Phylogeny and Evolution of the Cucurbitaceae

Susanne S. Renner and Hanno Schaefer

Abstract The Cucurbitaceae family contains about 1000 species in 96 genera. Representatives of all genera (except the extinct *Khmeriosicyos*) and a large percentage of the species have been sequenced for the ribosomal RNA transcribed spacer regions and variable regions of the plastid and mitochondrial genome. These data have allowed to infer evolutionary relationships in the family. The major phylogenetic structure of the family is now clear, and this chapter includes an up-to-date phylogenetic scheme with the placement of all genera. The Cucurbitaceae clade originated in mainland Southeast Asia sometime in the Late Cretaceous, and the five deepest evolutionary divergences in the family all date to the Late Cretaceous, 70–80 Ma. Two of these ancient clades, the Gomphogyneae and *Actinostemma*, are now almost restricted to Asia. A third ancient group, the Triceratieae, is mainly Neotropical, except one African genus; other clades and tribes are more widespread. The economically most important genera are concentrated in the Cucurbiteae and Benincaseae, and species of *Cucumis* and *Citrullus*, with well-annotated genomes, therefore have largely comparable (homologous) linkage groups. In contrast to the relatively good data on the family's phylogeny, data on its ecology, physiology and morphological evolution are scarce and collection and study of wild species, many of them in threatened habitats is much needed.

Keywords Collections • Molecular phylogenetics • Molecular clock • Publicly available herbarium specimens • Sister groups • Crop wild relatives

---

S.S. Renner (✉)
Systematic Botany and Mycology, Department of Biology,
University of Munich (LMU), 67 Menzinger Str,
80638 Munich, Germany
e-mail: renner@lmu.de

H. Schaefer (✉)
Biodiversity of Plants, Technical University Munich (TUM),
Emil-Ramann Strasse 2, 85354 Freising, Germany
e-mail: hanno.schaefer@tum.de

R. Grumet et al. (eds.), *Genetics and Genomics of Cucurbitaceae*,
Plant Genetics and Genomics: Crops and Models, DOI 10.1007/7397_2016_14

Introduction

The Cucurbitaceae are a tropical and subtropical family that is related to the Begoniaceae, Datiscaceae, and Tetramelaceae, with which it shares inferior ovaries and parietal placentation (Zhang et al. 2006). The precise relationships among these four families remain unresolved. Their tendrils readily distinguish Cucurbitaceae from their closest relatives, and the family's monophyly is well supported by molecular analyses that have included a dense sampling of both outgroups (potential relatives) and Cucurbitaceae themselves (Kocyan et al. 2007; Schaefer et al. 2009; Schaefer and Renner 2011a, b). Indeed, species from all genera of Cucurbitaceae except *Khmeriosicyos*, a genus only known from the type, a specimen collected in Cambodia in 1873 and now in the Paris herbarium, have been sequenced for at least one nuclear DNA region and one or more plastid regions. Maximum likelihood and Bayesian phylogenies inferred from these large data matrices reveal five statistically well-supported clades. This chapter summarizes the phylogenetic placement of all genera as well as the ages of the family's major clades based on fossils and molecular clock approaches. We conclude with a brief review of morphological trends and historical geographic expansion of the family.

The Main Clades (and Taxonomic Tribes) of the Cucurbitaceae

The most comprehensive molecular phylogenetic analysis of the Cucurbitaceae is that of Schaefer and Renner (2011b) who included ribosomal RNA transcribed spacer regions, two mitochondrial regions, and nine regions of the plastid genome for 664 species of Cucurbitales (most of them Cucurbitaceae, which were represented with 95 genera). Figure 1 shows the placement of all currently recognized genera and is up-dated from the most recent taxonomic classifications of the Cucurbitaceae (Schaefer and Renner 2011a, b). The deepest phylogenetic divergences in the family can be 'captured' in five major groups of genera, namely, (I) a group that includes *Alsomitra*, *Bayabusua*, and *Neoalsomitra*, which corresponds to tribe Gomphogyneae of Bentham & Hooker; (II) a group of one African genus and five Neotropical genera, including *Fevillea* and *Sicydium*, which corresponds to tribe Triceratieae of A. Rich.; (III) a group of four or five genera from Madagascar, continental Africa, Asia, and South America, corresponding to tribe Zanonieae of Bentham and Hooker; (IV) a clade consisting of the Asian *Actinostemma*; and (5) a group of c. 80 genera that has traditionally been ranked as subfamily Cucurbitoideae of Kosteletzky. Before molecular data, the groups (1) to (4) (above) were placed together in a subfamily called Zanonioideae (Benth. & Hook.f.) Luerss. or Nhandiroboideae (Kosteletzky 1833; Jeffrey 1980, 1990, 2005), however, Nhandiroboideae is an illegitimate name, and Zanonioideae is a taxonomic synonym of Fevilleoideae Burnett (Burnett 1835). Neither morphological data nor molecular phylogenetic results support the division of the family Cucurbitaceae into

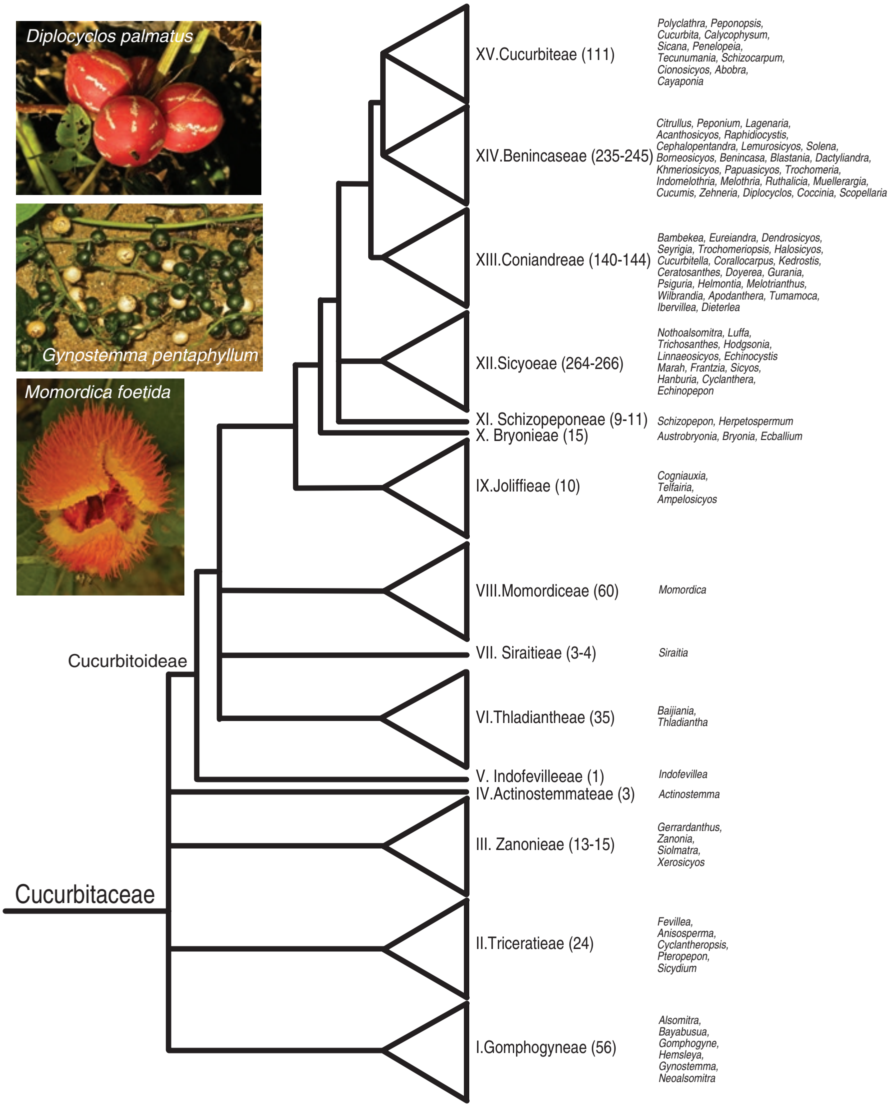

Fig. 1 Cladogram showing the tribal classification of the Cucurbitaceae based on 14 DNA regions from chloroplast, nuclear and mitochondrial DNA sequences. Up-dated from Schaefer and Renner (2011a, b, the latter paper showing the statistical support for this tree). Numbers in parentheses refer to species numbers (Photos by H. Schaefer)

two equal-aged or otherwise equivalent groups, and the morphological characters thought to distinguish Zanonioideae from Cucurbitoideae, namely, striate pollen, winged seeds, and "zanonioid" tendrils (tendrils in which the lower section is capable of curving), all occur also in Cucurbitoideae. We therefore recommend not using any subfamily division in this relatively small family. Brief descriptions of the 15 tribes (Fig. 1), including comments on geographic occurrence, and chromosome numbers are provided in Schaefer and Renner (2011b).

Morphological Evolutionary Trends in the Cucurbitaceae

Sexual Systems

Cucurbitaceae are usually hairy climbers with simple or branched, lateral tendrils (very rarely, the tendrils are lost, e.g. in the cucumber tree, *Dendrosicyos socotranus*), yellow or whitish unisexual flowers, an inferior ovary with parietal placentation and numerous, relatively large seeds. About 50 % of their species are monoecious and 50 % dioecious; no wild Cucurbitaceae have only bisexual flowers although a few have individuals with bisexual flowers and others with staminate flowers (individuals with bisexual flowers regularly occur in *Schizopepon bryoniifolius* and *Zehneria hermaphrodita*; Schaefer and Renner 2011a). Dioecy appears to be the ancestral condition in the family, with much back and forth between dioecy and monoecy (Zhang et al. 2006; Volz and Renner 2009; Schaefer and Renner 2010), and a dioecious mating system may even go back to the common ancestor of Begoniaceae, Cucurbitaceae, Datiscaceae, and Tetramelaceae, all of which have normally unisexual flowers and are entirely or mostly dioecious (Zhang et al. 2006). Spontaneous mutations that modify flower sex phenotype are common and were favored by breeding targeted towards femaleness (see also The Genomics of Wood Formation in Angiosperm Trees). In *Cucumis*, a genus of 66 species, most of them monoecious but a few dioecious, e.g. *Cucumis hirsutus*, (Sebastian et al. 2010), breeders have selected gynoecious or ‘all-female’ cultivars of *C. sativus* because of their high fruit yield. Gynoecy, coupled with parthenocarpy, is valued for greenhouse production. Field production of gynoecious varieties requires a few androecious plants (with only male flowers) or monoecious plants with both types of flowers to ensure fertilization. Their sexual lability and economic importance have made cucurbits an important system for the developmental genetics of sex determination (The Genomics of Wood Formation in Angiosperm Trees). The ancient presence of unisexual flowers and dioecious populations in Cucurbitaceae may be the evolutionary ‘reason’ for the absence of genetic self-incompatibility in this family. All species that have been investigated in this regard are self-compatible. However, the sexual systems of most species are only inferred from a few herbarium specimens rather than field observations of wild populations.

Flower Morphology and Its Evolutionary Trends

Floral symmetry is mostly actinomorphic (radially symmetric), although zygomorphy (mirror symmetry) has evolved in a few species, for example, in *Gerrardanthus* (Fig. 2a), *Xerosicyos,* and a few species of *Momordica.* Male and

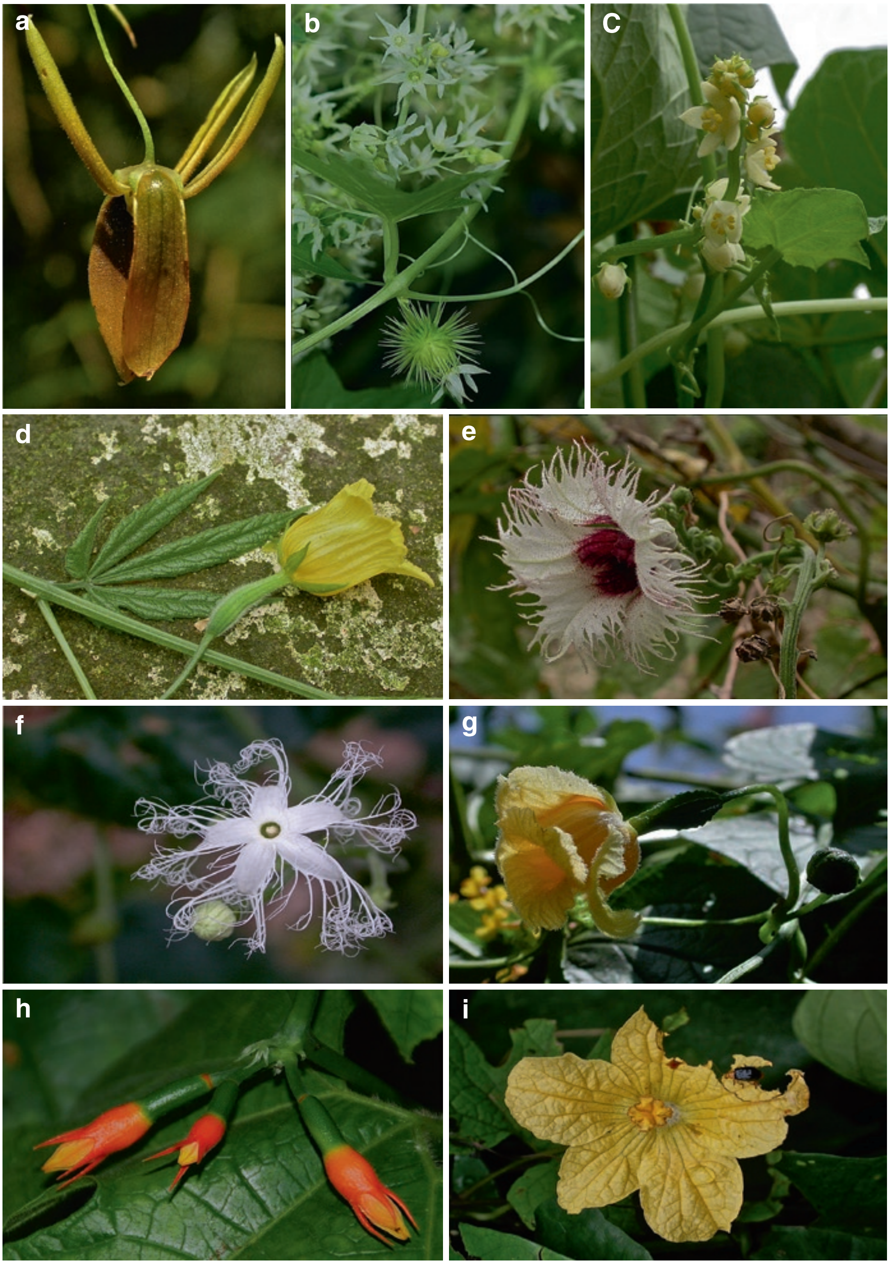

Fig. 2 Diversity of flower morphology in Cucurbitaceae: (**a**) *Gerrardanthus grandiflorus*, male flower (Tanzania); (**b**) *Echinocystis lobata*, male and female flowers (USA); (**c**) *Sicyos edulis* (syn. *Sechium edule*), male flowers (Brazil); (**d**) *Thladiantha hookeri*, female flower (China); (**e**) *Telfairia occidentalis*, male flower (Nigeria); (**f**) *Trichosanthes cucumerina*, male flower (China); (**g**) *Momordica leiocarpa*, female flower (Tanzania); (**h**) *Gurania makoyana*, female flower (Peru); (**i**) *Ruthalicia eglandulosa*, male flower (Sierra Leone); all photographs Hanno Schaefer

female perianths are usually similar, probably to make pollinators visit the often rewardless female flowers; occasionally, they differ in size and exceptionally also in shape. At about day six of floral development (at least in *Cucumis*), either the stamen primorida or the carpel primordia begin to expand rapidly, while the primorida of the other sex are arrested (Kater et al. 2001). In female flowers, the aborted stamens are visible as staminodes. The calyx and corolla are usually pentamerous, and the corolla consists of distinct or more or less fused petals that are highly variable in size and shape, but rather uniformly white, yellow, or orange, rarely red or pink (Fig. 2). Especially striking are the long-fringed petals of the nocturnally flowering species of *Trichosanthes* (Fig. 2f), *Linnaeosicyos*, *Hodgsonia*, and *Ampelosicyos*, which are pollinated by long-tongued hawkmoths (De Boer et al. 2012; Mitchell et al. 2015).

The hypanthium derives from the expansion of sepal and petal bases, and their receptacular insertion area (cf. Schaefer and Renner 2011a for references to morphological studies). In male flowers, stamens arise at the bottom of the hypanthium or are inserted at different levels on the hypanthium wall, with the stamen bases then contributing to the hypanthium. These "appendicular" hypanthia may take a wide range of shapes: from flat and patelliform (*Cyclanthera*) to long and tubular (*Ceratosanthes*). The hypanthium floor typically bears a nectary, which can be mesenchymal (most genera) or trichomatous (Sicyoeae). In female flowers, the hypanthium includes the ovary wall, and the gynoecia consist of 1–5 carpels, the 3-carpellate condition being the most common.

A taxonomically useful character is the number of stylodia: Gomphogyneae, Fevilleeae, and Zanonieae usually have three (sometimes two or five) distinct stylodia. The more derived clades (Fig. 1) have a single style with 2–3(−5) stigmas that can be enlarged to mimic an androecium, probably to attract pollen-seeking bees. Stigma shape is diverse and likewise taxonomically useful.

Ovules are anatropous and bitegmic, their number ranging between 1 to several hundreds (Matthews and Endress 2004). In the more derived clades, the ovules are embedded within individual chambers that at maturity can be liquid filled (e.g, *Cionosicyos macranthus*). Ovule orientation in the *Actinostemma* clade, Fevilleeae, Gomphogyneae, and Zanonieae (as well as in the derived clade Sicyoeae) is mostly pendent. Ovule orientation in the remaining clades is typically horizontal or entirely erect (*Cayaponia*). However, ovule orientation is not known for many groups.

A family-wide evolutionary trend is an increasing fusion of neighboring stamens, and an enlargement of the pollen-producing space through sigmoid coiling of the thecae. Five distinct, bithecal stamens probably is the ancestral state, and as far as is known, all cucurbit flowers initiate five distinct stamen primordia, even those with highly connate stamens (Matthews and Endress 2004). The condition survives in a few unrelated groups (*Anisosperma* and some *Telfairia*; see Fig. 1 for their placement). Five distinct monothecal stamens occur only rarely, while androecia with three stamens, four stamens (via the loss of one), or two stamens evolved repeatedly and are common. Another type of fusion involves the filaments, which may form a central column, a condition that has evolved repeatedly.

Fossils, Biogeography, and Divergence Times of Major Groups of Cucurbitaceae

The oldest fossils of Cucurbitaceae are seeds from the Uppermost Paleocene and Lower Eocene London Clay (65 Ma) that, based on their shape and testa morphology, represent Cucurbitaceae (Collinson et al. 1993). The earliest pollen of Cucurbitaceae is *Hexacolpites echinatus* from the Oligocene of Cameroon (Salard-Cheboldaeff 1978); these grains under the light microscope are hexacolpate or stephanocolpate, and resemble polycolpate pollen of New World Sicyoeae (Schaefer et al. 2008a). Seeds of various species of *Cucurbitospermum* have been described from the Early Miocene (17.8 Ma) sites of Rusinga Island in Lake Victoria, Kenya (Collinson et al. 2009). *Bryonia*-like seeds from fossil beds at Tambov, Western Siberia (Dorofeev 1963, 1988) date to the Lower Sarmat, 15–13 Ma ago. A relatively high geologic age for the clade comprising *Austrobryonia, Bryonia*, and *Ecballium* (Fig. 1) matches its geographically distant and biogeographically unusual range in Eurasia and Australia (Schafer et al. 2008b; Volz and Renner 2009).

Subfossil records of *Cucurbita pepo* have been dated to 8000–7000 B.P. at Guilá Naquitz, and to about 7000–6500 B.P. at Ocampo Cave, Tamaulipas (Smith 1997), those of *C. moschata* in the northern Peruvian Andes to up to 9200 B.P. (Dillehay et al. 2007; Paris, The Cucumber Genome). *Lagenaria siceraria* rind fragments from Mesoamerican archaeological deposits have been radiocarbon-dated to 10,000 B.P, indicating that the bottle gourd was present in the Americas as a domesticated plant by that time.

Cucurbitaceae apparently originated in Asia sometime in the Late Cretaceous (Schaefer et al. 2009). The five deepest evolutionary divergences in the family all date to the Late Cretaceous, 70–80 Ma. Two of these ancient clades [the Gomphogyneae (I) and *Actinostemma* (IV) clade; Fig. 1] are now almost restricted to Asia. A third, the Triceratieae (II), is mainly Neotropical, except for a small African genus, *Cyclantheropsis*. The ancestors of another early-diverging clade (Fig. 1), the Zanonieae (III), apparently reached the African continent early, and from there dispersed to Madagascar (the early Eocene *Xerosicyos* lineage). Later, in the Oligocene, at least two long-distance dispersal events brought two members of this clade, the *Siolmatra* lineage, to America, and the *Zanonia* lineage, back to tropical Asia. The younger tribes towards the top of the tree (Coniandreae, Benincaseae, Cucurbiteae) in Fig. 1 all have relatively large geographic ranges that they often extended by transoceanic dispersal (Schaefer et al. 2009). Striking examples of such transoceanic dispersal are found in the sponge gourd genus, *Luffa*, three of whose eight species occur in the New World, four in tropical and subtropical Asia, and one in northern Australia (Telford et al. 2011a, b; Filipowicz et al. 2014), and in *Sicyos*, which has 14 species, all descending from a single ancestor that arrived c. three million years ago, two species on Galapagos that arrived independently, and three species in Australia and New Zealand (Sebastian et al. 2012; Telford et al. 2012). Finally, the bottle gourds, *Lagenaria*, are of African origin but very likely arrived in Central America with sea currents and were domesticated there some 10.000 years ago (Clarke et al. 2006; Kistler et al. 2014).

The native European cucurbit flora belongs to a single clade, *Bryonia*, with 10 species, and its monotypic sister *Ecballium*, the squirting cucumber, which diverged from a sister group that reached Australia (*Austrobryonia*) c. 36 (50–24) million years ago (Schaefer et al. 2008b). The remaining cucurbit species occurring in Europe are the result of recent introductions (*Echinocystis lobata*, *Sicyos angulatus*, *Thladiantha dubia*), or casual escapes from cultivation (*Citrullus lanatus*, *Cucumis melo*, *C. sativus*, *Cucurbita pepo*).

African Cucurbitoideae, classified in some 25 genera, evolved from five successful dispersals from Asia to Africa, and two from America to Africa (in *Melothria* and *Cayaponia*; Schaefer and Renner 2010a; Duchen and Renner, 2010). The famous cucumber tree, *Dendrosicyos socotranus*, endemic on Socotra some 350 km from the Arabian peninsula, was thought to have diverged from its closest relative 34 (47–22) Ma, while the Socotra archipelago is only some 10 million years old (Schaefer et al. 2009) but more comprehensive sampling revealed previously overlooked close relatives in the genus *Kedrostis*, which led to a much reduced age estimate of *Dendrosicyos* of 14 (8–19) Ma in accordance with the age of Socotra (Schaefer et al. in prep.). Madagascar has 50 native species of Cucurbitaceae that are currently classified in 16 genera. Based on molecular sequence data, it appears that this diversity evolved from 13 ancestral lines that reached Madagascar from the African mainland (Schaefer et al. 2009).

South America has about 360 species of Cucurbitaceae that descend from just a few transoceanic dispersal events, mostly from Africa to South America. These events involved the ancestors of the Cucurbiteae, lineages of the Sicyoeae, part of the Coniandreae, and *Melothria*, *Lagenaria*, and *Luffa* (see under these genera). For *Melothria*, it appears that its ancestors came across the Pacific, since the sister group of *Melothria*, *Indomelothria*, is endemic in Southeast Asia. North American cucurbits descend from seven expansions of Central and South American lineages that occurred at widely different times (Schaefer et al. 2009).

The indigenous Australian Cucurbitaceae flora, finally, consists of 30 species in 12 genera of which two are endemic, *Nothoalsomitra*, a single liana species of Queensland's humid rainforests, and *Austrobryonia*, four species of trailers or creepers in the dry regions of (mostly) Central Australia (Schaefer et al. 2008b).

A 'time tree' or 'chronogram' for the Cucurbitaceae, which provides divergence times in million years, along with confidence intervals, is shown in Schaefer et al. (2009), and more detailed chronograms, all calculated using Bayesian molecular clock approaches, are available for the c. 66 species of *Cucumis* (Renner et al. 2007, Sebastian et al. 2010), all 47 species of *Momordica* (Schaefer and Renner 2010a, b), all 27 species of *Coccinia* (Holstein and Renner 2011), 52 of the 90–100 species of *Trichosanthes* (De Boer et al. 2012), all seven species of *Citrullus* (Chomicki and Renner 2015). Additional studies will be published in the coming months for the three species of *Dactyliandra* (Lindner et al. 2017), the six species of *Siraitia* (Schaefer, unpublished), and all species of *Kedrostis* and *Corallocarpus* (Schaefer, unpublished).

The Need for Fieldwork and Sequencing of Publicly Available Herbarium Vouchers

Even though the phylogeny and geographic history of the cucurbit family is now reasonably well understood (especially when compared to other tropical clades of similar species richness), every sequencing project so far has resulted in the discovery of overlooked species, including completely unexpected wild relatives of crop species such as cucumber, melon, and watermelon (Sebastian et al. 2010; Chomicki and Renner 2015). There is an urgent need to collect (and DNA-sequence) wild material, but also to sequence the type specimens (housed in herbaria) of the many overlooked existing species names. This would help breeders and genomics researchers to become aware of the correct names of the entities they are studying. Knowing the precise phylogenetic position of a taxon allows better choices for crossing experiments, facilitates genome annotation, and permits inferences about area of geographic origin or likely native climate niche. One example of this need is an entity often discussed as *Cucumis sativus* L. 'var. *xishuangbannanesis*' (e.g, most recently by Bo et al. 2015). This name has never been validly published, meaning it does not exist under the *Codes of Nomenclature*. To validate any scientific name requires a diagnosis, which need not comprise a lengthy text, but instead can consist of clearly stated and publicly verifiable DNA differences (characters) linked to one or more specimens deposited in a permanent and public collection (a herbarium, not a germplasm collection, which is not permanent) (Renner 2016). A similar case, now solved, was the watermelon, where the fully sequenced genome (Guo et al. 2013) was in fact not the species represented by the type specimen of *Citrullus lanatus* collected by one of Linnaeus's students (Chomicki and Renner 2015). The watermelon name problem can be rectified by selecting a new type for this name that agrees with our current usage as proposed to the International Nomenclature Commission (Renner et al. 2014). Lastly, and most importantly, more fieldwork, especially in the diversity centers of the family, the Himalayan foothills of India, the Australasian region, West Africa, and Madagascar, is needed to better understand the evolution of the family.

Literature Cited

Bo K, Ma Z, Chen J, Weng Y. Molecular mapping reveals structural rearrangements and quantitative trait loci underlying traits with local adaptation in semi-wild Xishuangbanna cucumber (*Cucumis sativus* L. var. *xishuangbannanesis* Qi et Yuan). Theor Appl Genet. 2015;128:25–39. doi:10.1007/s00122-014-2410-z.

Burnett GT. Outlines of Botany, including a general history of the vegetable kingdom in which plants are arranged according to the system of natural affinities. London: J. Churchill; 1835.

Chomicki G, Renner SS. Watermelon origin solved with molecular phylogenetics including Linnaean material: Another example of museomics. New Phytol. 2015;205(2):526–32. doi:10.1111/nph.13163.

Clarke AC, Burtenshaw MK, McLenachan PA, Erickson DL, Penny D. Reconstructing the origins and dispersal of the Polynesian bottle gourd (*Lagenaria siceraria*). Mol Biol Evol. 2006;23:893–900.

Collinson ME, Boulter MC, Holmes PR. Magnoliophyta (Angiospermae). In: Benton MJ, editor. The fossil record 2. London: Chapman and Hall; 1993. p. 809–41, 864.

Collinson ME, Andrews P, Bamford MK. Taphonomy of the early Miocene flora, Hiwegi Formation, Rusinga Island, Kenya. J Hum Evol. 2009;57:149–62.

De Boer HJ, Schaefer H, Thulin M, Renner SS. Evolution and loss of long-fringed petals: a case study using a dated phylogeny of the snake gourds, *Trichosanthes* (Cucurbitaceae). BMC Evol Biol. 2012;12:108. doi:10.1186/1471-2148-12-108.

Dillehay TD, Rossen J, Andres TC, Williams DE. Preceramic adoption of peanut, squash, and cotton in Northern Peru. Science. 2007;316:1890–3.

Dorofeev PI. The Tertiary floras of western Siberia. vol 271. Izdvo Akademii Nauk SSSR, Moscow-Leningrad, Russian Academy of Sciences, USSR; 1963.

Dorofeev PI. Mioz ä ne Floren des Bezirks Tambov. Akademija Nauka SSSR, Leningrad, Russian Academy of Sciences, USSR; 1988.

Duchen P, Renner SS. The evolution of *Cayaponia* (Cucurbitaceae): repeated shifts from bat to bee pollination and long-distance dispersal to Africa 2–5 million years ago. Am J Bot. 2010;97(7):1129–41.

Filipowicz N, Schaefer H, Renner SS. Revisiting *Luffa* (Cucurbitaceae) 25 years after C. Heiser: species boundaries and application of names tested with plastid and nuclear data. Syst Bot. 2014;39(1):205–15.

Guo S, Zhang J, Sun H, Salse J, Lucas WJ, Zhang H, et al. The draft genome of watermelon (*Citrullus lanatus*) and resequencing of 20 diverse accessions. Nat Genet. 2013;45:51–8.

Holstein N, Renner SS. A dated phylogeny and collection records reveal repeated biome shifts in the African genus *Coccinia* (Cucurbitaceae). BMC Evol Biol. 2011;11:28.

Jeffrey C. A review of the Cucurbitaceae. Bot J Linn Soc. 1980;81:233–47.

Jeffrey C. Appendix: an outline classification of the Cucurbitaceae. In: Bates DM, Robinson RW, Jeffrey C, editors. Biology and utilization of the Cucurbitaceae. Ithaca: Comstock Publication Associates, Cornell University Press; 1990. p. 449–63.

Jeffrey C. A new system of Cucurbitaceae. Bot Zhurn. 2005;90:332–5.

Kater MM, Franken J, Carney KJ, Colombo L, Angenent GC. Sex determination in the monoecious species cucumber is confined to specific floral whorls. Plant Cell. 2001;13:481–93.

Kistler L, Montenegro A, Smith BD, Gifford JA, Green RE, Newsom LE, et al. Transoceanic drift and the domestication of African bottle gourds in the Americas. Proc Natl Acad Sci U S A. 2014;111:2937–41.

Kocyan A, Zhang LB, Schaefer H, Renner SS. A multi-locus chloroplast phylogeny for the Cucurbitaceae and its implications for character evolution and classification. Mol Phylogenet Evol. 2007;44:553–77.

Kosteletzky VF. Allgemeine medizinisch-pharmazeutische Flora, vol. 6. Prag: Borrosch & Andre; 1833.

Lindner K, Hu Y, Pandey AK, Schaefer H. The Namib-Thar desert disjunction in Dactyliandra (Cucurbitaceae) is the result of a recent introduction to India. Systematic Botany; 2017 (in press).

Matthews ML, Endress PK. Comparative floral structure and systematics in Cucurbitales (Corynocarpaceae, Coriariaceae, Tetramelaceae, Datiscaceae, Begoniaceae, Cucurbitaceae, Anisophylleaceae). Bot J Linn Soc. 2004;145:129–85.

Mitchell TC, Dötterl S, Schaefer H. Hawk-moth pollination and elaborate petals in Cucurbitaceae: the case of the Caribbean endemic *Linnaeosicyos amara*. Flora. 2015;216:50–6.

Renner SS. A return to Linnaeus's focus on diagnosis, not description: the use of DNA characters in the formal naming of species. Syst Biol. 2016. doi:10.1093/sysbio/syw032, online 4 May 2016.

Renner SS, Chomicki G, Greuter W. Proposal to conserve the name *Momordica lanata* (*Citrullus lanatus*) (watermelon, Cucurbitaceae), with a conserved type, against *Citrullus battich*. Taxon. 2014;63(4):941–2.

Renner SS, Schaefer H, Kocyan A. Phylogenetics of *Cucumis* (Cucurbitaceae): cucumber (*C. sativus*) belongs in an Asian/Australian clade far from melon (*C. melo*). BMC Evol Biol. 2007;7:58. http://www.biomedcentral.com/1471-2148/7/58/.

Salard-Cheboldaeff M. Sur la palynoflore Maestrichtienne et Tertiaire du bassin sédimentaire littoral du Cameroun. Pollen Spores. 1978;20:215–60.

Schaefer H, Renner SS. A gift from the New World? The West African crop *Cucumeropsis mannii* and the American *Posadaea sphaerocarpa* (Cucurbitaceae) are the same species. Syst Bot. 2010a;35(3):534–40.

Schaefer H, Renner SS. A three-genome phylogeny of *Momordica* (Cucurbitaceae) suggests seven returns from dioecy to monoecy and recent long-distance dispersal to Asia. Mol Phylogenet Evol. 2010b;54(2):553–60.

Schaefer H, Renner SS. Cucurbitaceae. In: Kubitzki K, editor. Families and genera of flowering plants, vol. 10. Berlin: Springer; 2011a. p. 112–74.

Schaefer H, Renner SS. Phylogenetic relationships in the order Cucurbitales and a new classification of the gourd family (Cucurbitaceae). Taxon. 2011b;60(1):122–38.

Schaefer H, Heibl C, Renner SS. Gourds afloat: a dated phylogeny reveals an Asian origin of the gourd family (Cucurbitaceae) and numerous oversea dispersal events. Proc Royal Soc B. 2009;276:843–51.

Schaefer H, Kocyan A, Renner SS. *Linnaeosicyos* (Cucurbitaceae): a new genus for *Trichosanthes amara*, the Caribbean sister species of all Sicyoeae. Syst Bot. 2008a;33(2):349–55.

Schaefer H, Telford IRH, Renner SS. *Austrobryonia* (Cucurbitaceae), a new Australian endemic genus, is the closest living relative to the Eurasian and Mediterranean *Bryonia* and *Ecballium*. Syst Bot. 2008b;33(1):125–32.

Sebastian PM, Schaefer H, Telford IRH, Renner SS. Cucumber and melon have their wild progenitors in India, and the sister species of *Cucumis melo* is from Australia. Proc Natl Acad Sci U S A. 2010;107(32):14269–73.

Sebastian P, Schaefer H, Lira R, Telford IRH, Renner SS. Radiation following long-distance dispersal: the contributions of time, opportunity, and diaspore morphology in *Sicyos* (Cucurbitaceae). J Biogeogr. 2012;39:1427–38. doi:10.1111/j.1365-2699.2012.02695.x.

Smith BD. The initial domestication of *Cucurbita pepo* in the Americas 10,000 years ago. Science. 1997;276:932–4.

Telford IRH, Schaefer H, Greuter W, Renner SS. A new Australian species of *Luffa* (Cucurbitaceae) and typification of two Australian *Cucumis* names, all based on specimens collected by Ferdinand Mueller in 1856. PhytoKeys. 2011a;5:21–9.

Telford IRH, Sebastian PM, Bruhl JJ, Renner SS. *Cucumis* (Cucurbitaceae) in Australia and eastern Malesia, including newly recognized species and the sister species to *C. melo*. Syst Bot. 2011b;36(2):376–89.

Telford IRH, Sebastian P, de Lange PJ, Bruhl JJ, Renner SS. Morphological and molecular data reveal three rather than one species of *Sicyos* (Cucurbitaceae) in Australia, New Zealand and the islands of the South West Pacific. Aust Syst Bot. 2012;25(3):188–201.

Volz SM, Renner SS. Phylogeography of the ancient Eurasian medicinal plant genus *Bryonia* (Cucurbitaceae) inferred from nuclear and chloroplast sequences. Taxon. 2009;58(2):550–60.

Zhang LB, Simmons MP, Kocyan A, Renner SS. Phylogeny of the Cucurbitales based on DNA sequences of nine loci from three genomes: Implications for morphological and sexual system evolution. Mol Phylogenet Evol. 2006;39:305–22.