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REVIEW

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 *Cannabis* centre of origin 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 either *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, Robinia*, *Juglans*) was identified as *Humulus*. *C–H* pollen curves that upsurged alongside crop pollen were identified as cultivated hemp. Subfossil seeds (fruits) at archaeological sites also served as evidence of cultivation. All sites were mapped using geographic information system software. The oldest *C–H* pollen consistent with *Cannabis* dated to 19.6 ago (Ma), in northwestern China. However, *Cannabis* and *Humulus* diverged 27.8 Ma, estimated by a 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 *Cannabis* centre of origin, in the general vicinity of Qinghai Lake. This co-localizes with the first steppe community that evolved in Asia. From there, *Cannabis* first dispersed west (Europe by 6 Ma) then east (eastern China by 1.2 Ma). *Cannabis* pollen in India appeared by 32.6 thousand years (ka) ago. The earliest archaeological evidence was found in Japan, 10,000 BCE, followed by China.

Keywords Cannabis sativa · Humulus lupulus · Cannabaceae · Biogeography · Centre of origin · GIS

Introduction

Cannabis 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 fibres, for cordage and textiles. Carbonized hemp fibres, found with silk and spinning wheels, date to 5,600 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 2,700 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 centre of origin remains under 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 *Cannabis* species (Hillig and Mahlberg 2004; Clarke and Merlin 2013). Hypotheses regarding the *Cannabis* centre of origin began with Ibn Wahshīyah in 930 CE. He proposed that *šāhdānaj* was brought to Babylon from India or perhaps China (Hämeen-Anttila 2006). De

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Candolle (1883) offered Central Asia as the centre 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 *Cannabis* 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 (Ma) ago. Palamarev (1982) identified a fossil seed (fruit) as "*Cannabis* sp." in Bulgaria. He dated the find to the late Miocene ("Pontian age", 7.3–5.3 Ma). Dorofeev (1969) reported a fossil seed, "*Cannabis* sp.", from the Miocene in Siberia. He subsequently re-identified 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 labelling bias also arises: Chinese FPS 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 studies of Asian *Cannabis* (*C. sativa* ssp. *indica*) indicate that pollen grain diameter is smaller than that of European hemp (*C. sativa* ssp. *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 threshold 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 FPSs 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). Bottema et al. (2003) specifically mentioned *C–H* pollen in the "problem of long-distance transport". Several FPSs located in south-western Asia had three or fewer *C–H* pollen grains. These rare grains likely blew in from Europe. The Etesian winds blow from the Balkans (harbouring 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 pinpoint the *Cannabis* centre 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 Ma, out of the worldwide Antemideae (Miao et al. 2011). *Cannabis* also evolved in Central/East Asia, ca. 27.8 Ma, 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 travellers; 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*+). Analysing *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), 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 Karolímek 2008; Kim et al. 2010; Oh et al. 2010; Jeong et al. 2012; Lee et al. 2013), *Quercus* (Lee et al. 1976; Kolbek and Karolímek 2008; Kim et al. 2010; Oh et al. 2010), *Robinia* (Lee et al. 1976; Kolbek and Karolímek 2008; Kim et al. 2010; Jeong et al. 2012; Lee et al. 2013; Lee and Ahn 2014), and *Camellia* (Lee et al. 1976; Kim et al. 2010; Lee and Ahn 2014; Eom and Kim 2017).

However, *H. japonicus* sometimes colonizes habitats that overlap with those of *Cannabis.* These include ruderal (Kolbek and Sádlo 1996; Oh et al. 2008) and riverside communities (Jung and Kim 1998). Some riverside communities include Poaceae*, Artemisia,* or Chenopodiaceae in the ground layer (Song and Song 1996; Jarolímek and Kolbek 2006; Balogh and Dancza 2008; Andrek et al. 2010). One phytosociological study reports *H. japonicus* co-localizing with *C. sativa*—a ruderal community in Korea (Kolbek and Sádlo 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 palaeobotanists 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 non-arboreal 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, palynologist have shown that *Alnus* and *PAC* demonstrate oppositional characters (literature in McPartland et al. 2018).

C–H 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 fibres 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 *Cannabis* when it appeared de novo along with crop pollen, or increased at least twofold 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 twofold 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. $\geq$ 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. $\leq$ 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, fibre, 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-analysed seeds, phytoliths, and stem fragments were considered the most robust evidence. Fibre, cordage, and textiles were problematic. For example, Song et al. (2017) unearthed a few plant fibres identified as hemp, *C. sativa,* at a site occupied by Palaeolithic hunter-gatherers that dates to 28.5 ka. This could be the oldest hemp fibre ever found, but their photomicrograph of a "hemp" fibre is by no means convincing. Song et al. (2017) report plentiful flax fibres at their site. McPartland and Hegman (2018) detail the difficulties in differentiating hemp from flax fibre. 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 Ma), Miocene (23.03–5.3 Ma), Pliocene (5.3–2.58 Ma), and Pleistocene (2.58 Ma–11.6 ka) 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 ka, a period of improved climate, re-emerging 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 ka, 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 (r8 s version 1.70), calibrated with four fossil date intervals (*Boehmeria* 60–34 Ma, *Morus* 56–34 Ma, *Celtis* 65–56 Ma, *Humulus* 28–16 Ma). The molecular clock estimated that *Cannabis* and *Humulus* evolved (diverged) 27.8 Ma. This date is bracketed by other estimates: 87.3 Ma (Boutain 2014), 24.8 Ma (Wu et al. 2018), and 18.2 Ma (Zhang et al. 2018b). Most of these estimates predate the oldest *Cannabis* fossil pollen found in this study (19.6 Ma). Molecular-based divergence dates are expected to predate fossil evidence, because fossil records are fragmentary and incomplete (Parham et al. 2012). To deduce the location of *Cannabis* during the temporal "missing link" between the molecular divergence date and the oldest fossil pollen, 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 Ma. 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 palaeogeographic 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 Ma), latest Eocene (34 Ma), early Oligocene (34–28 Ma), Oligocene (34–23 Ma), early Miocene (23–20 Ma), and mid-Miocene (14 Ma).

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 11 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 (ESM Table 1). Excluded studies were also tabulated, with exclusion criteria (ESM Table 2).

Bin 1 (19.6 Ma–11.6 ka, Fig. 1). The oldest *C–H* pollen consistent with *Cannabis* dated to 19.6 Ma (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 ESM Table 1, citation #1. During the Pliocene, *Cannabis* pollen occurs in Northwest China (Ningxia, 2.6 Ma, ESM Table 1, #2). During the first half of the Pleistocene (i.e. the Gelasian and Calabrian ages, 2.58 Ma-781 ka), *Cannabis* pollen is located in Bashkorostan, Russia (1.5 Ma #156), Hebei Province (1.2 Ma #3), and the Russian Altai (787 ka, #4).

During the latter half of the Pleistocene, *Cannabis* pollen appears in four of six Chinese regions: ***Northwest China*** (Shaanxi, 342 ka, #5; Gansu, 145 ka, #6; Shaanxi, 50 ka, #8; Shaanxi, 25 ka, #12; Tibet, 20 ka, #13; Xinjiang, 14.5 ka, #20; Gansu, 12 ka, #28). ***North China*** (Inner Mongolia, 35 ka, #9). ***Northeast China*** (Liaoning, 16 Ma, #16; Jilin, 13 ka, #24). ***East China*** (Shanxi, 15 ka, #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 ka, ESM Table 1 #10); as well as Kazakhstan (130 ka, #152), Southwest Asia (Turkey, 111 ka, #7; Black Sea near Turkey, 17 ka, #152; Caspian Sea near Iran, 14 ka, #23; Georgia, 13 ka, #154; Syria, 11.9 ka, #30); South Asia (India, 32.6 ka, #11; Sri Lanka, 18 ka, #14; India, 12.8–11.9 ka, #25, #26, #27, #29); and Central Siberia (Altai, 16–15 ka, #15, #17, #18).

One FPS in Bin 1 (ESM Table 1, #9) conflicted with our algorithm's designation of a retting-site (*Cannabis* pollen ≥ 15% of TLP). That study reported *C–H* pollen reaching

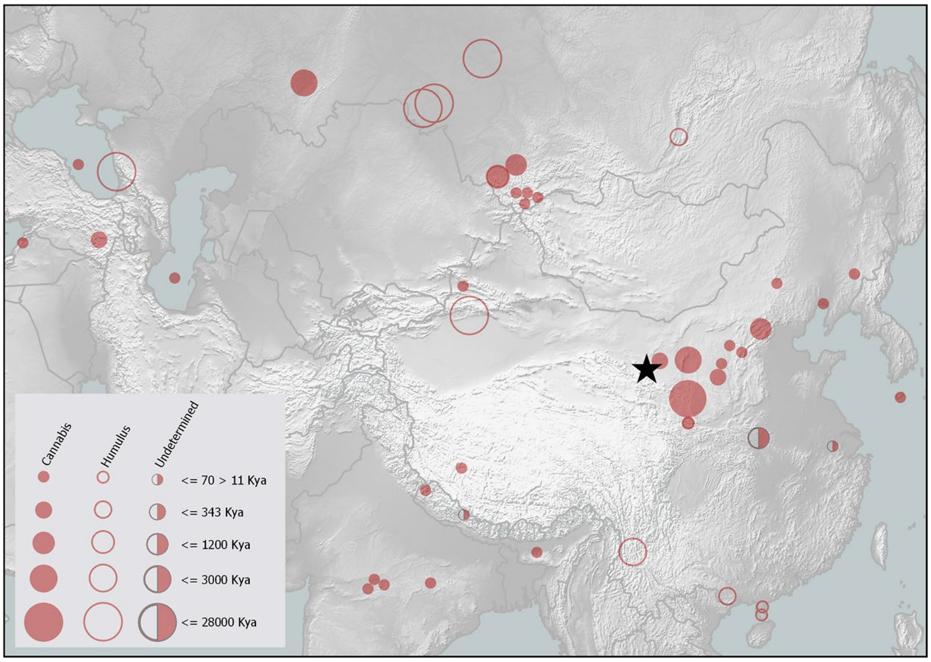

Fig. 1 Bin 1 (19.6 Ma–11.6 ka). Age-weighted geographical centroid for *Cannabis* data is marked by a star. Background base map by Natural Earth, free open-source map data, https://www.naturalearthdata.com

61%, but it was clearly not a retting-site, because it occurred 34 ka, long before agriculture began. The short-lived *C–H* pollen spike was superseded by *Artemisia* reaching 80% of TLP, another unusual finding.

Bin 2 (11.5–5 ka, 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, ESM Table 1 #142) and China (Henan, 7,850 BP, #132). Somewhat younger artifacts are found in Japan (Fukui, 7,200 BP, #144; Aomori, 5,900–4,300 BP, #146), and in China (Hunan, 6,400–5,300 BP, #104; Gansu, 5,000 BP, #109; and Inner Mongolia 5,000 BP, #134).

Bin 3 (4.5–0 ka, 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 11 of those sites, *Humulus* in a forested environment gave way to land clearance and *Cannabis* cultivation, resulting in two symbols at the same site within this time slice.

The oldest sites with pollen suggesting cultivated *Cannabis* are located in the lower Yangtze River basin, dating to 5,330 BP (#125) and 5,000 BP (a retting-site, with 15% TLP, #130). In Northwest China, cultivated *Cannabis* is located in Xinjiang (3,720 BP, #20; 2,600 BP, #129) and Qinghai (3,000 BP, #97). In East China, it appears in Shanxi (2,800 BP, #19). Outside of China, pollen consistent with cultivated *Cannabis* appears in Russia (3,700 BP, #155), Turkey (3,200 BP, #45; 2,300 BP, #153), Korea (3,150 BP, a retting-site, with 25% TLP, #139), and India (2,500 BP, a retting-site, with 28% TLP, #71).

The oldest archaeological sites within this time slice are located in Gansu (5,000–4,700 BP, #108, #110), Qinghai (4,200–3,500 BP, #115, #116), Inner Mongolia (3,900–3,400 BP, #133), Shandong (3,600–3,000 BP, #124), and Xinjiang (2,800–2,500 BP, #135, #136). Outside of China, relatively old sites are found in central Korea (4,590–4,240 BP, #138), the Ganges River basin in India (4,600–3,200 BP, #62–65), Japan (3,500–3,000 BP, #147, #148), Nepal (2,400 BP, #76), and the Russian Far East (2,500 BP, #79).

Extrapolating into the Oligocene

Next we deduced the location of *Cannabis* during the temporal "missing link" between its divergence date (27.8 Ma) and oldest pollen (19.6 Ma), 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 palaeogeographic zone was transferred to a modern map in Fig. 4. The oldest *C–H* pollen consistent with *Cannabis* (site #1) is located at the south-eastern 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

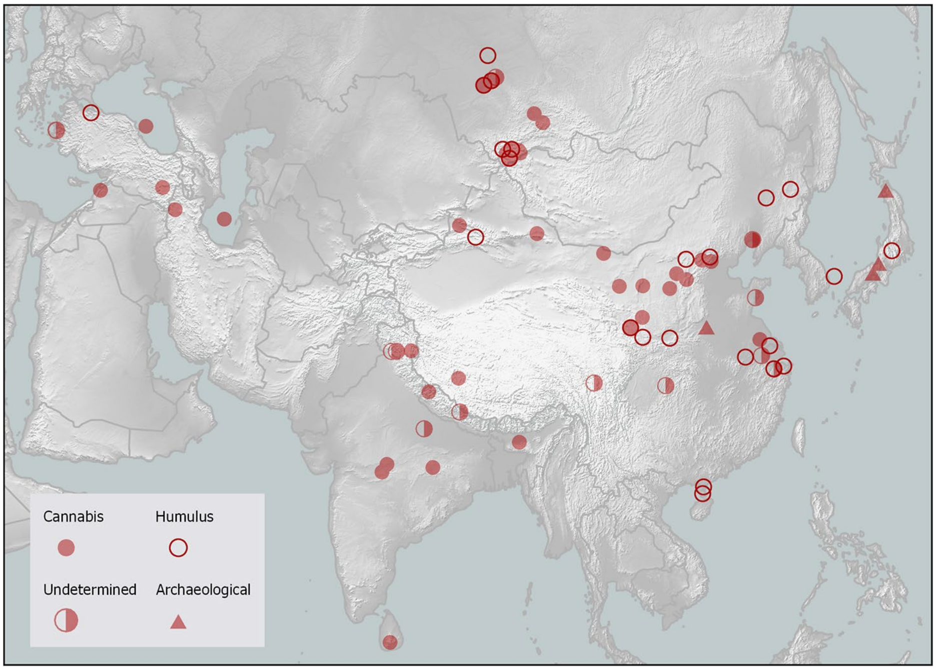

Fig. 2 Bin 2 (11.5–5 ka). Background base map by Natural Earth, free open-source map data, https://www.naturalearthdata.com/

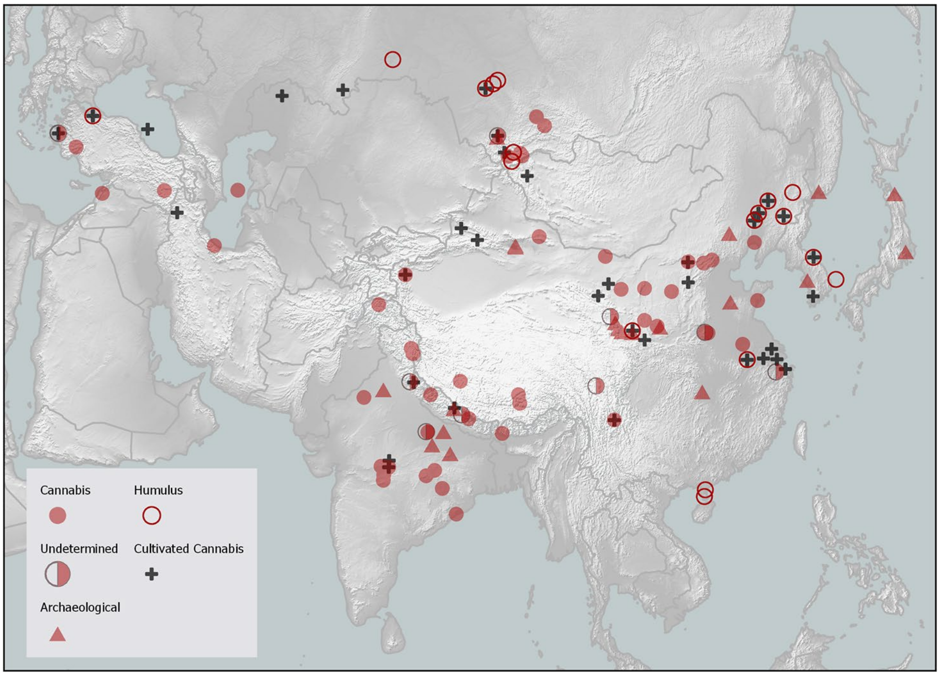

Fig. 3 Bin 3 (4.5–0 ka). Background base map by Natural Earth, free open-source map data, https://www.naturalearthdata.com/

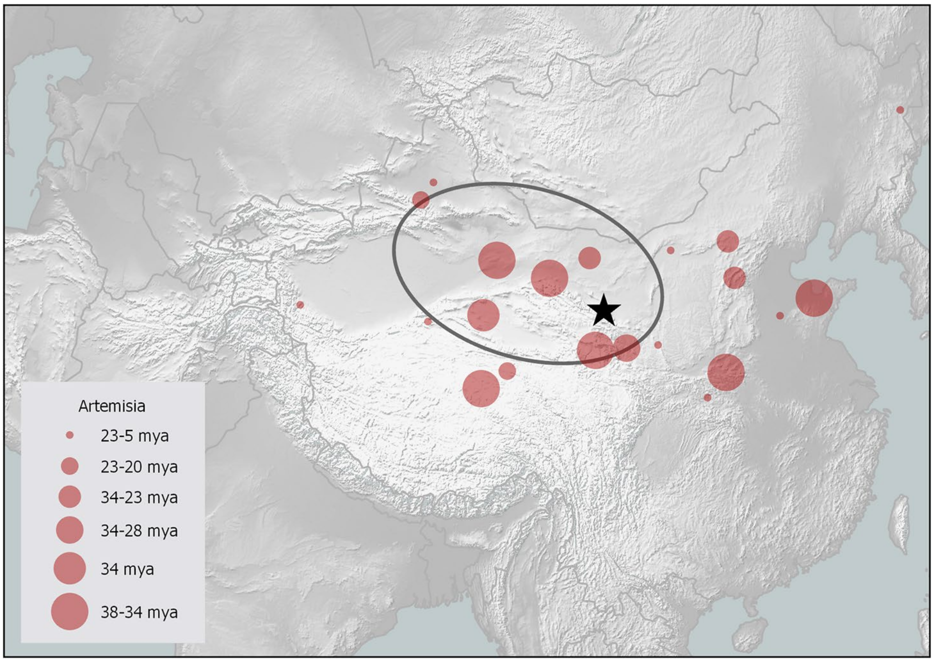

Fig. 4 Black ellipse: aridification zone arising at the Eocene–Oligocene boundary (Bosboom et al. 2011) transferred to a modern map. Age-weighted geographical centroid for *Artemisia* data is marked by a star. Background base map by Natural Earth, free open-source map data, https://www.naturalearthdata.com/

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.

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 climatic requirements of modern *Cannabis, Humulus, PAC,* and *ASP*+ can be extrapolated to past populations—the nearest living relative method (Mosbrugger and Utescher 1997).

Cannabis pollen has an age-weighted geographical centroid located in the north-eastern Tibetan Plateau (Fig. 1). However, the evolution of *Cannabis* predates these data. We applied Miao's *Artemisia* data as a proxy for the location of *Cannabis* during this temporal "missing link". The age-weighted geographical centroid for *Artemisia* pollen is also located in the north-eastern Tibetan Plateau (Fig. 4). Both centroids fall within Bosboom's aridification zone. The oldest *Cannabis* pollen lies at the zone's periphery. Thus, we deduce the centre of origin of *Cannabis*, along with that of *Artemisia,* as the north-eastern Tibetan Plateau, in the general vicinity of Qinghai Lake.

Cannabis expanded westward from its centre of origin. *C–H* pollen consistent with *Cannabis* appeared in central Russia (the cis-Ural region; ESM Table 1, #156) by 1.5 Ma. Further west, a fossil seed (fruit) assigned to *Cannabis* in Bulgaria dated to 7.3–5.3 Ma (Palamarev 1982). *Cannabis* expanded eastward from its centre of origin. 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; Bakshi and Atal 1985; Khuroo et al. 2007). The introduction of non-native *Humulus* was also reported in Pakistan (Steward 1971), Nepal (Sood and Thakur 2015), and Burma (Kress et al. 2003). Floras of Bangladesh and Thailand omit *Humulus* (Khan and Halim 1990; Santisuk and Balslev 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 (ESM Table 1, #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 ≤ 0.5 (#71). 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 ESM Table 1, #60).

Whether *Cannabis* is native to South Asia, versus an introduced species, is a long-standing debate (Watt 1889; Hooker 1890). Experts still argue whether Himalayan *Cannabis* 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 ka, which suggests an indigenous species.

Cannabis in South Asia by 32.6 ka begs the question of when it actually arrived. Early floristic exchanges between India and Asia were shaped by plate tectonics. As the Indian plate migrated towards the Asian plate, it made a "glancing contact" with Sumatra 57 Ma, followed by Burma, and then a "hard collision" with Tibet 35 Ma (Ali and Aitchison 2008). The glancing contact between continents resulted in floristic exchanges during the Eocene (Bande 1992; Morley and Dick 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 Ma, which was the primary cause of Bosboom's aridification zone. The Tibet uplift, followed by the Pamir uplift (35 Ma) created a dispersal barrier between Central Asia and India. Perhaps the biogeographical dispersal patterns of related plants, which we discuss below, might reveal how *Cannabis* hurdled the dispersal barrier into South Asia.

In contrast to the north-eastern Tibetan Plateau as the centre of origin of *Cannabis*, Zhang et al. (2018b) offered "low latitude" China as the centre of origin. Their estimate was based on genetic variation in cpDNA sequences of 52 extant *Cannabis* accessions. Spatial analysis of molecular variance (SAMOVA) determined the optimal number of haplogroups to divide the accessions; the data best fit K = 3. Phylogenetic tree topology placed the "L" (low latitude) haplogroup basal to the other haplogroups, 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 south-eastern fringe of the Tibetan Plateau, so our estimation of the *Cannabis* centre of origin differs little from that of Zhang et al. (2018b).

The south-eastern fringe of the Tibetan Plateau, however, was the last sector uplifted, ca. 8 Ma (Xing and Ree 2017). Prior to that, low altitude China was warmer and wetter than today, and covered by subtropical broad-leaved forests (Sun et al. 2011; Huang et al. 2016). We suggest 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).

The south-eastern fringe of the Tibetan Plateau is called the Henduan Mountains. Clarke and Merlin (2013) proposed a Pleistocene glacial refugium in the Henduan Mountains. Congruent with this, Zhang and colleagues estimated a *Cannabis* crown date (divergence of the three haplogroups) of 2.24 Ma—the early Pleistocene. Given this scenario, the "L" haplogroup should have expressed the greatest π (nucleotide diversity). Instead, greatest π was expressed by the "M" haplogroup, whose accessions primarily came from Xinjiang (n = 5) and Tibet/Qinghai (n = 4). Disparity between stem age and crown age is exampled by *Ginkgo biloba*, with uncertain range dynamics arising from cpDNA sequences of extant relictual populations (Hohmann et al. 2018).

Turning to cultivated *Cannabis,* the oldest pollen signal identified by our methods dated to 5,330 BP (ESM Table 1, #125). 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).

Archaeological findings (seeds) predate 5,330 BP. Perhaps the seeds were collected from wild-type *Cannabis*. A Jōmon Culture site yielded the oldest seeds (ESM Table 1 #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 fibre is not easily extracted from wild-type growth, which branches excessively. Densely sown crops, with minimal branching, yield the best fibre. The clearest palynological signal of fibre use comes from FPSs with *Cannabis* pollen ≥ 15% of TLP, indicative of a retting-site. The oldest retting-site, dating to 5,000 BP, is located in the Yangtze River delta (ESM Table 1, #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 fibres (excluded in this study)—dates to 5,600 BP, in Henan (Zhang and Gao 1999). Intact rope and cloth dates to 5,000 BP, in the Yangtze River delta (Zhou 1980).

Archaeological evidence of ceremonial or drug use dates to 2,700 BP, in Xinjiang (ESM Table 1, #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 centre of origin (Crisci et al. 2003). The *Humulus* centre 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 a tall canopy tree limited to China and Mongolia. A phylogeographical reconstruction of 28 extant populations identified southern China as the species's centre of origin (Li et al. 2012). 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 *C. aspera*, 64–56 Ma) 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* centre 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 Ma (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 Ma, and into South Asia by 18.1 Ma. 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 *Cannabis* resembles that of *H. lupulus*, except *Cannabis* 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 north-eastern 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 south-eastern 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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