

Article

Exploring the Origins of Hexaploid Wheats: Typification of Archaeological *Triticum vulgare* var. *antiquorum* and Description of Modern *Triticum sphaerococcum* subsp. *antiquorum* (Poaceae: Triticeae)

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Abstract: This study addresses a critical issue in plant taxonomy and phylogeny: the relationship between archaeological materials and potentially analogous living populations. Given the current limitations in definitively establishing the identity between archaeological and contemporary materials, we propose an intermediate approach. This approach serves as a useful framework while scientific methods advance towards definitively assessing whether an archaeological wheat sample, approximately 5000 years old from Central Europe, belongs to the same species as a modern wheat currently endemic to Central Asia. This approach consolidates the taxonomic validity of both archaeological and living materials, allowing them to be treated as distinct taxa while preserving the possibility of future identification convergence. *Triticum vulgare* var. *antiquorum*, an archaeobotanical small-grained, free-threshing wheat, was originally described in 1865. The 1982 discovery of morphologically similar living wheat in Tajikistan raised questions about their taxonomic relationship. Our study reviews the nomenclature of both taxa, designating an illustration from the original description of *T. vulgare* var. *antiquorum* as the lectotype to align with the traditional concept of the name. We address the ambiguity surrounding “*Triticum antiquorum*” as used by Russian agronomists and botanists, proposing a more precise circumscription within the current systematic framework of the genus based on cytogenetic data. Consequently, we describe a new taxon, *Triticum sphaerococcum* subsp. *antiquorum*. The holotype, selected from material with available cytogenetic data and grown from Professor Udachin’s original Pamir (Tajikistan) collection, is preserved in the N.I. Vavilov All-Russian Institute of Plant Genetic Resources (WIR) collection. It is deposited at the I.M. Krasnoborov Herbarium of Central Siberian Botanical Garden SB RAS (NS), with an isotype at the WIR. This taxonomic revision and new subspecies designation provide a robust framework for reconciling archaeological and contemporary wheat diversity, advancing our understanding of wheat evolution and agricultural history.



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1. Introduction

1.1. Overview

The discovery of living plants resembling archaeological type specimens presents a taxonomic challenge. This situation arises when the following conditions are met: 1. A taxon’s

original type material consists of plant remains from archaeological sites. 2. Contemporary populations have been unknown for years. 3. A living individual or population is found that appears similar or identical to the type material, accounting for preservation-related differences. In such cases, researchers face a dilemma. They must choose between the following: 1. adopting the existing name and rank for the living specimens, or 2. proposing a nomenclatural revision, such as reclassifying at a different rank, or introducing a new name with a modified rank. This decision involves a high degree of uncertainty. Assuming the identity between archaeological and living specimens, while tempting, requires careful consideration of the limitations in our ability to definitively establish such connections across vast time spans.

This is the situation that Udachin [1] faced concerning the ancestral original material of the hexaploid free-threshing wheat named *Triticum vulgare* var. *antiquorum* Heer. Von Heer described this taxon in 1865 [2] from archaeological findings of grain remains in Switzerland. In 1982, plants morphologically similar to this previously presumed extinct wheat taxon were collected in the western Pamirs region of Tajikistan. However, given the inherent uncertainty in comparing archaeological specimens with living plants, we cannot definitively assert that these modern samples belong to the same species as the ancient taxon. This discovery highlights the complex relationship between archaeological materials and potentially analogous living populations, underscoring the need for careful taxonomic consideration [1,3] (Appendix C). As a result of the study of the new material collected, Udachin [3] proposed the species rank for von Heer's taxon as *T. antiquorum* (Heer) Udachin ("*Triticum antiquorum* Heer ex Udachin"). The author abbreviation for R.A. Udachin has been standardised as Udachin [4] and is the one we follow, although Udaczin or Udacz. would be more correct.

Flaksberger [5], when combining *T. vulgare* var. *antiquorum* under *T. compactum* Host (as *T. compactum* var. *antiquorum* (Heer) Flaksb.), argued that the plant closely resembles that of hexaploid wheats, based on glume morphology and spike density. It differs from typical *T. compactum* particularly regarding the former's spherical grains.

Both the archaeological material from Switzerland and the living specimens collected in Pamir (Tajikistan) exhibit distinctive characteristics of the "inflatum" wheat type. These features include an awnless, dense spike and a clearly perceptible spikelet keel extending to its base. At the keel's base, there is an indentation characteristic of hexaploid wheat [6–8]. Similar longitudinal wrinkling is observed along the sides of the keel and at the base of the scales. Each spikelet contains 3–4 grains, distinguished by their somewhat rounded shape. The striking morphological similarities between the archaeological and contemporary samples underscore the potential taxonomic relationship while also highlighting the challenges in definitively establishing their identity across millennia.

The presence of basally indented keels in glumes is frequently cited as a distinguishing characteristic between tetraploid and hexaploid wheat. Tetraploid wheat typically exhibits glumes that are firmly coriaceous and distinctly carinate at the base, devoid of longitudinal folds or transverse depressions. As a result, the texture and consistency of these glumes remain uniform to the very base. In contrast, hexaploid wheat is characterised by glumes that possess an indistinct, narrow keel, which may sometimes disappear at the base, presenting an indented appearance [7].

While not all characters are exclusive to hexaploid wheats [9], the presence of these traits in both archaeological and modern Tajik wheat indicates a close relationship. Subsequent genetic analyses have confirmed the hexaploid nature of Tajik wheat. As a result, the dense-ear, round-grain wheat from West Pamir (Tajikistan) was identified as belonging to *T. vulgare* var. *antiquorum* Heer by Udachin [3] on p. 50.

Some authors assign a leading role to this ensemble in solving problems of domestication of cultivated hexaploid wheats and believe that Asia occupied the principal place in this process [3,7–10]. Clearly, *T. vulgare* var. *antiquorum* and the new wheat material found in western Pamir (Tajikistan), either identical or merely similar, are relevant in the study

of hexaploid wheats' origins and evolution [10–14], and it is possible that *T. vulgare* var. *antiquorum* was among the first cultivated hexaploid wheats in Europe [12,15].

1.2. Background

Triticum L. (Poaceae: Triticeae) is an extraordinarily complex genus of approximately 25 wild and domesticated species [16]. Currently, the classification of wheat species is artificial and very subjective, even with the molecular genetics tools currently available [17]. A possible cause is the evolutionary youth of the cultivated wheat species, all of which came into being within the last 6000–12,000 years [10].

Swaminathan and Rao [18] showed that differences in taxonomically important traits of hexaploid wheats are controlled by four pairs of nonallelic genes [12,19,20]. The four taxonomically important genes not only control the conspicuous morphological traits; they also have considerable pleiotropic effects [12,21]. The morphology of individual plants is determined by the combination of the alleles of such genes present. Consequently, it becomes easier to accurately identify individual plants, even in experimental plantings or during archaeological excavations [17].

The bread wheat *T. aestivum* L. (incl. *T. vulgare* Vill. as synonym), sect. *Triticum* [hexaploid $2n = 6x = 42$; BAD genomes] [8,18,20,22,23], is generally treated as a species that is not found in nature and its genome has been shown to be composed of those of several wild species (*T. dicoccoides* (Körn. ex-Asch. and Graebn.) Schweinf. [tetraploid $2n = 4x = 28$; BA genome], *T. speltooides* (Tausch) Gren. ex K. Richt. ($\equiv$ *Aegilops speltooides* Tausch) [diploid $2n = 2x = 14$; B genome] and *T. tauschii* (Coss.) Schmalh. ($\equiv$ *Aegilops tauschii* Coss.) [diploid $2n = 2x = 14$; D genome]) [24–28].

In this sense, the existence of archaeological wheat varieties (e.g., *T. vulgare* var. *antiquorum*) included currently within *T. aestivum* [1–3,6,10,12] confirms that this species grows always in anthropised habitats and is never wild in nature.

Recent studies by Goncharov and Gaidalenok [10] and Goncharov et al. [11] have shed light on the genetic similarities between modern hexaploid wheat from Central Asia and the ancient wheat variety *Triticum vulgare* var. *antiquorum*. Their research focused on the inheritance patterns of two domesticated traits that are significant for taxonomic classification. The investigators demonstrated that the recessive gene responsible for spherical grain shape in the Central Asian wheat was allelic to the *s* gene, which determines the same characteristic in *T. sphaerococcum* Perciv., an endemic species found in India and Pakistan. Furthermore, they examined the dominant genes controlling compact ears in specimens collected from western Pamir (Tajikistan) and in *T. sphaerococcum*. These genes were found to be nonallelic to the corresponding dominant gene in *T. compactum*. Additionally, molecular biological analyses conducted by the researchers indicated a close phylogenetic relationship among all hexaploid wheat species. These findings contribute to our understanding of the genetic linkages and evolutionary history of various wheat taxa.

This study aims to address the taxonomic ambiguity between archaeological plant materials and their potential modern analogues within the *Triticum* genus. Our primary objective is to revise and clarify the nomenclature of two significant *Triticum* taxa: the archaeological taxon, originally described as *Triticum vulgare* var. *antiquorum* in 1865, and a related modern taxon, which we propose to describe as *Triticum sphaerococcum* subsp. *antiquorum*. Through this research, we seek to establish a nomenclatural framework that harmonises historical taxonomic conventions with contemporary cytogenetic findings.

The expected results of this study include the resolution of nomenclatural inconsistencies between the archaeological and modern taxa, and the establishment of a clear taxonomic relationship between the historical *T. vulgare* var. *antiquorum* and the newly proposed *T. sphaerococcum* subsp. *antiquorum*. This will create a more precise and dynamic framework for understanding wheat phylogeny that integrates both historical and contemporary perspectives.

2. Materials and Methods

Despite its economic value and agronomic importance, *T. vulgare* var. *antiquorum* has not yet been typified. In this paper, we fix the application of this through typification. The designation of type is based on the consultation of original elements used by the author to describe this taxon. This material has been carefully evaluated for the purpose of fixing the precise taxonomic application of the name. We also clearly separate von Heer's variety from Udachin's taxonomic proposal which is here validated; although, being both similar and clearly located within the hexaploid wheats, we cannot rule out that future studies may confirm Udachin's statement that both are identical.

This study is based on a thorough literature review and the examination of materials and databases from the following herbaria, collections and museums: Datenbank Erdwissenschaftliche Sammlungen, Department of Earth Sciences, ETH Zürich; British Museum of Natural History-V; Komarov Botanical Institute; N.I. Vavilov All-Russian Institute of Plant Genetic Resources (Saint Petersburg) (WIR); I.M. Krasnoborov Herbarium of Central Siberian Botanical Garden, the Siberian Branch of Russian Academy of Sciences (NS); and the University of Murcia (MUB).

One of us (N. Goncharov) cultivated seeds from the K-56398 original accession of *T. antiquorum* in the greenhouse at the Institute of Cytology and Genetics, Siberian Branch of the Russian Academy of Sciences, Novosibirsk. After 1.5–2 months of growth, we were able to prepare herbarium sheets from this newly grown material and designate the holotype of *T. sphaerococcum* subsp. *antiquorum*.

3. Results and Discussion

3.1. Typification of the Name *Triticum vulgare* var. *antiquorum*

The existence of unusually small-grained wheats in archaeobotanical materials was disclosed by von Heer [2,29]. Details of “*Der kleine Pfahlbauweizen*”, provided, mainly, by Robenhausen but also Moosseedorf, Montelier and Olomouc [Olmuz], were published by von Heer in 1865 [2]; pages 13–14, fig. 1 [1] [on page 5] and figs. 14–18 [on page 55] (Appendix A) show grains that were typified as *Triticum vulgare* (var.) *antiquorum*, based on archaeological findings of grain remains in Switzerland (Appendix B), Figures 1 and 2. Following the best practice protocol, we proposed [30], we proceed with the typification of this taxon based on archaeobotanical material. Archaeobotanical remains are contemporary with modern living plants, including their nomenclatural requirements, and are not fossils. This distinction is supported by numerous reasons analysed in detail by Rivera et al. [30] for this and other taxa in similar situation.

Unfortunately, no specimens eligible for typification are known to be extant, and thus the fructified spike illustrations published in the protologue on pages 5 (fig. 1 [1]) and 55 (figs. 14–18 in table 1) are the only original elements (Figures 1 and 2).

Oswald von Heer (1809–1883), a Swiss paleobotanist, entomologist and theologian, was the first curator of the Zürich universities' joint herbaria; from 1834, he was connected with the University of Zürich, and from 1855, he was linked with the ETH (Geological Institute of the Technische Hochschule), Zürich, where he was a professor of Botany and director of the botanical garden. We did find some original *Triticum* materials at the Datenbank Erdwissenschaftliche Sammlungen, Website Erdwissenschaftliche Sammlungen, Departement Erdwissenschaften, ETH Zürich, but no one complete wheat ear nor grains were found belonging to “*Der kleine Pfahlbautenweizen*”. Wheat is present in von Heer's collection in (1) a box with carbonised grains labelled “*Triticum vulgare* Weizen Neolithische Pfahlbaute Lüscherz an Bielersee” [31]; (2) another box labelled “(Steinzeit) 17301/? Schütz/? *Triticum compactum*” [32]; and (3) an unlabelled box with carbonised grains [33]. Other materials can be found at the British Museum of Natural History-V (e.g., *Rhus bella* in the Paleobotany collection) but nothing related with *Triticum*. Flaksberger [5] mentions that part of the original material (or all) was transferred or bequeathed to the Museum of the Botanical Garden in Leningrad [Saint Petersburg], presently Komarov Botanical Institute, but these samples are no longer extant. Flaksberger [5], in photograph 2 on page 75, presents, in

figs. 2–4, very low-quality photographic images of these materials (two incomplete spikes and 33 grains), under the name “*Triticum aestivum* L. subsp. *compactum* (Host) Alef. var. *antiquorum* (Heer) Flaksb.” Therefore, the most reliable original elements of *T. vulgare* var. *antiquorum* are the figures included in the protologue by von Heer in 1865, on pages 5 and 55 [2].



Figure 1. (A) Image of the lectotype of *Triticum vulgare* var. *antiquorum* Heer; illustration in von Heer (1865: 55, table 1, fig. 14) [2]; Original material: (B) completed (reconstructed) ear; illustration in Heer (1865: 55, table 1, fig. 17) [2]; (C) a second fragment from the inside, which shows the thick position of the ears; illustration in von Heer (1865: 55, table 1, fig. 15) [2]; (D) a single ear with four grains; illustration in von Heer (1865: 55, table 1, fig. 16) [2]; (E) husks considerably enlarged, illustration in von Heer (1865: 55, table 1, fig. 16b) [2].

Thus, among the illustrations published by von Heer in 1865, the first drawing appears on page 5, labelled as “*Getreide-Ärten der Pfahlbauten aus der Steinzeit. 1. Kleiner Pfahlbauweizen (Triticum vulgare antiquorum)*” [Cereal species of the pile dwellings of the Stone Age. 1. Small pile-dwelling wheat. . .]. The remaining illustrations, shown in figs. 14–18, are printed on page 55. figs. 14–16 and 16b depict details of the ears and bracts, fig. 17 shows a complete ear and fig. 18 is a table with nine drawings (a, aa, b, c, d, e, f, g and h) illustrating the fruits. References to the original material are provided in the figure captions by von Heer [2] on page 51 as follows: “fig. 14. Fragment of ear from Robenhausen. fig. 15. A second piece from the inside, showing the thick position of the ears. fig. 16. A single ear with four grains. fig. 16. b. Husks enlarged. fig. 17. Ear complete. fig. 18. Individual grains; a. b. c. e. f. g. from Robenhausen, aa. from Moosseedorf, d. from Montelier, h. from Olomouc”. Among these illustrations, drawing number 14, which illustrates a large

spike fragment, on page 55 [2] is designated as the lectotype of the name *Triticum vulgare* var. *antiquorum*.



Figure 2. Original material of *Triticum vulgare* var. *antiquorum* Heer., Images of individual grains. (A) from Robenhausen; illustration in von Heer (1865: 55, table 1, fig. 18a) [2]; (B) from Moosseedorf; illustration in von Heer (1865: 55, table 1, fig. 18aa) [2]; (C,D) from Robenhausen; illustration in von Heer (1865: 55, table 1, fig. 18b,c) [2]; (E) from Montelier; illustration in von Heer (1865: 55, table 1, fig. 18d) [2]; (F–H) from Robenhausen; illustration in von Heer (1865: 55, table 1, fig. 18e–g) [2]; (I) from Olomouc; illustration in von Heer (1865: 55, table 1, fig. 18h) [2].

Triticum aestivum (subsp. *compactum*) var. *antiquorum* (Heer) H. Messik. (1913: 81) [34].

≡ *T. vulgare* var. *antiquorum* Heer (1865: 13) [2]. This represents the basionym of the currently accepted name.

≡ *T. compactum* var. *antiquorum* (Heer) Flaksberger (1930: 72) [5].

≡ *T. antiquorum* (Heer) Anonymous (1870: 162) [35].

≡ *T. aestivum* f. *antiquorum* (Heer) Neuweiler (1935: 104) [36].

Lectotype, designated here: [illustration] in von Heer (1865: 55, table 1, fig. 14) [2] Figure 1A.

3.2. Description of a New Hexaploid Free-Threshing Wheat: *Triticum sphaerococcum* subsp. *antiquorum*

3.2.1. Relevant Material and Types

Udachin [1] reported the existence of living wheats in Pamir (Tajikistan) that closely match the morphology of the parts described and figured from *T. vulgare* var. *antiquorum*. Later, Udachin [3] mentioned this archaeological variety under the name of *Triticum antiquorum* seemingly at the level of species. This reclassification has been accepted in numerous papers by Russian researchers and databases [37]. This taxon typically has a compact spike shape [38]. Specifically, Udachin [3] noted on page 52 that this material presents awnless, pubescent ears with grey hairs on a white background, an *inflatum* type, and white caryopsis (see Flaksberger [5] for comparison with the European material).

From the nomenclatural point of view, Udachin [3] on page 52 published “*Triticum antiquorum* Heer ex Udacz.”, which some authors incorrectly cite as “*T. antiquorum* Heer” [39]. Udachin [3], however, clearly indicates a full and direct reference to the author and place of valid publication, with a page number and date, namely “*T. vulgare* var. *antiquorum* Heer et *T. compactum* var. *muticum* Heer, 1865, Pflanz. Pfahlbaut.: 13–14.”, but does not designate a basionym (see ICN Art. 41.5 [40]). Thus, although some databases erroneously report “*T. compactum* var. *antiquorum* Heer” (see Tropicos) [4,41], Udachin included *T. compactum* var. *antiquorum* (Heer) Buschan as another synonym. But Buschan [42] on page 10 merely wrote

“However, it seems to me that these grains belong to *Triticum compactum* more naturally”, without formally publishing the combination. The combination under *T. compactum* was effectively published by Flaksberger [5] on page 72.

On the other hand, Udachin [3], on page 52, explicitly indicated that the “type” of “*T. antiquorum* Heer ex Udacz. var. *antiquorum*” was the material collected in 1965 in Pamir (Tajikistan) and preserved in the N.I. Vavilov All-Russian Institute of Plant Genetic Resources (Saint Petersburg) (VIR). The seeds are stored at the VIR, while the herbarium specimen cultivated from them was housed at the WIR herbarium (Figure 3). Thus, Udachin excluded the original material of von Heer, and therefore this “typification” is ineffective, as it is contrary to Art. 9.3 of the ICN [40].

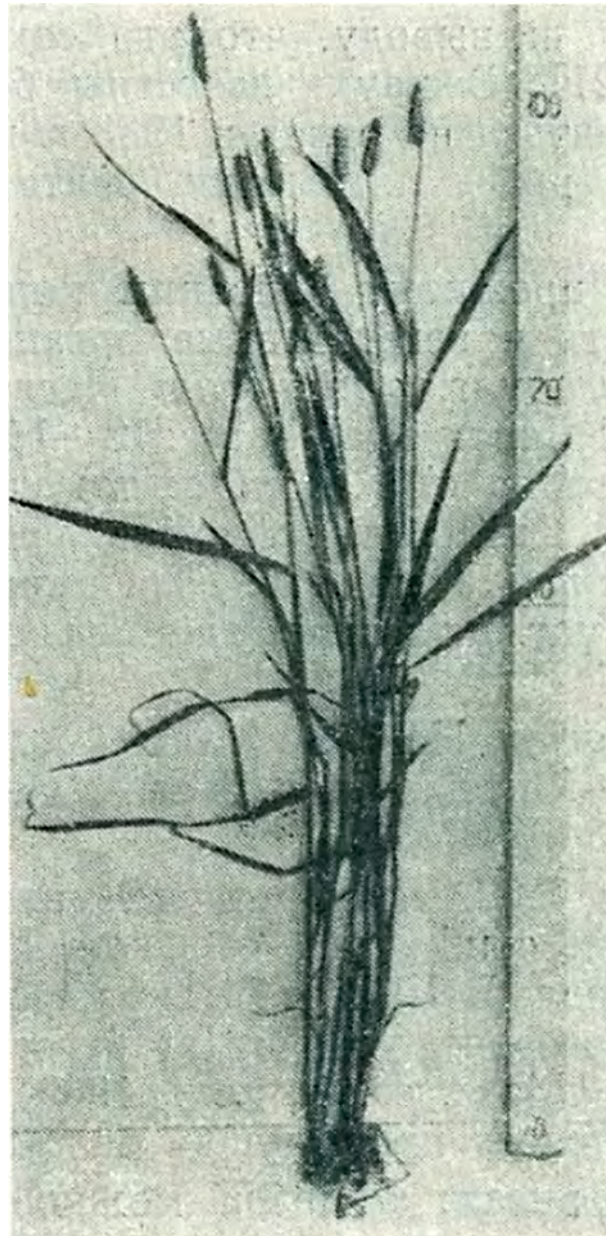


Figure 3. Image of the lost specimen of *Triticum sphaerococcum* subsp. *antiquorum* Udachin ex N.P.Gontsch.; WIR—photography published by Udachin [3] on page 51.

Udachin’s taxonomic action is notable for several reasons. Firstly, he explicitly excludes von Heer’s original material in his designation of a new type, using von Heer’s work merely as a reference. This decision effectively creates a new taxon at the species level,

despite employing the same final epithet “*antiquorum*” as von Heer. While this practice is permissible under taxonomic rules, it introduces a degree of confusion in this particular case. However, it is crucial to note that this newly created name lacks validity in a taxonomic sense. At the time of Udachin’s publication, the International Code of Nomenclature (ICN) required a Latin diagnosis for new taxa (Art. 39.1 of the ICN [40]). The absence of this Latin diagnosis renders Udachin’s new name invalid, despite its otherwise legitimate creation.

However, Udachin’s decision goes further because by choosing a new herborised material from modern living plants as a type, he drew attention to the Asian taxon which was well characterised from the genetic and morphological point of view. If we want to respect Udachin’s original idea, we must separate the two taxa and focus on the status of “*T. antiquorum*” in the sense of the type proposed by Udachin. The most prudent approach is to place the Asian taxon in the most appropriate taxonomic context (*T. sphaerococcum*), which is what we do in the present work. While *T. antiquorum* sensu Udachin and von Heer’s original concept of *T. vulgare* var. *antiquorum* Heer exhibit high morphological similarity, current taxonomic principles and the absence of conclusive evidence necessitate their treatment as distinct entities at present. This situation underscores the complexities of botanical nomenclature and the importance of adhering to the formal requirements for establishing new taxa. It also highlights how historical taxonomic actions can have lasting implications for plant classification and nomenclature.

The specimen preserved at the WIR could have been a good holotype for the name *T. sphaerococcum* subsp. *antiquorum*. This specimen, consisted in several complete and well-developed plants, with leaves and inflorescences (Figure 3, see also Udachin [3] page 51), clearly represents the current use and application of *T. antiquorum* [1,3]. In assessing the congruence between the material which could be selected as the type for the new subspecies and the traditional concept of *T. vulgare* var. *antiquorum* [2,5,34], it is important to recognise the significant differences between a compactum-like primitive wheat and the *Triticum sphaerococcum* Percival group.

The specimen (voucher code K-56398) is missing from the WIR herbarium according to its curators. With Professor Udachin’s passing, further search for this specimen is not possible. N. Goncharov planted seeds from K-56398, the original accession of *T. antiquorum*, at the Institute of Cytology and Genetics greenhouse (Siberian branch, Russian Academy of Sciences, Novosibirsk). After 1.5–2 months of growth, new material was prepared as herbarium sheets.

The holotype of *T. sphaerococcum* subsp. *antiquorum*, “*T. antiquorum* Heer ex Udacz. var. *antiquorum*”, is designated as material raised from seeds collected in 1965 in Pamir (Tajikistan), cultivated at the aforementioned greenhouse, collected and prepared by Nikolay Goncharov and deposited in the I.M. Krasnoborov Herbarium of Central Siberian Botanical Garden SB RAS (herbarium code NS) (Figure 4). This specimen (voucher code K-56398 B), with available cytogenetic data, belongs to the same accession used and cited by Russian authors [1,3,12,13,43].

Finally, according to the current systematic of the genus [44–46] and the cytogenetic data on the type [12,13], the taxon validated as *T. sphaerococcum* subsp. *antiquorum* is proposed.

***Triticum sphaerococcum* subsp. *antiquorum* N.P.Gonch., subsp. nov.**

– ‘*Triticum antiquorum* Heer ex Udacz.’

The holotype, designated here, is from TAJIKISTAN. The specimen, with awnless ears, was raised at the Institute of Cytology and Genetics, Siberian branch of the Russian Academy of Sciences, Novosibirsk, Russia, and collected on 25 March 2021 by N.P. Goncharov, from seeds collected in Barushan village, Rushan district, Gorno-Badakhshan Autonomous Region, Tajikistan, at 2020 m. a. s. l. on 11 August 1965 by R. Udachin 56398, at the WIR [K-56398 B] (NS barcode NS0000483). For an image of the holotype, see Figure 4 in this manuscript and a high-resolution image in Figure S1. The holotype [labelled Epitypus] was deposited at the I.M. Krasnoborov Herbarium of Central Siberian Botanical Garden SB RAS, Novosibirsk (with NS as the herbarium code). An isotype [labelled Isoepitypus]

was deposited at the herbarium of the N.I. Vavilov All-Russian Institute of Plant Genetic Resources, Saint Petersburg (WIR), as WIR-69644.



Figure 4. Image of the holotype of *Triticum sphaerococcum* subsp. *antiquorum* N.P.Gonch.; NS0000483 (photography by N. P. Goncharov; image courtesy of the herbarium NS, reproduced with permission). Note that although the specimen is labelled “Epitypus”, it is the specimen designated as the holotype.

3.2.2. Diagnosis

Two basic traits—spherical grains and a compact spike—make this wheat distinct from all other ones. It is characterised by a small (less than 5 mm long), almost spherical grain.

The vegetative organs of the plants of this subspecies are those typical for *T. sphaerococcum*, as is the appearance of the ear, whose spikelet scales are rounded with signs of flattening.

This diagnosis validates the creation of the new subspecies—see Art. 39.2 of the ICN [40].

A critical reassessment of Udachin's labelling system for the accession and associated herbarium material is warranted. Udachin's 1991 paper consistently references K-56398, linking it to the WIR. However, this designation actually pertains to the VIR seed bank. Concurrently, a herbarium specimen image in the same publication bears an identical code, presumably deposited at the WIR. Thus, K-56398 primarily denotes a VIR seed voucher.

In an earlier publication in 1969, Udachin employed the taxonomic combination "*T. compactum* Host ssp. *armeno-turkestanicum* Vav. Prol *pamiro-badakschanicum* Vav. var. *vavilovianum* Udacz. var. nov", associated with № 052189k [47]. While the significance of № 052189k remains unclear, it likely represents an earlier VIR seed voucher corresponding to K-56398.

K-56398 serves a dual purpose: it designates both the accession in the VIR seed bank and a herbarium specimen, the latter being illustrated in the 1991 publication and cultivated by Udachin from a K-56398 subsample. Notably, Udachin utilised the VIR seed voucher code K-56398 for this illustration. It is important to note that 'K' denotes 'catalogue', as in VIR catalogue number 56398. The alternative notation VIR-56398 is also acceptable.

K-56398B represents a subsample from the original accession, provided to N. Goncharov by Professor Udachin as an authentic specimen of "*T. antiquorum*". The absence of a herbarium sheet at VIR may be attributed to Udachin's potential lack of interest in the original specimen beyond its seeds.

Lastly, WIR 69644 designates the specimen submitted by N. Goncharov to the WIR, derived from new material cultivated from K-56398B seeds.

This revised labelling system elucidates the complex relationships between seed bank accessions, herbarium specimens and their respective identifiers, facilitating more precise reference and study of these materials in future research.

3.2.3. Implications of the Typification of the Archaeobotanical Taxon and the Description of the New Taxon

Flaksberger [5], on page 72, reclassified European *Triticum vulgare* var. *antiquorum* under *T. compactum* (as *T. compactum* var. *antiquorum* (Heer) Flaksb.), and not *T. sphaerococcum*, due to the belief that *T. sphaerococcum* was an Indian endemic species with a limited distribution. Indeed, current research and the proposed typification indicate that *Triticum sphaerococcum* subsp. *antiquorum*, from Central Asia, is genetically closer to *T. sphaerococcum* than to *T. compactum* [12,46,48,49], sharing the same species-forming genes with *T. sphaerococcum*.

While we cannot entirely dismiss the possibility that the same genetic and morphological characteristics apply to the taxon from Swiss archaeological sites, specifically *T. aestivum* var. *antiquorum*, there is currently insufficient evidence to confirm this. Notably, wheat traces from Neolithic Swiss lake sites, such as the Early Cortaillod culture level (3906 BC) at Lake Zurich, include both tetraploid and hexaploid species. These findings are supported by both morphological assessments and molecular markers [49].

If *T. sphaerococcum* subsp. *antiquorum* was present among these Neolithic wheats of Central Europe, it would suggest a wider geographical distribution of the *T. sphaerococcum* group during this period, which later became extinct in the western part. This hypothesis necessitates further archaeobotanical research in this area, the application of advanced molecular techniques for ancient DNA analysis and detailed morphometric analyses to provide clearer insights.

4. Conclusions

This study addresses a fundamental challenge in plant taxonomy and phylogeny: elucidating the relationships between archaeological materials and potentially analogous

living populations. The complexity of this issue is particularly evident when dealing with taxa initially described from archaeological specimens, followed by the subsequent discovery of extant materials that may belong to the same taxa. We emphasise that archaeobotanical materials, while ancient, should not be classified as fossil taxa, necessitating a nuanced approach to their taxonomic treatment. Archaeobotanical remains represent a distinct category of biological evidence, differentiated from fossils by their nature as preserved organic materials rather than mineralised remnants. These botanical artefacts persist through time due to specific environmental conditions that inhibit decomposition processes. The preservation mechanisms vary widely, encompassing scenarios such as carbonisation, which occurs in oxygen-poor environments often associated with burning; submersion in acidic aquatic ecosystems, where low pH levels retard microbial activity; and exposure to extremely arid climates, where desiccation precludes biological breakdown.

In the specific case of Oswald von Heer's pioneering work, the archaeobotanical specimens under examination were retrieved from lacustrine sediments in Central Europe. These lake environments provided ideal conditions for the long-term preservation of plant remains, likely due to a combination of factors including low oxygen levels, stable temperatures and protection from physical disturbances. Von Heer's studies of these well-preserved organic materials laid the groundwork for paleoethnobotany and significantly advanced our understanding of prehistoric flora and human–plant interactions in the region.

Given the current limitations in unequivocally establishing the identity between archaeological and contemporary materials, we propose an intermediary solution. This approach validates the taxonomic status of both archaeological and living materials, treating them as distinct taxa while maintaining the possibility of future identification convergence. This framework not only advances our understanding but also ensures the effective utilisation of both historical and current botanical data in taxonomic and phylogenetic research.

Specifically, we have typified *Triticum vulgare* var. *antiquorum* Heer within the context of *Triticum aestivum* subsp. *compactum* var. *antiquorum* (Heer) H. Messik. and described *Triticum sphaerococcum* subsp. *antiquorum* Udachin ex N.P. Gonch. These taxonomic revisions not only resolve long-standing nomenclatural issues but also establish a methodological framework for future research in this field.

The clarification of these taxa and the establishment of a new subspecies provide a robust foundation for future investigations into wheat evolution and diversity. This work bridges the gap between archaeological findings and contemporary plant genetics, offering valuable insights into the historical development and current state of wheat varieties. By reconciling archaeological and contemporary wheat diversity, this study contributes significantly to our understanding of wheat evolution and agricultural history, paving the way for more comprehensive and integrated approaches in plant taxonomy and phylogenetic research.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/taxonomy4040042/s1>, Figure S1: High-resolution image of the holotype of *Triticum sphaerococcum* subsp. *antiquorum*.

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Appendix A. List of Original Material

Translated from the original in German language (von Heer, 1865: 51).

14–18. *Small pile-dwelling wheat* (*Triticum vulgare antiquorum* m.). Fig. 14. Ear fragment from Robenhausen; Fig. 15. shows a second piece from the inside, which shows the thick position of the ears. Fig. 16. A single ear with four grains. Fig. 16. b. Husks considerably enlarged. Fig. 17. Ear completed. Fig. 18. Individual grains; a. b. c. e. f. G. von Robenhausen, a. a. of Moosseedorf, h. from Montelier, b. from Olomouc.

Appendix B. Protologue of *Triticum vulgare* var. *antiquorum*

Translated from the original in German language (von Heer, 1865: 13–14) [2].

“It has a short, densely packed, small but many-grained, awnless ear with sharply keeled husks and deviates just as far from ordinary wheat as the “miracle” and hard wheat, therefore represents a very excellent and, as it seems, perished form of wheat.

It differs from ordinary wheat not only in the small size of the grains, but also in the sharply protruding back keel of the husks and the fact that 3 to 4 grains are formed in each ear, whereas in ordinary wheat only 2 to 3.

In the formation of the husks, it comes closer to that of hard wheat, from which it clearly differs in the much smaller, namely shorter grains and the lack of awns.

The whole ear was probably about 44 millimeters in length, with a thickness of 10 millimeters but the individual ears are 6 to 7 millimeters high and 9 to 10 millimeters broad, see Fig. 16) but the outer glume is 5 millimeters long. It has a very sharp dorsal keel extending from the base and a short, somewhat inwardly curved, sharp point (Fig. 16. b enlarged); next to the keel there is a more or less distinct longitudinal stripe on each side. The outer lemma protrudes considerably beyond the glume and also ends in a short, curved tip, therefore has no awn. The grain is on average 5 millimeters, but sometimes only 4 millimeters long and 3 1/2 millimeters thick. It is bluntly rounded, curled deeply, and strongly arched on the back side. The three- to four-seeded ears (Fig. 16) stand together very closely (Fig. 15) and completely cover the spindle.

Due to the short, densely packed, awnless ear, it stands closest to the spelt wheat in the appearance.

This is probably the oldest type of wheat, which forms the predominant grain in all the older pile dwellings but was also still cultivated in the Helvetian-Roman times, as the healthy grains in Buchs show”.

Appendix C. Description of the Finding of *Triticum antiquorum* in Tajikistan

Supposedly related with *T. vulgare* var. *antiquorum* (Udachin, 1982: 72–73) [1] [in Russian followed by an English translation].

О ВОЗМОЖНОМ СУЩЕСТВОВАНИИ *TRITICUM ANTIQUORUM* HEER В НАШИ ДНИ

В 1865 г. при археологических раскопках свайных поселений в Швейцарии были найдены колосья и фрагменты их, свидетельствовавшие о возделывании в эпоху неолита пшеницы с легким обмолом. Эта пшеница имела небольшой плотный колос с округлыми колосковыми чешуями (*Triticum inflatum*) и мелкими округлыми зерновками, почти сферическими по форме. Она получила наименование *Triticum antiquorum* Heer. Автор этого вида О. Heer считал его сходным с *T. compactum* Host, т. е. он предполагал его гексаплоидную природу.

Общепринято считать, что *T. antiquorum* исчез из культуры еще в первом тысячелетии нашей эры. Однако во время обследования пшениц Горно-Бадахшанской автономной области (Таджикская ССР) в посевах мягкой пшеницы в кишлаке Барушан Рушанского района на высоте 2020 м над ур. м. нами были найдены

растения, определенные нами прежде как *T. compactum* var. *vavilovianum* и var. *griseovavilovianum*, но характеризующиеся мелким (длина менее 5 мм), почти сферическим зерном. Вегетативные органы растений этих разновидностей типичны для *T. compactum*, как и внешний вид колоса, колосовые чешуи которого округлые, с признаками инфлятности.

Нахождение пшеницы, сходной с ископаемым видом *T. antiquorum*, может быть связано с сохранением его в живом виде в отдаленном горном районе или же со вторичным появлением, согласно закону гомологических рядов в наследственной изменчивости, открытому Н. И. Вавиловым.

THE POSSIBLE EXISTENCE OF *TRITICUM ANTIQUORUM* HEER TODAY

In 1865, archaeological excavations of pile dwellings in Switzerland uncovered ears and fragments indicating the cultivation of light-threshing wheat during the Neolithic period. This wheat had small, dense ears with rounded spikelet scales (*Triticum inflatum*) and small, almost spherical grains. It was named *Triticum antiquorum* Heer. The author of this species, O. Heer, believed it to be like *T. compactum* Host, suggesting its hexaploid nature.

It is accepted that *T. antiquorum* disappeared from cultivation as early as the first millennium AD. However, during our survey of the Gorno-Badakhshan Autonomous Region (Tajik SSR), we found plants previously identified as *T. compactum* var. *vavilovianum* and var. *griseovavilovianum* in common wheat crops in the village of Barushan in the Rushan district, at an altitude of 2020 m above sea level. These plants were characterized by small (less than 5 mm long), almost spherical grains. The vegetative organs of these plants are typical of *T. compactum*, as is the appearance of the ear, with rounded spikelet scales showing signs of inflation.

The discovery of wheat like the fossil species *T. antiquorum* may be related to its preservation in a living form in a remote mountainous region or to its secondary occurrence, according to the law of homologous series in hereditary variability discovered by N. I. Vavilov.

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