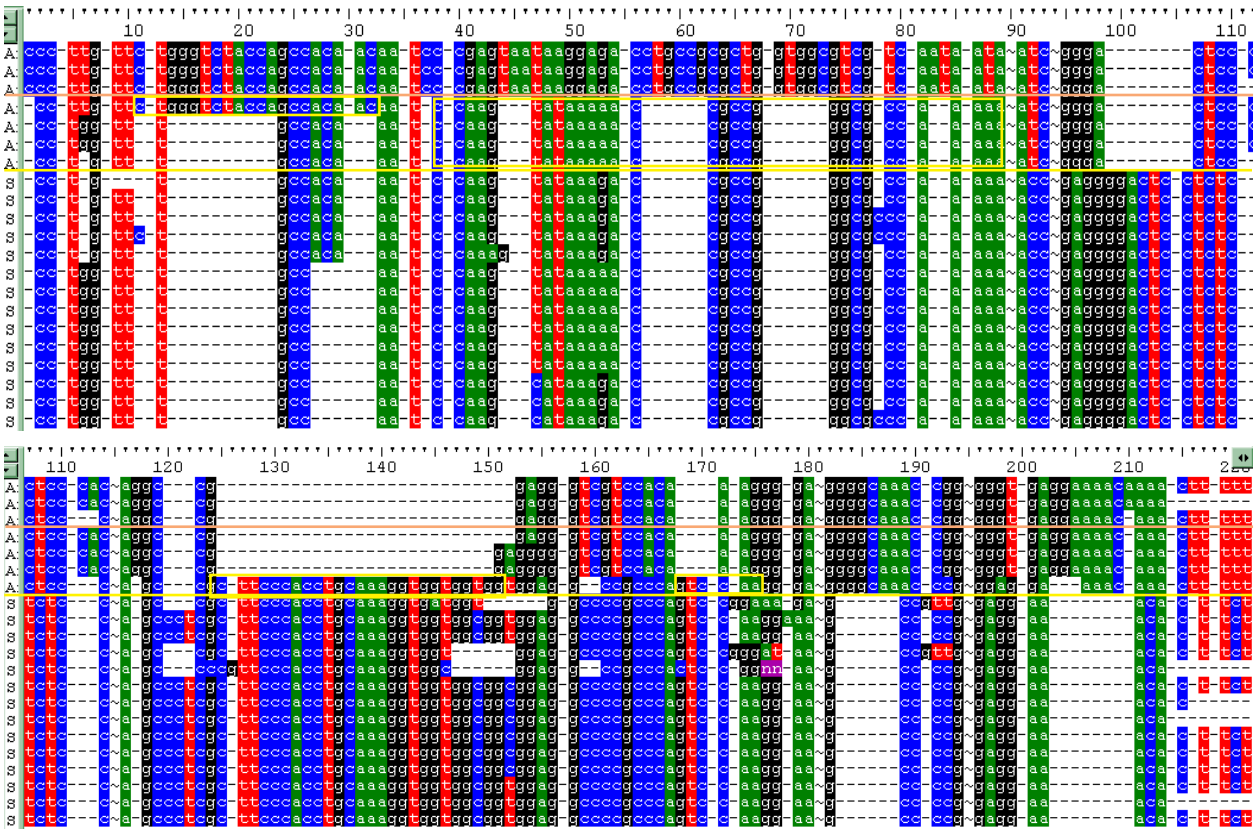

Fig. 3. Parts of the alignment of ITS and seven last columns of *trn*M-V, for *Anoectangium aestivum* and *A. stracheyanum* (A and S in the left column, separated by the yellow horizontal line). It shows that some specimens of *A. aestivum* have at places the motifs of *A. stracheyanum*, especially the specimen from Norway (immediately above the yellow line).

A comparison of sequences of *Anoectangium aestivum* and *A. stracheyanum* revealed that a certain gene flow between them may occur. Figure 3 comprises a selection of variable parts from the alignment, where a sharp difference between *A. stracheyanum* and *A. aestivum* (separated from each other by yellow line) is observed in the end of ITS2 (positions 168–220). However, some motifs of *A. stracheyanum* are seen in some samples of *A. aestivum* (between yellow and orange lines in Fig. 3). Especially enriched by *A. stracheyanum*-motifs is the Norvegian specimen from GenBank (immediately above the yellow line in Fig. 3), which is sister to seven other specimens of *A. aestivum* s. str., the latter forming a maximally supported clade within *A. aestivum* (Fig. 1). The Austrian and the Caucasian specimens also have some motifs of *A. stracheyanum* (in yellow frames in Fig. 3), compared to the 'pure *A. aestivum*' (above the orange line in Fig. 3), which is comprised by three specimens: from Norway, UK, and the Baikal Lake area in southern Siberia.

Discussion

A resurrction of Anoectangium laetevirens Besch. & Card.

The results of the present study suggest that *Anoectangium* is represented in Russia by at least three distinct species. Besides *A. aestivum* and *A. stracheyanum*, the earliest divergent clade formed of one Japanese and three Russian Far Eastern specimens comprises a species which needs an appropriate name (Fig. 1). Its leaves have a shape different from both *A. aestivum* and *A. stracheyanum*, being widest well above midleaf (Fig. 2, red frame). It fully agrees with the description and illustrations of *A. thomsonii* provided by Saito (1975). However, Zander (2019) stated that the lectotype of *A. thomsonii* is identical with *A. aestivum*; this point of view was later accepted by Sollmann (2023). Thus, another name had to be chosen for the plants in question from the earliest divergent clade. This can be done from the names of species described from Japan and adjacent areas and listed by Saito (1975). The earliest of the validly described ones is *A. ikaoense* Besch., 1900, but this species is described as monoicous. Four other *Anoectangium* species were described by Cardot and Bescherelle & Cardot in Cardot (1907). Among them, *A. dichroum* Card. is a rather robust plant, and *A. microphyllum* Card. otherwise has leaves only 0.5–0.8 mm long. Two remaining species, *A. laetevirens* Besch. & Card. and *A. sublaetevirens* Card. differ in costa dorsally papillose in the former one vs. smooth to slightly papillose in the latter one, which definitely suggests the former name for our plants. Hence, with only a slight hesitation we apply the former name; moreover, leaf shape in the syntype of *A. laetevirens* provided by Saito (1975, Fig. 34–16) fits well our speci-

mens from the earliest divergent clade (Figs. 1 & 2, red frame).

Anoectangium aestivum* and *A. stracheyanum. The second interesting conclusion from the present analysis concerns *A. aestivum* and *A. stracheyanum*. The latter species has been discovered in Europe only recently (Sollman, 2023). Our dataset does not include any specimens of *A. stracheyanum* from Europe; however, the diversity of sequences points a certain gene flow. In Fig. 3, some intermediates are observed, making separation of these species by sequence data somewhat uncertain. Currently, the distributions of *A. aestivum* and *A. stracheyanum* are mostly not sympatric and generally these species are well differentiated. Their possible introgression require further studies with the more dense sampling.

Northern and southern A. stracheyanum in Asian Russia. The third interesting observation is rather sharp geographic differentiation of *A. stracheyanum* populations on its northern limit. In Fig. 1 it is represented by two subclades, which comprise specimens from 'northern' (light blue frame) and 'southern' (dark blue frame) areas, respectively (see also map in Fig. 2). The representatives of the northern clade differ only in few substitutions in ITS. Northern plants are, expectedly, smaller (cf. Fig. 2), but the difference in leaf size is not enough for any taxonomic recognition.

As the descriptions and illustrations of *A. aestivum* and *A. stracheyanum* from Russia were already published by Ignatova (2009), here we provide the full morphological description only for *A. laetevirens*.

TAXONOMY

ANOECTANGIUM Schwägr., Sp. Musc. Frond. Suppl. 1(1): 33. 1811.

Type species: *A. compactum* Schwägr. (= *A. aestivum* (Hedw.) Mitt.)

Plants in dense or loose tufts, yellow-green in upper part, brownish below. Stems 0.5–4 cm, weakly branched, usually moderately tomentose, rounded-triangular in transverse section, with more or less strong central strand, weak sclerodermis, hyalodermis absent. *Leaves* distantly or densely arranged, straight or contorted and twisted when dry, erect-spreading when wet, uneven in size along the stem, forming alternating zones of smaller and larger leaves, ovate, ovate-lanceolate or oblong-lanceolate, with not differentiated or differentiated base, occasionally constricted above base, widest below or above midleaf, acute or acuminate, strongly keeled, narrowly grooved along costa ventrally; margins plane, entire or slightly crenulate at leaf base, sometimes uneven proximally; *costa* strongly projecting abaxially, ending few cells below apex, percurrent or shortly excurrent, with only dorsal stereid band, dorsal and ventral epidermis, occasionally ventral epidermis absent and guide cells exposed, ventral surface cells elongate, smooth, dorsal surface cells elongate, smooth proximally, slightly to strongly papillose distally; *lamina* unistratose, distal and median laminal cells subquadrate, densely papillose, papillae low and wide, bifid, rarer loosely papillose, basal laminal cells short rectangular, shorter to the margins, smooth. KOH laminal reaction yellow. *Specialized asexual reproduction* rare, by multicellular gemmae on rizhoids in leaf axils. *Dioicous*. Gametangia and sporophytes terminal on short lateral branches. Perichaetial leaves convolute-sheathing, ovate-acuminate. *Setae* yellow-brownish. *Urns* yellow-brown, with red rim, elliptic, smooth and glossy, exothecial cells rectangular, thin-walled, annulus of two rows of slightly vesiculose cells, peristome absent. *Spores* 12–16 μm, finely papillose. *Opercula* with long oblique beak.

KEY TO IDENTIFICATION OF *ANOECTANGIUM* SPECIES IN RUSSIA

1. Leaves lanceolate to oblong lanceolate, (1.0–)1.5–2.5 mm long, often constricted above base .... *A. stracheyanum*
— Leaves ovate-lanceolate to oblong-lanceolate, 0.8–1.2(–1.8) mm long, not constricted above base 2
2. Leaves incurved when dry, distantly arranged, stem exposed at places; leaves widest below midleaf .... *A. aestivum*
— Leaves contorted when dry, densely arranged, stem not exposed; leaves widest at or above midleaf .... *A. laetevirens*

Anoectangium laetevirens Besch. & Card., Bull. Herb. Boissier, sér. 2, 7: 712. 1907.

Type: Japan "Japon: Yezo (n. 599); Kofu (n. 2552). Corée: île Quelpaert (n. 5, 6, 74, 80)" (not seen, one of syntypes illustrated by Saito, 1975, figs. 34–16).

Plants small, in dense tufts or cusions, yellowish-green in upper part, dark brownish below. *Stems* 1–2 cm, erect, simple or rarely forked. *Leaves* densely arranged and hiding the stem, contorted when dry, sometimes slightly spirally twisted, patent when wet, narrowly lanceolate, widest at or above mid-leaf, narrowed to the base, acute, strongly keeled, carinate, (0.45–)0.8–1.3(–1.6) mm long, 0.14–0.28 mm wide; margins plane, entire; costa ±strong, 30–35 μm wide at base, excurrent into short apiculus to 3–4 cells long or percurrent, densely or loosely papillose dorsally in distal 2/3; upper and median laminal cells rounded-quadrate or transversely elliptical, 6–8×7–12 μm, ±thick-walled, opaque, densely covered by massive, low, bifid papillae; basal juxtacostal cells smooth, with moderately thickened walls, short rectangular, 12–20×6–11 μm, becoming quadrate and transversely rectangular towards margins. Gametangia and sporophytes unknown in Russia. [*Perichaetial leaves* broad-ovate, narrowly acute at apex, 0.5–0.7 mm long, 0.3–0.4 mm wide at middle. *Setae* 3–5 mm long. *Capsule* short-cylindrical, 0.6–0.8 mm long, ca. 0.4 mm thick at middle. *Opercum* 0.7 mm long. *Spores* 9–12 μm (Saito, 1975)].

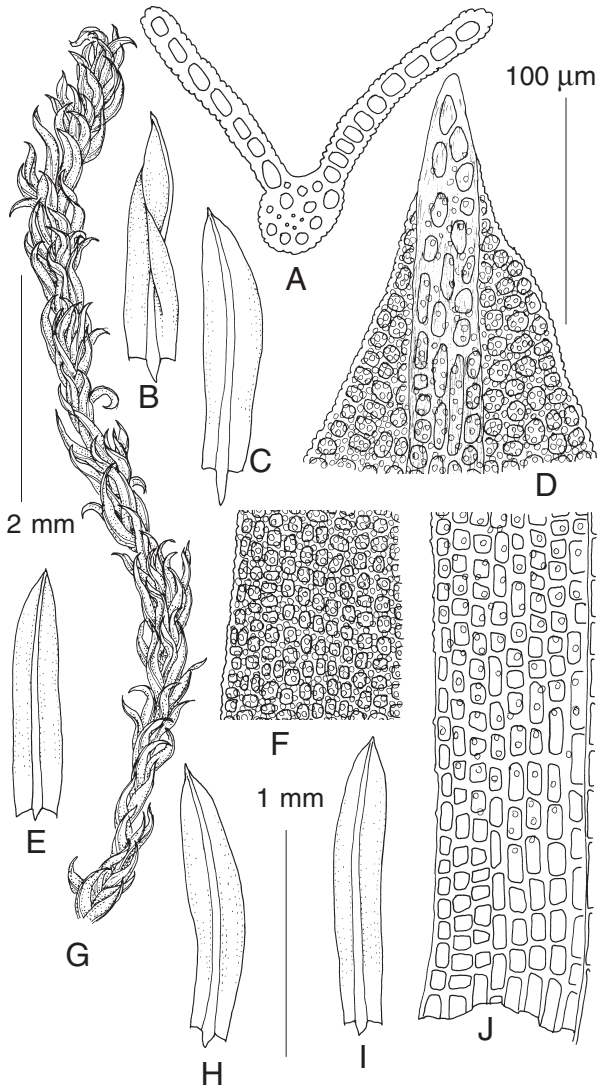

Fig. 4. *Anoectangium laetevirens* (from: Russia, Sakhalinskaya Province, Kuril Islands, Shikotan Island, *Bakalin K-45-13-07*, MHA9001556, isolate OK3884). A: leaf transverse section; B–C, E, H–I: leaves; D: upper leaf cells; F: midleaf cells; G: habit, dry; J: basal leaf cells. Scale bars: 2 mm for G; 1 mm for B–C, E, H–I; 100 µm for A, D, F, J.

Specimens examined: RUSSIA: Primorsky Territory: Olga District, waterfall on Milogradovka Creek, 310–370 m alt., *Ignatov #07-311, 07-295* (MW9001560, MW9001559); Sakhalinslaya Province, South Kuril Islands, Shikotan Island, Notoro Mt., 320 m alt., *Bakalin K-42-28-07* (MW9001567); same place, area of Tomari Mt., 300 m alt., *Bakalin K-45-13-07* (MW9001568) and *Bakalin K-45-3-07* (MW9001569); JAPAN, Kyushu, Miyazaki Prefecture, Inohae Valley, *Ignatov & Ignatova 98-509* (MW9001570).

Differentiation. *Anoectangium laetevirens* is similar to *A. aestivum* in plant size and leaves lacking constriction above their bases, but differs from it in leaf arrangement (dense, hiding stem vs. ± spaced, exposing stem at places); leaf shape (widest above mid-leaf, not widened at base vs. widest below mid-leaf, usually widened at base); and costa length (percurrent or excurrent into short mucro vs. ending below apex). Ignatova (2009) tentatively referred these specimens to *A. stracheyanum* despite the absence of constriction in their leaves, considering them as an extreme variation of the latter species in harsh environments, but the present study confirms their separate species identity. The distinctions of *A. laetevirens* from *A. stracheyanum* include smaller size of plants, shorter and narrower leaves and absence of constriction above leaf base.

Distribution and ecology. In Russia, *A. laetevirens* occurs mostly in Kuril Islands; its single locality in the mainland is in a valley near waterfall (albeit not very big one), providing high and constant air humidity, where some other rare mosses were found.

Acknowledgements

The study of Ignatov was carried out within institutional research project of MSU no. 121032500090-7 and of Kuznetsova within the MBG project no. 122042700002-6. The work of Ignatova was supported by RSF project 23-14-00043.

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Recieved 10 May 2024 *Accepted 15 July 2024*

Appendix 1. Specimens sequenced *de novo* and their GenBank accession numbers.

Species	Isolate	Geolocation	Voucher	ITS	*trn*M-*trn*V
Anoectangium aestivum	OK3963	USA, Alaska	Schofield 117615, LE	PQ034492	PQ096824
A. aestivum	OK3887	Russia, Karachaevo-Cherkessia	Korotkov s.n., 25 Aug 1999 MW9001522	PQ034493	PQ119828
A. aestivum	OK3881	Russia, Irkursk, Slyudyanka	Ignatov et al. 18-4465 MHA9027372	PQ034494	–
A. aestivum	OK3897	Norway	Fedosov & Hoitomt 17-00-12, MW9078832	PQ034495	PQ096825
A. laetevirens	OK3884	Russia, Kuril Islands	Bakalin K-45-13-07, MHA 9001556	PQ034488	PQ096826
A. laetevirens	OK3885	Russia, Kuril Islands	Fedosov 21-1033, MW9119488	PQ034489	PQ096827
A. laetevirens	OK3898	Russia, Primorsky	Ignatov 07-311, MW9001560	PQ034490	–
A. laetevirens	OK3903	Japan, Kyushu	Ignatov & Ignatova 98-509, MW9001570	PQ034491	PQ096828
A. cf. *aestivum*	OK3907	China, Yunnan	Shevock 30945, MW9115092	PQ034487	PQ096829
A. cf. *aestivum*	OK3953	Colombia	Muñoz 93-321, MHA9050352	PQ034497	PQ096830
A. cf. *aestivum*	OK3914	Colombia	Muñoz 98-293, MHA9050351	PQ034498	PQ096831
A. cf. *stracheyanum*	OK3906	India	Lüth 6677, MW9115593	PQ034496	–
A. stracheyanum	OK3878	Russia, Yakutia, Suntar-Khayata	Ignatov & Ignatova 15-59, MHA9001558	PQ034475	PQ096832
A. stracheyanum	OK3882	Russia, Khabarovsk, Bureya	Ignatov 97-848, MHA9001541	PQ034476	PQ096833
A. stracheyanum	OK3899	Russia, Irkutsk, Vitim	Bardunov sn, 30 Aug 1986, MW9001533	PQ034477	PQ096834
A. stracheyanum	OK3905	Russia, Amurskaya, Stanovoi	Dudov 2018_Br_0644, MW9118678	PQ034478	PQ096835
A. stracheyanum	OK3912	Russia, Khabarovsk, Bureya	Ignatov 97-837, MHA9001528	PQ034479	PQ096836
A. stracheyanum	OK3883	Russia, Khabarovsk, Botchi	Ignatov & Ignatova 13-746, MHA9001536	PQ034480	PQ096837
A. stracheyanum	OK3902	Russia, Primorsky	Ignatov & Ignatova 06-2909, MW0001554	PQ034481	PQ096838
A. stracheyanum	OK3913	Russia, Khabarovsk, Bureya	Ignatov 97-838, MHA9001540	PQ034482	PQ096839
A. stracheyanum	OK3880	Russia, Amurskaya, Nora	Bezgodov 17 June 2011 #257, MHA 9001573	PQ034483	PQ096840
A. stracheyanum	OK3879	Russia, Primorsky	Ignatov 08-, MHA9001561	PQ034484	PQ096841
A. stracheyanum	OK3901	Russia, Primorsky	Ignatov et al. 06-2155, MW9001558	PQ034485	PQ096842
A. stracheyanum	OK3904	Russia, Amurskaya, Zeya	Dudov & Kozhin 2016_Br_0944, MW9079718	PQ034486	–
Gymnostomum aeruginosum	OK3877	Russia, Perm	Bezgodov 28 July 2018 #197 MHA 9018369	PQ034473	PQ096822
G. aeruginosum	OK3546	Russia, Zabaikalsky Territory	Zabaikalsky, Afonina 5913 LE	PQ034474	PQ096823