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Linnaeosicyos (Cucurbitaceae): a New Genus for *Trichosanthes amara*, the Caribbean Sister Species of all Sicyeae

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Abstract—The Old World genus *Trichosanthes* has flowers with strikingly fringed petals, and Linnaeus therefore placed a species from Hispaniola that he only knew from an illustration (showing such fringed petals) in that genus. The species remained hidden from the attention of subsequent workers until acquiring new relevance in the context of molecular-biogeographic work on Cucurbitaceae. Based on molecular data, it is the sister to all Sicyeae, a New World clade of about 125 species in 16 genera. We here place this species in a new genus, *Linnaeosicyos*, describe and illustrate it, and discuss its phylogenetic context using molecular and morphological data. Judging from Dominican amber, elements of the flora of Hispaniola date back 15–20 my, and the occurrence on the island of at least five endemic species of Cucurbitaceae (*Linnaeosicyos amara*, *Melothria domingensis*, *Sicana fragrans*, and the sister species *Anacaona sphaerica* and *Penelopeia suburceolata*) points to its long occupation by Cucurbitaceae.

Keywords—Flora of Hispaniola, fringed petals, lectotypification, Linnaeus, Plumier.

With about 100 accepted species, *Trichosanthes* L. is the largest genus of the family Cucurbitaceae (Rugayah and De Wilde 1999; Huang et al. 2007). It is endemic in Asia and Australia, except for *T. amara* L., a species from the Caribbean island of Hispaniola in the Greater Antilles. Linnaeus (1753) described *T. amara* based on an illustration from Plumier's *Description des plantes de l'Amerique* (1693, pp. 86–87) and placed it in the genus *Trichosanthes* because of its striking fringed petals, otherwise then only known from *Trichosanthes*. Wild species of *Trichosanthes* are restricted to eastern Asia, tropical Australia, and Fiji (Jeffrey 1980, 1990; Rugayah and De Wilde 1997, 1999), and Linnaeus only knew them from illustrations. Thus, he described *T. cucumerina* and *T. nervifolia* from plates in Rheede's *Hortus Indicus Malabricus* (Jarvis 2007). These species have white flowers with deeply divided petals, similar to the fringed petals in the Hispaniola species. Of the latter, Linnaeus apparently only saw Plumier's plate, a plate also cited by Ray (1704). Because *T. amara* L. was treated in very few floras (with the notable exception of Liogier 1986) and was never studied in a broader context, it was never formally excluded from *Trichosanthes*. The most recent monographer of the family, Cogniaux (1881), placed it under *Species dubiae*, and the broadest modern specialist on the family, Charles Jeffrey, suspected that it did not belong in *Trichosanthes* but could not decide in which genus it belonged (C. Jeffrey, St. Petersburg, personal communication, March 2006).

For a molecular phylogenetic study of the family (Kocyan et al. 2007) we sought to include as many geographically disjunct entities as possible, which led to the sequencing of modern material of *T. amara*. In the resulting trees, *T. amara* was placed closer to the New World clade Sicyeae (125 species in 16 genera) than to any of the three Asian species of *Trichosanthes* included. Here, we test this result with much broader sampling of the Trichosantheae (as circumscribed by Jeffrey 2005) and conclusively show that *Trichosanthes* is not monophyletic, even after exclusion of Linnaeus's Caribbean *T. amara*. We therefore transfer *T. amara* to a new genus, *Linnaeosicyos*, redescribe and illustrate the species based on newly available collections, and discuss the implications of a Hispaniola taxon being sister to the Sicyeae.

Materials and Methods

Morphology—Specimens were borrowed from JBSD, NY, S, and U. All measurements are from dry herbarium specimens. Pollen was taken from a single male flower bud, mounted on a carbon film, coated with gold in a sputter coater (SCD 050, BAL-TEC, Witten, Germany) and observed and photographed using a scanning electron microscope (LEO 438 VP, ZEISS, Oberkochen, Germany).

Taxon Sampling and Sequencing—DNA extraction and sequencing followed standard procedures, using the *rbcL*, *matK*, *rpl20–rps12*, and *trnL* and *trnL–F* primers and polymerase chain reaction (PCR) protocols listed in Kocyan et al. (2007). Total genomic DNA was isolated from silica-dried leaves or from herbarium specimens with a commercial plant DNA extraction kit (NucleoSpin, MACHEREY-NAGEL, Düren, Germany), following the manufacturer's manual. PCR Reaction products were purified using the Wizard SV PCR clean-up kit (PROMEGA GmbH, Mannheim, Germany), and cycle sequencing was performed with BigDye Terminator v3.0 cycle sequencing kit on an ABI Prism 3100 Avant automated sequencer (Applied Biosystems, Foster City, California). Fifty-eight sequences were newly generated for this study, representing twelve species of Trichosantheae not included in our previous studies. Genbank accession numbers and vouchers are listed in appendix 1. Accession numbers for all other sequences used for the analyses are given in Kocyan et al. (2007). Parsimony and maximum likelihood analyses were conducted with the family dataset of Kocyan et al. (2007), which includes 123 of the 132 genera of Cucurbitaceae (representing all tribes and subtribes) and 171 of the c. 960 species. Additional sequences come from a biogeographical analysis of the Cucurbitaceae (Schaefer and Renner, unpubl.), including those of the genera *Anangia*, *Austrobryonia*, *Gomphogyne*, *Indomelothria*, *Pseudosicydium*, *Urceodiscus*, and *Zanonia*, which augmented our sampling to 130 of 132 genera currently recognized in Cucurbitaceae. The two genera of Cucurbitaceae that have not yet been sequenced are *Khmeriosicyos* De Wilde & Duyfjes, a monotypic genus from Cambodia, known only from the type, and *Papuasicyos* Duyfjes, a monotypic genus from Papua New Guinea. Judging from their floral morphology, both are expected to fall in Benincaseae, far from *Trichosanthes*, *Linnaeosicyos*, and the Sicyeae. In a second analysis for the present study, we used a reduced dataset of 90 species that represent all tribes, major subtribes, and genera containing Caribbean species.

Sequence Alignment and Phylogenetic Analyses—Sequences were edited with Sequencher (4.6; Gene Codes, Ann Arbor, Michigan) and aligned by eye, using MacClade 4.06 (Maddison and Maddison 2003). The aligned plastid matrix comprises 4733 nucleotides after exclusion of a poly-T run in the *matK* gene, a poly-A and a poly-G run in the *trnL* intron and a TATATA microsatellite region in the *trnL–F* intergenic spacer. Data matrix and trees have been deposited in TreeBASE (study number S1883).

Equally weighted parsimony (MP) 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,

Dedicated to Linnaeus on the occasion of his 300th birthday

saving all optimal trees. For the parsimony analyses, gaps were treated as missing data. To assess node support, parsimony bootstrap analyses were performed using 1000 replicate heuristic searches, each with 10 random addition replicates and TBR branch swapping, saving all optimal trees. Maximum likelihood (ML) analyses (and ML bootstrap searches) were performed using GARLI 0.951 (Zwickl 2006) available at www.bio.utexas.edu/faculty/antisense/garli/Garli.html and RAxML-VI-HPC v4.0.0 (A. Stamatakis 2006, available at http://phylobench.vital-it.ch/raxml-bb/). GARLI and RAxML searches relied on the GTR + G + I model. Model parameters were estimated over the duration of specified runs.

To test the phylogenetic position of *Trichosanthes* (*Linneaosicyos*) *amara*, we performed additional ML analyses with constrained topologies that forced the new genus to group with *Trichosanthes* and compared the likelihood scores of the respective trees with that of the unconstrained tree.

Results

Morphologically, *Linnaeosicyos* matches neither Trichosantheae nor Sicyeae. Sicyeae have filaments united into a central column (Jeffrey 1962) and pollen grains that are 4- to 16-colporate or -colpate with a mostly echinate exine or perforate to reticulate exine (Stafford and Sutton 1994; Khunwasi 1998; subtribes Sicyinae and Cyclantherinae, which were characterized by these different exine types, are not mutually monophyletic; Kocyan et al. 2007). In Trichosantheae, the filaments are free, pollen grains are 3- or 4-colporate or porate, but never colpate, and the exine structure is variable (Marticorena 1963; Huang et al. 1997; Pruesapan and van der Ham 2005). In *Linnaeosicyos*, the filaments are free as in *Trichosanthes* and the pollen is 4-colporate with a reticulate exine (Fig. 1); as far as known, no other Cucurbitaceae shows the pattern of ridges and margines seen in *Linnaeosicyos* (R. van der Ham, Nationaal Herbarium Nederland, Leiden, personal communication, Sep. 2007).

In the phylogenetic analyses, we obtained congruent topologies from the 130 species and the 90 species data sets (for overlapping taxa), and hence we discuss only the results from the smaller data set. Parsimony and likelihood analyses of the 90-taxon data set also yielded congruent topologies (Fig. 2). The Asian/Australian *Trichosanthes* species form two clades, one of them including two species of the Asian genus *Gymnopetalum*, while the Neotropical *Trichosanthes amara* is sister to the New World Sicyeae (represented with all their genera). Bootstrap support for the sister relationship *Linnaeosicyos*-Sicyeae is around 80% in the parsimony and likelihood analyses.

The likelihood score for the best ML topology under the GTR+G+I model is -25626, while constrained trees with *Trichosanthes* (*Linneaosicyos*) *amara* embedded in either of the two *Trichosanthes* clades have likelihood scores of -25644 and -25665. A polytomy of Sicyeae, *Linnaeosicyos* and the two *Trichosanthes* clades has a score of -25640. The placement of *L. amara* as sister to the Neotropical Sicyeae is thus favored.

We therefore here transfer *Trichosanthes amara* from *Trichosanthes* (Trichosantheae) to a new genus without, however, assigning it to one of the currently accepted tribes (Jeffrey 2005). New circumscriptions of the tribes Trichosantheae and Sicyeae based on a broader sampling will be made in a forthcoming treatment of the Cucurbitaceae for *The Families and Genera of the Vascular Plants* series.

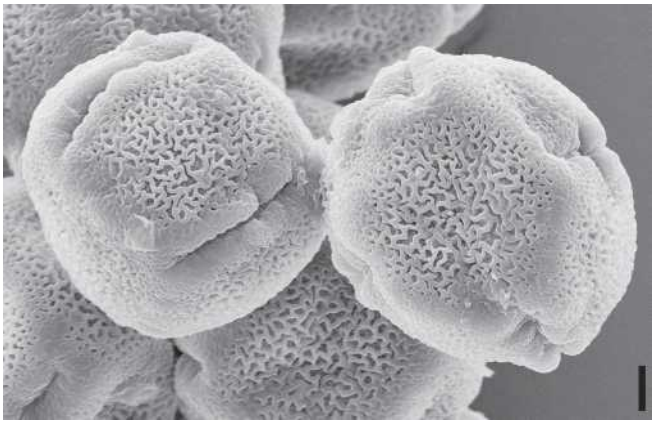

Fig. 1. Scanning electron microscope photo of the pollen of *Linnaeosicyos amara* (scale bar = 5 μm). Collection: *García 589* (JBSD).

Linnaeosicyos H. Schaef. & Kocyan, gen. nov.—TYPE: *Trichosanthes amara* L., Sp. Pl. 1008. 1753.

Planta cirrhis scandens, corolla alba longe et eleganter fimbriata, a *Trichosanthes* differt patria neotropica, foliis minoribus (c. 4.5 × 4.2 cm), pustulis in ambo latere foliorum conspicuis orbicularibus albis.

Perennial dioecious climbers or trailers. Tendrils simple. Leaves alternate, petiolate; lamina reniform to suborbicular, simple, entire to 3-lobed. Epidermis pustulate with numerous trichomes on multicellular, discoidal, cystolith-bearing bases. Flowers solitary, unisexual, pedicellate, white; calyx tube cylindrical, 5-lobed, lobes entire, dentate or laciniate; corolla funnel-shaped, deeply 5-parted with fimbriate segments. Fruit cylindrical-ellipsoidal, indehiscent, many-seeded. Seeds linear-oblong, compressed.

Distribution—Endemic to the Caribbean island of Hispaniola, Greater Antilles (Dominican Republic).

Etymology—The genus is named in honor of the Swedish botanist Carolus Linnaeus (1707–1778) on the occasion of his 300th birthday.

Linnaeosicyos amara (L.) H. Schaef. & Kocyan, comb. nov. *Trichosanthes amara* L., Sp. Pl. 1008. 1753.—HOLOTYPE, here designated: *Trichosanthes pomis turbinato-ovatis. Colocynthis flore albo fimbriato, fructu oblongo* in Plumier, Descr. Pl. Amér.: 86, t. 100. 1693 (reproduced as Fig. 3). Epitype, here designated: DOMINICAN REPUBLIC. Sierra Martín García: Barahona: 2 km antes de las salinas [Locality on road to Puerto Alejando, S of Canoa]. 30 Oct. 1985. *R. G. García 589 with J. Pimentel & G. Caminero* (JBSD), our Fig. 4.

Notes—There is a typographical error in Linnaeus's protologue; he cites Fig. 101 of Plumier, when it is actually Fig. 100.

Blanco (1837) misapplied the name to a mixture of *Trichosanthes* (the flowers) and *Luffa* (the fruit), with the flowers

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Fig. 2. Maximum likelihood tree for *Trichosanthes* and relatives based on 4692 nucleotides from combined chloroplast loci (*rbcL* gene, *matK* gene, *trnL* intron, *trnL–F* spacer, and *rpl20–rps12* spacer; enlarged data set of Kocyan et al. 2007). The tree is rooted on Datiscaceae + Begoniaceae. Parsimony bootstrap support ≥ 60% is indicated above branches, likelihood bootstrap support below branches. An asterisk (*) indicates species from the Caribbean region and genera containing Caribbean species.

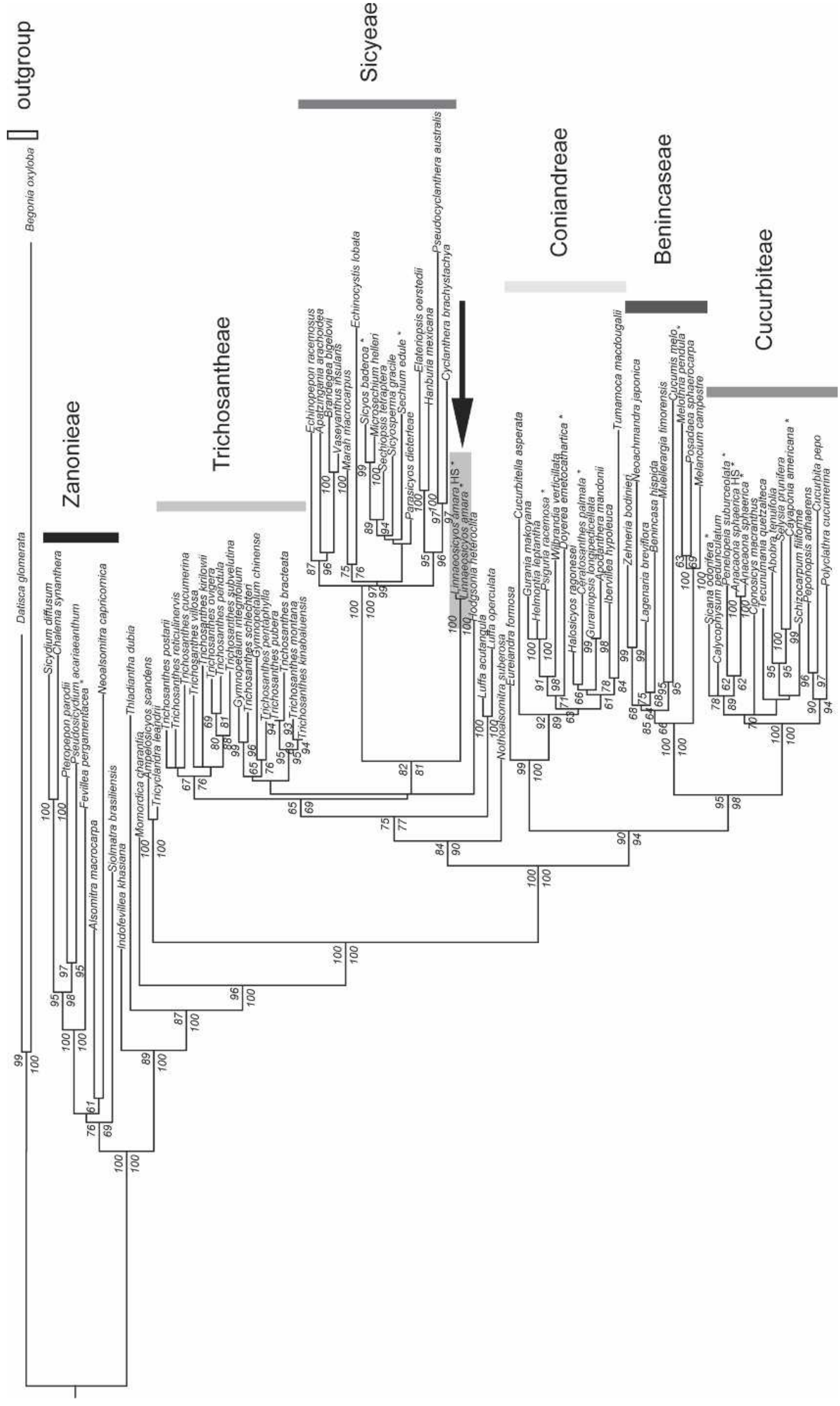
outgroup
Begonia oxyloba
Datisca glomerata
Zanonieae
Sicydium diffusum
Chalema synanthera
Pteropepon parodii
Pseudosicydium acariaeanthum
Fevillea pergamentacea *
Alsomitra macrocarpa
Neoalsomitra capricornica
Siolmatra brasiliensis
Indofevillea khasiana
Thladiantha dubia
Momordica charantia
Ampelosicyos scandens
Tricyclandra leandrii
Trichosantheae
Trichosanthes postarii
Trichosanthes reticulinervis
Trichosanthes cucumerina
Trichosanthes villosa
Trichosanthes kirilowii
Trichosanthes ovigera
Trichosanthes pendula
Trichosanthes subvelutina
Gymnopetalum integrifolium
Gymnopetalum chinense
Trichosanthes schlechteri
Trichosanthes pentaphylla
Trichosanthes pubera
Trichosanthes bracteata
Trichosanthes montana
Trichosanthes kinabaluensis
Sicyeae
Echinopepon racemosus
Apatzingania arachoidea
Brandegea bigelovii
Vaseyanthus insularis
Marah macrocarpus
Echinocystis lobata
Sicyos baderoa *
Microsechium helleri
Sechiopsis tetraptera
Sicyosperma gracile
Sechium edule *
Parasicyos dieterleae
Elateriopsis oerstedii
Hanburia mexicana
Pseudocyclanthera australis
Cyclanthera brachystachya
Linnaeosicyos amara HS *
Linnaeosicyos amara *
Hodgsonia heteroclita
Luffa acutangula
Luffa operculata
Nothoalsomitra suberosa
Eureiandra formosa
Coniandreae
Cucurbitella asperata
Gurania makoyana
Helmontia leptantha
Psiguria racemosa *
Wilbrandia verticillata
Doyerea emetocathartica *
Halosicyos ragonesei
Ceratosanthes palmata *
Guraniopsis longipedicellata
Apodanthera mandonii
Ibervillea hypoleuca
Benincaseae
Tumamoca macdougalii
Zehneria bodinieri
Neoachmandra japonica
Lagenaria breviflora
Benincasa hispida
Muellerargia timorensis
Cucumis melo
Melothria pendula *
Posadaea sphaerocarpa
Melancium campestre
Cucurbiteae
Sicana odorifera *
Calycophysum pedunculatum
Penelopeia suburceolata *
Anacaona sphaerica HS *
Anacaona sphaerica *
Cionosicys macranthus
Tecunumania quetzalteca
Abobra tenuifolia
Selysia prunifera
Cayaponia americana *
Schizocarpum filiforme
Peponopsis adhaerens
Cucurbita pepo
Polyclathra cucumerina

FIG. 3. Scan of the holotype: *Trichosanthes pomis turbinato-ovatis. Colocynthis flore albo fimbriato, fructu oblongo* in Plumier, Descr. Pl. Amér.: 86, t. 100. 1693.

most likely representing *Trichosanthes cucumerina* L. (Merrill 1918).

Perennial dioecious climber or trailer with fleshy rootstock. Stems up to 6 m long, up to 8 mm diam., ribbed, scabrid to glabrescent, woody when old, with 5 prominent cork-ridges. Tendrils simple, to 12 cm long. Leaves glabrous, petioles 20–32 mm long, sparsely hairy; lamina reniform to suborbicular, simple, entire to deeply 3-lobed, 12–45 mm × 16–42 mm, the lobes dentate, scabrid, the upper epidermis distinctly pustulate with short trichomes on whitish-grey, discoidal, multicellular, cystolith-bearing hair bases, up to 4 per square mm, each up to 0.3 mm in diameter, looking green from below (Fig. 5). Male flowers solitary, seen as buds only with pedicels up to 25 mm long; hypanthium broadly campanulate, in buds up to 20 mm long, glabrous. Stamens 3 inserted 10 mm below the throat of the receptacle tube; filaments free, c. 1 mm long, glabrous; anthers connate into a synandrium, c. 9 mm long; thecae S-shaped, 2 anthers are 2-thecous, one is 1-thecous. Female flowers solitary; pedicels 15–40 mm long; hypanthium above constriction c. 30 mm long, glabrous; ovary ellipsoidal, c. 25 mm long, placentas 3, ovules numerous; calyx lobes narrow-triangular, c. 10 mm long, glabrous; corolla lobes ovate, 30 mm × 12 mm, white with green veins, fimbriate; staminodes minute; stigma 3-lobed, the stigmatic lobes capitate. Fruit turbinate to ellipsoidal, green, pendent, 8–12 cm long, 3–4 cm diam.; fruiting pedicel 20–42 mm long. Seeds in soft, whitish pulp, many (several hundreds), yellowish-brown, linear-oblong, compressed, with distinct, flat margin, 4–5 × 1.5–2 mm (Fig. 6), resembling in shape the seeds of *T. subrosea* C. Y. Cheng & C. H. Yueh and *T. uniflora* K. S. Hao; seed coat consisting of an outer epidermal layer, a hypodermis with sclerotic cells, a well-developed aerenchyma and a thin chlorenchyma. Pollen reticulate, 4-colporate, c. 30 μm in diameter (pole-pole) (Fig. 1).

Phenology—Ripe fruits in April, June, October. Flowering specimens have been collected between December and May.

Distribution—Endemic to the island of Hispaniola, Greater Antilles (Dominican Republic). According to label information on the collection *Mejía et al. 1877* (JBSD, NY), it is locally common at Sierra Martín García in southern Hispaniola.

Habitat—Collected in thickets among cacti and herbs on a limestone hill, 300–400 m above sea level, along roadsides in dry forest with *Prosopis juliflora* DC. (Fabaceae) and *Senna atomaria* (L.) H. S. Irwin & Barneby (Fabaceae), or in dry forest close to sea level.

Local name—Calabacita amarga, Pepinito amargo, Pepinito de San Gregorio (Liogier 1986).

Specimens Examined—DOMINICAN REPUBLIC. San Cristóbal: Azua, east of town. 14 Mar. 1913. *J. N. Rose 3880 with W. R. Fitch & Paul G. Russell* (NY). Santiago: Jaiquí Picado, 20 miles West of Santiago. 23 May 1969. *A. H. Liogier* 15328 (NY). Santiago: Jaiquí Picado, 20 miles West of Santiago. 27 Nov. 1969. *A. H. Liogier 17034* (NY). Sierra Martín García: Barahona: 2 km antes de las salinas [Locality on road to Puerto Alejando, S of Canoa]. 30 Oct. 1985. *R. G. García 589 with J. Pimentel & G. Caminero* (JBSD, NY, U). Sierra Martín García: Barahona. En los alrededores de las salinas del Puerto Alejandro, al sur de Canoa. 29 Oct. 1986. *M. M. Mejía Pimentel 1877 with J. Pimentel & R. García* (JBSD, NY). Sierra Martín García: Barahona. 28 Jun. 2000. *B. Peguero & F. Jiménez 1623* (JBSD).

Notes—In his 1986 Flora of Hispaniola, Liogier discussed several additional specimens that he thought might represent a new species close to *T. amara*. Later, however, he annotated most of them as *Sicana odorifera* (Vell.) Naudin, but also described a new *Sicana fragrans* A. H. Liogier, M. Mejía, and R. García (see *Discussion*). These specimens are *Ekman 15471* (S, US, photo seen), *Liogier 14712* (NY, photo seen), *Liogier 18426* (NY, photo seen), *Liogier & Liogier 27501* (NY, photo seen), *Ekman 9980* (S, US, photo seen) and *Ekman 15228* (S). Three further collections from Haiti (*Ekman 3604*, *Ekman 7032*, *Ekman 9161*, all at S) and a collection from Ile la Gonave (*Ekman 8833* (S)) belong to *Doyerea emetocathartica* Grosourdy (identified by HS based on morphology). Finally, two specimens cited by Liogier (1986) as belonging to *T. amara*, namely *Ekman 13975* (S, U) and *Ekman 14113* (S), both from Constanza, represent *Anacaona sphaerica* A. H. Liogier, as verified by morphology and sequencing of the *rpl20*, the *trnL*, and the *matK* plastid locus. The sequences are 100% identical between *Ekman 13975* and *Zanoni et al. 39300* (NY), an undoubted specimen of *A. sphaerica*.

There is one other report of *Trichosanthes* for the West Indies, *T. tamnifolia* Poiret in Lamarck (Encycl. Méth., Bot., Suppl. 1: 386. 1810), which according to the protologue was

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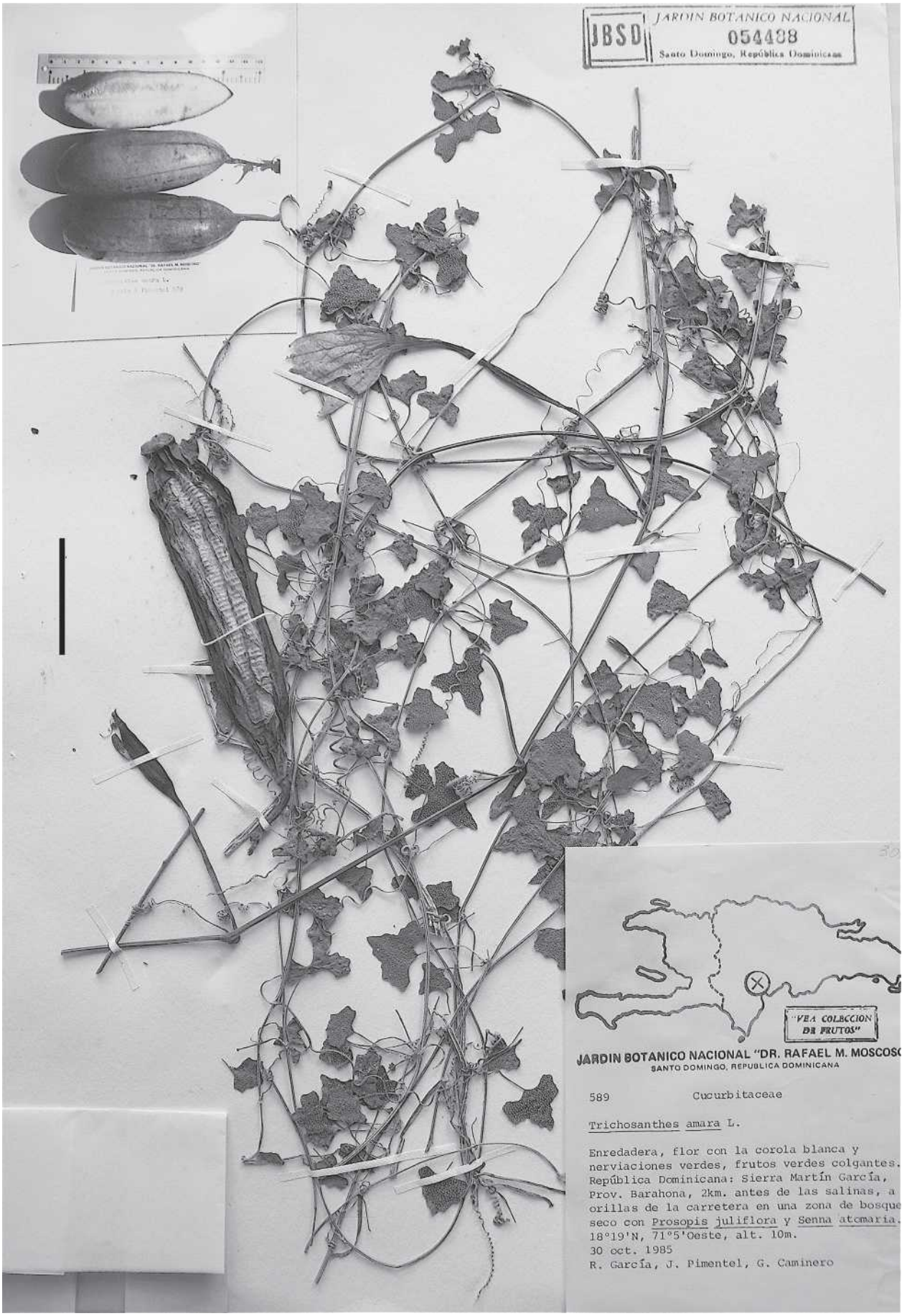
FIG. 4. Photo of the epitype, *García 589* (JBSD), of *Linnaeosicyos amara* (scale bar = 5 cm).


JBSD
JARDIN BOTANICO NACIONAL
054408
Santo Domingo, República Dominicana
"VEA COLECCION DE FRUTOS"
JARDIN BOTANICO NACIONAL "DR. RAFAEL M. MOSCOSO
SANTO DOMINGO, REPUBLICA DOMINICANA
589 Cucurbitaceae
Trichosanthes amara L.
Enredadera, flor con la corola blanca y nerviaciones verdes, frutos verdes colgantes. República Dominicana: Sierra Martín García, Prov. Barahona, 2km. antes de las salinas, a orillas de la carretera en una zona de bosque seco con Prosopis juliflora y Senna atomaria. 18°19'N, 71°5'Oeste, alt. 10m.
30 oct. 1985
R. García, J. Pimentel, G. Caminero

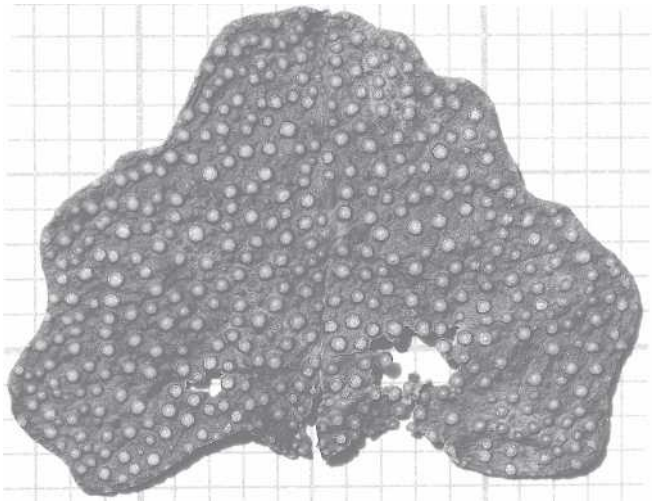


FIG. 5. Photo of the leaf of *Linnaeosicyos amara* (on 1 × 1 mm grid) with conspicuous discoidal hairbases. Collection: *García 589* (JBSD).

based on a Riedlé collection from Puerto Rico in the Desfontaines herbarium at Paris (P-Desfont.). This specimen was long lost, causing Cogniaux (1881) and Urban (1911) to place the name under *Species dubiae*, but a renewed search turned up a Riedlé collection from Puerto Rico labeled *T. tamnifolia* in the herbarium P Moquin-Tandon. This collection matches Poiret's protologue and represents *Cayaponia racemosa* (Mill.) Cogn., which still occurs on Puerto Rico today. Riedlé was a gardener on the Baudin expedition to the West Indies, which arrived in Puerto Rico in 1797 and spent less than a year there; his collections are among the earliest documents of the flora of from Puerto Rico (Liogier 1996).

DISCUSSION

The Cucurbitaceae of Hispaniola, while only comprising a few species, are highly relevant for inferring the phylogenetic and biogeographic history of the family. Apart from *Linnaeosicyos amara*, the island harbors 14 indigenous species in ten genera plus several escaped vegetable species (Liogier 1986). Of the indigenous species, the monotypic endemics *Anacaona sphaerica* and *Penelopeia suburceolata* (Cogn.) Urban (Cucurbiteae) are sister taxa (Kocyan et al. 2007; our Fig. 2), and might be treated as two species of the genus *Penelopeia*. The recently described *Sicana fragrans* (also in the tribe Cucurbiteae) differs from the widespread *S. odorifera* (Vell.) Naudin in having glabrous leaves and branches, 7-lobed leaves, and 9–10 cm long ellipsoid fruits (Liogier 1994). Two further species of Cucurbiteae, *Cayaponia racemosa* (Mill.) Cogn. and *C. americana* (Lam.) Cogn., occur throughout the Antilles, with the former reaching Central and northern South America, and the latter Florida (www.plantatlas.usf.edu). *Fevillea cordifolia* L. (Zanonieae) is widespread throughout the Antilles and tropical America; *Doyerea emetocathartica* Grosourdy (Coniandreae) is known from the Caribbean region south to Colombia and Venezuela; *Psiguria pedata* (L.) Howard, *P. trilobata* (L.) Howard, and *P. trifoliata* (L.) A. H. Liogier (also Coniandreae) occur on many Caribbean islands, and so does *Sechium edule* (Jacq.) Sw. (Sicyeae), which is known throughout the Caribbean and Mesoamerican region, although the native range of this popular vegetable may have been much smaller than its current distribution. *Sicyos laciniatus* L. (Sicyeae) occurs in Hispaniola, Mexico, and the southwestern United States of America. Finally, *Melothria pendula* L. and *M. domingensis* Cogn. (Benincaseae) belong to a Neotropical genus of currently unclear circumscription; the latter species is an endemic of Hispaniola.

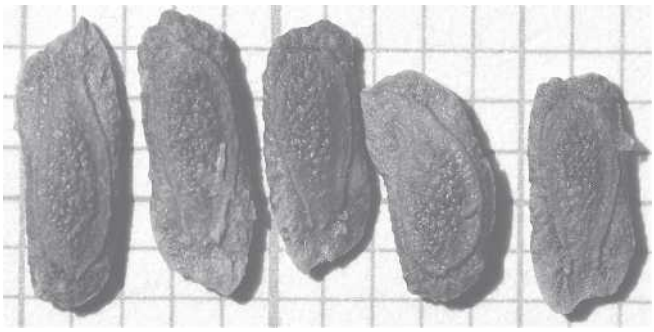


FIG. 6. Photo of the seeds of *Linnaeosicyos amara* (on 1 × 1 mm grid). Collection: *García 589* (JBSD).

Judging from Dominican amber, elements of the flora of Hispaniola date back at least 15–20 my (Iturralde-Vinent and MacPhee 1996), and the occurrence on the island of an endemic clade of Cucurbitaceae (namely the sister taxa *Anacaona* and *Penelopeia* from the Cucurbiteae) and three other endemic species (*Linnaeosicyos amara*, *Melothria domingensis* from Benincaseae, and *Sicana fragrans* from Cucurbiteae) points to its long occupation by Cucurbitaceae. Hispaniola might represent a refuge for at least some Cucurbitaceae. Among the earliest fossils of Cucurbitaceae is the pollen *Hexacolpites echinatus* from the Oligocene of Cameroon (Salard-Cheboldaeff 1978; Muller 1985); these grains under the light microscope are 6-colpate and resemble polycolpate pollen of Sicyeae (Salard-Cheboldaeff 1978). It is therefore conceivable that Sicyeae in the Oligocene ranged from West Africa to the New World, and that *L. amara* represents an early lineage of Sicyeae that survived on Hispaniola, while the remainder of the tribe diversified on the mainland.

The fringed petals and large, many-seeded fruits of *Linnaeosicyos amara* differ from the petals and fruits of most other Sicyeae and might represent adaptations to pollinators and seed dispersal conditions on Hispaniola. White, nocturnally open flowers with conspicuous fringed petals evolved in several genera of Cucurbitaceae, including *Trichosanthes*, *Hodgsonia*, *Telfairia,* and at least three island endemics, namely *Tricyclandra* and *Ampelosicyos* from Madagascar, and *Linnaeosicyos* from Hispaniola (Vogel 1954; Endress and Matthews 2006; this paper). Although it is unknown whether *Linnaeosicyos* flowers open at night or during the day, hawk-moth pollination seems likely because of the elongate perianth tube. Fringed petals have evolved in several sphingid-pollinated flowers and probably enhance their visibility (Vogel 1954; further examples are given in Endress and Matthews 2006).

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Appendix 1 Taxa, Genbank accession numbers (*rbcL, matK, trnL, trnL–F, rpl20–rps12*; "—" = sequence not obtained), and sources of plant materials from which DNA was extracted for sequencing. To facilitate data location, taxa are listed in alphabetical order by genus and species. Abbreviations for herbaria follow the *Index Herbariorum* at http://sciweb.nybg.org/science2/IndexHerbariorum.asp.

Anacaona sphaerica A. H. Liogier; EU036995, EU036997, EU036998, EU036999, EU036996; Dominican Republic, *Ekman 13975* (U); *Gymnopetalum chinense* Merr.; EU155601, EU155606, EU155630, EU155621, EU155612; Peoples' Republic of China, Guangdong Province, *Schaefer 2005/661* (M); *Hodgsonia heteroclita* Hook.f. & Thomson; —, EU155607, EU155631, —, EU155613; Bangladesh, *Loeffler s. n.* (M); *Trichosanthes* (=*Linnaeosicyos*) *amara* L.; EU037000, EU037001, EU037003, EU037004, EU037002; Dominican Republic, *Liogier 15328* (NY); *Trichosanthes bracteata* (Lam.) Voigt.; EU155602, EU155608, EU155632, EU155622, —; India, Kochin, *Haegele 20* (M); *Trichosanthes cucumerina* L.; EU155603, EU155609, EU155633, EU155623, EU155614; India (cultivated at Munich Botanical Garden), *Schaefer 2007/327* (M); *Trichosanthes kinabaluensis* Rugayah; —, —, EU155634, EU155624, EU155615; Malaysia, Sabah, *Postar et al. 144260* (L); *Trichosanthes montana* Rugayah; —, —, EU155635, EU155625, EU155616; Malaysia, Sabah, *Postar et al. 144259* (L); *Trichosanthes pendula* Rugayah; —, —, EU155636, EU155626, EU155617; Malaysia, Sabah, *Postar et al. 144100* (L); *Trichosanthes pentaphylla* F. Muell.; EU155604, EU037012, EU037010, EU037011, EU037013; Australia, Queensland, *Schaefer 2007/09* (M); *Trichosanthes postarii* de Wilde & Duyfjes; —, —, EU155637, EU155627, EU155618; Malaysia, Sabah, *Postar et al. 144066* (L); *Trichosanthes schlechteri* Harms; EU155605, EU155610, EU155638, EU155628, EU155619; Papua New Guinea, *Takeuchi 15663* (GIFU); *Trichosanthes subvelutina* F. Muell.; —, EU155611, EU155639, EU155629, EU155620; Australia, Queensland, *Schaefer 2007/17* (M); *Trichosanthes villosa* Blume; EU037005, EU037007, EU037008, EU037009, EU037006; Thailand, *Phonsena, De Wilde & Duyfjes 4669* (L).