

## A Gift from the New World? The West African Crop *Cucumeropsis mannii* and the American *Posadaea sphaerocarpa* (Cucurbitaceae) are the Same Species

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**Abstract**—The biogeographical history of several important vegetables is still unclear. In the gourd family, Cucurbitaceae, this applies to melon and cucumber, but also to many species of more regional importance. *Cucumeropsis mannii* is cultivated in West Tropical Africa for its nutritious seeds. Family-wide phylogenetic analyses suggested that it is closest to *Posadaea sphaerocarpa* from Central and South America, the seeds of which are also eaten and the fruit of which is made into bowls. To reconstruct these species' historical biogeography, we sequenced six plastid markers and the nuclear ribosomal ITS region for several accessions of both species, plus all relevant outgroups. Morphological traits were studied in 102 herbarium specimens representing both species. A 5,155 nucleotide-long matrix of chloroplast and nuclear DNA contained a single informative mutation in a poly-C region of nuclear ITS among six accessions that covered the species' native ranges. Next-closest species differed in all plastid markers and by  $\geq 34$  mutations in ITS1 and ITS2. Study of the morphology revealed a possible small difference in fruit shape (cylindrical-ovate versus spherical), presumably resulting from human selection on the African populations. The closest outgroups *Melanium* and *Melothria* are endemic to the neotropics, and maximum likelihood area reconstruction indicates that *Cucumeropsis mannii* also originated there. The near-absence of genetic and morphological differentiation implies that gene flow between *Cucumeropsis mannii* and *Posadaea sphaerocarpa* stopped relatively recently, and taxonomically they should (or could) be treated as one species. Transport of seeds during the transatlantic slave trade is a possible scenario, although we cannot reject natural dispersal.

**Keywords**—Benincaseae, DNA barcoding, egusi, long distance dispersal, molecular phylogenetics, oil-rich seeds.

The gourd family (Cucurbitaceae) comprises some of the most important vegetables of Western cultures, including melon (*Cucumis melo* L.), cucumber (*C. sativus* L.), pumpkin (*Cucurbita pepo* L.), and chayote (*Sechium edule* (Jacq.) Sw.), but also a range of traditional crops in Native American, Asian, and African cultures. Among the latter is the West African *Cucumeropsis mannii* Naudin. In Sub-Saharan Africa, *C. mannii* is prized for its oleaginous seeds that, together with seeds of *Citrullus* Schrad. and *Cucumis* L. species, are used to thicken a traditional soup called "egusi soup" in Cameroon, Nigeria, and Benin, and "pistachio soup" in Côte d'Ivoire (Zoro Bi et al. 2003; Koffi et al. 2008). In Bas-Congo province (D. R. Congo), a traditional dish is made of *Cucumeropsis* seeds and caterpillars, grasshoppers, shrimp, or winged ants (Adriaens 1951). The composition and nutritional value of *C. mannii* seeds have been analyzed in numerous studies (e.g. Mbuli-Lingundi et al. 1983; Badifu and Ogunsua 1991; Kapseu and Parmentier 1997; Zoro Bi et al. 2003; Osuji et al. 2006); up to 36% of the seed weight consists of protein and up to 50% consists of fat (Okoli 1984; Koffi et al. 2008). The species is well adapted to cropping systems characterized by minimal inputs (Zoro Bi et al. 2003).

Like *Cucumeropsis*, the South American *Posadaea* comprises a single species, but different from the African crop, *P. sphaerocarpa* Cogn. has received no attention from chemists and agronomists, and only limited attention from ethnobotanists (Patiño 1964; Piperno et al. 2000). A study of Wayãpi people from the Tupi-Guarani language group (in French Guiana and extending into northern Brazil) reports that according to myth *P. sphaerocarpa* was brought to the Wayãpi people by a shaman as a gift from another world (Grenand 2001/2002). The seeds of *Posadaea sphaerocarpa* are also eaten roasted and even the fruit is eaten sometimes, but mostly serves as bowls (Table 1). The species is treated in several floras and is well collected compared to other neotropical species of the family

(Wunderlin 1978; Jeffrey and Trujillo 1992; Delascio Chitty and Reyes López 2007).

*Cucumeropsis* and *Posadaea* are similar in morphology, but since there is no modern revision of the Cucurbitaceae, the two species were never directly compared. However, Charles Jeffrey (St. Petersburg), the only living taxonomist to have worked on Cucurbitaceae worldwide, expressed doubt as to whether the two species should be placed in separate genera (Jeffrey 1967: 117). The question of the best generic disposition of *Cucumeropsis* and *Posadaea* arose again some 30 yr later, when we compared them for a global treatment of the Cucurbitaceae (Schaefer and Renner, in press). As with other isolated species long forgotten by systematists (Schaefer et al. 2008), family-wide DNA sequencing led to unexpected insights also about *Cucumeropsis* and *Posadaea*. For the three most promising plant barcoding markers, *rbcL*, *matK* and *trnH-psbA*, an accession of *Cucumeropsis mannii* from the Congo basin and one of *Posadaea sphaerocarpa* from Venezuela yielded identical sequences (Kocyan et al. 2007; Schaefer et al. 2009).

DNA barcoding is often used to detect cryptic species and sometimes even thought to result in an artificially inflated number of species (Hansen et al. 2007). The combination of two or three of these markers in other Cucurbitaceae clades provided excellent phylogenetic signal (e.g. Kocyan et al. 2007; Schaefer et al. 2009, Schaefer and Renner 2010; Nee et al. 2010), and it therefore was surprising that they would fail to distinguish samples from different genera, whose geographic ranges are separated by the Atlantic Ocean. We thus obtained additional samples from South America and tropical Africa and studied over 100 herbarium collections to find out if material had been misidentified or confused, if the barcodes fail in this case, or if the African crop and the neotropical entity represent a single species. Anthropogenic dispersal across the trans-Atlantic, perhaps with slave ships or modern

TABLE 1. Local names and uses of the crops known as *Cucumeropsis mannii* in Africa and *Posadaea sphaerocarpa* on the American continent (information from specimen labels in the herbaria listed in Materials and Methods; specimens seen are listed in Appendix 2).

Vernacular name	Tribe/Language	Country	Use
White Egusi	Creole	Sierra Leone	Roasted seeds eaten; dry fruit blown as horn
Ma-Tent-M-Temne	Temne	Sierra Leone	Unknown
Koja-Mumui	Mende	Sierra Leone	Unknown
Kō-Sa	Kono	Sierra Leone	Unknown
Sāhū-Tuntun-de	Sherbro	Sierra Leone	Unknown
Ito	Unknown	Nigeria	Roasted seeds eaten
Nzaka	Nzebi?	Gabon	Unknown
Teri	Bapounou?	Gabon	Unknown
N'viélé	Unknown	Ivory Coast	Unknown
Bora axi	Yanomami	Brazil (Amazonas)	Fruit eaten
Jamaru	Canamarís	Brazil (Amazonas)	Unknown
Jere'a	Ka'apor	Brazil (Maranhão)	Dry fruit used as bowls
Yeluapapa	Wayãpi	French Guyana	Roasted seeds eaten
Jo-Macam	Kekchí	Guatemala	Dry fruit used as bowls
A'ha	Piaroa	Venezuela	Dry fruit used as bowls
Falada	Makiritari	Venezuela	Unknown
Taparo de choco	Unknown	Venezuela	Unknown
Taparilla	Unknown	Venezuela	Dry fruit used as bowls
Tarralí	Spanish	Colombia	Dry fruit used to hold coca leaves & chalk
Brujito	Spanish	Panama	Unknown

transport, has been suggested for at least some of the 108 species of angiosperms that occur on both sides of the Atlantic (Thorne 1973; Renner 2004), and for nonweedy and useful species, such as *Cucumeropsis mannii* and *Posadaea sphaerocarpa*, it seemed worth testing. We also used formal biogeographic reconstruction (using likelihood optimization) to infer the direction of spread between tropical America and Africa.

#### MATERIALS AND METHODS

**Morphology**—One-hundred-and-two herbarium specimens from BM, BR, E, K, M, MO, P, W, WU, and WAG were obtained on loan or studied during herbarium visits. In addition, seeds of African origin were obtained from the USDA germplasm bank and five plants cultivated at Munich botanical gardens in 2007/2008. Measurements were taken from cultivated plants and herbarium specimens.

**Sampling and DNA Extraction**—We chose four samples of African *Cucumeropsis mannii* and three samples of South and Central American *Posadaea sphaerocarpa* for DNA extraction. Based on a family-wide phylogeny that included all but one genus of Cucurbitaceae (Schaefer et al. 2009), the closest outgroups of *Cucumeropsis* and *Posadaea* are *Melothria* L., *Indomelothria* W. J. de Wilde & Duyfjes, and *Melanium* Naudin. We included two to four species of the larger of these genera and the single species of the monotypic genus *Melanium*. Trees were rooted with the West African *Ruthalicia* C. Jeffrey (Schaefer et al. 2009). Total genomic DNA was isolated from herbarium specimens or from silica-dried leaves of cultivated plants following standard procedures described in Kocyan et al. (2007). Amplification and sequencing of the *rbcl*, *matK*, *trnL*, *trnL-trnE*, *rpl20-rps12*, *trnH-psbA*, and ITS1–5.8S–ITS2 regions followed standard protocols. Primers used are given in Kocyan et al. (2007) and Schaefer et al. (2009). Fifty-five sequences were generated for this study. Appendix 1 lists the relevant taxonomic names with authors, plant sources, and GenBank accession numbers.

**Sequence Alignment and Phylogenetic Analyses**—Sequences were edited with Sequencher (4.9; Gene Codes, Ann Arbor, Michigan) and aligned by eye in MacClade 4.08 (Maddison and Maddison 2005) following the similarity criterion (Simmons 2004). The aligned plastid matrix comprised 4,388 nucleotides, the aligned ITS matrix 767 nucleotides with a total of 25% gaps or missing data in the combined alignment.

Equally weighted parsimony analyses for matrices of nucleotides were conducted using PAUP\* 4.0b10 (Swofford 2002). The search strategy involved 100 random addition replicates with TBR branch swapping, saving all optimal trees. Gaps were treated as missing data. To assess node support, parsimony bootstrap analyses (Felsenstein 1985) were performed using 1,000 replicate heuristic searches, each with 10 random addition replicates and TBR branch swapping, saving all optimal trees.

Maximum likelihood (ML; Felsenstein 1973) tree searches and ML bootstrap searches were performed using RAxML 7.0.3 (Stamatakis et al. 2008). Based on the Akaike Information Criterion (Akaike 1974) as implemented in jModeltest (Posada 2008) we selected the GTR +  $\Gamma$  model (six

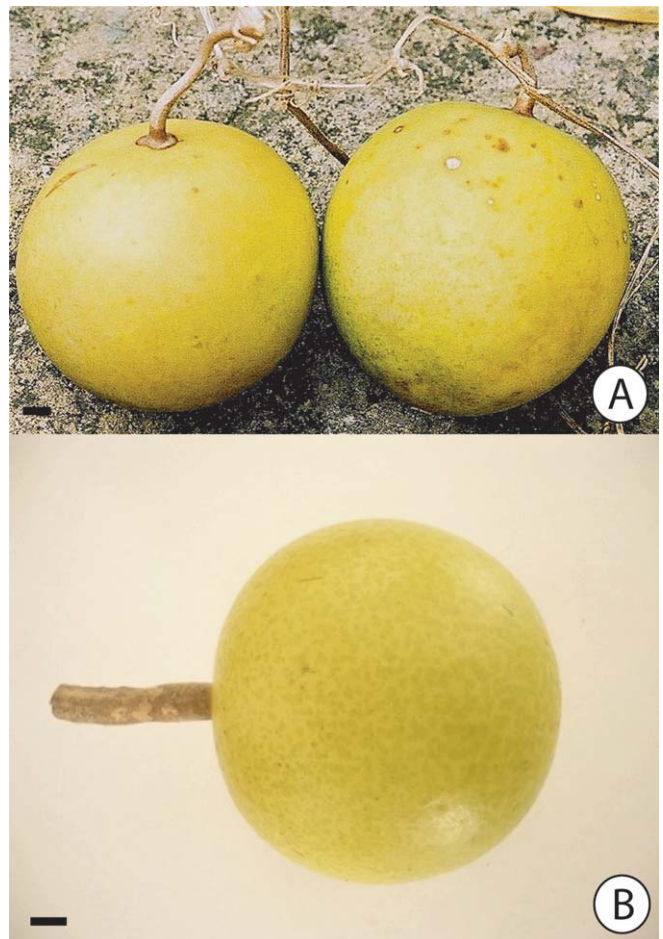


FIG. 1. A. Mature fruits of *Cucumeropsis mannii* cultivated in Bas-Congo province (D. R. Congo). B. Mature fruit of *Posadaea sphaerocarpa* collected in Ecuador (scale bars 1 cm; photos 1A: P. Latham; 1B: N. Gerstl).

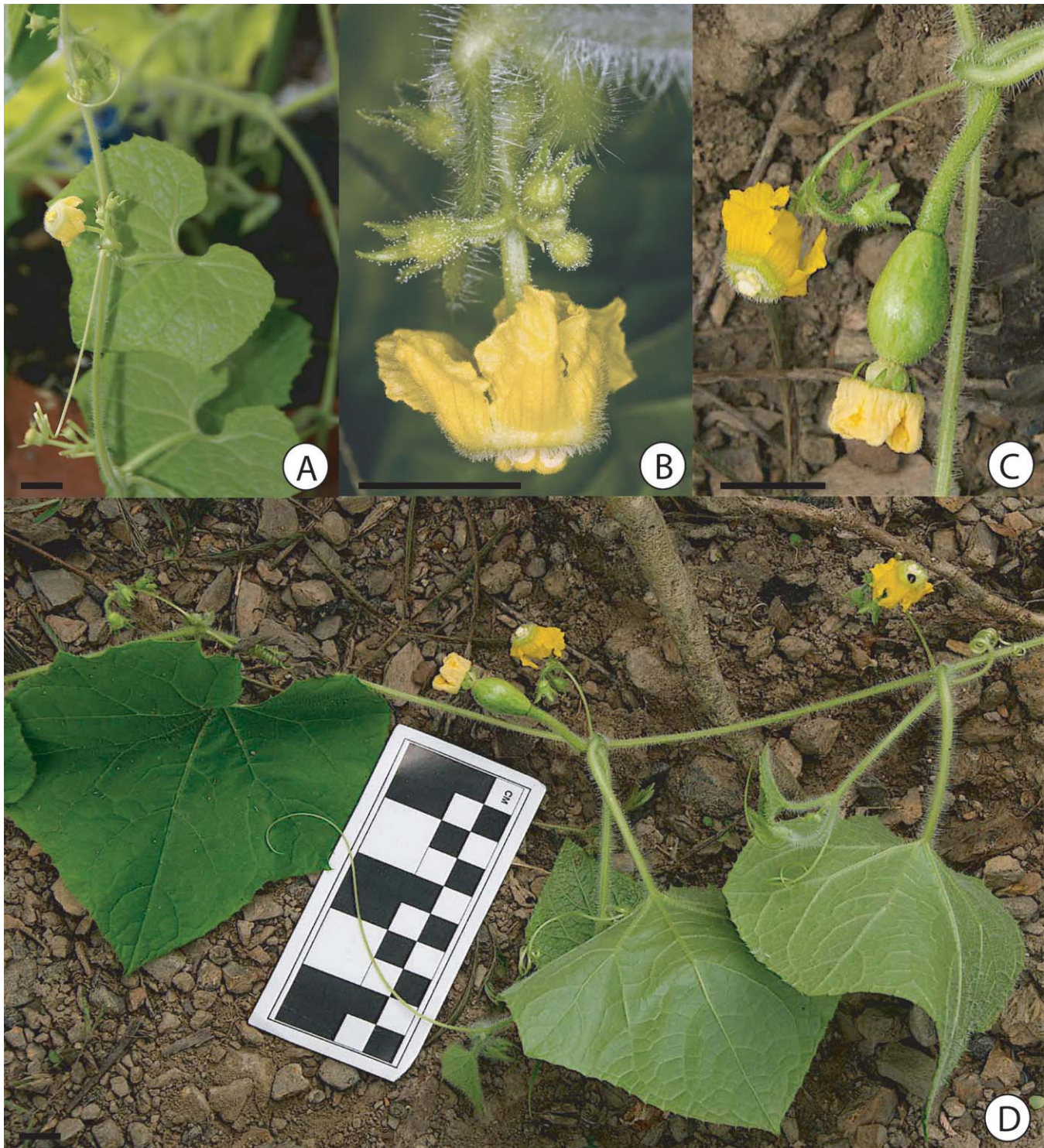


FIG. 2. A. Habitus of *Cucumeropsis mannii* cultivated at the Munich Botanical Garden from seeds collected in D. R. Congo (USDA-PI532721). B. Detail of male flower of the same plant as in (A). C. *Posadaea sphaerocarpa* collected in Venezuela, detail of male and female flowers. D. Habitus of the same plant as in (C) (scale bars 1 cm; photos 2A: H. Schaefer; 2B: B. O. Schlumpberger; 2C, 2D: T. C. Andres).

general time-reversible substitution rates, assuming gamma rate heterogeneity), with model parameters estimated over the duration of specified runs. Analyses in RAxML were run both with the combined unpartitioned data and with a model that partitioned the plastid data from the ITS data.

Bayesian MCMC inference (Yang and Rannala 1997) used the GTR +  $\Gamma$  model (with the default four rate categories) plus a proportion of invariable sites and relied on MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001).

Markov chain Monte Carlo (MCMC) runs started from independent random trees, were repeated twice, and extended for five million generations, with trees sampled every 100th generation. We used the default priors in MrBayes, namely a flat Dirichlet prior for the relative nucleotide frequencies and rate parameters, a discrete uniform prior for topologies, and an exponential distribution (mean 1.0) for the gamma-shape parameter and branch lengths. Convergence was assessed as in our earlier studies (e.g. Schaefer and Renner 2010).



FIG. 3. Seeds of *Cucumeropsis mannii* ('white egusi') collected in D. R. Congo - USDA-PI532721 (scale bar 1 cm; photo: H. Schaefer).

The data matrix and trees have been deposited in TreeBASE (study number S10330).

**Biogeographic Analysis**—To reconstruct the biogeographical history of *Cucumeropsis* and *Posadaea*, we coded species' geographic ranges as an unordered multistate character, using the following character states: (i) Southeast Asia, (ii) West Africa, (iii) Central and Tropical South America. We then imported the highest likelihood tree with branch lengths into Mesquite 2.72 (Maddison and Maddison 2009) and used the Markov k-state one-parameter model (Lewis 2001), which assumes a single rate for all character state transitions to infer the probabilities of shifts between biogeographic regions.

## RESULTS

**Morphology**—The comparison of herbarium material and the original descriptions for *Cucumeropsis* (Naudin 1866) and *Posadaea* (Cogniaux 1890) did not yield any morphological differences between the two taxa with the possible exception of fruit shape. While mature African fruits are usually described as cylindrical-ovate and longer than wide, American material seems to be mostly spherical. However, at least some of

the African fruits are also spherical (Fig. 1A), and fruit shape varies considerably in cultivated cucurbit species (e.g. Paris 1989). Unfortunately, cucurbit fruits are poorly represented in herbaria, therefore preventing a statistical analysis of the shape differences.

*Cucumeropsis* and *Posadaea* are monoecious annual herbaceous climbers or trailers that grow 2–5 m long. The leaves are simple, petiolate, the blade broadly ovate, unlobed (Fig. 2A, D) or palmately five-lobed, with characteristic, unpleasant odour. The tendrils are usually simple (rarely bifid) and solitary (rarely two per node). Based on a family-wide molecular phylogeny, *Cucumeropsis* and *Posadaea* belong in the Benincaseae, where they appear to be embedded in *Melothria* (Schaefer et al. 2009; Schaefer and Renner, in press).

The small flowers are borne in few-flowered racemes or umbels (male) or solitary in the leaf axils (female). The receptacle-tube is campanulate. Each flower has five sepals and petals and three stamens. The sepals are lanceolate, 2–3 mm long and green, while the petals are 3–7 mm long, fused at the base, reflexed, and bright yellow (Fig. 2B,C). The stamens are inserted halfway up the receptacle-tube on free filaments. Two of the three anthers are bitheous; one is monotheous. The thecae are straight, apically hooked, and fringed with hairs. The pollen is large (polar axis 51–67  $\mu\text{m}$ , equatorial axis 62–69  $\mu\text{m}$ ), 3-colporate, reticulate (Khunwasi 1998). The female flowers have a cylindrical ovary, a single three-lobed stigma and three short staminodes. The fruit is fleshy, spheroid or cylindrical-ellipsoid, up to 20 cm long, indehiscent, smooth, ripening cream, and often has paler green stripes or markings (Fig. 1A, B). Each fruit holds ca. 250–300 ovate, compressed, oil-rich seeds (Fig. 3) with smooth, white testa.

Chromosome counts have been published only for African material, where Osuji et al. (2006) found a diploid number of 24.

**Distribution and Habitat**—The northernmost American collections come from the Dominican Republic and Guatemala, the southernmost ones from Bolivia (Fig. 4, Appendix 2: Collections seen). In Africa, most collections come from tropical and subtropical West and Central Africa (Ivory Coast, Sierra Leone, Nigeria, Democratic Republic of Congo) with single collections from Uganda and Zambia (both cultivated plants). Little is known about the natural habitat in Africa and tropical America. The majority of herbarium collections seem

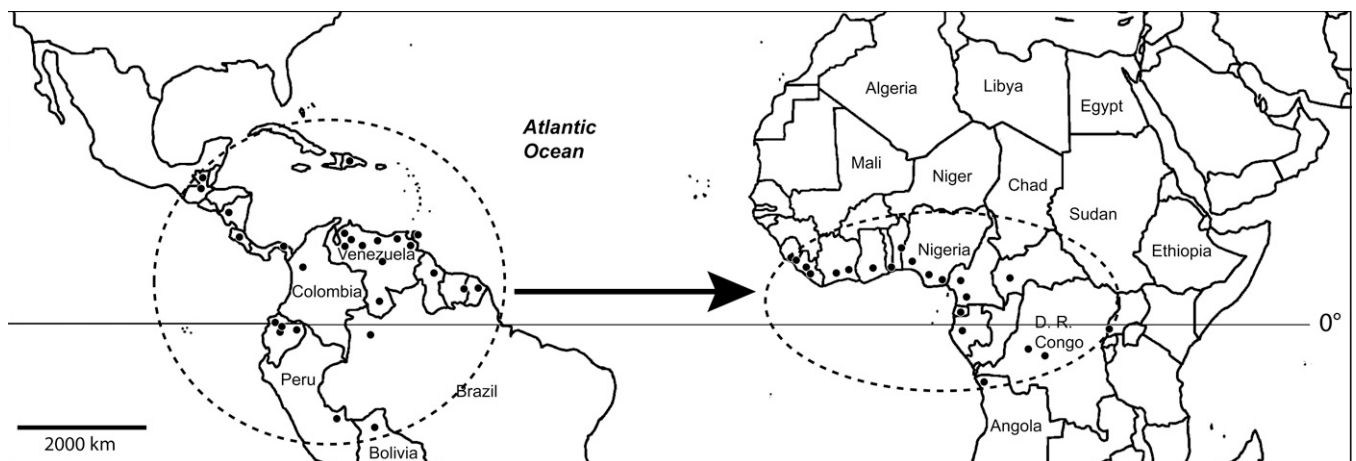


FIG. 4. Geographic range of *Cucumeropsis mannii*/*Posadaea sphaerocarpa* (African and American range). Black dots indicate studied herbarium specimens. The arrow shows the presumed direction of the human-mediated transport across the Atlantic.

—0.0010

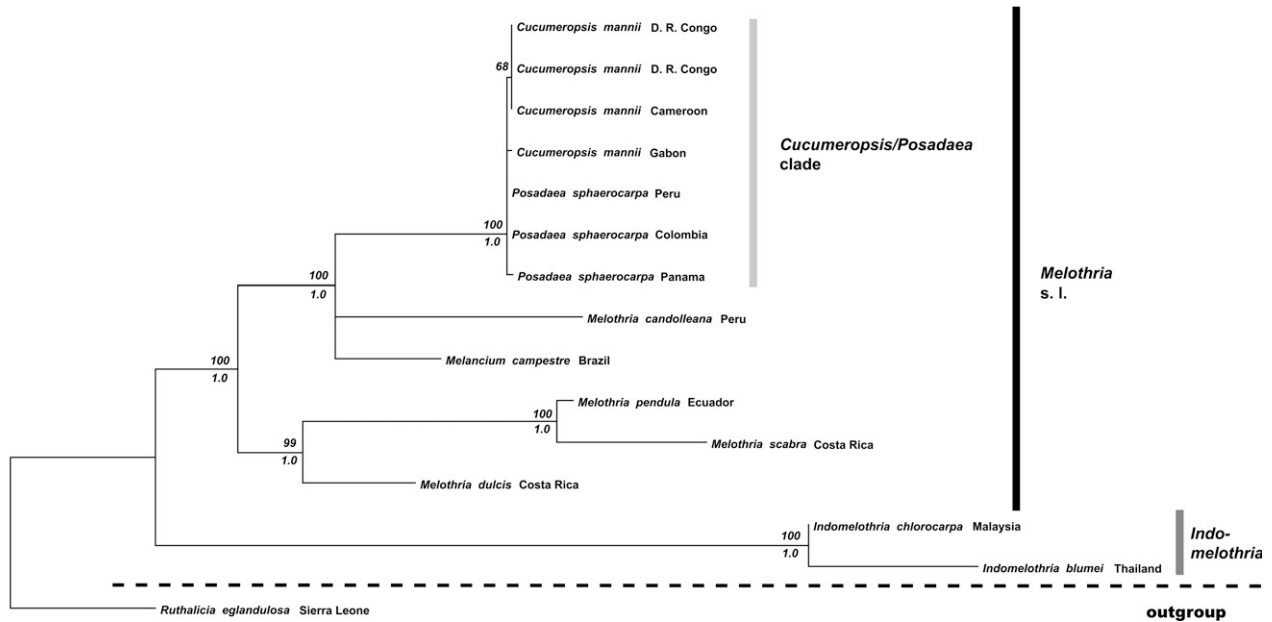


FIG. 5. Maximum likelihood phylogram of combined plastid and ITS sequences (5,155 nucleotides) analyzed under the GTR +  $\Gamma$  model. Likelihood bootstrap support values > 60% are given above the nodes, Bayesian posterior probability values > 0.95 below the nodes.

to come from cultivated material or from riverside thickets, forest edges, or roadsides in forest from 250–1,200 m.

**Phylogenetic Analyses**—The analyzed *Cucumeropsis* and *Posadaea* samples were identical except for a poly C region at the 5' end of the ITS2 region, which is composed of six cytosines in the three *Cucumeropsis* samples but seven cytosines in the three *Posadaea*. Other substitutions characterized single African or American accessions. A 35-nucleotide inversion was found in the *trnL-F* spacer region of one *Cucumeropsis* sample and a poly-A region in the *trnH-psbA* spacer varied from eight nucleotides (in three of the four *Cucumeropsis* samples) to nine (one *Cucumeropsis*, two *Posadaea*) to ten (one *Posadaea*). All analyses (MP, ML and Bayesian) produced a single *Cucumeropsis* and *Posadaea* clade with all accessions from Africa and America (Fig. 5). The *Cucumeropsis/Posadaea* clade was nested in a grade of *Melothria* and *Melancium* species. The sister group to all these species is the Southeast Asian *Indomelothria*.

**Biogeographic Analyses**—The geographic origin of the African *Cucumeropsis* is unambiguously reconstructed as American (Fig. 6). For the deepest nodes in the phylogeny, however, an African or Asian character state becomes also likely as expected from the Asian sister group of the *Melothria* + *Melancium* + *Cucumeropsis/Posadaea* clade and the African outgroup, *Ruthalicia*, used to root the tree.

#### DISCUSSION

Morphological and phylogenetic data show that *Cucumeropsis mannii* and *Posadaea sphaerocarpa* must be placed in the same genus if the goal is a maximally informative classification of Cucurbitaceae. The single nucleotide difference in a poly-C region of the nuclear ITS2 intergenic spacer also hardly justifies species-level rank for *Cucumeropsis mannii* and *Posadaea sphaerocarpa*. In all well sampled cucurbit species (i.e.

sequenced for several accessions: *Cucumis*, Renner et al. 2007; *Bryonia*, Volz and Renner 2009; *Melothria*, H. Schaefer, unpublished data), ITS sequences vary slightly within species, but much more between species, so that ITS is useful for

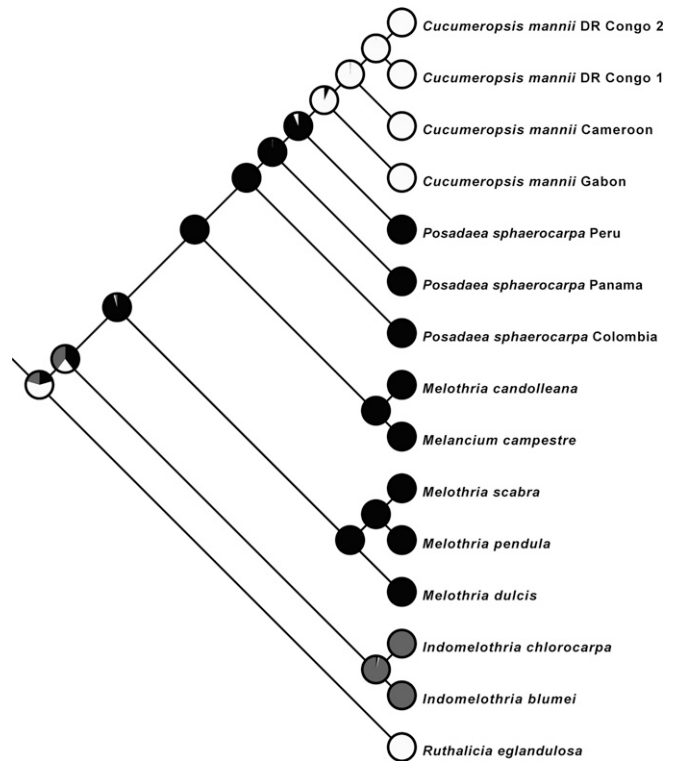


FIG. 6. Ancestral area reconstruction for *Cucumeropsis mannii* and its relatives on the preferred ML tree (Fig. 3 using maximum likelihood optimization and a one-rate model (character states: West Africa – white, Southeast Asia – grey, Tropical America – black).

species-level phylogenetics. The observed inversion in the *trnL-F* spacer region of a single accession of *Cucumeropsis mannii* is known from other cucurbit species (Kocyan et al. 2007) and so far is uninformative in our ingroup. Following a genealogical species concept (Baum and Shaw 1995), one could therefore treat the African and American populations as representing a single taxonomic species, perhaps with two subspecies. In this case, the name *Posadaea* Cogniaux (1890) would become a synonym of *Cucumeropsis* Naudin (1866). Another taxonomic issue is that in their current circumscription, the genera *Cucumeropsis* (*Posadaea*) and *Melancium* render *Melothria* paraphyletic (Fig. 5), so that all these genera are probably best included in a more broadly circumscribed *Melothria* (as done in Schaefer and Renner, in press).

The most parsimonious explanation for the presence of these highly similar entities on both sides of the Atlantic is recent, perhaps human-mediated transatlantic dispersal, most likely from the neotropics to Africa. Slave ships coming with their human cargo and the necessary provisions from West Africa are thought to have brought the following vegetables and grains to the Americas: cabbage (*Brassica oleracea* L.), sorghum (*Sorghum bicolor* (L.) Moench), okra (*Abelmoschus esculentus* Moench), cowpea (*Vigna unguiculata* (L.) Walp.), and some cucurbit crops like bittergourd (*Momordica charantia* L.), balsam gourd (*M. balsamina* L.), West Indian Gherkin (*Cucumis anguria* L.), and water melon (*Citrullus lanatus* (Thunb.) Matsumura and Nakai (Kiple and Ornelas 2000). Slave traders often followed a triangular route and went from the Americas to European ports before going back to West Africa, but some also commuted directly between Brazil and the West African coast (Klein 1999). This led to the African introduction of plants from the New World, including cassava (*Manihot esculenta* Crantz) and corn (*Zea mays* L.), which slave traders brought from, respectively, Brazil and the Caribbean (Kiple and Ornelas 2000). The African Melastomataceae genus *Nerophila* Naudin, with a single species in Guinea-Bissau and Sierra Leone, is another entity for which recent arrival from a neotropical population (of *Chaetolepis* Miq.) has been suggested (Jacques-Félix 1994).

While we prefer the hypothesis that *Cucumeropsis* was introduced to West Africa by Brazilian ships (Fig. 4) and then distributed further inland through trade, natural dispersal cannot be ruled out. Naturally occurring long-distance dispersal, perhaps via sea currents, has been suggested for a number of cucurbit lineages (Schaefer et al. 2009), including *Cayaponia* Silva Manso, where the *C. africana* (Hook. f.) Exell lineage is thought to have crossed the Atlantic from South or Central America to West Africa less than five million years ago (Duchen and Renner 2010). Given the single difference in >5,100 nucleotides between the American and African samples, however, such natural dispersal would have to have happened recently. Population-level studies using a micro-satellite approach or AFLP techniques on samples collected throughout the American and African ranges in the future may reveal a more precise picture of the biogeographic history of this interesting crop (i.e. *Cucumeropsis mannii* s. l.).

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- APPENDIX 1. Taxa, sources of plant materials from which DNA was extracted, GenBank accession numbers (*rbcL*, *matK*, *trnL* and *trnL-F*, *rpl20-rps12*, *trnH-psbA*, ITS1-5.8S-ITS2; “—” = sequence not obtained). Abbreviations for herbaria follow Thiers (2010).
- Cucumeropsis mannii* Naudin, J. J. Wieringa 5514 (WAG), Gabon, EU436376, EU436402, EU436350, EU436323, GU799520, GU799493; *Cucumeropsis mannii*, USDA-PI532719, D. R. Congo, GU799533, GU799540, GU799512, GU799505, GU799521, GU799494; *Cucumeropsis mannii*, USDA-PI532721, D. R. Congo, GU799534, GU799541, GU799513, GU799506, GU799522, GU799495; *Cucumeropsis mannii*, E. & J. Westphal 9620 (BR), Cameroon, —, GU799542, GU799514, GU799507, GU799523, —; *Posadaea sphaerocarpa* Cogn., R. Vasquez et al. 10924 (MO), Peru, GU799535, GU799543, GU799516, GU799508, GU799524, GU799501; *Posadaea sphaerocarpa*, B. Hammel 4373 (MO), Panama, GU799536, GU799544, GU799517, GU799509, GU799525, GU799502; *Posadaea sphaerocarpa*, M. Monsalve 579 (MO), Colombia, DQ535836, DQ536718, DQ536850, DQ536581, GU799526, GU799503; *Indomelothria blumei* (Ser.) W. J. de Wilde & Duyfjes, A. F. G. Kerr 3735 (BM), Thailand, GU799532, GU799539, GU799515, GU799510, GU799527, GU799496; *Indomelothria chlorocarpa* W. J. de Wilde & Duyfjes, W. J. de Wilde et al., SAN no. 143729 (L), Malaysia (Sabah), —, EF 065456, —, —, —; *Melancium campestre* Naudin, G. F. Pabst et al. 8741 (M), Brazil, GU799537, GU799545, DQ536838, DQ536567, GU799528, —; *Melothria candolleana* Cogn., J. Schunke Vigo 5822 (MO), Peru, GU799538, GU799546, GU799518, GU799511, GU799529, GU799497; *Melothria dulcis* Wunderlin, M. Blanco 1456 (M), Costa Rica, EU436386, EU436410, EU436360, EU436336, —, GU799498; *Melothria pendula* L., E. Cotton et al. 1741 (AAU), Ecuador, DQ535828, DQ536699, DQ536839, DQ536839, DQ536568, —, GU799499; *Melothria scabra* Naudin, R. Chacón & C. Pineda 427 CR (MO), Costa Rica, —, GU799547, GU799519, —, GU799531, GU799500; *Ruthalicia eglan-dulosa* (Hook. f.) C. Jeffrey, H. Schaefer 06/438 (M), Sierra Leone, EU436393, EU436418, EU436369, EU436341, —, GU799504.
- APPENDIX 2. Material studied.
- Cucumeropsis mannii* Naudin (African material).** Angola: F. Welwitsch 808 (K); Monteiro s. n. (K); Cameroon: E. & J. Westphal 9620 (BR, K); R. Letouzey 7744 (BR); G. L. Bates 261 (K); H. Jacques-Félix 4212 (K, P); Central African Republic: J. M. Fay et al. 5235, 5236 (K, MO); Democratic Republic of Congo: R. Devred 705 & 709 (BR); Vanderyst 22516 (BR); G. Chalou 409 (BR); Y. & T. Ankei 79/1083 (BR); Bequaert 1409 (BR); Léonard 775 (BR, K); D. van der Ben 1068 (K); R. Germain 1893 (BR, K); J. Louis 2257 (BR, K); Kesler 1032 (BR, K); J. Lebrun 1953 (BR, K); G. Gilbert 2334 (BR, K); G. Zenker 584 (B, K); Equatorial-Guinea: Carvalho 2118 (BR, K); G. Tessmann 79 (B, K); Gabon: N. Hallé 3397 (K); J. J. Wieringa 5514 (WAG); Ghana: F. R. Irvine 4771 (K); J. B. Hall 2706 (K); F. N. Howes 1040 (K); Ivory Coast: A. Chevalier 22387 (BR), 21123 (K); Liberia: D. H. Linder 1060 (K); Nigeria: N. W. Thomas 672 (K); W. H. Johnson s. n. (K); J. M. Dalziel 738 (K); W. MacGregor 307 (K); J. D. Clarke 17 (K); C. Barter 1752 (K); Sierra Leone: Deighton 2379 (K); Uganda: R. B. Drummond & J. H. Hemsley 4593 (BR, K); Zambia: D. B. Fanshawe F. 10.144 (K).
- Posadaea sphaerocarpa* Cogn. (American material).** Brazil: I. L. Amaral et al. 415 (K, MO); G. Davidse et al. 11564 (MO); W. L. Balée & A. Gely 913 (K); C. A. Cid & J. Lima 3467 (K); W. Milliken 1868 (K); J. Murca Pires & P. B. Cavalcante 52552 (K); Co-operative Republic of Guyana (British Guyana): Jenman 6288 (K); Colombia: R. Fonnegra et al. 1777 (MO); A. E. Brant et al. 1663 (K, MO); A. Gentry & E. Renteria A. 24142 (MO); A. Juncosa 1163 (MO); W. A. Córdoba & F. García 304 (MO); W. A. Córdoba 498 (MO); A. Gentry et al. 47913 (MO); A. Gentry et al. 47986 (MO); M. Monsalve 579, 634 (MO); F. C. Lehmann 5274 & 137955 (K); A. E. Laurance 545 (K); Costa Rica: A. F. Skutch 3956 (K); Ecuador: A. Alvarado 40 (K); C. Dodson et al. 14431 (K); D. Rubio & C. Quelal 1495 (K); French Guyana: M. J. Jansen-Jacobs et al. 1802 (K); M. F. Prévost & P. Grenand s. n. (K); Guatemala: J. A. Steyermark 45220 (F); Nicaragua: R. Rueda et al. 3983 (MO); J. J. Pipoly 3636 (K, MO); Panama: B. Hammel 4373 (MO); M. Nee & T. Andres 46316 (MO); Peru: V. Huashikat 235 (MO); A. Gentry et al. 28830 (MO); A. Gentry & J. Revilla 16406, 16506 (K, MO); N. Jaramillo & M. A. Wright 10924 (MO); R. Vasquez et al. 10924 (K, MO); Trinidad & Tobago: R. E. D. Baker 1506 (K); Venezuela: J. R. A. Lister 151, 360, 485 (K); J. A. Steyermark & R. Liesner 119087 (K); G. Aymard & N. Cuello 4992 (K); B. Trujillo 14200 (F), 14528 (K); F. D. R. López & R. Jackson 4548 (K); C. Jeffrey et al. 2040, 2210, 2544 (K).