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## Article

# The First Genome from the Basal Monocot Family Has Been Misnamed: Taxonomic Identity of *Acorus tatarinowii* (Acoraceae), a Source of Numerous Chemical Compounds of Pharmaceutical Importance

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**Abstract:** The basalmost monocot genus *Acorus* is well-known for its use in traditional oriental medicine. It comprises the groups of *A. calamus* and *A. gramineus*. A recent study recognized three species in the latter group, *A. gramineus*, *A. macrospadiceus*, and *A. tatarinowii*. The material currently known as *A. tatarinowii* has been extensively studied as a source of various chemical compounds and for producing the first published genome of *Acorus*, which is important for understanding the origin and evolution of monocots. Using the data from morphology, anatomy, and biogeography, we argue that the type material of *A. tatarinowii* does not match the interpretation of the species name as adopted in the current literature and herbarium collections (to a taxon of the *A. gramineus* group from Southeast Asia) but rather belongs to the *A. calamus* group. Moreover, the name *A. macrospadiceus* also cannot be used because it was invalidly published. Under a narrow species concept, other appropriate species names should be found or proposed for the plants currently named *A. tatarinowii* and *A. macrospadiceus*. However, we discourage the use of a narrow species concept in the *A. gramineus* group as insufficiently justified and suggest recognizing a single polymorphic species, *A. gramineus* s.l., at least until a comprehensive taxonomic revision of the group is available. Apart from the presentation of our revised taxonomic framework, we update the geographical distributions of *Acorus* species in Vietnam, Laos, and Thailand.



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## 1. Introduction

Accurate naming of plant material used in genomic, biochemical, pharmaceutical, ethnobotanical, and other studies is essential for the replicability of the results and their proper use. The naming of plant material is regulated by the principle of nomenclatural priority along with the use of reference specimens called types [1]. Type specimens are plant collections used by the author while describing a particular plant species and proposing its scientific name. Such specimens serve as a permanent link between the original publication, in which a plant name is established, and the biological species as a natural phenomenon. Due to this link, a plant name remains permanently attached to the species in a certain and unambiguous way. When some essential information on plant characters is not indicated

in the original species description (=protologue), the missing information can be obtained by an examination of its type specimens. This procedure is legally formalised in the International Code of Nomenclature for algae, fungi, and plants [1], whose rules have a binding effect.

The basal monocot order Acorales Reveal includes a single family, Acoraceae Martinov, and the only genus, *Acorus* L. [2,3]. An early phase of taxonomic studies of *Acorus* (then classified in Araceae Juss.) culminated in an important monograph by H.W. Schott published in 1860 that recognized as many as nine species of the genus [4], of which five were established by Schott as new to science. In a follow-up publication, Schott described four more species of the genus [5]. Diagnostic characters of species recognized by Schott mainly included the size and shape of basic organs, such as the leaf, inflorescence (spadix), and spathe as well as the spathe-to-spadix length ratio. In addition, some seed and ovule characters were mentioned, but those of ovules provided little differentiation between species while those of seeds were very inconsistently mentioned. In the next fundamental monograph of Araceae published in 1905, A. Engler recognized only two species of the genus, *A. calamus* L. and *A. gramineus* Sol. ex Aiton [6]. He considered that the size and shape parameters used by Schott were not convincing, and concluded that for the most part, the species proposed by Schott and others cannot be recognised even as varieties. Even when some subsequent authors recognised more than two species in the genus, Engler's idea of two major groups of *Acorus* was commonly accepted.

The *A. gramineus* group is native to Japan (except Hokkaido), southern Korea, mainland China (except its northern and western parts), Hainan, Taiwan, Luzon Island in the Philippines, Vietnam, Laos, Cambodia, Thailand, Myanmar and northeast India [7–9]. There are also reports of *A. gramineus* from E Siberia (Russia) [7,8,10,11], but Russian regional floristic accounts do not support them [12,13] and we were unable to find any herbarium specimens from Russia. The *A. calamus* group has a wide native range in temperate N America and in temperate to mountain tropical Asia, extending northwards up to ca 63° N in Yakutia (Russia) [7–9,12–16]. Members of both groups are cultivated in various parts of the world as medicinal and ornamental plants; as a result of ancient medicinal use, *A. calamus* is widely naturalized in Europe [17–21]. This human-assisted dispersal complicates taxonomic studies of the genus and obscures the natural distribution areas of its species.

Among the most comprehensive literature sources on plants of Southeast Asia, *Flore générale de l'Indo-Chine* [22], *Flora of China* [7], *Flora Malesiana* [8], and *Flora of Thailand* [9] followed Engler [6] in accepting one polymorphic species in each of the two groups of *Acorus* (*A. calamus* s.l. and *A. gramineus* s.l.). Some other authorities, most notably in China, recognized more than one species within the *A. gramineus* group [10,21,23–29]. For example, a recent study by Cheng et al. used data on two plastid markers and comparative metabolomics to support the recognition of three species of the *A. gramineus* group in China, namely, *A. gramineus*, *A. tatarinowii* Schott, and *A. macrospadiceus* (Yamam.) F.N. Wei & Y.K. Li [27]. Unfortunately, Cheng et al. [27] did not cite and discuss an earlier molecular-based study that revealed a polyphyletic nature of *A. tatarinowii* [30], a paper that described two more species of the *A. gramineus* group from China (*A. latifolius* Z.Y. Zhu and *A. xiangyeus* Z.Y. Zhu) [28], and a morphology-based paper that suggested combining *A. macrospadiceus*, *A. latifolius* and *A. tatarinowii* as one and the same species [29].

Plants currently assigned to *A. tatarinowii* [10,23–27] are widely used in Chinese herbal medicine and have been extensively studied as a source of various chemical compounds of, for example, pharmacological importance [31–45]. A recent study provided a detailed analysis of the genome of *A. tatarinowii* [46]. Being the first published genome of the basal monocot order Acorales, it is highly important for understanding the origin and evolution of monocots [46].

Due to the lack of a recent taxonomic revision, the nomenclature of some species in *Acorus* accepted in the current literature is problematic and requires clarification. For example, some publications regard *A. gramineus* as a synonym or potential synonym of

*A. tatarinowii* [43–46], an approach that contradicts the principle of nomenclatural priority because the species name *A. gramineus* was published in 1789 [47], long before the publication of the species name *A. tatarinowii* in 1859 [48]. Even if considered distinct from *A. gramineus*, the use of the name *A. tatarinowii* is not straightforward because the original description of *A. tatarinowii* provided by Schott [48], as well as the description of the species in his monograph [4], does not include the most important taxonomic character, namely the presence or absence of a midrib on the leaf blade. Therefore, it is difficult to figure out based solely on the descriptions whether Schott named a member of the *A. calamus* group or a member of the *A. gramineus* group. The only way of resolving this problem is a thorough examination of the original (type) material. We traced the type material of *A. tatarinowii* in herbarium collections of the Komarov Botanical Institute, St.-Petersburg (LE). Its detailed analysis and taxonomic identity are provided in the present paper, together with an updated overview of morphological differences between the two major groups of the genus *Acorus*, and the nomenclatural implications of our discoveries.

## 2. Materials and Methods

### 2.1. Morphology and Anatomy

Herbarium collections of the Komarov Botanical Institute (LE) and Moscow State University (MW) were used to study the morphology of *Acorus* specimens. In addition, digital herbarium collections (E, L, M, MO, P, PE) were used to verify the geographical distributions of *Acorus* in Southeast Asia. For the leaf anatomy, leaf fragments taken from isotype specimens of *A. tatarinowii* (LE) were rehydrated in hot water and transferred into 70% ethanol. Free-hand cross sections were made and observed in glycerol with an Olympus SZX-4 microscope. In addition, free-hand sections of leaves of *A. calamus* s.l. and *A. gramineus* s.l. were made using material from the spirit collection of the Department of Higher Plants of Moscow University.

### 2.2. Nomenclatural Analysis

As the curatorial history of old collections at LE had seldom been described, we analysed herbarium labels of the original specimens in order to uncover their history of owning, curatorial handling, and taxonomic studies. This analysis was based on the published history of herbarium collections [49–54] and the first-hand curatorial experience and expertise of the authors. On the occasion of the present work, the collections of A.A. Tatarinov from China were examined and treated by one of us (ANS) in detail in a separate paper [55]; this treatment was used here as a historical background. The protologue of *A. tatarinowii* [48] was analysed and the nomenclatural status of the original herbarium collections was determined according to the rules of plant nomenclature [1].

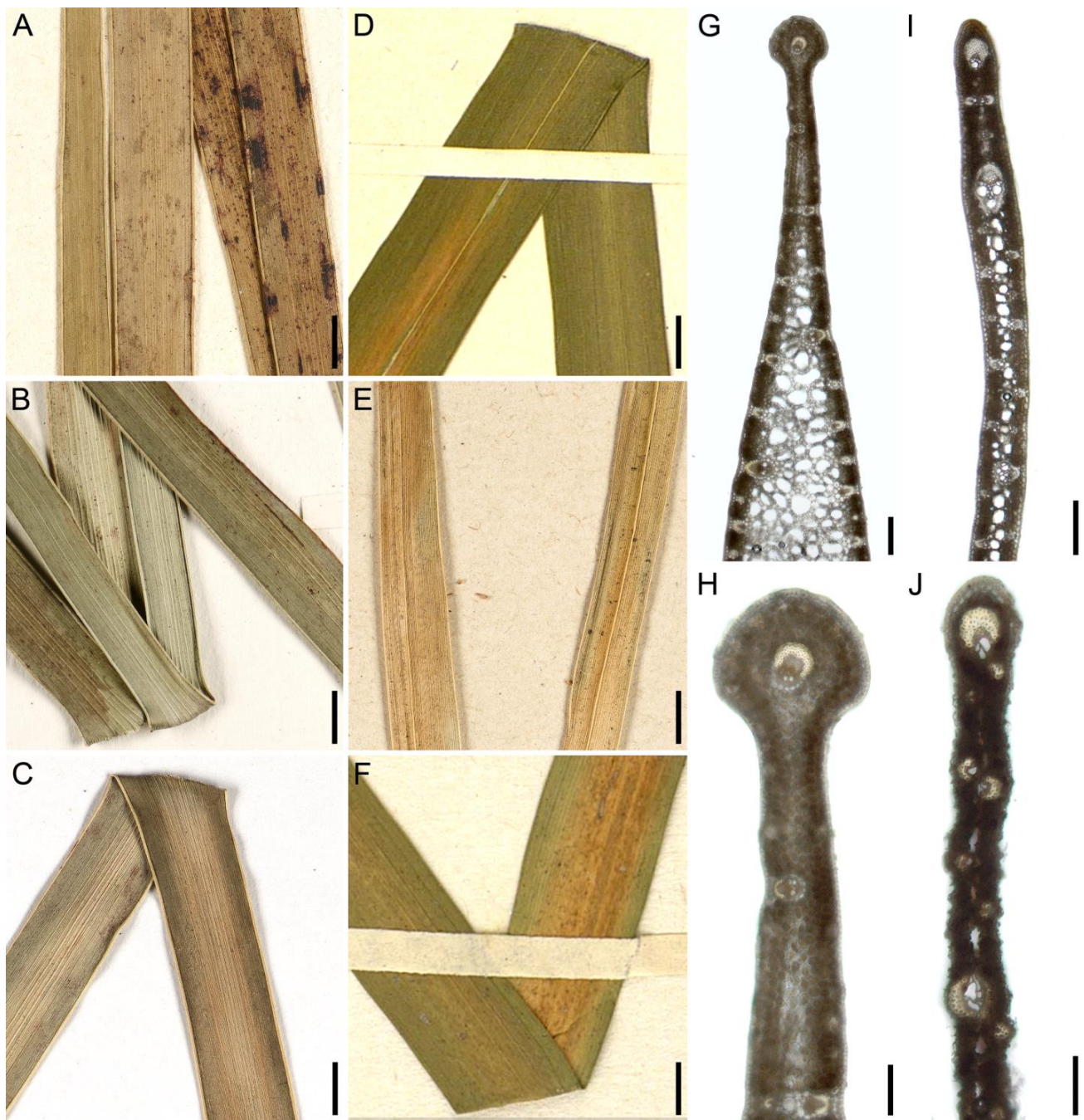
## 3. Morphological Differences between the *Acorus calamus* Group and the *A. gramineus* Group

The *A. gramineus* group and the *A. calamus* group are morphologically well-defined. Although the ranges of their variation overlap, the *A. calamus* group includes generally taller plants (with longer leaves) than the *A. gramineus* group. The leaf length ranges between 45 and 175 cm in the *A. calamus* group and between 15 and 85 cm in the *A. gramineus* group [7,9,19,24].

In the Old World, where their distribution ranges partially overlap, the *A. calamus* group can be distinguished from the *A. gramineus* group by the presence (vs. absence) of a secondary midrib on its leaf blade (Figures 1 and 2A–E) [6–9,16,22]. The midrib in *Acorus* is a more complex structure than just a large vascular bundle and represents a prominent swelling of the leaf blade with separate vascular bundles (often more than one) on either side of a leaf [16,56]. The leaf blade of *Acorus* is ensiform (unifacial) and thus flattened in a vertical plane. Its midrib is therefore not homologous to that of a typical bifacial angiosperm leaf. It should be better called a secondary midrib [56].



**Figure 1.** Morphological differences between the *Acorus gramineus* group (A) and the *A. calamus* group (B–D). (A) Narrow, yellow anthetic inflorescence and leaves lacking a midrib; N Vietnam, Lao Cai province, Sa Pa district (Nuraliev and Sokoloff 259; MW: MW0734438). (B) Fruiting inflorescence and leaves; Russia, Primorsky Krai, Mikhaylovsky district. (C) Broad and green anthetic inflorescence; Russia, Moscow region, Odintsovky district (naturalized). (D) Leaf blades with midribs; same plant as in (C). Photos by D.D. Sokoloff.



**Figure 2.** Taxonomically useful characters of the leaf blade in *Acorus*. (A–F) details of leaf blades in herbarium collections. (A–C) the *A. gramineus* group: a secondary midrib is absent, marginal swellings are conspicuous. (A) Japan, Maximowicz s.n. (LE: LE 01193002). (B) N Vietnam, Soviet-Vietnamese Expedition LX-VN 3883 (LE: LE 01193022). (C) S Vietnam, Averyanov et al. VH 015 (LE: LE 01193215). (D–F) the *A. calamus* group. (D) European Russia, Tikhomirov et al. 13833 (MW: MW0281203): a secondary midrib is present, marginal bundles inconspicuous (such leaves are also common in Asian plants). (E) Bhutan, Griffith 5941 (LE: LE 01082877): a secondary midrib is present, marginal bundles conspicuous. (F) Canada, Boivin and Mosquin 10866 (MW: MW0572409, *A. americanus*): a secondary midrib is absent, marginal bundles inconspicuous. (G–J) Anatomy of a secondary margin of the leaf blade. (G,H) *Acorus gramineus* (spirit collection: Japan, Remizowa et al. s.n., MW). (I) *Acorus calamus* s.l. (spirit collection: Russia, Primorsky Krai, Krestov et al. D47, MW). (J) Isotype of *A. tatarinowii* (LE: LE 01182327). Scale bars: 5 mm (A–F), 0.2 mm (G,I), 0.1 mm (H,J).

There is a native North American member of the *A. calamus* group that apparently deserves recognition at the rank of species, i.e., *A. americanus* (Raf.) Raf. [19,57]. The main diagnostic character of *A. americanus* is the absence of a secondary midrib (Figure 2F). In this respect, the species resembles the *A. gramineus* group, but in spadix morphology (see below), *A. americanus* is similar to the Asian members of the *A. calamus* group. An analysis based on ample material revealed that the leaf length in *A. americanus* varies between 45 and 145 cm with a mean value of 94.31 cm [19], which exceeds the maximum leaf length observed in the *A. gramineus* group [24]. To our knowledge, the placement of *A. americanus* into the *A. calamus* group has never been questioned in previous studies, and we hereby support this view. This placement is well justified by molecular phylogenetic data [30].

We revealed an additional leaf character that allows distinguishing members of the *A. gramineus* group from those of the *A. calamus* group, including *A. americanus*. It was not mentioned in the latest account on the vegetative anatomy of Acoraceae [58]. In the *A. gramineus* group, the leaf blade has prominent marginal swellings (Figure 2A–C). More precisely, these are swellings of secondary leaf margins, because the leaf blade of *Acorus* is ensiform and its margins are not homologous to true leaf margins of bifacial leaves; in ensiform leaves, one margin is adaxial and the other one is abaxial [56]. Anatomically, a vascular bundle surrounded by abundant chlorenchyma is present along either leaf margin (Figure 2G,H). Figure 2I shows a leaf margin of *A. calamus* s.l. without such a swelling, for comparison. Note that the presence of a marginal bundle as such has no taxonomic significance. In this case, it is an amount of parenchymatous (photosynthetic) tissue surrounding the marginal bundle that has diagnostic value. As shown in illustrations in our earlier paper (Figure 14 in [16]), the size and arrangement of marginal bundles vary among specimens belonging to the *A. calamus* group. The marginal bundles are either inconspicuous (Figure 2D) or conspicuous but not forming pronounced swellings (Figure 2E) in the *A. calamus* group. It is important that the presence or absence of marginal swellings can be examined using herbarium material without making anatomical sections, i.e., leaving the specimen intact (Figure 2A–F). The marginal swellings are especially easily recognisable by running a fingernail toward the edge of the leaf blade. In particular, the absence of marginal swelling distinguishes the leaf blade of *A. americanus* from that of *A. gramineus* s.l. despite the absence of the secondary midrib (Figure 2F).

The spadix axis is narrower in the *A. gramineus* group than in the *A. calamus* group (Figure 1). Bogner [8] reported the spadix to be 0.6–1.2(–1.5) cm in diameter in *A. calamus* s.l. and (0.3–)0.4–0.6(–0.7) cm in diameter in *A. gramineus* s.l. These measurements apparently cover both anthetic and postanthetic inflorescences of each species. The spadix diameter increases after anthesis [16].

A spadix character that is not biased by developmental stages is the number of vertical rows (orthostichies) of flowers (Figure 1A,C). According to our observations, as few as 5–9(10) vertical rows (orthostichies) of flowers are typically seen in the side view of the spadix in *A. gramineus* s.l. (i.e., approximately in a longitudinal half of the spadix). In contrast, 11 or more vertical rows of flowers are typically observed in the side view of the spadix in *A. calamus* s.l. In addition, the anthetic spadix is yellow to white in *A. gramineus* and greenish in *A. calamus*.

#### 4. Nomenclatural Treatment of *Acorus tatarinowii*

##### 4.1. Formal Nomenclature

*Acorus tatarinowii* Schott, Oesterr. Bot. Z. 9: 101 (1859).

**Type:** CHINA. Beijing, Changping District: “in a small river near hot springs in Tangshan [Xiaotangshan]”, 1840s, A.A. Tatarinov s.n. (holotype LE: LE 01182329!; isotypes LE: LE 01182325!, 01182326!, 01182327!) Figure 3.



**Figure 3.** Type gathering of *Acorus tatarinowii* (Tatarinov s.n.). (A–C) holotype (LE 01182329); (D) isotype (LE 01182326); (E) isotype (LE 01182325); (B–E) are four times magnified relative to (A), for which a scale is provided. (A) complete specimen. (B) spadix. (C) detail of the leaf blade with a pronounced midrib. (D) spadix. (E) detail of the leaf blade with a pronounced midrib and detail of the spadix. Blue dots are added on (D,E) to show centres of individual flowers. About 14 vertical rows (orthostichies) of flowers can be recognized in (E) each passing through one of the blue dots.



#### 4.2. Nomenclatural History

*Acorus tatarinowii* was described by Schott in 1859 [48] on the basis of herbarium material collected by Alexander A. Tatarinov (contemporary German spelling ‘Tatarinow’). The provenance of the material was indicated in the protologue as “China (Pekin)”, implying that the material was collected in or near Beijing City in China.

As Tatarinov was a Russian collector and Schott’s herbarium of aroid plants was destroyed in Vienna during the Second World War [59], we searched for the original material of *A. tatarinowii* at the Herbarium of the Komarov Botanical Institute (LE), where the early Russian collections from China are known to be deposited [60]. Four historical specimens (herbarium sheets) relevant to this species and collected in China near Beijing were found. Their label information, shown in Figure 4, is transcribed and analysed in detail in Table 1. This information allowed us to determine the history of these specimens, their collector’s name, collection locality and period, and their relevance to the typification of the species name.



**Figure 4.** Herbarium labels from the original collections of *Acorus tatarinowii*. (A,B) LE 01182327. (C) LE 01182325. (D,E) LE 01182329. (F) LE 01182326. For scripts and comments, see Table 1.

**Table 1.** Analysis of the label information from the original collections of *Acorus tatarinowii* at LE. Handwritings are identified according to Sennikov [55]. For label images, see Figure 4.

Specimen Barcode	Script Verbatim	Translation or Transcription	Authority of Handwriting	Notes
LE 01182325	Аcorus Calamus L. (кит. сянь-пу) Июнь. близъ теплыхъ водъ, въ 25 верстахъ отъ Пекина	Acorus Calamus L. (Changpu in Chinese) June, near hot springs, 25 versts [=26.5 km] from Beijing	unknown copyist	original label
	Кирилов	P.Ye. Kirilov	V.L. Komarov	erroneous collector's name, curatorial annotation
LE 01182326	non remitt[endum]	should not be given away	F.J. Ruprecht	curatorial annotation, applied by Ruprecht to most important specimens which cannot be used for exchange
	Acorus Calamus var.?		F.J. Ruprecht	curatorial annotation
	Herb. Acad. Petrop. Fl. Pekin. Dr. Tatarinow, acc. 1856.	Herbarium of the Imperial Academy of Sciences in St.-Petersburg Flora of Beijing Dr. A.A. Tatarinov, acquired in 1856		printed curatorial label of the Botanical Museum, with collecting area, collector's name, and accession year
LE 01182327	Acorus Calamus L.		A.A. Tatarinov	taxonomic revision, identification label
	Herb. Acad. Petrop. Fl. Pekin. Dr. Tatarinow, acc. 1856.	Herbarium of the Imperial Academy of Sciences in St.-Petersburg Flora of Beijing Dr. A.A. Tatarinov, acquired in 1856		printed curatorial label of the Botanical Museum, with collecting area, collector's name, and accession year
	сянь-пу. Июнь-в рѣчкѣ близъ теплых[ъ] водъ въ Тань-Шанѣ	Changpu. June—in a small river near hot springs in Tangshan	A.A. Tatarinov	original label
LE 01182329	Acorus Tatarinowii Schott		H.W. Schott	taxonomic revision, identification label
	Hb. Fischer. Pekin. Kirilow?	Herbarium of F.E.L. von Fischer [Collected from the vicinity of] Beijing. By P.Ye. Kirilov?	F. Körnicke	curatorial annotation, Herbarium Fischer accession to the Botanical Garden in 1855
	Jun. сянь-пу Acorus Calamus? в рѣчкѣ близъ тепл[ыхъ] водъ в[ъ] Тань-Шанѣ	June. Changpu. Acorus calamus? In a small river near hot springs in Tangshan	A.A. Tatarinov	original label

The specimens, denoted by their curatorial barcodes, are analysed in detail below. The history of each specimen is described and interpreted according to the historical analysis of Tatarinov's herbarium collection [55]. Based on its history of treatment and handling, the total collection of Tatarinov was subdivided into three main sets [55], which are represented in the original material of *A. tatarinowii*. This history accounts for the striking differences

observed in the style, handwriting, and even text of the labels in individual specimens, thus obscuring their attribution and type status [55].

#### 4.3. Original Material

**(1) LE 01182329.** The specimen bears an original label in Tatarinov's hand, which allows its attribution to the first set of his collections as recognized by Sennikov [55]. LE 01182329 also bears a taxonomic annotation written by Schott. The label is annotated curatorially to indicate that the specimen belonged to the personal herbarium of F.E.L. von Fischer, which was incorporated into the Imperial Botanical Garden in St.-Petersburg after Fischer's death, thus agreeing with the history of the first set [50,55]. The curatorial annotation, written by F. Körnicke [55], erroneously assumes that the specimen was probably collected by Porphyri Ye. Kirilov, a physician at the 11<sup>th</sup> Russian Orthodox Ecclesiastical Mission in Beijing, who resided in China during 1830–1840 [51]. The inflorescence of this specimen is slightly damaged, indicating that its flowers were used by Schott for his taxonomic analysis.

Heinrich Wilhelm Schott, then Director of the Imperial Gardens at Schönbrunn Palace (Hietzing, Vienna, Austria), received several specimens of various aroids on loan from the Imperial Botanical Garden in St.-Petersburg, which were cited in his monograph [4]. Three of these specimens, referred to three species newly described by Schott, were cited as collected from "Pekin" (Beijing). We traced these specimens at LE and realised that, according to their labels, they all belonged to the same set of Tatarinov's collection kept at the Botanical Garden, in agreement with the statement in [51]. Indeed, their original labels written in the same style were annotated by Körnicke who was an assistant curator at the Garden under the directorship of E. Regel during 1856–1858 [50]. This fact overturns the erroneous statement in Schott's monograph [4] that two of these specimens, including the material of *A. tatarinowii* (LE 01182329), were received from the Botanical Museum in St.-Petersburg; the specimens kept at the Museum were labelled differently [55] and were actually not sent on loan to Schott.

The first species of Araceae described by Schott from Beijing, *Pinellia pedatisecta* Schott dated 1857 [61], was published with the correct statement of the holding institution (Imperial Botanical Garden in St.-Petersburg) but without the collector data, since the collector's name was originally absent from the label and was not added to the label curatorially. For the other two species, *Acorus tatarinowii* Schott [48] and *Arisaema tatarinowii* Schott [62], both published in 1859, the holding institution was omitted but the collector's name was indicated correctly, in spite of the erroneous curatorial statement; this correction may be explained by the follow-up correspondence with St.-Petersburg, most probably from F. Ruprecht, Director of the Botanical Museum, who was already experienced with the collections of Tatarinov [55].

**(2) LE 01182327.** This specimen of *A. tatarinowii* bears a different label but also in Tatarinov's hand. It belongs to the second set of his collections as recognized by Sennikov [55], which was handled separately from the first set by Pavel F. Horaninov at the Imperial Medico-Chirurgical Academy in St.-Petersburg and subsequently sold to the Botanical Museum of the Imperial Academy of Sciences in St.-Petersburg, most likely in 1856 [55].

**(3) LE 01182326** has the same curatorial label as LE 01182327. The lack of original labels on this specimen indicates that it was curatorially separated from LE 01182327 because of its exceedingly large amount of plant material, which did not fit a single herbarium sheet.

**(4) LE 01182325** was attributed by V.L. Komarov, then Curator at the Botanical Garden, to P.Ye. Kirilov. This attribution is erroneous, and the specimen actually belongs to the third set of Tatarinov's collections as recognized by Sennikov [55], which was labelled differently in another hand and acquired separately by the Botanical Garden [55]. This specimen was not available to any researcher during the 19th century, including Schott [55].

#### 4.4. Nomenclatural Discussion

Since the labels of *A. tatarinowii*, which belong to the first (LE 01182329), second (LE 01182326 and LE 01182327), and third (LE 01182325) sets of Tatarinov's collections, contain

the same essential information, we conclude that these plants were collected in the same place by Tatarinov himself. As the plants and their label data are practically identical, we assume, in the absence of any counter-evidence, that they were collected at the same time. This conclusion agrees with the practice of handling herbarium specimens in Tatarinov's collections when a single bulk of plants of the same species was subsequently divided into separate sets with the same label data, which therefore denote parts of the same original collection [55]. In curatorial practice, such herbarium specimens are called duplicates of the same gathering. According to the rules of plant nomenclature, such specimens in the type collection are also duplicates in the nomenclatural sense [1].

As discussed above, only the first set of Tatarinov's collections, kept at the Imperial Botanical Garden in St.-Petersburg, was examined by Schott and became the basis of his new species described from "Pekin". Based on this analysis, we conclude that the only specimen examined by Schott for the original description of *A. tatarinowii* was LE 01182329, which is necessarily the holotype, whereas its duplicates (LE 01182325, 01182326, 01182327) are therefore isotypes. This specimen determines the taxonomic application of the species name *A. tatarinowii* according to the rules of plant nomenclature [1].

The type locality of *A. tatarinowii* is a small river near the Xiaotangshan hot springs [40.175° N, 116.39° E], ca. 25 km north of Beijing (Figure 5), which was a fashionable resort at that time. This place is situated close to the road from Beijing to Kiakhta, which was used by Russian travellers in the 19th century. The plants were repeatedly collected or observed in the same locality by various botanists starting from Bunge [63].



**Figure 5.** Geographical localities of plant material currently (and erroneously) assigned to *Acorus tatarinowii* as provided by GBIF (<https://www.gbif.org/>, accessed 26 November 2022). The map is based on 106 georeferenced records of '*A. tatarinowii*', 37 of which were supplied with images of herbarium specimens. Manual inspection revealed that all 37 specimens in fact belong to the *A. gramineus* group. White star indicates the type locality of *A. tatarinowii* (belonging to the *A. calamus* group).

### 5. Taxonomic Identity of *Acorus tatarinowii*

The morphology of the holotype and all three isotypes of *A. tatarinowii* leave no doubt that they belong to the *A. calamus* group.

In all four specimens, leaves have a well-defined secondary midrib (Figure 3). This feature has never been recorded in any member of the *A. gramineus* group [6–9,22–25,27–30]. Bundles at secondary leaf margins are inconspicuous (Figure 3E) or pronounced (Figure 3C) when examined in dry specimens, but no marginal swellings were found (Figure 2J). The leaf margin structure falls within the limits of the variation found in the *A. calamus* group (Figure 2D,E). We measured the length of the longest leaves in two specimens of the type collection, whereas the two other specimens (LE 01182326 and LE 01182329) have incomplete tips of the longest leaves. The longest leaf is 73 cm long in LE 01182327 and 76 cm long in LE 01182325. These measurements fall into the interval where the ranges of leaf length variation overlap between the *A. calamus* group and the *A. gramineus* group, but disagree remarkably with the range (20–50 cm) that was indicated for '*A. tatarinowii*' by Cheng et al. [27].

The spadix morphology of the holotype and all three isotypes of *A. tatarinowii* also supports their placement in the *A. calamus* group. Inflorescences of the type material of *A. tatarinowii* have more than 11 vertical rows of flowers in the side view (Figure 3) as characteristic of the *A. calamus* group. Thus, our data unambiguously suggest that the name *A. tatarinowii* cannot be applied to any segregate species belonging to the *A. gramineus* group.

Apart from the morphological evidence, the geographical locality of the type material of *A. tatarinowii* is also instructive. The material was collected in the northern part of China, near Beijing, and originated from a natural locality rather than from cultivation. However, according to *Flora of China* [7], the native occurrence of the *A. gramineus* group was not recorded from Beijing or the neighbouring Hebei and Tianjin provinces. The *Flora Reipublicae Popularis Sinicae* recognized '*A. tatarinowii*' as a distinct species within the *A. gramineus* group, and described its range as not extending beyond the Yellow River (the Huang He River) to the north [23]. More recent publications recognizing '*A. tatarinowii*' also implied that the species occurs south of the Yellow River [64–66]. This distribution range does not include the actual type locality of *A. tatarinowii*, indicating a misapplication of the species' name (Figure 5).

## 6. The Concept of Three Narrowly Defined Species in the *A. gramineus* Group Is Still Insufficiently Justified

The most recent taxonomic study on *Acorus* recognized three species of the *A. gramineus* group in China: *A. gramineus*, '*A. tatarinowii*' and *A. macrospadiceus* [27]. From a nomenclature standpoint, the current use of both segregate species names is incorrect. In addition to the misapplication of the name *A. tatarinowii* discussed above, the name '*A. macrospadiceus* (Yamam.) F.N. Wei & Y.K. Li' has not been properly published. Wei and Li [24] intended to publish a new combination based on '*A. gramineus* var. *macrospadiceus* Yamam.', but this varietal name was proposed by Yamamoto in 1943 [67] without a validating description or diagnosis in Latin, which was strictly required in 1935–2011. Although Wei and Li in 1985 [24] provided a Latin description for their species, which was technically new at that time, they did not designate its type as required for the publication of new species names since 1958. In spite of some use and limited acceptance, the species name '*A. macrospadiceus*' remains invalidly published and cannot be considered available under the rules of plant nomenclature [1].

The main morphological character proposed to distinguish the three species of the *A. gramineus* group is leaf dimensions, which were stated as 20–30 × <0.7 cm in *A. gramineus* s.str., 20–50 × 0.7–1.3 cm in so-called '*A. tatarinowii*' and 30–85 × 0.7–1.5 cm in '*A. macrospadiceus*'. The overlapping nature of this character makes its use in the identification of plant material problematic.

One cannot exclude that molecular and metabolomic data provide a better basis for recognizing narrowly defined species than can be offered by morphology. However, the two available molecular phylogenetic studies [27,30] showed contradictory results. The so-called '*A. tatarinowii*' is monophyletic according to Cheng et al. [27], but polyphyletic

according to Zhang [30]. This may be partly explained by differences in the sampling of plant material. Zhang [30] used some important accessions not employed in the study of Cheng et al. [27], including those identified as two additional members of the *A. gramineus* group, *A. latifolius* and *A. xiangyeus*, both described from Sichuan, China [28].

According to the protologue, *A. latifolius* is characterized by leaves 25–55 cm long and 1.5–2.5 cm wide. The leaf width range indicated for *A. latifolius* [28,30] is beyond the ranges of variation of all three species recognized by Cheng et al. [27]. *Flora of China* [7] treated *A. latifolius* as a synonym of *A. gramineus* s.l., whereas *Flora of Thailand* [9] placed it in the synonymy of *A. calamus* s.l. The photograph provided in the protologue [28] suggests that *A. latifolius* belongs to the *A. gramineus* group. This is further supported by the molecular phylogenetic data of Zhang [30] based on the material of *A. latifolius* from locus classicus. *Acorus xiangyeus* is described as resembling *A. gramineus* s.str., but is distinguished by even narrower leaves (0.2–0.4(0.5) mm wide), shorter spadix and spatha, and the absence of normally developed fruits [28].

According to Zhang [30], an accession of '*A. tatarinowii*' from Sichuan was closest to *A. latifolius* whereas two other accessions of '*A. tatarinowii*' (from Hong Kong and Hainan) were closer to accessions identified as *A. gramineus*, *A. xiangyeus* (material from locus classicus), and '*A. macrospadiceus*'. Cheng et al. [27] did not study any material from Hong Kong or Hainan. They apparently did not include any sample identified as *A. latifolius* or *A. xiangyeus*. At least, these two names were not mentioned in their paper [27].

A study of leaf morphology and anatomy suggested combining '*A. macrospadiceus*', *A. latifolius* and '*A. tatarinowii*' as one and the same species [29], but this hypothesis cannot be properly tested using the molecular data of Cheng et al. [27] because of limited sampling in the latter study. Based on the above discussion, we conclude that the concept of three (or more) narrowly defined species of the *A. gramineus* group [27] is still insufficiently justified. This conclusion fits well with the ideas of Engler [6], Bogner [8], Boyce [9], and others who acknowledged the occurrence of a high morphological variation within *A. gramineus* s.l., but found it impossible to distinguish narrowly defined species based on this variation. In the current state of knowledge, the wide species concept is more appropriate to use, especially because the monophyly of the *A. gramineus* group has been convincingly demonstrated [27,30]. We, therefore, suggest that the plant material that was incorrectly referred to in recent publications as '*A. tatarinowii*' should be interpreted as belonging to a single polymorphic species, *A. gramineus* s.l., at least until a comprehensive taxonomic revision of the group is available.

## 7. Distribution of *Acorus* in Eastern Indochina and Thailand

Both the *A. calamus* group and the *A. gramineus* group occur in tropical Southeast Asia, but details of their distribution require further clarification.

The treatment of Boyce in *Flora of Thailand* [9] provides detailed morphological and ecological accounts of *A. gramineus* s.l. and *A. calamus* s.l. that fully agree with our observations on *A. gramineus* in Vietnam and Japan and *A. calamus* in Russia. According to Boyce [9], *A. calamus* s.l. is locally distributed in northern Thailand (Chiang Rai province) where it grows in swamps, along pond sides, and in standing water at elevations below 2800 m. It is also cultivated in Thailand [9]. *Acorus gramineus* s.l. has a wider distribution in Thailand and tends to occur at lower elevations (below 2600 m) where it grows in dense forests, moist rocky stream banks, and meadows, often occurring as a rheophyte [9]. Boyce correctly placed *A. tatarinowii* in the synonymy of *A. calamus* under the wide species concept adopted by him for the genus [9]. However, his view appeared to contradict the treatment in *Flora of China* [7] that placed *A. tatarinowii* in the synonymy of *A. gramineus*. Boyce also did not mention that the name *A. tatarinowii* has been widely used for a member of the *A. gramineus* group [9]. The synonymy provided by Boyce has been followed by POWO [68] and implemented by GBIF [69].

*A checklist for the seed plants of Cambodia* [70] accepted *A. calamus* (and separately *A. calamus* var. *angustatus* Besser, another invalidly published name) and *A. gramineus*. *A*

checklist of the vascular plants of Lao PDR [71] listed three species: *A. calamus*, *A. gramineus* and *A. verus* (L.) Raf. (the latter name is a synonym of *A. calamus* [9]). An illustrated flora of Vietnam [25] reported the presence of two native species in the country, *A. gramineus* and *A. tatarinowii*. We studied extensive collections identified as *A. tatarinowii* in LE and MW Herbaria and in available digital resources. Our examination demonstrated that specimens from Thailand, Laos, and Vietnam currently identified as *A. tatarinowii* belong to the *A. gramineus* group, which indicates the same misidentification as in China. Due to the discrepant interpretations, taxonomic algorithms used in GBIF [69], the greatest aggregator of biodiversity distribution data in the world, re-classify all specimens originally identified as *A. tatarinowii* (and belonging to *A. gramineus* s.l.) under the wide concept of *A. calamus* according to the synonymy from POWO [68]. Therefore, an impression of the abundance of *A. calamus* in southeast China and Indochina that comes from the analysis of GBIF data should be taken with caution.

Herbarium-based data on the distribution of *A. calamus* s.l. in Eastern Indochina and Thailand are further biased by incorrectly identified specimens. We re-identified as *A. gramineus* s.l. the following specimens originally named as *A. calamus*.

LAOS. Vientiane province: vicinity of Kasi (Na Mon), undergrowth semi-dense forest, ca. 450 m, 2 March 1994, J.E. Vidal and B. Svengsuksa 86 (P: P06491951).

THAILAND. Chiang Rai province: Khun Chae National Park, lower montane forest, nature trail from headquarters, on rocks near streams, 950 m, 16 March 2005, R. Pooma, K. Phattarahirankanok, S. Sirimongkol, M. Poopath 4845 (E: E00318527; L: L.1408913); [Chiang Mai province:] Doi Suthep, 500–800 m, 30 December 1904, C.C. Hosseus 286 (M: M-0168505); Chiang Mai province: Doi Inthanon, evergreen forest, epilithic in a stream, 18°40' N 98°25' E, 1400 m [mistake?], 3 January 1975, R. Geesink, P.H. Hiepkco, C. Phengklai 8053 (L: L.1408916); Chiang Mai province: [Doi Inthanon National Park], Siriphum waterfall, on stone along a stream, ca. 1400 m, 25 June 1978, C. Phengklai, M.N. Tamura, C. Niyomdham, B. Sangkhachand 4095 (L: L.1408915); Chaiyaphum province: Ban Nam Phrom, Chulaborn dam, the evergreen forest along a stream on sandstone, in streamlet, 15°40' N 102°00' E [mistake?], 800 m, 26 May 1974, R. Geesink, T. Hattink, C. Phengklai 7000 (L: L.1408914; P: P00251691).

VIETNAM. Quang Ninh province: Ha Tu, in the stream, T. Canh 260 (B: B100001586); Hoa Binh province: the road from Hanoi to Hoa Binh, Muong Thon, swamp at foot of limestone hill, 15 March 1941, in the stream bed, in the water, P.A. Pételot 7582 (P: P01797767, P01797768); [Khanh Hoa province:] Nha Trang area, West of Nha Trang, 4 July 1922, E. Poilane 4352 (L: L.3716329; P: P02074719); Lam Dong province: Don Duong, Ca Do, 2 January 1983, L.V. Averyanov et al. LX-VN 1126 (LE: LE01193210).

All the specimens listed above fit the diagnostic characteristics of the *A. gramineus* group as provided in Section 2 of the present paper. When ecology was indicated on herbarium labels, it was well compatible with the ecological preferences of *A. gramineus* mentioned by Boyce [9] (see above) and confirmed by our field observations in Vietnam. There was, however, an exception. The specimen Pételot 7582, according to the label, was collected in a habitat that is much more appropriate for *A. calamus* [9,27]. Re-collection of the plant from this locality along with detailed ecological observations may clarify the discrepancy.

For only a few specimens from Laos, Thailand, and Vietnam listed below, we hereby confirm the identification as *A. calamus* s.l.

LAOS. Sayaboury [Sainyabuli] province: Sayaboury [Sainyabuli], planted, 300 m, 26 October 1965, J.E. Vidal 4153 (P: P02136600); [Luang Prabang province:] Luang Prabang district, Sangkhalok village, 19°52.23' N 102°06.73' E, 530 m, 26 January 2000, B.H. Southavong, D.T. Kien, M.V. Sinh 082 (L: L0406783).

THAILAND. Chiang Rai province: South of Chiang Rai, irrigation-canal, on clayey soil, ca. 400 m, 2 March 1958, T.J. Sorensen, K. Larsen, B. Hansen 1812 (A: 01634206) (this is the only specimen from Thailand recorded in a recent checklist [72]); Chiang Mai province: Fang, ca. 350 m, 28 February 1958, T.J. Sorensen, K. Larsen, B. Hansen 1780 (A: 01634205).

VIETNAM. Thu Dau Mot [Binh Duong] province: Thu Dau Mot, Annamite gardens, 16 February 1919, *A.J.B. Chevalier* 39966 (P: P00251665); province unknown: Cochinchina, cultivated, 1862–1866, *C. Thorel* 327 (P: P00251664).

Specimens from Vietnam and Laos here confirmed as belonging to *A. calamus* were collected from cultivated plants as can be inferred from their labels (*Southavong 082* has no information on ecology, but the collection site is indicated as a village). Among the two specimens from Thailand, one has no information on ecology and the other was collected in an anthropogenic habitat (irrigation canal). Therefore, our data show that *A. gramineus* s.l. (= *A. gramineus* group) is the only native member of the genus in Eastern Indochina. The status of *A. calamus* s.l. in Thailand requires further clarification.

## 8. Conclusions

Our data show that the species name *A. tatarinowii* cannot be applied in the way adopted in recent publications and herbarium collections from SE Asia, because the type of this name belongs to the *A. calamus* group and is clearly distinct from the *A. gramineus* group. The material widely identified as *A. tatarinowii* should in fact be assigned to *A. gramineus* when a wide species concept is adopted. Under a narrow species concept, other appropriate species names should be found or proposed for the plants currently named *A. tatarinowii* and *A. macrospadiceus* (the latter name has not been validly published). We highlight the danger of merely proposing two new species names, because the names *A. latifolius* and *A. xiangyeus* are properly published and will have a nomenclatural priority over any newly published name.

However, the concept of three or more narrowly defined species in the *A. gramineus* group [24,27,28] is still insufficiently justified. In the current state of knowledge, the wide species concept is more appropriate to use. The wide species concept has been adopted in recent accounts on the floras of Japan [73] and northern Vietnam [74]. We, therefore, suggest that the plant material that was incorrectly referred to in recent publications as '*A. tatarinowii*' should be interpreted as belonging, along with other members of the *A. gramineus* group, to a single polymorphic species, *A. gramineus* s.l., at least until a comprehensive taxonomic revision of the group is available. We further suggest that all studies of chemical substances extracted from *Acorus* species should be accompanied by the preparation of voucher specimens deposited in appropriate Herbarium collections. This will allow updates of the taxonomic identity of the material along with refinements of the classification of the genus.

Some plants of *A. gramineus* (in a wide sense) from Vietnam, Laos, and Thailand have been sometimes mistaken for *A. calamus*, which is in fact only known in cultivation in Vietnam and Laos. The status of *A. calamus* in Thailand requires further clarification.

Further morphological, molecular, and metabolomic studies of the material from across its geographical range will be essential for comprehensive conclusions on species limits and distribution patterns in the *A. gramineus* group.

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