



Dasypyrum villosum (mosquito grass) in archaeobotanical assemblages from the Balkans and east-central Europe reveals aspects of human plant- and land use

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Abstract

Archaeobotanists working in the Balkans and the Carpathian Basin in the 1980s documented remains resembling wild rye caryopses in the deposits from the Bronze and Iron ages, and named them “weedy rye” or “small *Secale*”. It took years and more finds, including those of chaff, to identify these remains more precisely—as *Dasypyrum villosum* (mosquito grass). The first systematic overview of archaeobotanical records of this species in the Balkans and east-central Europe provided detailed description of the finds, emphasising the difficulty in distinguishing the grain and chaff of *D. villosum* from those of wheat (principally *Triticum monococcum*, einkorn) and *Secale*. Since this work, further finds of *D. villosum* have been discovered in this part of Europe, dating from prehistory but also later periods. The current paper combines the previous and new knowledge and examines the wider temporal, geographical, archaeobotanical and bioecological context of *D. villosum*. Our study confirms the earliest appearance of *D. villosum* from the Bronze Age and shows its continued presence through the late antique and medieval periods, mainly in the deposits containing large amounts of einkorn. We consider early finds of *D. villosum* as indicators of the changes in land use noted for the Bronze and Early Iron ages in our study region. These changes pertained to the advance of specialised, more extensive crop and animal husbandry, intensified metallurgy and growing urbanism, leading to modification of the environment and facilitating the expansion of *D. villosum* and other species associated with open, dry, disturbed habitats.

Keywords Archaeobotany · Charred/carbonised remains · SE Europe · Wild grasses · Land use · Disturbed habitats

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Introduction

Archaeobotanical research of the 1980s that flourished at the universities of Kiel, Germany, and Groningen, the Netherlands, pioneered respectively by Helmut Kroll and Willem van Zeist, was instrumental for early archaeobotanical programmes in different parts of Eurasia, including south-eastern Europe, where the interests of these two colossally erudite scholars converged, in the northern Serbian province of Vojvodina. Here, at the Bronze and Iron Age site of Feudvar (Fig. 1), Kroll recovered several thousand of small grass (Poaceae) grains, and a small amount of corresponding chaff elements, that he preliminary identified as rye (*Secale*). These “vorläufig genannt Roggen” (Kroll 1998, p 315) grains resembled those he had previously encountered at the Bronze and Iron age sites of Kastanas and Olynthos (Agios Mamas) in northern Greece, where he had considered them to be of ‘small rye’ or ‘weedy rye’ (Kroll



Fig. 1 Location of the sites with records of *Dasypyrum villosum* (mosquito grass) in the Balkans and east-central Europe (for site names see Table 1)

1983, p 93, 2016, p 150–151). While analysing the material from another site in Vojvodina, the Neolithic-through-Roman Gomolava (Fig. 1), van Zeist came across hundreds of “weedy *Secale*” grains in the Iron Age deposits, which he described as morphologically similar to the grains from Kastanas (Van Zeist 2001/2002, p 104–105).

It was only in 2012 that Kroll ascertained that the ‘weedy rye’ remains do not belong to a *Secale* species but to another annual wild member of Poaceae—*Dasypyrum villosum* (Kroll 2016, p 49). Soon after determination of the finds in Greece and Serbia, the discovery of a couple of grains and a spikelet fork of *D. villosum* at the Early Iron Age site of Győr-Ménfőcsanak in western Hungary was reported (Kenéz et al. 2014), and a register of archaeological finds of this species compiled, raising the possibility that more sites hold such evidence, including the already analysed assemblages. Indeed, re-evaluation of some of the collections confirmed the presence of *D. villosum* at other Iron Age or later sites in Vojvodina (e.g. Medović 2016). Since the first systematic overview, which also offered a detailed consideration of the distribution and ecology of *D. villosum* in Europe and southwest Asia (Kenéz et al. 2014), the species has been attested at a number of recently analysed sites in Bulgaria, Serbia and Hungary.

Here, we provide an updated overview of the archaeological finds of *D. villosum* in southeast and east-central Europe in order to increase the awareness of its potential presence in archaeobotanical assemblages from these regions from at least the Bronze Age onwards, and to encourage revisions of previously analysed collections. Additionally, we (a) refine the morphological criteria useful for determination of grains of mosquito grass and provide linear measurements of a subset of charred archaeological grains; (b) explore and discuss the composition of deposits containing *D. villosum* and its co-occurrence with some crop and wild taxa; and (c) consider the ecology of *D. villosum* in relation to the changes in land use and crop production in the Bronze and Early Iron ages in our study regions (e.g. Marinova et al. 2012; Gumnior et al. 2020; Bartosiewicz 2022; Filipović et al. 2022).

Materials and methods

Published and unpublished information on the archaeological occurrence of *D. villosum* in the study regions were collated in a spreadsheet, including: summary data on the location, site and archaeological deposit, as well as the deposit’s age, archaeological interpretation and broad archaeobotanical composition, the amount and type of *D. villosum* remains, and the source of information (Table 1; SI 1 Table S1). The assemblages containing remains of mosquito grass come from sites where archaeobotanical sampling was employed and the samples were processed by flotation (machine- or manually operated) or wet-sieving, with plant remains captured in 0.3–0.5 mm mesh, which enabled the recovery of smaller parts of *D. villosum*, namely spikelet forks and fragments of grains, alongside whole specimens. All of the remains encountered so far were charred in the past.

In their publications, Kroll and van Zeist reported a selection of measurements taken on the grains of *D. villosum* (length, breadth and height/thickness, and their ratios; Kroll 1983, 2016; Van Zeist 2001/2002). We compiled their data and added measurements on the grains from several of the sites we analysed, and use these to perform simple numerical comparisons within and between the sites, in order to propose the value ranges that can be expected in our study regions and that can potentially aid in identification. Building upon the previously presented identification criteria by Kroll, van Zeist and Kenéz and colleagues, we add more detail and highlight the most indicative morphological features.

Where available, fully quantitative data for the deposits containing 30 or more remains of *D. villosum* (grains and chaff) were considered and compared with the proportion of other taxa (cultivated and wild) also represented by at

Table 1 List of sites and summary records of *D. villosum* in east-central Europe and the Balkans; * for comments on identification issues (and summary of the archaeological context and archaeobotanical content of *D. villosum*-containing assemblages) see SI 1 Table S1; Gr: grain, Sf: spikelet fork, BA: Bronze Age, IA: Iron Age, E: early, M: middle, L: late

ID	Country	Site (some multi-period)	Arch. period/phase	Time span	D. v. (incl. cf.)		Deposits with D. v.	References
					Gr	Sf		
1	Hungary	Nyíregyháza-Oros, Keleti elkerülő	BA	2500/2400–900/800 BCE	1		1	Pető and Kenéz unpubl.
2	Hungary	Százhalombatta-Földvár	MBA	2500/2400–900/800 BCE	*37	*(11)	*2	Pető and Kenéz unpubl.
3	Hungary	Marcali-Halastói-dűlő	EBA	2300/2200–1700/1600 BCE	*156	*	1	Pető and Baktay unpubl.
4	Serbia	Feudvar	MBA–EIA	1700–500 BCE	4,898	31	*many	Kroll (1983, 2016)
5	Greece	Olynth	LBA–EIA	1500–800 BCE	*	*	*	Becker and Kroll (2008)
6	Greece	Kastanas	LBA–EIA	1500–800 BCE	*	*	*	Kroll (1983)
7	Hungary	Csanádpalota-Földvár	LBA	1300–1100 BCE	23		1	Szeverényi et al. (2015)
8	Serbia	Gomolava	LBA, IA (Hallstatt, La Tène), Roman	1300–1 BCE, 1st–2nd c.	*864	*several	*19	Van Zeist 2001/2002; Medović (2016)
9	Serbia	Hisar	LBA	1300–1000 BCE	33	*	2	Medović (2012)
10	Bulgaria	Vaskovo	EIA (Hallstatt)	1100/900–700 BCE	7		3	Hristova and Marinova unpubl.
11	Bulgaria	Tash Bair	EIA (Hallstatt), Roman Imperial (site 2), Early Medieval	1000–500 BCE; 2nd–3rd c. CE; 9th–10th c. CE	*61	*2	*5	Dankov et al. unpubl.; Marinova and Fischer unpubl.
12	Hungary	Győr-Ménfőcsanak	EIA (Hallstatt)	900–450 BCE	2	1	1	Kenéz et al. (2014)
13	Serbia	Gradina-on-Bosut	EIA (Hallstatt)	900–500 BCE	40	*	1	Medović (2011)
14	Hungary	Gyomaendrőd-Pavlik tanya	EIA (Scythian)	800/750–400/350 BCE	1		1	Pető and Gyulai unpubl.
15	Serbia	Čarnok	LIA (La Tène)	500–1 BCE	1	*	1	Medović (2006, 2016)
16	Bulgaria	Dana Bunar	LIA (La Tène)	6th–4th c. BCE	1		1	Hristova et al. (2017)
17	Bulgaria	Krepost	Early Hellenistic	4th–3rd c. BCE	1		1	Hristova (2012)
18	Hungary	Tiszagyenda-Lakhatom	Hunnic	4th–5th c. CE	1	1	1	Pető and Kenéz unpubl.
19	Serbia	Gornji Breg-Senta	Late Antiquity	4th–6th c. CE	14		2	Filipović et al. unpubl.
20	Serbia	Sterijino-Ada	Sarmatian	4th–6th ct. CE	5		2	Filipović et al. unpubl.
21	Hungary	Rákóczipfalva-Bagi-földek	Sarmatian	4th–6th c. CE	354	86	8	Pető et al. (2024)

least 30 remains in the same deposits. We use the results to infer association of *D. villosum* with other taxa and the ways in which it entered the archaeobotanical record. Botanical information on the ecology and geographical distribution of *D. villosum* is used to suggest the habitats the species occupied in the past and what they indicate in terms of the composition of the landscape and the methods of land use.

Results and discussion

Occurrences of *D. villosum* in the study regions

To the best of our knowledge, the data summarised in Table 1 and SI 1 Table S1 reflect the current state of archaeological records of *D. villosum* and its spatiotemporal distribution in the parts of Europe we studied (Fig. 1). On this evidence, the earliest archaeological presence of *D. villosum* in the Balkans and east-central Europe may be in the Early Bronze

Age, i.e. the last centuries of the 3rd millennium BCE, and the most recent is in the early medieval period, ca. 9–10 century CE. No absolute dating of mosquito grass remains has been performed and so the chronological attribution follows archaeological assignment of the deposits to cultural periods and their timespans. It is important to clarify here that, the three *D. villosum* grains van Zeist retrieved from the samples attributed to the Late Neolithic Vinča culture deposits at the site of Gomolava, Serbia, are almost certainly intrusions from the Early Iron Age (Hallstatt) pits that extended into the respective underlying Neolithic layers and that contained significant quantities of *D. villosum* grains (e.g. 1/4 of sample H2 yielded 590 grains) (Van Zeist 2001/2002, Tables 1, 2 and 4).

Table 2 Identification criteria for archaeological finds of *D. villosum*

Grain	
Shape	Short and slender; widest just below the apex, narrowing gradually towards the middle and tapering sharply at the embryo end (Fig. 2: a, b)
Apical end	Appears truncated unless well preserved, in which case the cone-shaped projection, clearly visible in modern specimens, can be observed (Fig. 2: b, c2, f1)
Embryo end	Scutellum is very narrow and short (Fig. 2: b, c2)
Ventral view	Flat and narrow, laterally compressed (Fig. 2: a, b, d)
Dorsal view	Narrow, straight or slightly curved, sometimes with discernible lengthwise 'ridge' (Fig. 2: c2, e)
Surface	Fragments of lemma sometimes preserved on the surface; furrow-like impressions of tough glumes sometimes visible on the lower part of the grain (Fig. 2: a)
Spikelet fork (Fig. 2: c1)	
Shape	Glumes thick, robust, forming 'U' or flared (Fig. 2: 3a); angles of glume insertion often unequal (Kenéz et al. 2014 Fig. 4a–c, e); glumes difficult to identify if broken-off
Disarticulation scar	Large, horizontal-oval, located at the level of glume insertion (Kenéz et al. 2014 Fig. 4)

Taxonomic determination of archaeological finds of *D. villosum*

The identification of *D. villosum* grains and chaff is

complicated by their morphological similarity to wild (and domesticated) rye and wheat (Kroll 1983, p 93; Nesbitt 2002, p 116; Van Zeist 2001/2002, pp 104–105), but clear differences exist and were defined by Kenéz and colleagues (Kenéz et al. 2014). Here, we expand on the published observations. Many more grains than chaff remains have been encountered in archaeological deposits (Table 1; SI Table S1), and so the descriptive criteria relate primarily to the grains (Table 2; Fig. 2). Finds of spikelet forks were reported and described (Kenéz et al. 2014), but individual glumes or rachis segments are generally too difficult to distinguish from those of other grasses.

The size and overall shape of the grains are the first to attract attention, e.g. during sample sorting, and to alert to a possible presence of *D. villosum* in the assemblage. The size of *D. villosum* is similar to that of unripe grains of cultivated rye or grains of wild rye (Kroll 2016) and, alone, not suitable for species determination. An additional complication is that *D. villosum* is characterised by grain dimorphism, where a single spikelet can develop grains of somewhat different sizes (and quite different colour) (De Pace et al. 2011). The size of larger grains can overlap with the size of *Secale cereale* grains. Therefore, it is essential to analyse the grains with respect to the other morphological features described (Table 2) before assigning them a taxonomic category.

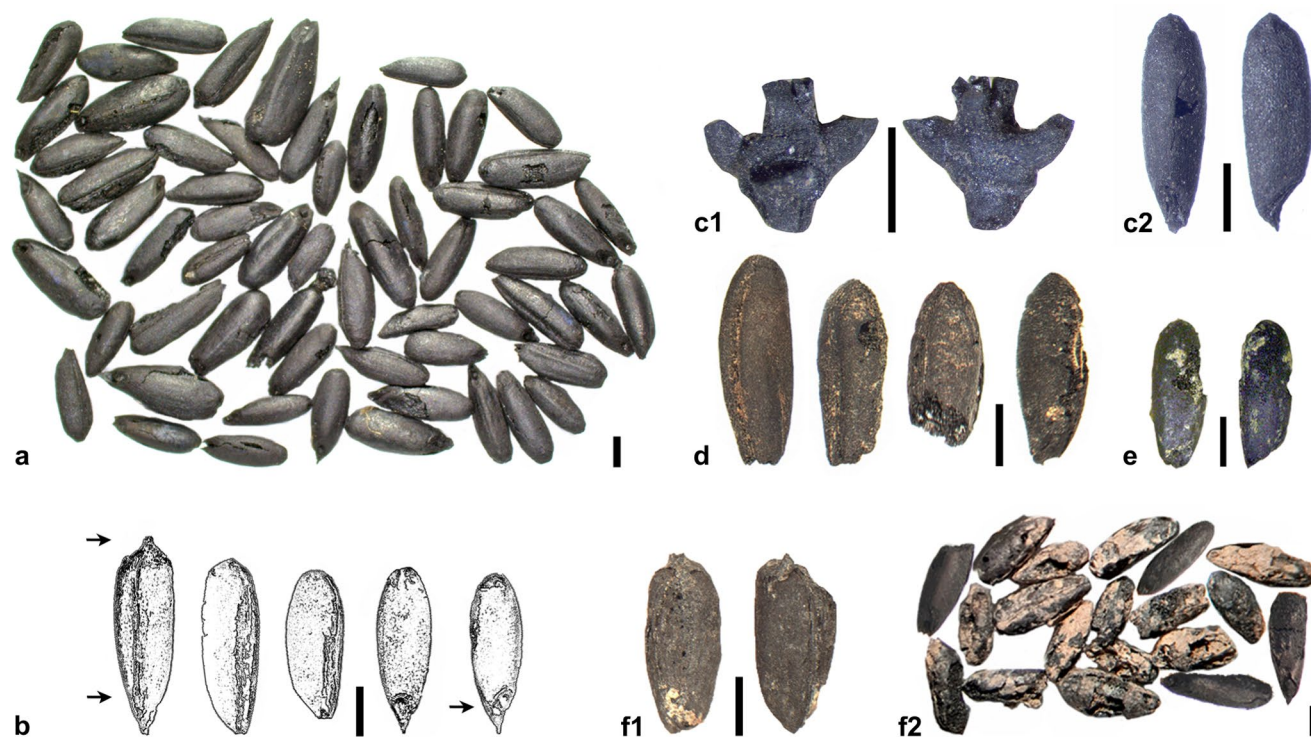


Fig. 2 Images and illustrations of some of the finds of *D. villosum* grain and chaff: **a–b** Feudvar (AI-created drawings, see SI 2 Appendix); **c1–2** Tash Bair site 2 (spikelet fork and grain); **d** Gornji Breg-

Senta; **e** Krepost; **f1–2** Gomolava (scale bars=1 mm, arrows indicate the cone-shaped apical end preserved in some specimens, and the tapered embryo end)

The natural variation in size among *D. villosum* grains would perhaps be possible to discern in archaeobotanical collections if large sets of measurements became available and if the modifications due to charring were explored. For now, we assembled a small set of values and compared them within and between the sites (SI 1 Table S2; Fig. 3). The minimum and maximum values for the grain length, as published for Kastanas (Kroll 1983), can diverge by as little as 0.7 mm and as much as 2.2 mm. Besides factors such as the position of grain in the spikelet, its degree of ripeness, and the plant growing environment, charring also affects the size and morphology and must be considered. A further taphonomic filter is crop processing, which separates both crops and weedy inclusions based on their size, weight and morphology (Jones 1984). In threshing, *D. villosum* shatters spikelets and behaves like a glume/hulled cereal through the subsequent stages in the crop processing sequence. Clean (i.e. dehusked) grains are generally smaller

than the grains of cultivated cereals (except millets), but their breadth is sometimes similar to or approaching that of cereals, and so larger specimens can be retained in the fine sieve used to eliminate glume bases and small weed seeds after dehusking. Smaller grains, especially narrower specimens, can pass vertically through the openings of such a sieve (Jones 1996, p 177). With this in mind, and accounting for the yet-to-be-explored charring effect on the grain, the size of archaeological *D. villosum* grains could be indicative of their position in the spikelet, and perhaps also of the crop processing stage they originate from.

D. villosum, crops and other wild/weed taxa in archaeological deposits

Among the sites with evidence of *D. villosum*, some had hundreds (Gomolava and Rákóczi-falva-Bagi-földek) or thousands (Feudvar) of the remains, others dozens or as few as one. For the sites that yielded ≥ 50 remains (grain and chaff) of *D. villosum*, we focus on the deposits with ≥ 30 remains (grain and chaff) of *D. villosum* and analyse their archaeobotanical composition by looking at *D. villosum* and all other taxa represented by at least 30 remains in the same deposits (SI 1 Table S3). *D. villosum* seems to have been a prominent inclusion in a wide range of crops. For instance, the Rákóczi-falva-Bagi-földek deposit (sample 1035) with 400 *D. villosum* grains and glume bases also contains large amount of *Linum* (flax) seeds (Fig. 4a), suggesting that *D. villosum* could have grown together with flax, perhaps as its weedy companion. At Gomolava, the analysed quarter of a single deposit (sample H2) contained nearly 600 *D. villosum* grains (Van Zeist 2001/2002, Tables 1 and 4) alongside numerous remains of the site's most prominent crops (*T. monococcum*, *Hordeum vulgare* and *Panicum miliaceum*), perhaps due to their association in the arable field (Fig. 4b). At Tash Bair site 2, the deposit with over 30 remains of *D. villosum* (sample TB 5) includes several dozen grains of free-threshing wheat, some *P. miliaceum* and traces of pulses; Fig. 4c); *D. villosum* may have shared the habitat with any or all of them. At Marcali-Halastói-dűlő, *D. villosum* grains occur in an exceptionally rich deposit (sample 705) consisting of 2.6 L of charred material likely representing burnt store of (semi)-cleaned cereals—over 80% of it consists of complete or fragmented cereal grains; chaff makes up 8% and weeds 9% of this assemblage. *Triticum dicoccum* (emmer) dominates among the cereals; besides *D. villosum*, grains of *Bromus* (*secalinus*, *tectorum* and indeterminate) are also present, and both species are understood as associated with emmer in the field (Pető and Baktay unpubl.).

At Feudvar, at least 39 deposits contain *D. villosum* grains and a couple of them also *D. villosum* chaff. Based on

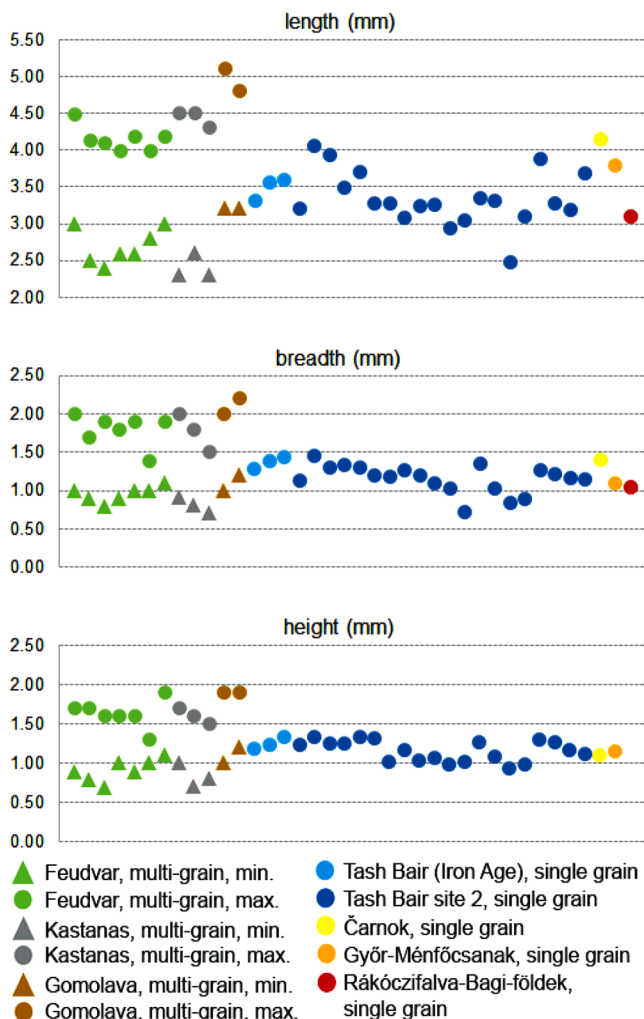


Fig. 3 Linear measurements of a subset of archaeological grains of *D. villosum* illustrating the varied grain size (the values are listed in SI 1 Table S2)

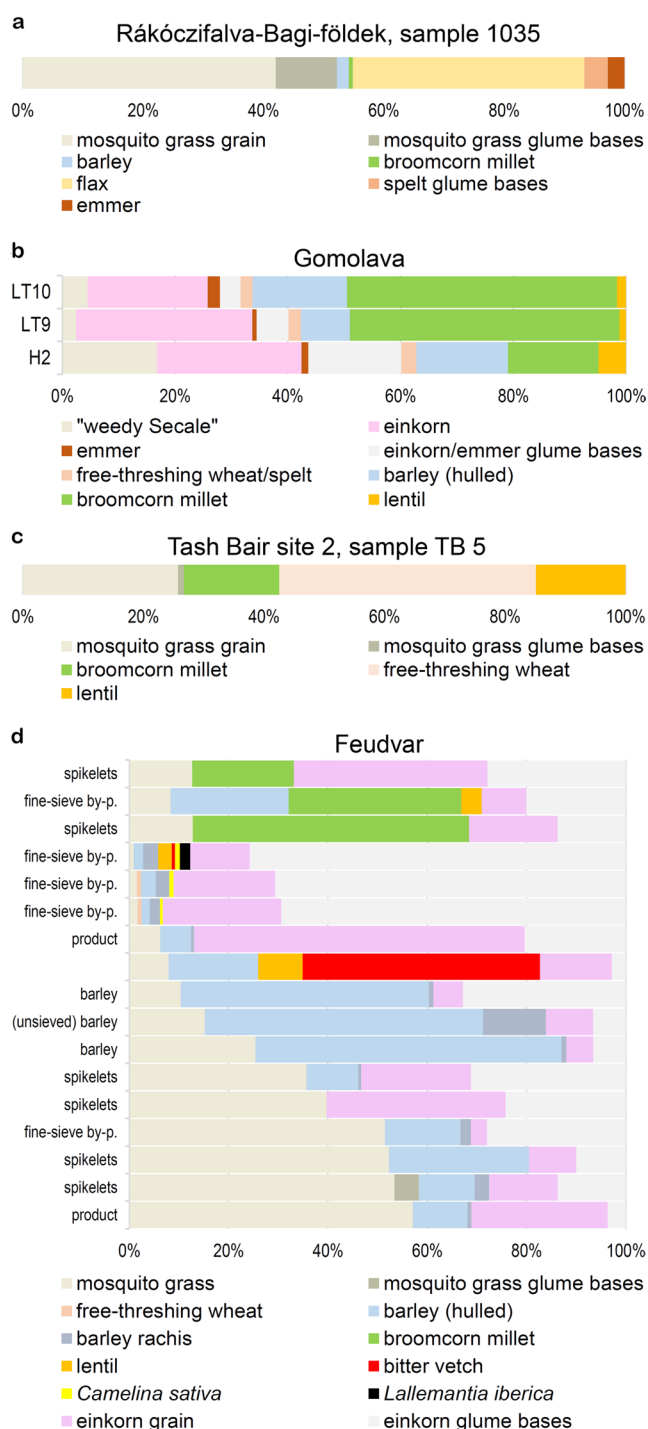


Fig. 4 Relative proportions of the main crops in the samples containing ≥ 30 remains of *D. villosum* at selected sites (for absolute counts see source publications)

its abundance in the einkorn-rich samples, Kroll concluded that *D. villosum* likely accompanied einkorn in the fields (Kroll 2016, p 151). We also observe that, the crop content of most of the samples with ≥ 30 *D. villosum* remains is largely made up of einkorn grains and chaff (Fig. 4d; SI 2).

In several of these, the percentage of einkorn glume bases is significantly higher than that of grain (70% or more), indicating that these deposits are by-products of fine sieving of einkorn (cf. Hillman 1981; Jones 1984; Reed 2013; Table 6.5, 2016). In several other einkorn-dominated samples, the percentage of chaff is similar or slightly lower than that of the grain, pointing to the possibility that these deposits were composed of einkorn spikelets and represent unprocessed (un-dehusked) crop.¹ Another two of the einkorn-dominated samples have a high percentage of grain and only a small proportion of glume bases; in these cases, the einkorn component may have derived from dehusked grain. The percentage of *D. villosum* grains in these samples varies, but is overall much higher in 'spikelets' and 'dehusked grain' than in 'fine-sieve by-products' (Fig. 4d). It seems that fine sieving had not removed *D. villosum* grains, or had removed the smaller ones and retained the larger within the einkorn grain awaiting hand cleaning. The emmer-dominated deposit from Marcali-Halastói-dűlő points to a similar scenario. It is useful to take account of the crop processing stage potentially represented in the sample when evaluating the size of *D. villosum* grains; vice versa—*D. villosum* grain measurements may suggest the cleaning steps the material underwent prior to deposition.

Several samples with ≥ 30 *D. villosum* remains from Feudvar consist mainly of *Hordeum* (barley) grains, with one containing many rachis segments (Fig. 4d; SI 2) and perhaps representing un-sieved barley (Reed 2013; Table 6.5, 2016). Some deposits contain high percentages of *P. miliaceum*; three other yielded appreciable amounts of pulses (*Lens culinaris*, lentil, and *Vicia ervilia*, bitter vetch). In the two deposits from Százhalombatta-Földvár (Pető and Kenéz unpubl.), *D. villosum* occurs in the einkorn chaff-dominated assemblage from a house (ID 5047) and in the pit fill containing mostly einkorn and barley grain (ID 6285). *D. villosum* may have grown among both cereals and pulses, or their differing combinations.

Beside *D. villosum*, both of the features at Százhalombatta-Földvár contain marked quantities of *Chenopodium album*, *Bromus* (*arvensis* and *secalinus*), *Setaria* (*viridis/verticillata*) and *Polygonum aviculare* remains. One of them (ID 6285) also had a high amount of *Glaucium corniculatum*. The Rákóczifalva-Bagi-földek deposit (sample 1035) rich in *D. villosum* and *Linum* contains a wide range of weedy flora, most prominently *Ch. album*, *Ballota nigra* and *Xanthium strumarium* (Fig. 5a). The Gomolava deposit

¹ One- and two-grained einkorn varieties were documented at Feudvar (Kroll and Reed 2016) and so, in a spikelet deposit, the number of glume bases could equate half, or the entire, quantity of the grain (i.e. two glume bases, or one, per grain); however, it is in any case likely to be lower than ideally expected due to a faster degradation of chaff fragments under high temperatures (Boardman and Jones 1990).

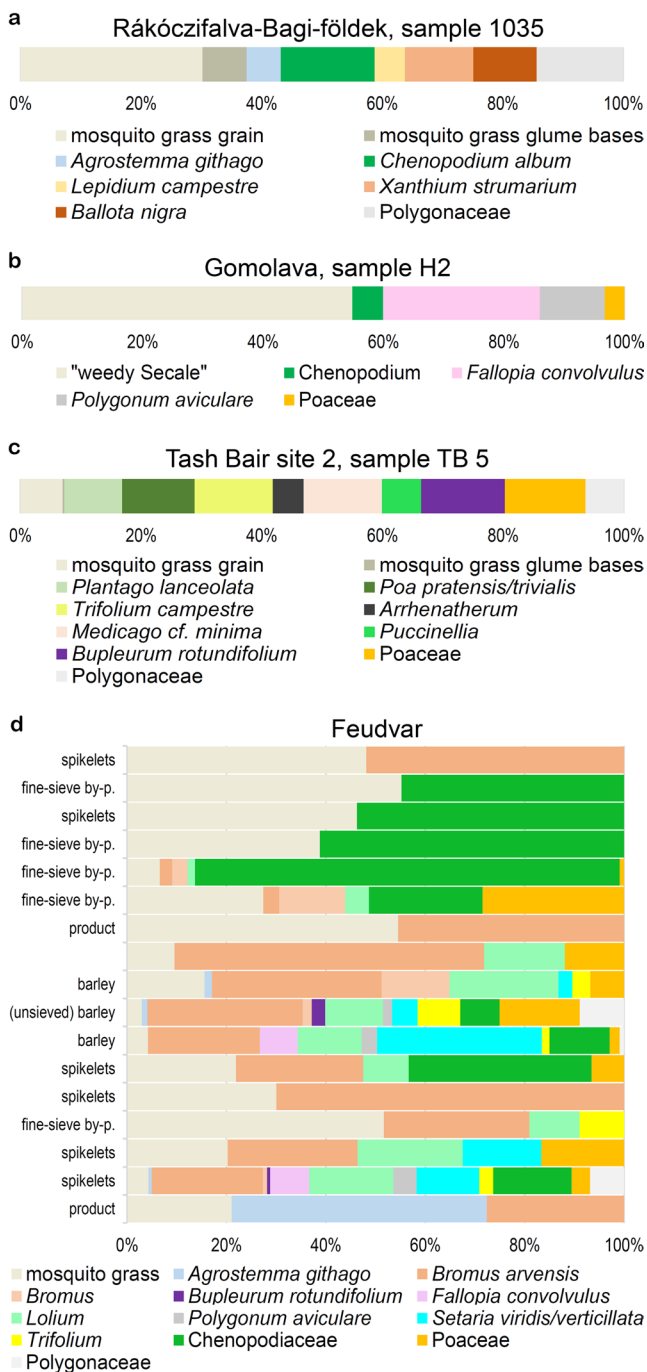


Fig. 5 Relative proportions of a subset of weedy species represented by ≥ 30 remains in the samples containing ≥ 30 remains of *D. villosum* at selected sites (for absolute counts see source publications)

(sample H2) with hundreds of *D. villosum* grains (Van Zeist 2001/2002, Tables 1 and 4) yielded numerous remains of the site's most common weeds: *Chenopodium*, *Fallopia convolvulus* and *P. aviculare* (Fig. 5b). The deposit from Tash Bair site 2 (sample TB 5) is composed of even more diverse wild flora, including arable, ruderal and dry grassland species, among which various small- and large-seeded Poaceae, wild

Fabaceae and *Bupleurum rotundifolium* are most abundant (Dankov et al. unpubl.; Fig. 5c). Each of the selected Feudvar deposits, and especially the 'einkorn fine-sieve by-product' and '(un-sieved) barley' comprise several dozen wild/weed taxa present with at least 30 remains—an exceptional diversity (Fig. 5d). *Bromus* (*arvensis*) and other Poaceae (*Digitaria*, *Lolium*, *Setaria viridis/verticillata*), Chenopodiaceae (mainly *Ch. album* and *Ch. hybridum*) occur in considerable proportions in most of the samples; also striking is the presence of *Agrostemma githago* and Polygonaceae (*F. convolvulus*, *P. aviculare*, *Persicaria maculosa*). While a prominent companion of a wide range of crops, mosquito grass was only one of many arable and ruderal species that flourished on and around cultivated land at these sites. They were perhaps also common elements of fallow ground and former forests, anthropogenically degraded to shrubland, both used for pasture.

Of our closer interest is the association of two large-seeded grasses, *D. villosum* and *Bromus*, visible particularly in the Feudvar deposits (SI 2) and the sample from Marcali-Halastói-dűlő. Like many Poaceae weedy species, *D. villosum* and *Bromus* plants closely mimic cereal plants and are difficult to avoid in harvest. Their grains are morphologically broadly similar, and are also similar to the grains of large-seeded cereals. It is no surprise we find them in archaeological deposits resulting from crop-cleaning. What is peculiar at Feudvar and Marcali-Halastói-dűlő is that, both *D. villosum* and *Bromus* occur in rather high percentages in crop processing products (i.e. dehusked and sieved cereal grain) awaiting subsequent hand cleaning, during which their grains may or may not have been removed, the latter implying their consumption together with cereals. This raises a question as to whether these large-seeded grasses really were unwanted inclusions in the harvest or if they were tolerated. Was there effort to eradicate them from the fields or remove them from harvested crop?

It is possible that these and similar taxa were tolerated or even desired inclusions in the harvest, serving to bulk out the (main) crop (Bogaard et al. 2018). Consumption and targeted collection of wild grasses, including *Bromus*, are known for the past (e.g. Behre 2008; Kroll 2017). An association of einkorn grain or spikelets and *Bromus* was observed at other coeval sites in the Carpathian Basin, such as at Middle Bronze Age Kakucs-Turján-mögött (Filatova 2020) and Early Iron Age Kalakača (Filipović 2015) and may have not been accidental. The 'einkorn spikelets' samples from Feudvar contain high percentage of *D. villosum* and *Bromus*; if these were remnants of seed corn kept as such for next year's sowing, then *D. villosum* and *Bromus* would have been re-sown as well. Alternatively, unsieved/semi-cleaned grain and spikelets may have been used as animal fodder (Reed 2013, 2016, p 236). Noteworthy, some

Fig. 6 Stands and inflorescence of *D. villosum* on the slopes of Osogovo mountain region, north-east North Macedonia (curtesy of Trajche Dimitrovski, © Trajche Dimitrovski)



modern growers of *D. villosum* experiment with the use of the grain for bread-making, alone or in a combination with wheat, and report agreeable taste (<https://www.wildgetreid.com/>).

In several of the Feudvar deposits, *D. villosum* is associated with large proportions of Chenopodiaceae seeds (Fig. 5d; SI 2), most probably coming from the two *Chenopodium* species found in large concentrations at the site—*Ch. polyspermum* and *Ch. album* (Kroll 1990, 1998, 2016). That some *Chenopodium* species were consumed as food or medicine in the past has long been recognised and analytically confirmed (e.g. Helbaek 1959; Kubiak-Martens et al. 2024), and was also proposed for Feudvar (Kroll 1990, 2016). Other sites in our study regions, including those from the same period as Feudvar (Kakucs-Turján-mögött, Vatin and Židovar; Filatova 2020; Filipović et al. unpubl.) yielded high quantities of, primarily, *Ch. album*, sometimes in the form of virtually pure ‘mass finds’ of hundreds of charred nutlets, preserved loose or fused into clumps. At Rákóczi-falva-Bagi-földek (Pető et al. 2024) and Százhalombatta-Földvár (Pető and Kenéz unpubl.), there are deposits rich in the remains of both *D. villosum* and *Ch. album*, suggesting their possible association in arable fields but also, or instead, their (combined) use as foodstuffs.

***D. villosum* and aspects of past agricultural land use**

Flora Europaea (Humphries 1980, p 203) describes *D. villosum* (L.) P. Candargy as an annual of dry grasslands, native to the Mediterranean and southeast Europe. De Pace et al. (2011, pp 185–186) observe its more expansive distribution—to the east, as far as the Caucasus, and to the north, to the Carpathian Basin and the Alpine belt. Modern botanical surveys in southeastern Europe document its presence in different parts of the region, but also reveal its absence in, for instance, much of northern Croatia (Nikolić 2015-onwards) where it has as yet not been reported archaeobotanically (Reed et al. 2022). In Hungary, it is considered introduced but naturalised taxon, and its modern occurrence

is only sporadic (Kenéz et al. 2014, p 848). *Flora of Serbia* lists it under the name *Triticum villosum* (Josifović 1976, p 469); more recent studies refer to the species also under another synonym (*Haynaldia villosa*) and observe its presence in eastern and southern Serbia, including at altitudes of around 1,000 m (Randelović et al. 2005; Holubec et al. 2021). Its distribution at and over such high altitudes is also documented in Albania and Bulgaria (De Pace et al. 2011; Holubec et al. 2021). In North Macedonia, vast stands of it have been observed on the dry, sunny slopes of the Osogovo Mountain and its river gorges (Fig. 6), occupying siliceous soils or rare limestone substrate and forming mountain pastures (T. Dimitrovski pers. commun.; <https://osogovonature.com/2021/10/18/dasypyrum-villosum-l-p-candargy/>). While preferring warm, dry, (sub-)Mediterranean conditions, the species can evidently thrive in (temperate) continental and suboptimal environments, thanks to its tolerance to shade, saline substrate, moisture stress, low-quality soils, high disturbance and resistance to pathogens (De Pace et al. 2011; Holubec et al. 2021). From its natural stands in grassland it colonises abandoned arable land and degraded forests, roadsides, sandy areas and dumps (Josifović 1976, p 469; Holubec et al. 2021). As a therophyte, *D. villosum* takes advantage of the warm season and goes through life-cycle rapidly: it flowers May–June and fruits June–July (Cabi et al. 2009). It may have accompanied crops between late spring and summer harvest and, if not removed from the seed corn, would have been replanted for the following agricultural cycle which, if incorporating winter (i.e. autumn sowing), it would have survived thanks to its long seed dormancy (De Pace et al. 2011).

Archaeological records of *D. villosum* in southeastern Europe are still very few and none have been reported for the periods preceding the Bronze Age. Specifically, its salient presence in Late Bronze–Early Iron Age deposits in our study area coincides with the significant changes in the environment and land use identified in parts of the region by archaeobotanical, anthracological and palynological analyses. A comprehensive study of long-term human impact

on the vegetation and landscape in southwestern Bulgaria clearly points to the second half of the 2nd millennium BCE, the Late Bronze Age, as the time when human activities began to exert visible and significant influence on the environment, and this trend continued through the Early Iron Age (Marinova et al. 2012). The dramatic rise in the number of settlements during these periods was accompanied by forest clearance in both low- and high-altitude zones, aimed at the creation of pastures and expansion of arable land. Similar developments were reconstructed at the northern end of our study area, the Carpathian Basin, where the period from the mid-2nd millennium BCE onwards was marked by growing urbanisation and increasing scale and extent of land use. Large, complex, often fortified settlements were sustained through expansion of the area under arable and pastoral use, and transformation of the landscape by practices such as deforestation, plough-based tillage, exploitation of a wider edaphic range, and establishment of field system and mobility/trade corridors (Magyari et al. 2012; Fischl et al. 2013; Reed 2016; Bartosiewicz 2022; Molloy et al. 2023; Cavazuti et al. 2025).

The disturbed, open environments created through these practices represented favourable ground for the spread of both *D. villosum* and other ruderal species it is commonly associated with, principally annual grasses and legumes (De Pace et al. 2011, pp 187–188, 248)—frequent components of our *D. villosum*-containing deposits (Table 1; SI 1 Table S1, SI 2). Indirectly indicating the low likelihood of *D. villosum* entering pre-Bronze Age archaeobotanical record in our study region is the overall character of land use prior to the Bronze Age, reconstructed as marked by spatially restricted, intensive and relatively permanent crop cultivation and animal husbandry, which exerted minimal impact on the surrounding vegetation (Marinova et al. 2012; Bogaard and Halstead 2015; Reed 2015; Filipović et al. 2020a). The limited extent of cultivated, cleared or otherwise disturbed habitats would have reduced the possibility or success of expansion of therophytes, like *D. villosum*, into anthropogenically altered landscapes. In other words, whether or not present in the natural vegetation in the times more ancient than the 2nd millennium BCE, *D. villosum* would have had little chance to be incorporated in crop harvests. Remarkably, it was again human intervention, principally in the second half of the 2nd millennium BCE, that resulted in such prevalence of *D. villosum* in anthropogenically created habitats to make it prominent in archaeobotanical samples, sometimes as prominent as crops.

Be it via introgression from pre-existing local vegetation or via arrival in the region, *D. villosum* became part of crop harvests at the time when crop diversity grew sharply in the mid-2nd millennium BCE—not just through the introduction of *P. miliaceum* and *Lallemantia* in the study region—but

also through re-introduction or greater reliance on plants already present and perhaps cultivated (locally), including pulses, free-threshing wheat, hulled barley, gold-of-pleasure (*Camelina sativa*), safflower (*Carthamus tinctorius*), chenopods (*Chenopodium* spp.), oak (*Quercus* spp.) and walnut (*Juglans regia*) (Marinova et al. 2012; Kroll 2016; Reed 2017; Filatova et al. 2019; Filipović et al. 2020b, 2022; Reed et al. 2024; Karanikola et al. 2026). The increase in the diversity of crops and respective cultivation systems and areas was mirrored among arable weeds. Together, crops and weeds reflect not just a change in the intensity of cultivation, but also in its ecology and organisation. For example: newly broken arable land may have been located in less fertile edaphic zone which, if not receiving manuring and (thorough) weeding—e.g. due to great distance from the settlement, or large size of the plot—would have offered lower crop yields and less pure harvest, but still useful as animal fodder or for fulfilling tax contributions (Hajnalová and Dreslerová 2010; Diffey et al. 2020). In this context, the archaeobotanical appearance of *D. villosum* can serve as an indicator of broader, fundamental shifts in agricultural management of the time. It is also an indicator of environmental transformation caused by changes in land use in the 2nd and early 1st millennium BCE. But perhaps most saliently, it is a document of plant biological opportunism that secured survival in novel, highly anthropogenic habitats.

D. villosum is nowadays highly valued in cereal improvement and breeding because of its flexibility, resilience and resistance to pathogens. Moreover, its genetic compatibility with wheat facilitates successful transfer of genes to wheat for production of improved varieties; there are a number of wheat cultivars created with *D. villosum* in their genetic matrix (De Pace et al. 2011). This has further contributed to the spread of the species beyond the area of its estimated natural, and archaeological, distribution.

Conclusions

Building upon the previously presented morphological criteria for determination of the remains of *D. villosum*, we refine them and add more detail, including a collection of linear measurements of archaeological grains, in order to facilitate future identifications. Although challenging and time-consuming, re-visiting old, and closely inspecting upcoming archaeobotanical collections for the presence of *D. villosum* is worthwhile and recommended for our study regions. One key reason to invest in this effort, as this paper highlights, is that it opens up a possibility not only to deepen our understanding of the distribution of this species in space and time, but also to explore the relationships between *D. villosum* and other taxa in the deposits. This exploration

can be rewarding, as we demonstrate, because it can show that the relationship between *D. villosum* and the crops it is associated with may be more complex than what the simple crop-weed distinction implies. In fact, *D. villosum* may have been a tolerated component of harvests, moreover—a welcome foodstuff. If so, association of *D. villosum* with other wild species in the deposits could point to further meal ingredients (e.g. *Bromus* and *Chenopodium*), in addition to elucidating such aspects of crop growing ecology as the disturbance and cultivation intensity.

For now it seems that the Bronze Age shift towards more extensive land use and the related, pronounced human influence on the landscape, coupled with significant increase in crop and weed diversity, constituted the agronomic context of appearance of *D. villosum* in archaeological deposits in our study region. Principally an element of dry, open grassland, *D. villosum* colonised the land newly cleared of forest for arable use which, between the planting seasons, may have been fallowed and used as pasture. Such setting naturally contained plentiful buried banks of shattered, long-dormancy grains of *D. villosum*. Disturbance, including ard/plough tilling, and low soil fertility do not affect its short-season growth and it thrives well on fallow ground. Virtually any dry man-made habitat could have attracted *D. villosum* and provided an environment for its early interaction with humans or animals. Whereas we cannot exclude the presence of *D. villosum* in the studied region before the 2nd millennium BCE, it seems that the time from the mid-2nd millennium BCE onwards was particularly favourable for its spread and integration in the archaeological layers, enabling us to chart its history further back in time. Expanding the dataset used here by looking at a larger region and deposits with smaller amounts of *D. villosum* remains would refine the observations we have made.

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References

- Bartosiewicz L (2022) Bronze Age novelties in animal exploitation in the Carpathian Basin in a European context. In: Kirleis W, Dal Corso M, Filipović D (eds) Millet and what else? The wider context of the adoption of millet cultivation in Europe. Sidestone, Leiden, pp 69–93
- Behre K-E (2008) Collected seeds and fruits from herbs as prehistoric food. *Veget Hist Archaeobot* 17:65–73. <https://doi.org/10.1007/s00334-007-0106-x>
- Boardman S, Jones G (1990) Experiments on the effects of charring on cereal plant components. *J Archaeol Sci* 17:1–11 [https://doi.org/10.1016/0305-4403\(90\)90012-T](https://doi.org/10.1016/0305-4403(90)90012-T)
- Bogaard A, Ater M, Hodgson JG (2018) Arable weeds as a case study in plant-human relationships beyond domestication. In: Stépanoff C, Vigne J-D (eds) Hybrid communities. Biosocial approaches to domestication and other trans-species relationships. Routledge, London, pp 97–112
- Bogaard A, Halstead P (2015) Subsistence practices and social routine in Neolithic southern Europe. In: Fowler C, Harding J, Hofmann D (eds) The Oxford Handbook of Neolithic Europe. Oxford University Press, Oxford, pp 385–410
- Cabi E, Doğan M, Başer B, Us E, Pehlivan S (2009) Morphological and palynological features of the genus *Dasypyrum* (Poaceae) in Turkey. *Phytologia Balcanica* 15:393–400
- Cavazzuti C, Horváth A, Gémes A et al (2025) Isotope and archaeological analysis reveal radical changes in mobility, diet and inequalities around 1500 BCE at the core of Europe. *Sci Rep* 15:17494 <https://doi.org/10.1038/s41598-025-01113-z>
- De Pace C, Vaccino P, Cionini PG, Pasquini M, Bizzarri M, Qualset CO (2011) *Dasypyrum*. In: Kole C (ed) Wild crop relatives: genomic and breeding resources: Cereals. Springer Berlin, Heidelberg, pp 185–292
- Diffey C, Neef R, Seeher J, Bogaard A (2020) The agroecology of an early state: new results from Hattusha. *Antiquity* 94:1204–1223. <https://doi.org/10.15184/aqy.2020.172>
- Filatova S (2020) Kakucs-Turján III: A case study of macrobotanical formation processes and plant economy from the Hungarian Bronze Age. *Studien zur Archäologie in Ostmitteleuropa/Studia nad Pradziejami Europy Środkowej* 20. Habelt, Bonn

- Filatova S, Gyulai G, Kirleis W (2019) Environmental imposition or an ancient farmers' choice? A study of the presence of inferior legumes in the Bronze Age Carpathian Basin (Hungary). In: Dal Corso M, Kirleis W, Kneisel J, Taylor N, Wieckowska-Lüth M, Zanon M (eds) How's Life? Living Conditions in the 2nd and 1st Millennia BCE. Sidestone, Leiden, pp 57–84
- Filipović D (2015) Granaries of Early Iron Age Kalakača, northern Serbia and the issue of archaeobotanical taphonomy. *Bulg e-J Archaeol* 5:99–115
- Filipović D, Bulatović J, Bulatović A (2020a) Food economy during and after the Neolithic- Eneolithic transition in the central Balkans: contextualising crops and domestic animals from Eneolithic Bubanj, southern Serbia. *J Serbian Archaeol Soc* 36:27–56
- Filipović D, Dal Corso M, Kirleis W (2022) Early cultivation of millet in Europe: What else and where next? Concluding the workshop proceedings. In: Kirleis W, Dal Corso M, Filipović D (eds) Millet and what else? The wider context of the adoption of millet cultivation in Europe. Sidestone Press, Leiden, pp 293–320
- Filipović D, Meadows J, Dal Corso M et al (2020b) New AMS ^{14}C dates track the arrival and spread of broomcorn millet cultivation and agricultural change in prehistoric Europe. *Sci Rep* 10:13698 <https://doi.org/10.1038/s41598-020-70495-z>
- Fischl KP, Kiss V, Kulcsár G, Szevérenyi V (2013) Transformations in the Carpathian Basin around 1600 B.C. In: Meller H, Bertemes F, Bork H-R, Risch R (eds) 1600 – Kultureller Umbruch im Schatten des Thera-Ausbruchs? (1600 – Cultural Change in the Shadow of the Thera-Eruption?). Tagungen des Landesmuseums für Vorgeschichte Halle 9. Landesamt für Denkmalpflege und Archäologie Sachsen-Anhalt. Landesmuseum für Vorgeschichte, Halle (Saale), pp 355–371
- Gumnior M, Herbig C, Krause R, Urdea P, Ardelean AC, Bălărie A, Stobbe A (2020) Palaeoecological evidence from buried topsoils and colluvial layers at the Bronze Age fortification Cornesti-Iarcuri, SW Romania: results from palynological, sedimentological, chronostratigraphical and plant macrofossil analyses. *Veget Hist Archaeobot* 29:173–188. <https://doi.org/10.1007/s00334-019-00762-1>
- Hajnalová M, Dreslerová D (2010) Ethnobotany of einkorn and emmer in Romania and Slovakia: towards interpretation of archaeological evidence. *Památky Archeologické* 101:169–202
- Helbaek H (1959) Comment on *Chenopodium album* as a food plant in prehistory. *Ber Geobot Inst ETH Stiftung Rübel* 31:16–19
- Hillman GC (1981) Reconstructing crop husbandry practices from the charred remains of crops. In: Mercer R (ed) Farming Practice in British prehistory. Edinburgh University, Edinburgh, pp 123–162
- Holubec V, Dvořák V, Svobodová Leišova L, Ercisli S (2021) Morphological, genetic and biochemical evaluation of *Dasyphyrum villosum* (L.) P. Candargy in the Gene Bank Collection. *Agronomy* 11:1316. <https://doi.org/10.3390/agronomy11071316>
- Hristova (Славова) I (2012) Археоботанични изследвания като източник на данни за палеосреда, палеодиета, и ползване на растенията в ритуален контекст от антични обекти в днешна Югоизточна България. Doctoral dissertation, University of Sofia, Sofia
- Hristova I, Atanassova J, Marinova E (2017) Plant economy and vegetation of the Iron age in Bulgaria: archaeobotanical evidence from pit deposits. *Archaeol Anthropol Sci* 9:1481–1494 <https://doi.org/10.1007/s12520-016-0328-x>
- <https://osogovonature.com/2021/10/18/dasyphyrum-villosum-l-p-candargy/>. Accessed 4 January 2026
- <https://www.wildgetreide.com/>. Accessed 4 January (2026)
- Humphries CJ (1980) *Dasyphyrum* (Cosson & Durieu) T. Durand (*Haynaldia* Schur). In: Tutin TG, Heywood VH, Burges NA, Moore DM, Valentine DH, Walters SM, Webb DA (eds) Flora Europaea, Vol 5: Alismataceae to Orchidaceae (Monocotyledones). Cambridge University Press, Cambridge, p 203
- Jones G (1984) Interpretation of archaeological plant remains: ethnographic models from Greece. In: van Zeist W, Casparie WA (eds) Plants and Ancient Man. Studies in Palaeoethnobotany. Balkema, Rotterdam, pp 43–61
- Jones G (1996) An ethnoarchaeological investigation of the effects of cereal grain sieving. *Circaea* 12:177–182
- Josifović M (ed) (1976) Флора СР Србије VIII (Flora of the SR Serbia 8). Српска академија наука и уметности, Београд
- Karanikola K, Valamoti S-M, Motuzaite Matuzeviciute G (2026) Earliest millet cultivation reflects steppe connections, dietary flexibility, and resilience in Bronze Age northern Greece. *PLoS ONE* 21:e0344099. <https://doi.org/10.1371/journal.pone.0344099>
- Kenéz Á, Malatinszky Á, Pető Á (2014) The first archaeobotanical evidence of *Dasyphyrum villosum* in Hungary: an archaeophyte weed or a native grass? *Veget Hist Archaeobot* 23:841–849. <https://doi.org/10.1007/s00334-014-0468-9>
- Kroll H (1983) Kastanas. Ausgrabungen in einem Siedlungshügel der Bronze- und Eisenzeit Makedoniens 1975–1979, Vol 1: Die Pflanzenfunde. Prähistorische Archäologie in Südosteuropa 2. Volker Spiess, Berlin
- Kroll H (1990) Melde von Feudvar, Vojvodina: Ein Massenfund bestätigt *Cbenopodium* als Nutzpflanze in der Vorgeschichte. *Prähist Z* 65:46–48
- Kroll H (1998) Die Kultur- und Naturlandschaft des Titeler Plateaus im Spiegel der metallzeitlichen Pflanzenreste von Feudvar. In: Hänsel B, Medović P (eds) Feudvar. Ausgrabungen und Forschungen in einer Mikroregion am Zusammenfluss von Donau und Theiss, 1: Das Plateau von Titel und Šajkaška. Prähistorische Archäologie in Südosteuropa 13. Oetker-Voges, Kiel, pp 305–317
- Kroll H (2016) Die Pflanzenfunde von Feudvar. In: Kroll H, Reed K (eds) Feudvar III: Die Archäobotanik. Würzburger Studien zur Vor- und Frühgeschichtlichen Archäologie 1. Würzburg University, Würzburg, pp 37–194
- Kroll HJ (2017) Ökologie?—Ökonomie! Zu den Beifunden der neolithischen Getreidewirtschaft. In: Lechterbeck J, Fischer E (eds) Kontrapunkte. Festschrift für Manfred Rösch. Universitätsforschungen zur prähistorische Archäologie 300. Habelt, Bonn, pp 159–164
- Kroll HJ, Reed K (2016) Feudvar III: Die Archäobotanik. Würzburger Studien zur Vor- und Frühgeschichtlichen Archäologie 1. Würzburg University, Würzburg
- Kubiak-Martens L, Oudemans TFM, Brozio JP, Filipović D, Müller J, Kirleis W (2024) Transformation of cereal grains: Botanical and chemical analysis of food residues encrusted on pottery from the Funnel Beaker settlement of Oldenburg LA 77, northern Germany. *PLoS ONE* 19:e0296986. <https://doi.org/10.1371/journal.pone.0296986>
- Magyari EK, Chapman JC, Fairbairn AS, Francis M, de Guzman M (2012) Neolithic human impact on the landscapes of North-East Hungary inferred from pollen and settlement records. *Veget Hist Archaeobot* 21:279–302. <https://doi.org/10.1007/s00334-012-0350-6>
- Marinova E, Tonkov S, Božilova E, Vajsov I (2012) Holocene anthropogenic landscapes in the Balkans: the palaeobotanical evidence from Southwestern Bulgaria. *Veget Hist Archaeobot* 21:413–427. <https://doi.org/10.1007/s00334-011-0345-8>
- Medović A (2006) Arheobotaničke analize četiri korpe ječma i jedne korpe prosa sa Čarnok. *Rad Muzeja Vojvodine* 47/48:41–52
- Medović A (2011) Biljna privreda Gradine na Bosutu (ili Savi?) u starijem gvozdenom dobu. In: Medović, P, Medović I (eds) Gradina na Bosutu: Naselje starijeg gvozdenog doba. Pokrajinski zavod za zaštitu spomenika kulture, Novi Sad, pp 329–355
- Medović A (2012) Late Bronze Age plant economy at the Early Iron Age hill fort settlement Hisar. *Rad Muzeja Vojvodine* 54: 105–118
- Medović A (2016) Was säen die Nachbarn von Feudvar? Metallzeitliche Pflanzenfunde aus der Vojvodina und Südserbien. In: Kroll

- HJ, Reed K (eds) Feudvar III: Die Archäobotanik. Würzburger Studien zur Vor- und Frühgeschichtlichen Archäologie 1. Würzburg University, Würzburg, pp 293–305
- Molloy B, Jovanović D, Bruyere C et al (2023) Resilience, innovation and collapse of settlement networks in later Bronze Age Europe: New survey data from the southern Carpathian Basin. PLoS ONE 18:e0288750. <https://doi.org/10.1371/journal.pone.0288750>
- Nesbitt M (2002) When and where did domesticated cereals first occur in southwest Asia? In: Cappers RTJ, Bottema S (eds) The Dawn of Farming in the Near East. Studies in Early Near Eastern Production, Subsistence, and Environment 6. Ex Oriente, Berlin, pp 113–132
- Nikolić T (2015) -onwards) Flora Croatica. database (<http://hirc.botanic.hr/fcd>). Prirodoslovno-matematički fakultet, Sveučilište u Zagrebu. Accessed 05 March 2026
- Pető Á, Masek Z, Kenéz Á, Daróczi-Szabó M, Daróczi-Szabó L, Rácz Z (2024) Subsistence strategies of the Sarmatians in the central region of the Carpathian Basin in the fourth–fifth centuries AD. <https://doi.org/10.1080/14614103.2024.2399976>. Environ Archaeol
- Randelović N, Avramović D, Đorđević V, Lilić A (2005) Flora Leskovika, 1. Proceeding of the 8th Symposium on Flora of South-eastern Serbia and Neighbouring Regions. Univerzitet u Nišu, Niš, pp 5–12
- Reed K (2015) From the field to the hearth: plant remains from Neolithic Croatia (ca. 6000–4000 cal BC). Veget Hist Archaeobot 24:601–619. <https://doi.org/10.1007/s00334-015-0513-3>
- Reed K (2016) Archaeobotanical analysis of Bronze Age Feudvar. In: Kroll HJ, Reed K (eds) Feudvar III: Die Archäobotanik. Würzburger Studien zur Vor- und Frühgeschichtlichen Archäologie 1. Würzburg University, Würzburg, pp 197–291
- Reed K (2017) Agricultural Change in Copper Age Croatia (ca. 4500–2500 cal B.C.)? Archaeol Anthropol Sci 9:1745–1765 <https://doi.org/10.1007/s12520-016-0330-3>
- Reed KA (2013) Farmers in Transition: The Archaeobotanical Analysis of the Carpathian Basin from the Late Neolithic to the Late Bronze Age (5000–900 BC). Doctoral dissertation, University of Leicester. Leicester. <https://hdl.handle.net/2381/28118>
- Reed K, Hršak T, Mihaljević M, Balen J (2022) Settlements and cemeteries in Bronze Age Croatia: The archaeobotanical evidence. Acta Palaeobotanica 62:108–122 <https://doi.org/10.35535/acpa-2022-0008>
- Reed K, Kudelić A, Essert S, Polonijo L, Karavanić S (2024) House of plenty: Reassessing food and farming in Late Bronze Age Croatia. Environ Archaeol 29:165–181. <https://doi.org/10.1080/14614103.2021.1979385>
- Szeverényi V, Priskin A, Czukor P, Torma A, Tóth A (2015) Subsistence, settlement and society in the late Bronze Age of southeast Hungary: a case study of the fortified settlement at Csanádpalota–Földvár. In: Kneisel J, Dal Corso M, Kirleis W, Scholz H, Taylor N, Tiedtke V (eds) The Third Food Revolution? Setting the Bronze Age Table: Common Trends in Economic and Subsistence Strategies in Bronze Age Europe. Habelt, Bonn, pp 97–117
- Van Zeist W (2001/2002) Plant Husbandry and Vegetation of Tell Gomolava. Vojvodina Yugoslavia Palaeohistoria 43/44:87–115 <https://doi.org/10.1201/9781003762522>

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