Cannabis in Asia: its center of origin and early cultivation, based on a synthesis of subfossil pollen and archaeobotanical studies

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Abstract

Biogeographers assign the center of origin of *Cannabis* to "Central Asia," mostly based on wild-type plant distribution data. We sought greater precision by adding new data: 155 fossil pollen studies (FPSs) in Asia. Many FPSs assign pollen of *Cannabis* or *Humulus* (*C-H*) to collective names (*e.g., Cannabis/Humulus* or *Cannabaceae*). To dissect these aggregate data, we used ecological proxies. *C-H* pollen in a steppe assemblage (with *Poaceae, Artemisia, Chenopodiaceae*) was identified as wild-type *Cannabis. C-H* pollen in a forest assemblage (*Alnus, Salix, Quercus, Betula, Robinia*, *Juglans*) was identified as *Humulus*. *C-H* pollen curves that upsurged alongside crop pollen were identified as cultivated hemp. Subfossil seeds (achenes) at archaeological sites also served as evidence of cultivation. FPSs and archaeological sites were mapped using geographic information system (GIS) software. The oldest *C-H* pollen consistent with *C. sativa* dated to 19.6 million years ago (mya), in northwestern China. However, *Cannabis* and *Humulus* diverged 27.8 mya, based on molecular clock analysis. We bridged the temporal gap between the divergence date and the oldest pollen by mapping the earliest appearance of *Artemisia*. These data converge on the northeastern Tibetan Plateau, which we deduce as the *C. sativa* center of origin. This co-localizes with the first steppe community that evolved in Asia. From there, *Cannabis* first dispersed west (Europe by 6 mya) then east (eastern China by 1.2 mya). *Cannabis* pollen in South Asia appeared by 32.6 kya. The earliest *Cannabis* seeds were found in Japan, 10,000 BCE, followed by China.

Electronic supplementary material The online version of this article contains supplementary material, which is available to authorized users.

Introduction

Cannabis sativa L. holds significance in human history and life today as a triple-use crop. First, its fruits (seeds) provide valuable protein and essential fatty acids. Archaeological evidence in a food context dates back to 10,000 BP, in Japan (Kobayashi et al. 2008). Its bast cells supply fiber, for cordage and textiles. Carbonized hemp fiber, found with silk and spinning wheels, dates to 5600 BP, in Henan Province, China (Zhang and Gao 1999). Its flowering tops produce cannabinoids, which have been used for medicinal, shamanic, and recreational purposes. Archaeological evidence of drug use dates to 2700 BP, in Xinjiang Region (Russo et al. 2008, Jiang et al. 2016).

Despite a voluminous literature emerging in the last three decades, the classification of *Cannabis* and its center of origin remains under continuous debate. A single species concept (Small and Cronquist 1976), has support from measures of population differentiation, such as F_{ST} (Sawler *et al.* 2015, Lynch *et al.* 2016) and barcode gaps (McPartland 2018). Other botanists recognize several species in the genus *Cannabis* (Hillig and Mahlberg 2004, Clarke and Merlin 2013). Hypotheses regarding the *Cannabis* center of origin began with Ibn Wahshīyah in 930 CE. He proposed that *šāhdānaj* was brought to Babylon from India and perhaps China (Hämeen-Anttila 2006). De Candolle (1884) offered Central Asia as the center of origin of *C. sativa*. His biogeographical theories were based upon the distribution of wild-type plants, as well as linguistic, historical, archaeological, and fossil data.

Print fossils (*i.e.,* impressions of leaves or fruits in rocks) of *C. sativa* are limited to only two collections: Friedrich (1883a,b) found fossil leaves in Germany that he named *Cannabis oligocaenica.* His species epithet indicates the Oligocene Epoch, 33.9–23.03 million years ago (mya). Palamarev (1982) identified a fossil seed (achene) as "*Cannabis* sp." in Bulgaria. He dated the find to the late Miocene ("Pontian age", 7.3–5.3 mya). Dorofeev (1969) reported a fossil seed, "*Cannabis* sp.," from the Miocene in Siberia. He subsequently reidentified the fossil

as an extinct species, *Humulus irtyshensis* (Dorofeev 1982). *Humulus* and *Cannabis* are sister genera, forming a phylogenetic clade within the family *Cannabaceae*.

Contrary to the paucity of print fossils, hundreds of fossil pollen studies (FPSs) have identified subfossil *Cannabis* pollen. Fröman (1939) first used pollen analysis to reconstruct the history of *Cannabis*. Following analytical refinements by Fries (1958), dozens of papers have been published. This culminated with the elaborate meta-analysis by Dörfler (1990), followed by our own meta-analyses (Long et al. 2017, McPartland et al. 2018).

Cannabis pollen is often straightforward to recognize (Mercuri et al. 2002), however, morphological similarities between *Cannabis* and *Humulus* pollen grains have prompted palynologists to use collective labels, *e.g., Cannabis/Humulus* or *Cannabaceae*. Significant labeling bias also arises: Chinese FPSs palynologists assign *Cannabis* pollen to "*Humulus*" (Li 1974), and northern European palynologists often assign *Humulus* pollen to "*Cannabis*" (Wilson 1975).

Parsing *Cannabis* from *Humulus* may be more difficult in Asia than in Europe. Five palynology studies of Asian *Cannabis* (*C. sativa* subsp. *indica*) indicate that pollen grain diameter is smaller than that of European hemp (*C. sativa* subsp. *sativa*), so the size of Asian *Cannabis* pollen falls within the range of *Humulus* (literature in McPartland et al. 2018).

FPSs resorting to collective labels (hereafter abbreviated *C-H* pollen) have thwarted the study of *Cannabis*. Clarke and Merlin (2013) reviewed dozens of Asian FPSs, and they were flummoxed by FPSs that lumped data as *C-H* pollen. Long et al. (2017) synthesized 46 FPSs in their pan-Eurasian study. They resolved the *C-H* dilemma by limiting FPSs to studies that explicitly identified pollen as *Cannabis*—a strategy that excluded a lot of *C-H* data.

McPartland et al. (2018) used ecological proxies, instead of grain morphology, to differentiate *C-H* pollen as either *Cannabis* or *Humulus* pollen. *Cannabis* flourishes in steppe— an open, treeless habitat. European phytosociologists and other field botanists report wild-type *C. sativa* cohabitating with *Poaceae, Artemisia,* and *Chenopodiaceae* (hereafter abbreviated *PAC*). Thus *C-H* pollen in a steppe assemblage (with *PAC* pollen) was identified as wild-type *Cannabis*. Conversely, *Humulus lupulus*, a perennial herbaceous scandent, requires trees to climb. European phytosociologists and other field botanists report *H. lupulus* associating with *Alnus*, *Populus*, and *Salix* spp. (abbreviated *ASP*). Thus *C-H* pollen in a mesophytic forest assemblage (with *ASP* pollen) was identified as *Humulus*.

Palynologists have noted correlations between *Cannnabis* and *PAC*, and between *Humulus* and *ASP,* and extended these associations into the past. For supporting palynological and phytosociological literature, see McPartland et al. (2018). In this study, we aim to further develop this method, focusing in particular on the Asia context. The ecological proxies method will be applied to a multilingual collection of Asian FPSs to reconstruct the evolutionary and human-related history of *Cannabis* in Asia.

Methods

FPS search strategy and data analysis

We collated an FPS database using several internet search engines (European Pollen Database, Web of Science, Google Scholar) using keywords and Boolean operators: Asia AND (palynology OR pollen) AND (*Cannabis* OR *Humulus* OR *Cannabaceae*). This was repeated with Chinese characters when searching Chinese-based references. Additional FPSs were obtained through citation tracking—references in retrieved publications were searched for antecedent sources, and these were retrieved. To map pollen in space and time, retrieved publications had to meet three inclusion criteria: 1) precise geographical coordinates, 2) accurate chronology, 3) a minimal threshhold amount of pollen grains.

1. Precise geographical coordinates were localized to within a hundredth degree of latitude and longitude. Some studies did not provide geographical coordinates. We obtained coordinates of those sites via Google Earth, which uses World Geodetic System of 1984 (WGS84) datum. Several FPS were conducted at deep-water sites, which explains sites located in seas and oceans. Geographers have debated the border between eastern Europe and western Asia. We included three studies on the edge: a deep-water site in the Black Sea off the coast of Turkey, a site in Georgia, and a cis-Ural site in Russia.

2. Accurate chronology necessitated restricting data to FPSs with absolute dating, such as radiocarbon (^{14}C), optically stimulated luminescence (OSL), or magnetostratigraphical methods. We excluded studies that assigned "relative dates" within sediments cores (*i.e.,* dates inferred by changes in vegetation, such as the start of the Holocene).

3. Palynologists debate the minimal amount of pollen required to determine the local presence of a plant species at a study site (versus pollen at a study site that arrived via long distance transport). Botemma *et al.* (2003) specifically mentioned *C-H* pollen in the "problem of

long-distance transport." Several FPSs located in southwestern Asia had three or fewer *C-H* pollen grains. These rare grains likely blew in from Europe. The Etesian winds blow from the Balkans (harboring endemic *Cannabis*) into Israel, Palestine, Lebanon, and Egypt (Zecchetto and De Blasio 2007). For a retrieved publication to be included in our study, *C-H* pollen had to appear in a minimum of five separate strata within a stratigraphic core (for details see McPartland et al. 2018).

Ecological proxies in the Asia context

In Central and East Asia, *Cannabis* seems to have a stronger alliance with *Artemisia,* less so with *Poaceae* and *Chenopodiaceae.* We took a closer look at *Artemisia*, to better pin-point the *Cannabis* center of origin. *Artemisia* and *Cannabis* share parallel evolutionary patterns: In phylogenetic studies, *Artemisia* nests within the *Antemideae* subfamily (Zhao et al. 2010), and *Cannabis* nests within the *Cannabaceae* family (Yang et al. 2013). *Artemisia* evolved in Central/East Asia during the late Eocene (*ca*. 36–33.9 mya) out of the worldwide *Antemideae* (Miao et al. 2011). *Cannabis* also evolved in Central/East Asia, *ca*. 27.8 mya, out of the worldwide *Cannabaceae* (McPartland 2018).

Artemisia and *Cannabis* are wind-pollinated and dioecious. Both genera exhibit phenotypic plasticity, with adaptive phenotypes that respond to environmental changes, enabling them to colonize new geographic locations. A meta-analysis of FPSs in Europe showed that *Cannabis* and *Artemisia* were fellow travelers; their geographic ranges expanded and contracted in unison during, respectively, glacial periods and warmer periods (McPartland et al. 2018).

Humulus pollen, in Central and East Asia, correlates with *ASP* pollen, as well as *Quercus, Betula, Juglans, Camellia,* and *Robinia* (abbreviated *ASP+*). Analyzing *Humulus* pollen in East Asia is complicated by two additional species, *H. yunnanensis* and *H. japonicus* (=*H. scandans*). *H. yunnanensis* is a tree-climbing species limited to Yunnan province (Zhou and Bartholomew 2003). It is a rare and endangered plant (Hu and Wu 1992). No phytosociological studies have been published that include *H. yunnanensis*.

H. japonicus is native to Japan, Korea, and eastern China (Zhou and Bartholomew 2003), the Russian Far East (Maximovich 1859), and Vietnam and Laos (Pételot 1954). Phytosociological and field studies report *H. japonicus* in communities dominated by trees—specifically *Alnus* (Lee et al. 1976, Kim et al. 2010, Jeong et al. 2012, Lee et al. 2013), *Salix* (Kolbek and

Karol ínek 2008, Kim et al. 2010, Oh et al. 2010, Jeong et al. 2012, Lee et al. 2013), *Quercus* (Lee et al. 1976, Kolbek and Karol ínek 2008, Kim et al. 2010, Oh et al. 2010), *Robinia* (Lee et al. 1976, Kolbek and Karol ínek 2008, Kim et al. 2010, Jeong et al. 2012, Lee et al. 2013, Lee and Ahn 2014), and *Camellia* (Kim et al. 2010, Lee et al. 1976, Lee and Ahn 2014, Eom and Kim 2017).

However, *H. japonicus* sometimes colonizes habitats that overlap with those of *C. sativa*. These include ruderal communities (Kolbek and S ádlo 1996, Oh et al. 2008), and riverside communities (Jung and Kim 1998). Some riverside communities include *Poaceae, Artemisia,* or *Chenopodiaceae* in the ground layer (Balogh and Dancza 2008, Andrek et al. 2010, Song and Song 1996, Jarol ínek and Kolbek 2006). One phytosociological study reports *H. japonicus* co-localizing with *C. sativa*—a ruderal community in Korea (Kolbek and S ádlo 1996). Maximovich (1859) reported *H. japonicus* growing with *C. sativa* in the Amur region of the Russian Far East, and Clarke and Merlin (2013) photographed feral hemp and *H. japonicus* growing together in Shandong Province.

Despite these intermittent associations with herbaceous plants, Asian paleobotanists characterize *Humulus* as a drought-intolerant climber of trees (Ni *et al.* 2010). They treat *Humulus* pollen as a botanical marker of deciduous broadleaved forests (Zhou *et al.* 2007), or tropical evergreen forests (Lee and Liew 2010).

The ratio of nonarboreal pollen (NAP, pollen from grasses, forbs, and sedges) and arboreal pollen (AP, tree pollen) serves as an indicator of landscape openness. NAP and AP percentages are oppositional—when one goes down, the other goes up. Similarly, palynologists have shown that *Alnus* and *PAC* demonstrate oppositional characters (literature in McPartland et al. 2018).

CH pollen can be identified as that of *cultivated* hemp when its pollen count surges or becomes a continuous curve in synchrony with pollen from other crop plants. This metric was first adopted by Fries (1958) and used in ten other palynological studies. Other crop plants include *Avena* (oats), *Hordeum* (barley), *Secale* (rye), *Triticum* (wheat), and *Cerealia*-type (undifferentiated cereal pollen).

The presence of *Cannabis* pollen in very high percentages indicates a former hemp retting site. Retting is a technical term for rotting, a process that separates fibers from the rest of the stalk. Soaking hemp stalks in water encourages bacterial growth and retting. When flowering male plants are soaked in a retting pond, large quantities of pollen settle into pond sediments.

Cannabis pollen ≥15% of TLP (total land pollen) is usually considered evidence of hemp retting, and percentages up to 97% have been reported (literature in McPartland et al. 2018).

Pollen algorithm

To differentiate *C-H* pollen, the algorithm by McPartland et al. (2018) was adjusted to account for Asian conditions. We identified *C-H* pollen as that of cultivated *C. sativa* when it appeared *de novo* along with crop pollen, or increased at least 2-fold over earlier pre-Neolithic counts. Several FPSs in South Asia report *Cerealia* pollen, attributed to agriculture, in ancient strata that clearly predate archaeological evidence of grain cultivation (*e.g.,* 12,000 BP, Quamar and Bera 2017). In these FPSs we looked for 2-fold increases and continuous curves of *C-H* pollen in the presence of *Cerealia* pollen.

To differentiate *C-H* pollen in pre-agricultural strata, we used ecological proxies. When *C-H* occurred in a pollen assemblage where the NAP-to-AP ratio ≥2 (*i.e.,* ≥ 66%/33%), dominated by steppe vegetation (*PAC*), we identified it as wild-type *Cannabis*. When *C-H* occurred in a pollen assemblage where the NAP/AP ratio ≤0.5 (*i.e.,* ≤ 33%/66%), in the presence of *ASP+*, we identified it as *Humulus*. In some ambiguous FPSs, pollen counts of *PAC* and *ASP+* rise and fall in near-synchrony, and the NAP/AP ratio approaches 1:1 (*i.e.,* 50%/50%). At these sites, we classified *C-H* pollen as unresolved *C/H*.

Archaeobotanical evidence

We also included botanical evidence from archaeological sites. Previous studies have collated archaeological reports of hemp seeds, phytoliths, stalk fragments, fiber, cordage, or textiles, and pottery impressions of those materials (Clarke and Merlin 2013, Long et al. 2017). McPartland and Hegman (2018) stratified the relative robustness or validity of these materials. Microscopically-analyzed seeds, phytoliths, and stem fragments were considered the most robust evidence. Fiber, cordage, and textiles were problematic. For example, Song et al. (2017) unearthed a few plant fibers identified as hemp, *C. sativa,* at a site occupied by Paleolithic hunter-gatherers that dates to 28.5 kya. This could be the oldest hemp fiber ever found, but their photomicrograph of a "hemp" fiber is by no means convincing. Song et al. (2017) report plentiful flax fibers at their site. McPartland and Hegman (2018) detail the difficulties in differentiating hemp from flax fiber. Regarding pottery impressions, identifying the plant species

that made the cord impression is even more difficult. At least 14 plant species were utilized for pottery cord impressions in Neolithic China (Kuhn 1988). In this current study, we limited archaeological findings to microscopic analyses of seeds, phytoliths, and stem fragments.

GIS mapping and binning strategy

Latitude and longitude (referencing WGS84 datum) of each FPS was plotted, using geographic information system (GIS) software, ArcGISPro 2.2. The FPS sites were plotted on three maps, corresponding to three binned time slices. Each FPS site was notated with a symbol indicating pollen interpretation—either wild-type *Cannabis*, *Humulus,* cultivated *Cannabis*, or unresolved *C/H* pollen. Archaeological sites with hemp seeds or phytoliths were notated with another symbol.

Stratigraphical data were binned into three time slices:

Bin 1. This period includes the Oligocene (33.9–23.03 mya), Miocene (23.03–5.3 mya), Pliocene (5.3–2.58 mya), and Pleistocene (2.58 mya–11.6 thousand years ago, kya) epochs. The symbols for these sites are sized according to the age of the pollen. A weighted centroid for *Cannabis* pollen data was also calculated (weighted by geographical location and age).

Bin 2. Early- to Mid-Holocene, 11.5–5.0 kya, a period of improved climate, reemerging forests, and the Mid-Holocene Climatic Optimum. This period includes the onset of agriculture in Asia and the earliest archaeobotanical evidence of *Cannabis* usage.

Bin 3. Late-Holocene, 4.5–0 kya, a period of profound anthropogenic impact on landscapes, and the earliest recorded Asian history.

Extrapolating into the Oligocene

McPartland (2018) constructed a maximum likelihood phylogenetic tree (PAUP* version 4.0b10) of 11 Rosales genera, using *rbcL+trnL-trnF* sequences, and a nonparametric variable rate-smoothing algorithm (r8s version 1.70), calibrated with four fossil date intervals (*Boehmeria* 60-34 mya, *Morus* 56-34 mya, *Celtis* 65-56 mya, *Humulus* 28-16 mya). The molecular clock estimated that *Cannabis* and *Humulus* evolved (diverged) 27.8 mya. This date considerably predates the oldest *Cannabis* pollen found in this study (19.6 mya). To deduce the location of *C. sativa* during this temporal "missing link," we used two sets of indirect data:

Bosboom *et al.* (2011) mapped an "aridification zone" arising in Central Asia at the Eocene-Oligocene boundary, 34 mya. Orogenic changes at that time—the rise of the Tibetan plateau and the retreat of the Tarim Sea—forced concomitant changes in climate, resulting in the evolution of steppe vegetation. China's first steppe communities originated at the Eocene-Oligocene boundary (Sun et al. 2014), and continued to develop through the Oligocene and Miocene (Wang 1996), spanning the temporal missing link. We transferred a best approximation of the paleogeographic map by Bosboom and colleagues onto a modern map of Asia.

Secondly, we applied a previously reconstructed history of *Artemisia* in Asia. Miao *et al.* (2011) tracked the spatiotemporal appearance of *Artemisia* pollen, beginning at the Eocene-Oligocene boundary, in a meta-analysis of 122 FPSs. As a proxy for the distribution of *Cannabis* prior to our oldest pollen, we mapped their distribution of *Artemisia* pollen, in six binned time slices used by Miao and colleagues: late Eocene (38-34 mya), latest Eocene (34 mya), early Oligocene (34-28 mya), Oligocene (34-23 mya), early Miocene (23-20 mya), and mid-Miocene (14 mya).

Results

The search strategy identified 173 FPSs that included *C-H* pollen or archaeological studies with seeds, phytoliths, or stem fragments. Seven studies did not meet our inclusion criteria, and another eleven studies reported duplicate data. The remaining 155 studies were tabulated, each with a citation number, study location, details regarding application of the algorithm, and duplicate reports (Online Resource, Table S1). Excluded studies were also tabulated, with exclusion criteria (Table S2).

Bin 1 (19.6 mya–11.6 kya, Fig 1). The oldest *C-H* pollen consistent with *Cannabis* dated to 19.6 mya (early Miocene). The site is located in Ningxia, China, on the border between the Tibetan Plateau and the Loess Plateau. For scholars interested in the original publication, see Table S1, citation #1. During the Pliocene, *Cannabis* pollen occurs in Northwest China (Ningxia, 2.6 mya, Table S1, #2). During the first half of the Pleistocene (*i.e.,* the Gelasian and Calabrian ages, 2.58 mya–781 kya), *Cannabis* pollen is located in Bashkorostan, Russia (1.5 mya #156), Hebei Province (1.2 mya #3), and the Russian Altai (787 kya, #4).

During the latter half of the Pleistocene, *Cannabis* pollen appears in four of six Chinese regions: ***Northwest China*** (Shaanxi, 342 kya, #5; Gansu, 145 kya, #6; Shaanxi, 50 kya, #8;

Shaanxi, 25 kya, #12; Tibet, 20 kya, #13; Xinjiang, 14.5 kya, #20; Gansu, 12 kya, #28). **North China** (Inner Mongolia, 35 kya, #9). **Northeast China** (Liaoning, 16 mya, #16; Jilin, 13 kya, #24). **East China** (Shanxi, 15 kya, #19). FPSs in two remaining provinces, South Central and Southwest China, have *Humulus* pollen but no *Cannabis* pollen.

FPSs from latter half of the Pleistocene show sites with *Cannabis* pollen elsewhere in East Asia (Korea, 32 kya, Table S1 #10); as well as Kazakhstan (130 kya, #152), Southwest Asia (Turkey, 111 kya, #7; Black Sea near Turkey, 17 kya, #152; Caspian Sea near Iran, 14 kya, #23; Georgia, 13 kya, #154; Syria, 11.9 kya, #30); South Asia (India, 32.6 kya, #11; Sri Lanka, 18 kya, #14; India, 12.8–11.9 kya, #25, #26, #27, #29); and Central Siberia (Altai, 16–15 kya, #15, #17, #18).

One FPS in Bin 1 (Table S1, #9) conflicted with our algorithm's designation of a retting site (*Cannabis* pollen ≥15% of TLP). That study reported *C-H* pollen reaching 61%, but it was clearly not a retting site, because it occurred 34 kya, long before agriculture began. The short-lived *C-H* pollen spike was superseded by *Artemisia* reaching 80% of TLP, another unusual finding.

Fig. 1 Bin 1 (19.6 mya–11.6 kya). Age-weighted geographical centroid for *Cannabis* data is marked by a star. Background base map by Natural Earth, free open-source map data, https://www.naturalearthdata.com.
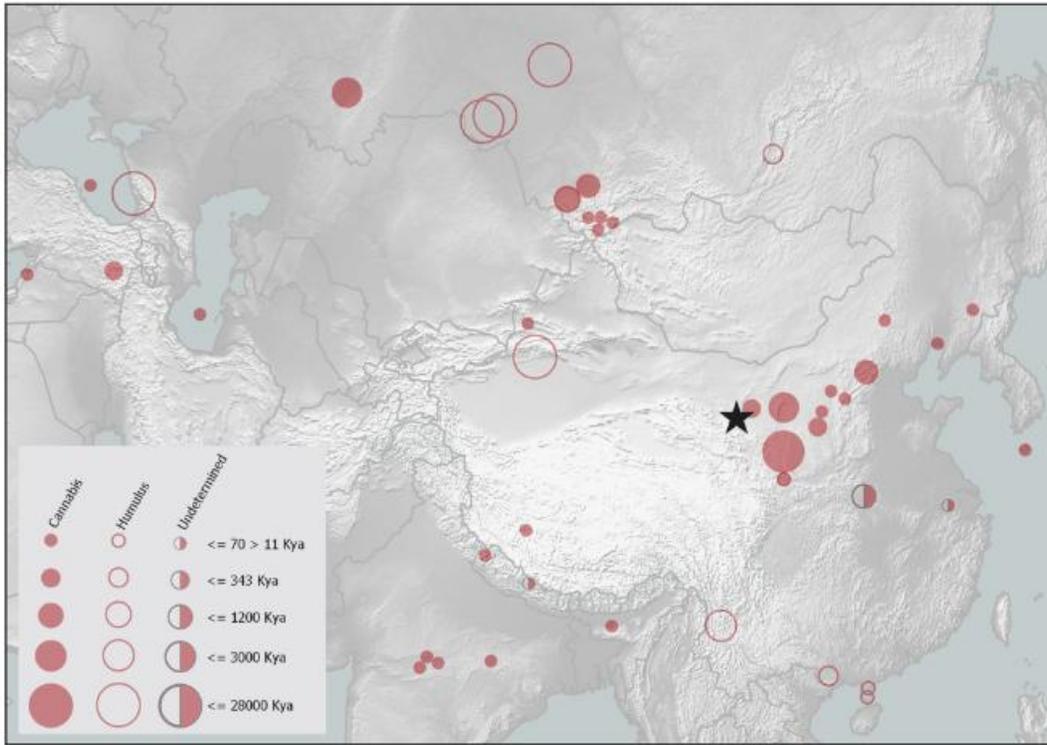
Bin 2 (11.5–5.0 kya, Fig 2). During the early Holocene, *C-H* pollen consistent with wild-type *Cannabis* occurs across Asia, from the Syrian and Anatolian steppes in the west to the Liaoning plains in the east, and from the Altai steppe in the north to the Central Highlands of India in the south, even the Horton Plains of Sri Lanka. No *C-H* pollen consistent with cultivated *Cannabis* is detected in Bin 2. However, several archaeological sites with *Cannabis* artifacts fall into Bin 2. The oldest sites are in Japan (Chiba, 10,000 BP, Table S1 #142) and China (Henan, 7850 BP, #132). Somewhat younger artifacts are found in Japan (Fukui, 7200 BP, #144; Aomori, 5900-4300 BP, #146), and in China (Hunan, 6400-5300 BP, #104; Gansu, 5000 BP, #109; and Inner Mongolia 5000 BP, #134).

Fig. 2 Bin 2 (11.5–5.0 kya). Background base map by Natural Earth, free open-source map data, https://www.naturalearthdata.com.
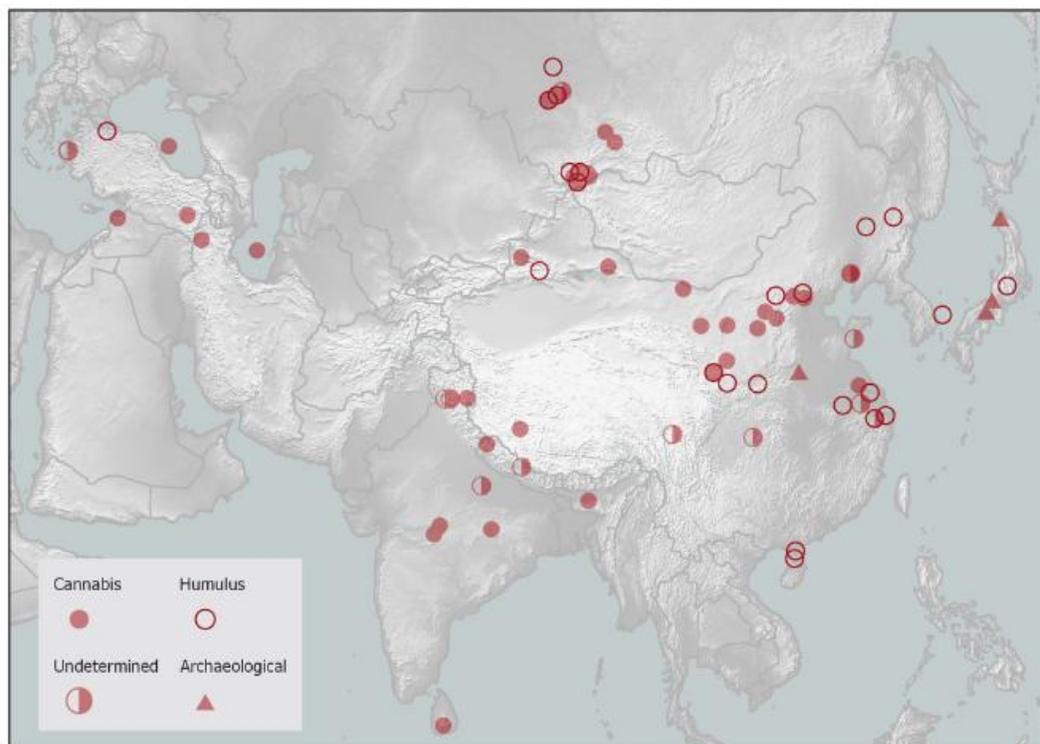
Bin 3 (4.5–0 kya, Fig 3) During the late Holocene, *C-H* pollen consistent with wild-type *Cannabis* occurs across the same range as Bin 2, excepting the loss of the Sri Lankan site. Pollen consistent with cultivated *Cannabis* appears at 35 sites. At eleven of those sites, *Humulus* in a forested environment gave way to land clearance and *Cannabis* cultivation, resulting in two symbols at the same site.

The oldest sites within this time slice are located in the lower Yangtze River basin, dating to 5330 BP (#125) and 5000 BP (a retting site, with 15% TLP, #130). In Northwest China, cultivated *Cannabis* is located in Xinjiang (3720 BP, #20; 2600 BP, #129) and Qinghai (3000 BP, #97). In East China, it appears in Shanxi (2800 BP, #19). Outside of China, pollen consistent with cultivated *Cannabis* appears in Russia (3700 BP, #155), Turkey (3200 BP, #45; 2300 BP, #153), Korea (3150 BP, a retting site, with 25% TLP, #139), and India (2500 BP, a retting site, with 28% TLP, #71).

The oldest archaeological sites within this time slice are located in Gansu (5000-4700 BP, #108, #110), Qinghai (4200-3500, #115, #116), Inner Mongolia (3900-3400 BP, #133), Shandong (3600-3000 BP, #124), and Xinjiang (2800-2500 BP, #135, #136). Outside of China, relatively old sites are found in central Korea (4590-4240 BP, #138), the Ganges River basin in

India (4600-3200 BP, #62–65), Japan (3500-3000 BP, #147, #148), Nepal (2400 BP, #76), and the Russian Far East (2500 BP, #79).

Fig. 3 Bin 3 (4.5–0 kya). Background base map by Natural Earth, free open-source map data, https://www.naturalearthdata.com/
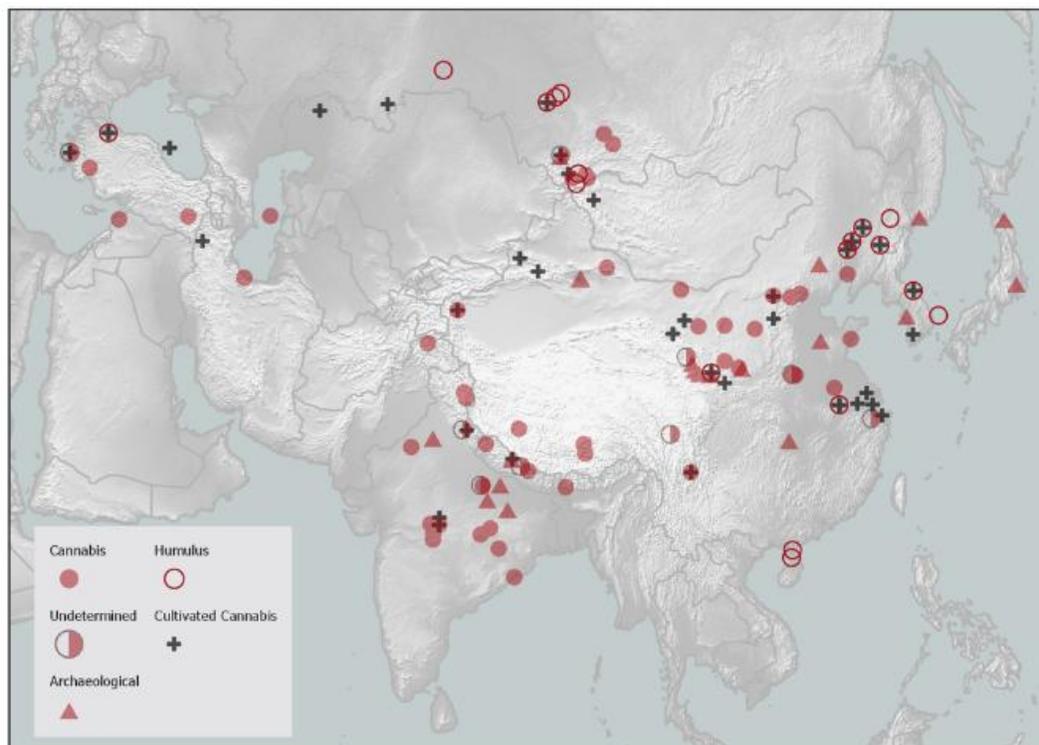

Extrapolating into the Oligocene

Next we deduced the location of *C. sativa* during the temporal "missing link" between its divergence date (27.8 mya) and oldest pollen (19.6 mya), using two sets of indirect data. Bosboom *et al.* (2011) mapped an aridification zone arising at the Eocene-Oligocene boundary. The periphery of their zone is demarcated by the central Tarim Basin, southern Mongolia, and southeast of the Xining Basin. A best approximation of this paleogeographic zone was transferred to a modern map in Fig 4. The oldest *C-H* pollen consistent with *Cannabis* (site #1) is located at the southeastern perimeter of the aridification zone (Fig 4).

Artemisia pollen during the late Eocene, Oligocene, and early/mid Miocene, based on data from Miao *et al.* (2011) is also mapped in Fig 4. The age-weighted centroid for these data is located within Bosboom's aridification zone. The *Artemisia* centroid, at 38.621 N, 102.205 E, is located 60 km north of the *Cannabis* centroid shown in Fig. 1 (38.186 N, 101.910 E). This

amazing proximity is somewhat spurious, because the data set of *Artemisia* and *Cannabis* pollen somewhat reflects the distribution of palynologists, and accessibility to related strata, rather than a theoretically complete distribution of pollen.

Fig 4. Black ellipse: aridification zone arising at the Eocene-Oligocene boundary (Bosboom *et al.* 2011) transferred to a modern map. Age-weighted geographical centroid for *Artemisia* data is marked by a star. Background base map by Natural Earth, free open-source map data, https://www.naturalearthdata.com/
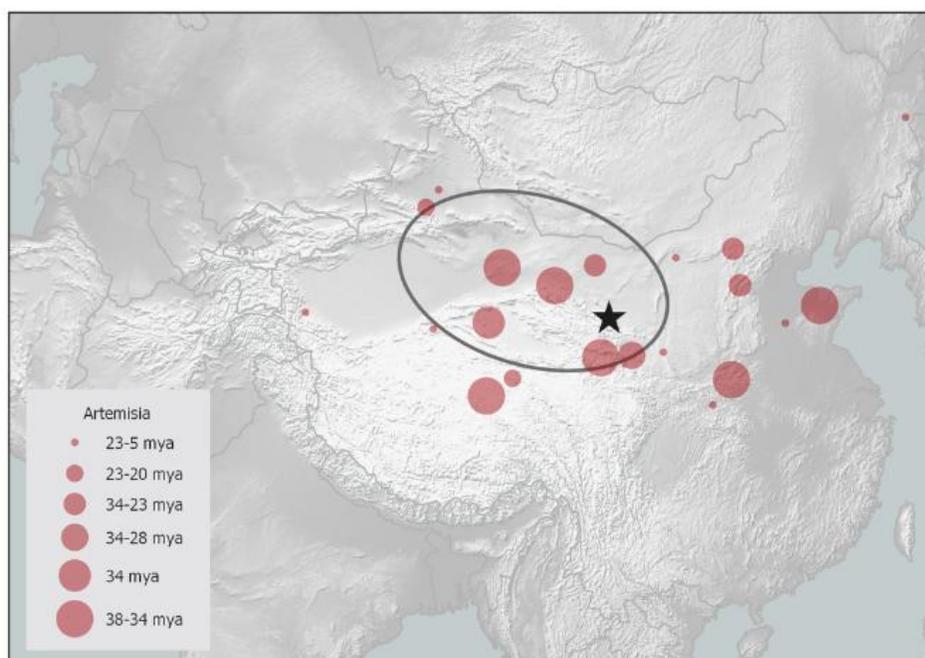
Discussion

The use of ecological proxies is an inferential method of differentiating *Cannabis* and *Humulus* pollen (McPartland et al. 2018). It offers a way to dissect *Cannabis/Humulus* and other collective names assigned by palynologists, due to the morphological similarities between *Cannabis* and *Humulus* pollen. However, the method is inherently probabilistic. The method also assumes that ecological niches of modern *Cannabis, Humulus, PAC,* and *ASP+* can be extrapolated to past populations—the nearest living relative method (Mosbrugger and Utescher 1997).

At some sites dominated by AP pollen, we may have misidentified pollen signals of *Cannabis* cultivation as *Humulus* pollen. Pollen-based detection of early agriculture in densely forested sites often shares this conundrum (e.g., Tarasov et al. 2018).

Cannabis pollen dating to the Miocene, Pliocene, and Pleistocene (Fig 1) has an age-weighted geographical centroid located in the northeastern Tibetan Plateau. However, the evolution of *Cannabis* predates these data. We applied Miao's *Artemisia* data as a proxy for the location of *Cannabis* during this "missing link." The weighted geographical centroid for the *Artemisia* data is also located in the northeastern Tibetan Plateau.

Thus we deduce the center of origin of *Cannabis*, along with that of her fellow traveler *Artemisia,* as the northeastern Tibetan Plateau, in the general vicinity of Qinghai Lake. The northeastern Tibetan Plateau, and the *Cannabis* and *Artemisia* pollen centroids, all fall within Bosboom's aridification zone. The oldest *Cannabis* pollen lies at the zone's periphery.

Zhang et al. (2018b) offered "low latitude" China as the *Cannabis* center of origin, based on haplotype data of 52 extant *Cannabis* accessions. They identified 25 haplotypes based on genetic variation in five cpDNA sequences (*rps16, psal-accD, rps11-rps8, rpl32-trnL, and ndhF-rpI32*). Spatial analysis of molecular variance (SAMOVA) was used to determine the optimal number of haplogroups to divide the haplotypes, based on cpDNA variation and geographical coordinates. The data best fit K = 3; a phylogenetic tree placed one of the haplogroups basal, whose accessions came from Tibet (n =7) and Yunnan (6), as well as Inner Mongolia (3), Gansu (1), Guangxi (1), and Shandong (1).

Tibet and Yunnan embrace the southeastern portion of the Tibetan Plateau, so the estimation by Zhang and colleagues differs little from our own. Their analysis may have been biased by relatively recent genetic bottlenecks: Clarke and Merlin (2016) proposed that the Henduan Mountains, which constitute the Tibetan Plateau in southeastern Tibet, Yunnan, and Sichuan, served as a Pleistocene glacial refugium. Zhang and colleagues utilized the phylogram as a molecular clock, anchored by one fossil date (*Aphananthe,* 66 mya), and estimated that *Cannabis* and *Humulus* diverged 18.2 mya. However, low altitude China at that time was warmer and wetter than today, and covered by subtropical broad-leaved forests (Sun *et al.* 2011, Huang *et al.* 2016). This ecosystem would not have driven the evolution of a steppe plant like *Cannabis*, according to the nearest living relative method (Mosbrugger and Utescher 1997).

Cannabis expanded westward from its center of origin. *C-H* pollen consistent with *Cannabis* appeared in central Russia (the cis-Ural region; Table S1, #156) by 1.5 mya. Further west, a fossil seed (achene) assigned to *Cannabis* in Bulgaria dated to 7.3-5.3 mya (Palamarev 1982). *Cannabis* expanded eastward from its center of origin. *C-H* pollen consistent with *Cannabis*

appeared in northeastern Ningxia by 2.6 mya (Table S1, #2), and Hebei by 1.2 mya (Table S1, #3). By the end of the Pleistocene, all regions of China except South Central and Southwest China showed evidence of *Cannabis*.

FPSs in South Asia merit special attention: *Humulus* is not native to India; *H. lupulus* was introduced as a cultigen by British colonists in the 1840s (Hooker 1890, Khuroo et al. 2007). In many areas the plants proved maladaptive and did not reach maturity, because flowering time coincided with the onset of monsoons (Bakshi and Atal 1985). The introduction of non-native *Humulus* was also reported in Pakistan (Stewart 1971), Nepal (Sood and Thakur 2015), and Burma (Kress et al. 2003). Floras of Bangladesh and Thailand omit *Humulus* (Khan and Halim 1990, Santisuk 2015).

The absence of *Humulus* in South India provided a "beta test" of our algorithm—all *C-H* pollen in South Asia should appear in pollen assemblages with a NAP/AP ratio ≥2, consistent with *Cannabis*. In fact, several sites showed NAP/AP ratios approaching 1:1 (Table S1, #42, #57, #59, #66, #67). The *C-H* pollen at these sites may be due to long-distance transport, or represent small steppe communities surrounded by forests. One South Asian study found *C-H* pollen in an assemblage with a NAP/AP ratio ≤2 (#71). This ratio would classify it as *Humulus*. But the *C-H* percentage surged to 28%, in the presence of crop pollen (*Cerealia, Fagopyrum*), which the algorithm identified as a hemp retting site, as did the original authors.

South Asian studies that recorded "*Cannabis*" in pollen assemblages with high AP values may have misidentified *Celtis* tree pollen. Notably, few South Asian FPSs included *Celtis* (family Cannabaceae) in their pollen diagrams. Three *Celtis* species are distributed in South Asia, *C. australis, C. tetrandra,* and *C. wightii* (Watt 1889, Hooker 1890). *Celtis* pollen grains resemble those of *Cannabis*—they are circular to elliptic, triporate with circular pores surrounded by an annulus, a thin exine, and smooth to verrucate surfaces. They have grain diameters whose sizes fall into the range of *Cannabis* and *Humulus* (see notes in Table S1, #60). Several FPSs in India provided photomicrographs of *Cannabis* pollen; measurements based on their bar scales show grain sizes smaller than *Cannabis* (range 16–23 μm, #55, #56), others are larger than *Cannabis* (range 70–180 μm, #57–59).

Whether *C. sativa* is native to South Asia, versus an introduced species, is a long-standing debate (Hooker 1890, Watt 1889). Experts still argue whether *C. sativa* in the Himalaya is indigenous (Zhou and Bartholomew 2003) or a naturalized alien (Khuroo *et al.* 2007). We found

pollen consistent with *Cannabis* appearing in India by 32.6 kya, which suggests an indigenous species, not introduced by humans. *Cannabis* pollen in South Asia by 32.6 kya begs the question of when it actually arrived. Early floristic exchanges between the Indian subcontinent and Asia were shaped by plate tectonics. As the Indian plate migrated towards the Asian plate, it made a "glancing contact" with Sumatra 57 mya, followed by Burma, and then a "hard collision" with Tibet 35 mya (Ali and Aitchison (2008). The "glancing contact" between continents resulted in floristic exchanges during the Eocene (Bande 1992, Morley 2003). The extant flora of India is often termed Indo-Malayan.

Cannabis arriving via Southeast Asia during the Eocene seems unlikely. Southeast Asian FPSs are bereft of *C/H* pollen, and the Indo-Malayan exchange occurred before *Cannabis* evolved. The migrating Indian plate initiated uplift of the Tibet plateau *ca.* 40–35 mya—the primary cause of Bosboom's aridification zone. The Tibet uplift, followed by the Pamir uplift (35 mya) created a dispersal barrier between Central Asia and India. Perhaps the biogeographical dispersal patterns of related plants, which we discuss below, might help answer this question.

The oldest pollen signal of cultivated *Cannabis* identified by our methods dated to 5330 BP (Table S1, #125). Archaeological findings (seeds) predate this. Perhaps the seeds were collected from wild-type *Cannabis*. A Jōmon Culture site yielded the oldest seeds (Table S1 #142). The seeds were found with other edible nuts and fruits, indicating food use. The Jōmon people made pottery but did not farm—their economy was based on wild resources and nut harvesting (Bleed and Matsui 2010). Contrary to this wild-type hypothesis, however, photomicrographs of the Jōmon seeds do not show wild-type traits, suggesting they were not only cultivated, but domesticated.

Serviceable fiber is not easily extracted from wild-type growth, which branches excessively. Densely-sown crops, with minimal branching, yield the best fiber. The clearest palynological signal of fiber use comes from FPSs with *Cannabis* pollen ≥15% of TLP, indicative of a retting site. The oldest retting site, dating to 5000 BP, is located in the Yangtze River delta (Table S1, #130). The pollen identification is problematic, yet the authors discuss hemp retting as the source of their pollen surge, as do other authors (Table S1, #71). Older non-palynological evidence— carbonized hemp fibers (excluded in this study)—dates to 5600 BP, in Henan (Zhang and Gao 1999). Intact rope and cloth dates to 5000 BP, in the Yangtze River delta (Zhou 1980).

Archaeological evidence of ceremonial or drug use dates to 2700 BP, in Xinjiang (Table S1, #135, #136). This interpretation is secured by the presence of processed leaves and female flowering tops, stored in a leather basket, wooden bowl, or earthenware pot.

Cannabaceae biogeography

The geographic ranges of related species may help locate an organism's center of origin (Crisci et al. 2003). The *Humulus* center of diversity lies in Southwest China: *H. lupulus* occurs in Sichuan; *H. japonicus* occurs in Sichuan, Yunnan, Chongqing, Guangxi, and Guizhou; *H. yunnanensis* is limited to Yunnan (Zhou and Bartholomew 2003). Small (1978) divided *H. lupulus* into five varieties, which collectively circumnutate the Northern Hemisphere at temperate latitudes. Gray (1859) noted the *Humulus* connection between East Asia and North America, foretelling the Bering land bridge theory.

Pteroceltis tatarinowii, the only extant species of that genus, is limited to China and Mongolia. However, fossils indicate that *Pteroceltis* is a relictual lineage that once had a wider geographic range, and similar to that of *H. lupulus*. Fossils of *Pteroceltis tertiaria* were found in Germany, and fossils of *Pteroceltis knowltonii* were found in the USA (Manchester *et al.* 2009).

Celtis is the largest genus in the *Cannabaceae*, with about 70 species, and 13 grow in China. *Celtis* also has the largest native range in the *Cannabaceae*, spanning temperate as well as tropical latitudes. In the Northern Hemisphere, Gray (1859) included *Celtis* in his proto-Bering land bridge theory. In the Southern Hemisphere, *Celtis* occurs in South America, Africa, and Australia (Stevens 2008). The oldest *Celtis* fossils (of *Celtis aspera*, 64-56 mya) have been found in the Russian Far East and the western USA (Manchester et al. 2002). This hints at an East Asian origin for the genus.

Trema and *Parasponia* are sometimes synonymized; a molecular study found both *Trema* and *Parasponia* paraphyletic, with no clear basal lineages (Yesson *et al.* 2004). Twelve *Trema* species grow in subtropical and tropical regions, in southern China, India, Southeast Asia, Africa, and Central America. China is the *Trema* center of diversity, with eight species growing there. *Parasponia* species do not occupy continental Asia; they are found in Indonesia, Papua New Guinea, Philippines, northern Australia, and some Melanesian and Polynesian islands.

Aphananthe species occur in China, Japan, Korea, India, Sri Lanka, Southeast Asia (including Philippines and Papua New Guinea), Mexico, Madagascar, and Australia. Fossils

indicate a wider distribution, with finds in western Siberia, Germany, and the USA (Yang et al. 2017). Phylogenetic studies place *Aphananthe* basal to the rest of the *Cannabaceae,* hence it is the oldest genus (Yang et al. 2013, Zhang et al. 2018a). A fossil from Germany, *Aphananthe cretacea*, dates to 66–72.1 mya (Knobloch and Mai 1986).

Yang et al. (2017) reconstructed the biogeography of *Aphananthe* using DNA sequences and other molecular methods. They identified East Asia as the ancestral area of extant *Aphananthe* species. Dispersal took *Aphananthe* across the Bering land bridge into North America around 19.1 mya, and into South Asia by 18.1 mya. A route from East Asia to South Asia was not delineated. *A. cuspidata* occupies contiguous areas spanning East Asia and South Asia—Yunnan, Burma, and India—so that is the likely route.

In summary, most *Cannabaceae* genera have origins in East Asia. The ancestral distribution of *C. sativa* resembles that of *H. lupulus*, except *C. sativa* dispersed to South Asia, and *H. lupulus* crossed the Bering land bridge. We propose that the progenitor of *Cannabis* dispersed from East Asia to the northeastern Tibetan Plateau, where it underwent parapatric speciation in Bosboom's aridification zone, amidst Asia's first steppe community.

Cannabis dispersed from the Tibetan Plateau, first to the west (Russia and Europe) and then to the east (China). By the end of the Pleistocene, *Cannabis* spread throughout Asia, except for Southeast Asia. Thus wild-type *Cannabis* was available for people across Eurasia to bring into cultivation and domesticate. Several sites in southeastern Europe, mostly associated with the Yamnaya Culture, suggest autochthonous domestication in Europe (Clarke and Merlin 2013, Long et al. 2017, McPartland and Hegman 2018). Vavilov (1926) would have agreed, "it is probable that the cultivation of hemp arose simultaneously and independently in several places."

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