

Bitter gourd from Africa expanded to Southeast Asia and was domesticated there: A new insight from parallel studies

Susanne S. Renner^{a,1}

Matsumura et al. (1) report a chromosome-level genome assembly of Momordica charantia, an important vegetable and medicinal plant in the family Cucurbitaceae, and then use resequencing to infer the divergence between wild samples with "[var.] muricata-type morphology" and cultivated samples (var. charantia). The initial domestication was dated to 6,000 y ago, followed by the separation of further cultivars 800 y ago. A parallel study by Cui et al. (2) (with partly overlapping authorship) instead inferred that wild bitter gourds and the lineage that gave rise to var. muricata and var. charantia diverged ~1.9 Mya (ref. 1, figures 2c and S10), while the split between muricata and charantia is again dated to ~6,000 y ago. The ~1.9-Mya-old wild lineage, called TR group, has seeds barely one-half the size of var. muricata and var. charantia seeds (Fig. 1).

Why these contrasting inferences? Matsumura et al. (1) included 44 cultivated bitter gourds from Asia and 1 from Belize, plus 15 supposedly wild accessions from Taiwan, Thailand, and the Philippines. No material is illustrated or vouchered in an herbarium, and some accessions (e.g., THMC170) are labeled as wild in the phylogenies but as cultivar in table S5. Cui et al. (2) included 187 accessions from Asia, Africa, and South America, and rooted their phylogeny on two African species. Including African material was important because *M. charantia* occurs wild in Africa, Madagascar, and India (and naturalized in many tropical regions; refs. 3 and 4), and is used as a medicinal plant and as a vegetable in Africa, too (3). Seeds of a wild accession from Tanzania are indistinguishable from wild Asian bitter gourds (Fig. 1, TR-8).

The studies use similar methods to infer divergence times, with a mutation rate per generation of either 2 x 10^{-8} (1) or 1 x 10^{-8} (2). The specific method used in ref. 1 assumes the absence of gene flow, which is problematic given that the study discovered admixture.

Such different conclusions in parallel work on the same species underscore the importance of geographic sampling that builds on existing taxonomic insights. Thus, an origin of M. charantia in Africa and natural dispersal to Asia was inferred in molecularphylogenetic work that included all 60 species of Momordica, most of which are endemic in Africa (4). The data brought forward so far (1) provide neither convincing evidence that the domestication of bitter gourd was "nonclassic" nor, indeed, that a quantitative trait locus said to affect the ratio of male to female flowers has found its way from cultivars back into wild populations. Neither inference can be drawn because it is unclear whether any truly wild populations were sampled. An insight from the combined studies, however, is that bitter gourd domestication first occurred in Asia. This is implied by the presence there of wild plants that completely match African wild plants (Fig. 1, TR-8). This now answers the question (5) whether bitter gourd more likely was first domesticated in Africa or in Asia.

^aSystematic Botany and Mycology, Faculty of Biology, Ludwig Maximilian University Munich, 80638 Munich, Germany Author contributions: S.S.R. designed research, performed research, analyzed data, and wrote the paper.

The author declares no competing interest.

This open access article is distributed under Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 (CC BY-NC-ND). ¹Email: renner@lmu.de.

First published September 29, 2020.



Fig. 1. The seeds of *Momordica charantia*, with those of the TR group on the *Left*, those of var. *muricata* in the *Middle*, and those of var. *charantia* on the *Right*. (Scale bar: 1 cm.) The seeds TR-8 are from wild Tanzanian material, while the remaining TR seeds are from Thailand (TR-2, TR-4, and TR-5), China (TR-9 and TR-10), Taiwan (TR-3), the Philippines (TR-1), and Columbia (TR-6 and TR-7). The seeds in the *Middle* are mostly from India and Nepal, except for Mu-8, Mu-9, and Mu-10 from Thailand, Vietnam, and China. The seeds on the *Right* are from India, Vietnam, China, and the Philippines, and Ch-7 is from cultivated Tanzanian bitter gourd plants. Reproduced from ref. 2, which is licensed under CC BY 4.0.

- 1 H. Matsumura et al., Long-read bitter gourd (Momordica charantia) genome and the genomic architecture of nonclassic domestication. Proc. Natl. Acad. Sci. U.S.A. 117, 14543–14551 (2020).
- 2 J. Cui et al., Whole-genome sequencing provides insights into the genetic diversity and domestication of bitter gourd (Momordica spp.). Hortic. Res. 7, 85 (2020).
- 3 E. Achigan-Dako, S. Ndanikou, A. Ahanchede, J. Ganglo, F. Blattner, Phenetic analysis of wild populations of *Momordica charantia* L. (Cucurbitaceae) in West Africa and inference of the definition of the new subspecies *macroloba* Achigan-Dako & Blattner. *Candollea* 63, 153–167 (2008).
- 4 H. Schaefer, S. S. Renner, A three-genome phylogeny of Momordica (Cucurbitaceae) suggests seven returns from dioecy to monoecy and recent long-distance dispersal to Asia. Mol. Phylogenet. Evol. 54, 553–560 (2010).
- 5 G. Chomicki, H. Schaefer, S. S. Renner, Origin and domestication of Cucurbitaceae crops: Insights from phylogenies, genomics and archaeology. New Phytol. 226, 1240–1255 (2020).