Cucurbitaceae

Cucurbitaceae Durande (1782), nom. cons.

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Tendril-bearing monoecious or dioecious climbers or trailers, rarely without tendrils, herbaceous annual vines or woody perennial lianas, exceptionally trees (*Dendrosicyos*), often with tuberous roots or rootstocks or with leafless and $\pm$ succulent stems. Shoots usually angulate, herbaceous, woody, or succulent, with bicollateral vascular bundles. Leaves spiral, estipulate, petiolate, membranaceous or succulent, simple and entire or palmately or pedately lobed, or palmati- or pedati-compound, the margins with small hydathodes (or glandular teeth); tendrils usually one per node. Inflorescences generally racemes, thyrses, panicles, fascicles, rarely spikes or umbels. Flowers with calyx and corolla, unisexual (very rarely bisexual), epigynous, usually pentamerous and actinomorphic, rarely zygomorphic; corolla aestivation valvate, contort, quincuncial; petals (3–)5(–10), entire, 2-lobed or fringed, rarely with a basal scale; nectary formed by mesophyll tissue or hairs; some species with floral oil glands; androecium of 3–5 alternipetalous stamens; thecae 1 or 2, distinct or connate along their filaments and/or anthers; stamens often joined or connate in two pairs, filaments or stamens sometimes connate into a central column; anthers typically basifixed and thecae longitudinally dehiscent, straight or variously bent or folded, rarely forming a horizontal ring; gynoecium with (1–)3(–5) carpels, inferior or semi-inferior; stylodia distinct or connate into a single style; stigma entire, lobulate, or divided; placentation parietal; ovules anatropous, bitegmic, and crassinucellar, horizontal, pendent, oblique, or ascendent. Fruit many-seeded, rarely 1-seeded, usually a soft-shelled or hard-shelled berry, less often a capsule, rarely samaras or achenes. Seeds with an exotestal seed coat, sometimes flattened, winged, or enclosed by mucilaginous tissue, exalbuminous; embryo straight, usually oily, with large, flat cotyledons. Producing oxygenated tetracyclic triterpenoids (cucurbitacins) with bitter taste and purging or abortive effect.

The family contains 97 genera and 940–980 species. Its distribution is essentially tropical and subtropical, with relatively few species reaching the temperate regions of the world. The aerial parts of all species are sensitive to frost.

Vegetative Morphology. Most Cucurbitaceae are annual or perennial herbs with relatively thin roots and shoots. Many perennial species have tuberous roots or pachypodia, and their herbaceous shoots die and re-grow in an annual cycle (hemicryptophytic life form). Pachypodia can reach well over a meter in diameter (e.g., in *Baijiania yunnanensis*). The family also includes a few shrub species (*Acanthosicyos horridus*, Fig. 29, *Corallocarpus glomeruliflorus*, *Momordica spinosa*) and lianas with woody, perennial stems up to 10 cm across (*Alsomitra*, *Bayabusua*, *Coccinia grandis*, *Siolmatra*, *Zanonia*; Carlquist 1992). The sole tree in the family, *Dendrosicyos socotranus* (Fig. 27), results from an extreme case of pachycauly, with stems up to 1 m in diameter (Olson 2003).

Phyllotaxy in Cucurbitaceae is spiral. Only the first leaves following the cotyledons may be opposite or rarely verticillate (*Bayabusua*). The cotyledons are often large, fleshy, ovate to elongate, green, and long-lived. Epigeal germination is the rule, hypogeal germination an exception (Zimmermann 1922; Parfitt et al. 1990). Cucurbitaceae leaves lack stipules and usually have

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well-developed petioles; sessile or subsessile leaves occur in a few species of *Coccinia*, *Momordica*, *Sicyos*, *Solena*, and *Cephalopentandra ecirrhosa*. The blade is simple or lobed, less often 3-foliolate, rarely up to 9-foliolate (*Momordica enneaphylla*), the venation is palmate. As is typical of climbers, leaf shape can vary strikingly along shoots of the same plant and between individuals growing under different environmental conditions (Jones 1993; Pozner 1998a, b). Probracts (usually foliar structures at the base of the peduncles, see Fig. 30D) occur in some inflorescences, and these bracts often bear extrafloral nectaries (Fig. 31B, H; see also Sexual Strategies, Pollination, and Herbivores). The indumentum of Cucurbitaceae is often pubescent or prickly, with trichomes that have calcified cell walls and cystolith-bearing bases; glandular hairs are also common, as are foliar nectaries and mucilage glands.

Most Cucurbitaceae have tendrils, and this ancestral condition presents a clear morphological synapomorphy for the family; evolutionarily, these tendrils are modified shoots (Kumazawa 1964; Lassnig 1997; Gerrath et al. 2008). Whether tendrils are simple or divided and how they coil is taxonomically useful (Fig. 21A–C illustrates the main types). Tendrils that coil below the tendril branching point are found in the more basal clades (see below), and have traditionally been referred to as zanonioid (from Zanonieae). In a few species, the tendrils have been transformed into thorns (*Acanthosicyos horridus*, Fig. 29, *Citrullus naudinianus*, *Momordica spinosa*) or were lost (*Citrullus ecirrhosus*, *Dendrosicyos socotranus*, *Ecballium elaterium*, *Melothria campestre*, *Cucumis messorius*, *Trochomeria polymorpha*). Sometimes, the tendrils form adhesive pads similar to those of *Parthenocissus* in the Vitaceae (*Alsomitra macrocarpa*, *Bayabusua clarkei*, *Neoalsomitra sarcophylla*, *Polyclathra cucumerina*, *Trichosanthes cucumerina*). The first tendrils usually appear on the 4th to 6th node of a seedling (Zimmermann 1922).

Anatomy. The wood anatomy of Cucurbitaceae reflects the climbing habit of most species (Carlquist 1992), with a wide vessel diameter compensating for a small transsectional area of secondary xylem. In some groups, parenchyma is abundant, with the vessels sheathed in thick-walled libriform fibers and vasicentric tracheids (Zimmermann 1922; Carlquist 1992). Uniseriate rays are absent. Large primary rays separate perennial vascular bundles, or large secondary rays are initiated within vascular bundles (Schweingruber et al. 2010). Successive cambia occur in *Bryonia* and *Ecballium*, and some genera have medullary phloem and bicollateral vascular bundles (Schweingruber et al. 2010). The phloem is mostly simply structured. Sieve tubes and

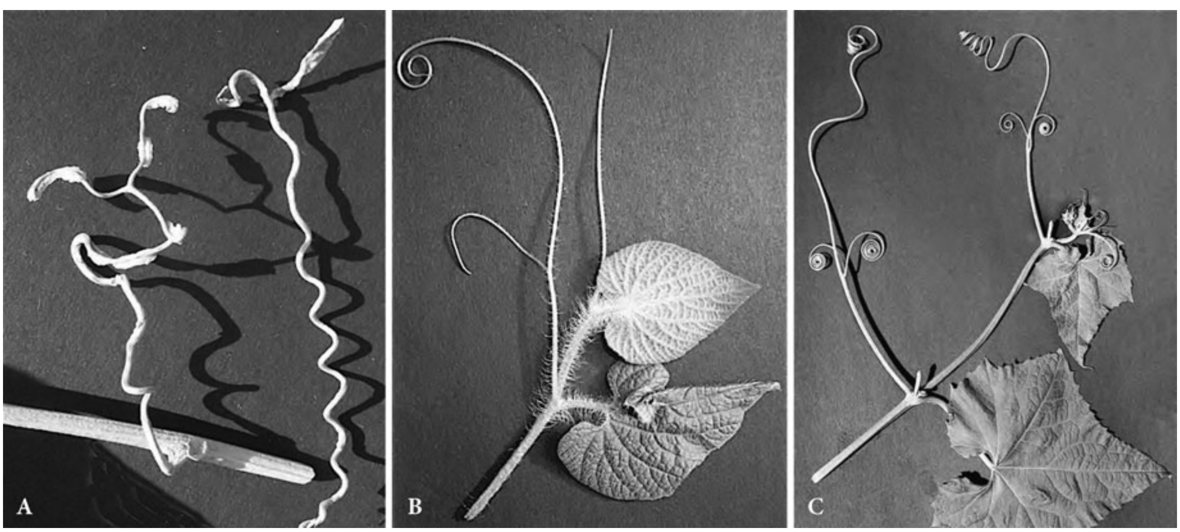

Fig. 21. The main tendrils type of Cucurbitaceae. **A** *Neoalsomitra sarcophylla* (Gomphogyneae, apically 2-fid (=zanonioid) tendril). **B** *Thladiantha dubia* (Thladiantha Clade, simple or 2-fid tendril). **C** *Luffa cylindrica* (Sicyoeae). (Photos G. Hausner)

parenchyma are difficult to distinguish. Raphids occur in the phloem of at least *Ecballium* and *Cucurbita pepo*. Calcium oxalate crystals as well as cystoliths, small calcium carbonate bodies of variable shape, are abundant in *Telfairia* (Okoli and McEuen 1986) and also occur in other genera, especially near the bases of hairs. At least *Cucurbita* contains crystalline silica grains (SiO_2), and in the fossil record, where they are called phytoliths, their shapes can document the presence of particular domesticated forms (Piperno et al. 2002; Piperno and Stothert 2003).

Inflorescences and Floral Structure. Flowers are generally borne in few- to many-flowered racemes, thyrses, panicles, or fascicles, rarely in spikes or umbels. The family's basic inflorescence type seems to be monotelic, and cases of "open" inflorescences are therefore best described as racemiform, spiciform or umbelliform cymes. About 50% of the c. 960 species are monoecious, and in these species, inflorescences can be cosexual or unisexual. The flowers of Cucurbitaceae are usually unisexual. Bisexual flowers are exceedingly rare. They regularly occur in *Schizopepon bryoniifolius* (Fukuhara and Akimoto 1999; Akimoto et al. 1999) and *Zehneria hermaphrodita* (de Wilde and Duyfjes 2006a; see also Sexual Strategies, Pollination, and Herbivores). Floral symmetry is mostly actinomorphic. Zygomorphy has evolved only in a few species, for example, in *Gerrardanthus* (Fig. 25) and *Xerosicyos*. Male and female perianths are usually similar; occasionally, they differ in size and exceptionally also in shape (*Momordica*, *Peponopsis*). 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. Analysis of cucumber floral homeotic mutants suggests that the inhibition of stamens or pistils depends on whorl position, not specific sexual organ identity (Kater et al. 2001). The calyx and corolla in Cucurbitaceae are usually pentamerous. Sepal aestivation is valvate or open, exceptionally overlapping (*Luffa*; Pozner 1998a). The corolla consists of ± connate or distinct petals highly variable in size, shape, and consistence, though rather uniform in color (usually white, yellow, or orange).

The hypanthium in Cucurbitaceae derives from the expansion of sepal and petal bases, and their receptacular insertion area (Leins and Galle 1971; Pozner 1993a, b). 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*; Vogel 1981a; Pozner 2004). The hypanthium floor typically bears a nectary, which can be mesenchymal (most genera) or trichomatous (Sicyoeae; Vogel 1981a, 1997; Pozner 2004). In female flowers, the hypanthium includes the ovary wall, producing a "hypanthial gynoecium" (Leins et al. 1972). 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, Triceratieae, and Zanonieae usually have three (sometimes two or five) distinct stylodia (e.g., Figs. 23F, 24G,25F). The more derived clades have a single style with 2–3(–5) stigmas (e.g., Fig. 30F), which can be enlarged to mimic an androecium, probably to attract pollen-seeking bees (Dukas 1987; Rust et al. 2003). Stigma shape is diverse and taxonomically useful. Ovules are anatropous and bitegmic, their number ranging between 1 to several hundreds. Placentae are typically large, and ovule numbers can be huge (Matthews and Endress 2004). In the more derived clades, the ovules are embedded within individual chambers (ovular or seminal chambers) formed by hypanthial-carpellary-placentary tissue (Pozner 1994). Ovule orientation in the *Actinostemma* Clade, Triceratieae, Gomphogyneae, and Zanonieae (as well as in the derived clade Sicyoeae) is mostly pendent. Ovule orientation in the remaining clades is typically horizontal, horizontal in the upper and middle region of the ovary, and erect at the base (*Cucurbita*) 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 may represent the ancestral state, which survives in a few unrelated groups (*Anisosperma* and some *Telfairia*; see Fig. 26C). Five distinct monothecal stamens, as in *Fevillea*, occur only rarely, while androecia with three stamens (two 2-thecous, one 1-thecous, e.g., Fig. 30B), four stamens (via the loss of one), or two stamens (below) evolved repeatedly and are common. Cucurbit flowers initiate five distinct stamen primordia, even those with highly connate stamens (Matthews and Endress 2004, and references therein), and it is assumed that the 3-merous androecia evolved from the fusion of two pairs of monothecal stamens, leaving one monothecal unpaired stamen (Eichler 1875). An analogous process may be observed in some genera with postgenital fusion of stamens, such as *Cucurbitella* (Pozner 1993b, 1994, 1998a), and double vascular bundles in filaments also fit with such an interpretation (*Thladiantha*; Vogel 1990; *Momordica charantia*; Deshpande et al. 1986). Another type of fusion involves the filaments, which may form a central column (in the unrelated genera *Echinopepon*, *Frantzia*, *Gynostemma*, *Hanburia*, *Ibervillea*, *Marah*, *Penelopeia*, and *Sicyos*). Not all filament columns are homologous: some derive from staminal filaments, while others are a receptacle expansion (Imaichi and Okamoto 1992). Striking is the independent evolution of circular anther heads in the unrelated genera *Cyclanthera*, *Cyclantheropsis*, and *Penelopeia*. Stamens of Cucurbitaceae often bear connective trichomes, which may arise in marginal rows, resulting in fringed connectives (*Cucumis*, *Melothria*), or else they may produce sticky secretions that agglutinate pollen grains (Zimmermann 1922; Vogel 1981b). Connective outgrowths are usually apical, and may be taxonomically useful, although this needs critical study (*Cucumis*, *Citrullus*).

Karyology. Chromosome numbers are available for at least 141 species from about half of the 97 genera (Beevy and Kuriachan 1996; Index to Plant Chromosome Numbers, http://mobot.mobot.org/W3T/Search/ipcn.html), mostly those of economic importance. Reported haploid (gametophytic) chromosome numbers range from 7 to 24, with $x = 12$ a prevalent number (Beevy and Kuriachan 1996). In the relatively basal Gomphogyneae, reported numbers for *Gynostemma* are $n = 11, 22, 33, 44, 66, 88$ (Gao et al. 1995), for *Gomphogyne* $n = 16$ (Thakur and Sinha 1973), and for *Hemsleya* $n = 14$ (Samuel et al. 1995). *Actinostemma* has $2n = 16$ (Probatova and Rudyka 1981), and the more derived clades, such as the *Thladiantha*, *Siraitia*, and *Momordica* Clades, have $n = 9$ in *Thladiantha*, $n = 12$ in *Siraitia*, $n = 16$ in *Baijiania* (Li et al. 1993), or $n = 11$ and 14 in *Momordica* (Beevy and Kuriachan 1996). *Telfairia* has $x = 12$ (Okoli 1987). Bryonieae have $x = 9$ (*Ecballium*) or 10 (*Bryonia*) (Volz and Renner 2008). Schizopeponeae have $x = 10$ in *Schizopepon* (Nishikawa 1981) and $x = 11$ in *Herpetospermum* (Thakur and Sinha 1973). In the Sicyoeae (as defined here), *Luffa* has $n = 13$ (Whitaker 1933; Samuel et al. 1995), *Hodgsonia* $x = 9$ (Chen 1993), *Trichosanthes* $x = 11$ or 12 (Beevy and Kuriachan 1996), *Echinopepon* and *Sicyos* $n = 12$ (Ward and Spellenberg 1988; Turala-Szybowska 1990), *Marah* $n = 15$ (Parfitt et al. 1990), and *Cyclanthera* and *Echinocystis* $n = 16$ (Samuel et al. 1995; Gervais et al. 1999). The few counted species of Coniandreae have $n = 13$ (*Corallocarpus*, *Kedrostis*; Beevy and Kuriachan 1996) or $n = 14$ (*Apodanthera*; Ward 1984). Benincaseae may have a base number of $n = 12$, as reported for eight of their genera (Beevy and Kuriachan 1996), but there is also much polyploidy and aneuploidy (Thakur and Sinha 1973; Beevy and Kuriachan 1996). The Cucurbiteae may have fixed polyploidy, with $n = 20$ (*Sicana*; Mercado and Lira Saade 1994; *Cucurbita*; Samuel et al. 1995).

Pollen Morphology. (contributed by C.B. Mennes and R.W.J.M. van der Ham). The morphology of the pollen grains is known for all but one very rare genus (*Tumamoca*). Pollen of Cucurbitaceae is tectate to intectate, and grains are shed as monads, rarely as tetrads (*Borneosicyos*, *Gurania*, *Psiguria*). Pollen grain size can reach up to very large (to 200 µm; some *Cayaponia* and *Polyclathra*; Khunwasi 1998; Barth et al. 2005), but most species have large grains (50–100 µm in diam.). When describing the pollen of individual genera for this treatment, we have applied Erdtman's (1952) subdivision: 10–25 µm = small, 25–50 µm = medium-sized, 50–100 µm = large, 100–200 µm = very large. Pollen of the phylogenetically early-branching *Actinostemma* Clade, the Triceratieae, Gomphogyneae, and Zanonieae is always tricolporate and, different from the more derived clades, usually small to medium-sized, with diameters less than 40 μm. The exine in these clades is usually striate, although *Gerrardanthus* (Zanonieae) has reticulate exines, and *Alsomitra macrocarpa* (Gomphogyneae) a perforate to indistinctly rugulate exine (van der Ham 1999). Nevertheless, striate-reticulate exines are also found in a few genera in more derived clades, such as *Kedrostis* in the Coniandreae and *Peponium*, *Scopellaria*, and *Papuasicyos* (including *Urceodiscus*) in the Benincaseae (Duyfjes et al. 2003). Clades V–XV in Fig. 22 usually have pollen with reticulate or echinate exines, and porate, colporate or colpate apertures. Thus, Coniandreae (including *Bambekea* and *Eureiandra*) and Benincaseae tend to have reticulate 3-colporate pollen, and Cucurbiteae echinate 3-porate to periporate pollen. An African member of Benincaseae with unusual 6-aperturate pollen is *Zehneria peneyana* (van der Ham and Pruesapan 2006). Echinate exines also occur in *Benincasa* (including *Praecitrullus*) and *Diplocyclos* (Benincaseae). Other examples of parallel evolution are the pollen tetrads in *Gurania* and *Psiguria* (Coniandreae) and in *Borneosicyos* (Benincaseae; van der Ham and van Heuven 2003). Another striking case of morphological similarity (or parallel evolution) is the intectate, gemmate pollen with 3 operculate pori that is found in the Asian Schizopeponeae and in the African *Cephalopentandra ecirrhosa* (Benincaseae) (van der Ham and Mennes, unpubl. data). Pollen of Sicyoeae is rather heterogeneous, as expected in an old and species-rich group. Thus, *Trichosanthes* has 3 (4)-colporate to 3(4)-porate pollen (Pruesapan and van der Ham 2005), and the New World *Linnaeosicyos* and Sicyoeae have 4- to 16-colporate or -colpate pollen (Stafford and Sutton 1994; Schaefer et al. 2008a). Such New World sicyoid pollen is also known as *Hexacolpites echinatus* from the Oligocene of Cameroon (Salard-Cheboldaeff 1978; Muller 1985).

Embryology. Important aspects of floral structure and embryology are unknown for most Cucurbitaceae, especially the early-branching lineages (Matthews and Endress 2004). In all species studied, ovules are anatropous, bitegmic, and crassinucellar (Johri et al. 1992; Matthews and Endress 2004). Typically, ovules of Cucurbitaceae develop a nucellar beak: a more or less cylindrical protuberance of the nucellus that fills the micropylar channel, and in some cases also contacts the epidermis of the ovular chamber (Pozner 1993a). The outer integument has a vascular bundle running from the funiculus around the chalaza and reaching the opposite, distal end of the integument. The outer integument, and particularly its outer epidermis, forms the testa (resulting in the family's characteristic exotestal seed coat; Johri et al. 1992). The inner integument is typically 2-layered (but thicker around the micropyle) and disintegrates by the time of fertilization. Megaspores are arranged in a linear tetrad (Johri et al. 1992), and megaspore selection is usually by postmeiotic competition (Pozner 1994). As far as known, embryo sacs are of the Polygonum type, except in *Benincasa hispida*, which can have a Polygonum type or an Allium type embryo sac (Chopra and Basu 1965). The endosperm is of the nuclear type (Johri et al. 1992). Shortly after fertilization, the lower part of the embryo sac of many (most?) cucurbit genera forms a chalazal endosperm haustorium, which can be coenocytic or become cellular (Chopra 1955; Chopra and Basu 1965; Chopra and Seth 1977). The haustorium functions until the growing embryo reaches the heart-shaped stage and then disorganizes or is pressed to the base of the endosperm. In the studied genera, the endosperm is completely consumed during embryo development and the mature seeds are non-endospermic (Chopra 1955). Embryo development follows the onagrad, asterad, or solanad type (Johri et al. 1992). Embryos are straight and have flat cotyledons.

The anthers are bi- or tetrasporangiate, and in *Cucumis sativus* and *Echinocystis lobata* both conditions may occur in the same flower (Davis 1966). Anther wall development corresponds to Davis's basic type (Davis 1966; Johri et al. 1992), although the pattern of cell layer segregation is unstable (Pozner 1993b). The endothecium develops fibrous thickenings, and anther dehiscence has some variations particularly in species with tightly folded thecae (Pozner 1993b). The 1–3 middle layers are ephemeral, and the tapetum is glandular, with uni- to multinucleate cells. The microspore mother cells after meiosis undergo simultaneous cytokinesis, and the microspore tetrads are tetrahedral. Pollen grains are 2- or

3-celled when shed (Johri et al. 1992). The pollen tube is persistent within the nucellar beak after fertilization, and in some species it may grow as a swollen structure the function of which is unclear (Pozner 1993a).

Fruits and Seeds. The morphology of cucurbit fruits and seeds is highly variable and often useful for identifying genera. Fruits are typically many-seeded, the ancestral condition in the clade formed by Begoniaceae, Cucurbitaceae, Datiscaceae, and Tetramelaceae (Zhang et al. 2006). One-seeded fruits evolved in *Hodgsonia* (1–3 seeds per pyrene), *Sicyos*, and *Sicydium*. Berries are the most common fruit type, and they can be hard-shelled, then called gourd or pepo (*Citrullus*, *Cucumis*, *Cucurbita*), or leathery with a fibrous mesocarp (*Sicyos*). Especially the commercially important species often have hard-shelled berries that can reach huge dimensions (to 1 m diameter in *Cucurbita pepo*). In the seasonally dry habitats, where most of these species occur, hard-shelled water-storing fruits allow for prolonged protected seed maturation, which continues even after the remainder of the vegetative shoot has mostly dried out and died off. Dehiscent berries that expose seeds surrounded by a showy, fleshy, arilloid jacket characterize *Momordica*, and explosive fruits *Ecballium* and *Hanburia*. In the latter, the seeds are ejected while the fruit stays on the plant, whereas in *Ecballium* and some species of *Cucumis* the mature fruits separate from the peduncle and eject the seeds by elastic contraction. Capsules are less common (e.g., Figs. 23G, 25G), and they may open apically by 3-radiate slits (*Gerrardanthus*, *Siolmatra*), or the upper part may fall off to release the seeds (pyxidium; *Actinostemma*, *Echinopepon*, *Luffa*). Achenes are found in *Sicydium*, samaras in *Cyclantheropsis*, *Pteropepon*, and *Pseudosicydium*, and geocarpic fruits evolved independently in a few species of *Echinopepon*, *Kedrostis*, and *Cucumis*. Vivipary occurs in chayote, *Sicyos edule*, when the testa does not differentiate sclerenchymatous layers, and the epidermis of both the testa and cotyledons differentiate as haustorial epitelium (Giusti et al. 1978).

Seed morphology is extremely variable, and a few seed shapes are unique to Cucurbitaceae, which may permit the assignment of fossil seeds to particular genera (cf. Fossils and Biogeography). Seeds of fleshy fruits may be globose, ovoid, pyriform (*Halosicyos*), falcate (*Abobra*), compressed (most cases), or even winged (*Cyclanthera* p.p.), usually surrounded by an arilloid jacket derived from the closest carpellary tissue (the ovular or seminal chamber) around the ovule. That arilloid jacket is usually fleshy, hyaline (*Cucumis*), green (*Cucurbitella*), yellow or red (*Momordica*) and sticky with mucilage, which contributes to seed dispersal by adhesion (see Dispersal). Seeds from dry, dehiscent fruits do not have an arilloid jacket. They may be more or less globose (*Echinopepon* p.p.), compressed (*Luffa*), or frequently winged. Seeds with wings predominate in Triceratieae, Gomphogyneae, and Zanonieae. The wings can be huge and unilateral (*Gerrardanthus*, *Neoalsomitra*, *Zanonia*), bilateral (*Siolmatra*), or peripheral (*Alsomitra*). The testa can be smooth, tuberculate, or scrobiculate, and it can bear spongy outgrowth (*Apodanthera*) or hairs (some species of *Cucumis*, *Melothria*, *Indomelothria*, *Tecunumania*, and *Zehneria*). Seeds of *Ecballium* contain mucilage in their testa cells that rapidly hydrates, surrounding seeds with a jelly coat. The testa can also be thin and delicate, especially in the 1-seeded undehiscent fruits (*Pteropepon*), or it can be hard and highly lignified (*Cayaponia*). The tegmen is always thin and delicate (see Embryology).

Sexual Strategies, Pollination, and Herbivores. Throughout the evolution of Cucurbitaceae, there have been numerous changes between dioecy and monoecy (Roy and Saran 1990; Zhang et al. 2006; Kocyan et al. 2007; Volz and Renner 2008; Schaefer and Renner 2010a), and the phylogenetic distribution of monoecy and dioecy on the family phylogeny suggests that dioecy may be the ancestral condition. A cucurbit, *Bryonia dioica*, was the first experimental system for the genetic analysis of the inheritance of sex in any organism (Correns 1903, 1907; Rheinberger 2000), and it was from the sex ratios of the offspring from reciprocal pollinations between this species and the monoecious *B. alba* that Correns inferred that half the pollen grains of *B. dioica* must carry a "female tendency," the other half a "male tendency." Correns's results were confirmed in a series of later studies that also inferred XY sex determination in *Bryonia*, with the male the heterogametic sex. While the chromosomes of *Bryonia* are not morphologically differentiated, those of *Coccinia grandis* are. Male individuals of this species have a pair of different-sized chromosomes, with one, interpreted as the Y-chromosome, 2.5-times longer than its homolog and all autosomes (Bhaduri and Bose 1947; N. Holstein and S. Renner, pers. obs.). Very few Cucurbitaceae have functional bisexual flowers, and these may occur only in some populations (see Inflorescences and Floral Structure). Deviations from pure monoecy (every individual with functional male and female flowers) and pure dioecy (every individual either male or female) have been reported (Morimoto et al. 2004), but there is surprisingly little fieldwork on the role of such deviations (Schaefer and Renner 2010a). In the cultivated species, especially of *Cucumis*, hormone application has permitted the planting of large fields of female (gynoecious) individuals of *C. sativus*. All species of Cucurbitaceae that have been investigated in this regard are self-compatible, fitting with little heterosis being known in the family (Gusmini and Wehner 2008; cf. Phytochemistry and Economic Importance).

Pollen of Cucurbitaceae is usually covered with a thick layer of oily yellow to orange-colored pollenkitt (Zimmermann 1922; Vasil 1960), and pollen-foraging bees are the predominant pollinators of Cucurbitaceae, with several clades more or less oligolectic on cucurbits (below). Cucurbit flowers usually open early in the morning, and anthers usually dehisce hours before the flowers open; evening or nocturnal flowering are less common, but occur in bat- and hawkmoth-pollinated species.

About 86 species of *Momordica*, *Thladiantha*, and a few other genera have oil-secreting trichomes on the petal bases, and are pollinated by specialized oilbees of the genus *Ctenoplectra* (Vogel 1990; H. Schaefer and S. Renner, unpubl. data); over the course of its evolution, *Ctenoplectra* has broadened its host spectrum from *Momordica* to the unrelated clades *Thladiantha*, *Siraitia*, and *Telfairia*. The squash bees *Xenoglossa* and *Peponapis* are specialized on the extremely coarse pollen of *Cucurbita*, and *Andrena florea* depends on the pollen and nectar of *Bryonia*. Hawkmoth pollination evolved independently in several genera that all have pale, usually fragrant flowers opening at night, often with nectar in elongated receptacle-tubes: *Cayaponia*, *Dieterlea fusiformis*, *Hodgsonia*, some *Lagenaria*, some *Momordica* species, *Peponium*, *Selysia*, *Trichosanthes*, *Tricyclandra*, and *Trochomeria*. The conspicuously fringed petals of several of these species (*Hodgsonia*, *Linnaeosicyos*, *Telfairia*, *Tricyclandra*, most *Trichosanthes*) likely are an adaptation to moth pollination (Vogel 1954; Endress and Matthews 2004). For *Lagenaria siceraria*, pollination by the sphingids *Agrius convolvuli* and *Hippotion celerio* has been confirmed by field observations in Kenya (Morimoto et al. 2004). The Indonesian cucurbit *Bayabusua* with purple-red, hairy, fleshy flowers of unknown scent may be adapted to pollination by flies. Bird pollination is characteristic for *Gurania* and *Psiguria*; their bright orange to red flowers, often in dense heads or umbels, attract straight-billed hummingbirds. Species in these genera are also visited by butterflies of the genus *Heliconius* that depend on their pollen for protein (Murawski and Gilbert 1986). Bat pollination has been reported for species in the South American genera *Calycophysum*, *Cayaponia*, and *Cionosicys* (Vogel 1958, 1969; Sazima et al. 1996), which form a clade, and a phylogeny of *Cayaponia* implies that bat pollination may be ancestral in this genus, with bee pollination evolving repeatedly as species entered more open habitats (Duchen and Renner 2010).

Cucurbits often attract nectary-tending ants with extrafloral nectaries on bracts, petioles, leaf bases, or flower buds (Zimmermann 1922; Okoli and Onofeghara 1984; Ilyas 1992; Agarwal and Rastogi 2008). Other insects feed on cucurbit shoots, leaves, and flowers. From Tanzania, Zimmermann (1922) lists species of *Orthezia* and *Helopeltis* (Hemiptera); *Epilachna* species (Coccinellidae), chrysomelid beetles, and gall-inducing Curculionidae. Several species of the ladybird beetle genus *Epilachna* (Coccinellidae) also specialize on cucurbits, with larvae and adults both feeding on the leaves of their hosts: *E. borealis*, the squash ladybird beetle, feeds on *Cucurbita*, *E. argus*, the bryony ladybird beetle, mainly on *Bryonia* and *Ecballium*, and *E. chrysomelina*, the melon ladybird beetle, mainly on *Citrullus lanatus*. Cucumber beetles or rootworms (Chrysomelidae, Luperini) feed on leaves and pollen of several cucurbit genera, and the larvae of some species feed on cucurbit roots (Metcalfe 1986; Gillespie et al. 2003). Larvae of the melon fly *Bactrocera cucurbitae* (Diptera, Tephritidae), a native of India, Southeast Asia, New Guinea, and Australia (introduced in Hawaii, Egypt, Kenya, and Tanzania), develop in the fruits and fleshy stems of many species, causing considerable economic damage (Heppner 1989). Whiteflies (Aleyrodidae) feed on most species of the family and can be a big problem in cultivation. The most common whitefly species on Cucurbitaceae seem to be the polyphagous *Aleurodicus dispersus*, *Bemisia tabaci*, and *Trialeurodes vaporariorum* (Evans 2007). In the neotropics, larvae of *Blepharoneura*, a genus of tephritid fruit flies, feed within the flowers or fruits of Cucurbitaceae, especially *Gurania* and *Psiguria* (Condon et al. 2008). Snails and slugs also feed on many cultivated cucurbit species.

Dispersal. Dispersal is mostly by animals, more rarely by wind or gravity (ballistic). Wind dispersal of fruits or seeds occurs in *Alsomitra*, *Bayabusua*, *Neoalsomitra*, *Pseudosicydium*, *Pteropepon*, *Siolmatra*, *Zanonia*, and *Sicyos*. Typical bird fruits, i.e., red small fleshy berries, are common in *Bryonia*, *Cucumis*, *Diplocyclos*, and *Zehneria*. Larger fruits may be swallowed entirely by large birds, such as ostriches, emus, and bustards (*Cucumis*, *Austrobryonia*). Others are picked open by birds that feed on the pulp, sometimes also the seeds, e.g., *Dieterlea* (Lott 1986). Large seabirds, such as albatrosses, shearwaters and storm petrels, nest in habitats were *Sicyos* occurs and probably disperse the seeds, which can be glandular sticky or ornamented with retrorse barbs. The pigeon *Zenaida maculata* eats, and occasionally disperses, the seeds of the *Cayaponia* species that occurs on the island of Fernando de Noronha (Ridley 1930), and similar occasional dispersal on or in birds likely explains the presence of cucurbits on other ocean islands. Mammals are also important dispersal agents of Cucurbitaceae, although they probably destroy most seeds. Spider monkeys (*Ateles*) feed on *Cayaponia* (Link and Di Fiore 2006), and rodents burry and disperse *Marah* seeds (Borchert 2004). The Maned wolf (*Chrysocyon brachyurus*) in Goias, Brazil, occasionally feeds on *Cayaponia espelina* fruits (Rodrigues et al. 2007). The geocarpic fruits of *Cucumis humifructus* are dug out and eaten by the aardvark (*Orycteropus afer*), which apparently also disperses the seeds (Meeuse 1962). Fruit bats and flying foxes feed on, and disperse, species of *Guriana*, *Coccinia*, and probably quite a few other cucurbits (Condon and Gilbert 1988; Medellín and Gaona 1999; Elangovan et al. 2001). Herbivorous fishes in Suriname feed on the fruits of *Cayaponia cruegeri* (herbarium specimen label N.M. Heyde 469, Herbarium Utrecht), and there is evidence of *C. cruegeri* plants occurring on floating mats in the Suriname River, already close to the Atlantic ocean (herbarium specimen label J. van Donselaar 3854, Herbarium Utrecht). In *Luffa* and *Cayaponia*, the fruit veins persist as a spongy web enclosed in the papery or leathery exocarp, which enables the fruit to float for many days in fresh or salty water (Ridley 1930). Other genera (*Hodgsonia*, *Fevillea*, *Sicana*) evolved large fleshy buoyant fruits apparently adapted to water dispersal. These observations fit well with the inferred transoceanic dispersal of several Cucurbitaceae between South America to Africa, and between the Malesian region or India and Madagascar and Africa (Schaefer et al. 2009).

Phytochemistry and Economic Importance. Probably the most characteristic chemicals are cucurbitacins, saponins, especially triterpenesaponins, and non-proteinogenic aminoacids (Hegnauer 1964, 1989). Cucurbitacins are a group of bitter triterpenes confined mainly to the seeds of Cucurbitaceae (Chen et al. 2005). Biologically, they are effective herbivore deterrents, although certain chrysomelid beetles are adapted to, and even require, these substances (e.g., Metcalfe 1986; Gillespie et al. 2003). Cucurbitacins are effective in slowing or stopping cell division, and there is much research on their medical uses, with hundreds of papers just in the past few years. Cucurbits that have been studied usually also contain saponins, e.g., *Bryonia dioica* (Oobayashi et al. 1992), *Gynostemma pentaphylla*, *Hemsleya chinensis*, and many others. The cucurbitane-type triterpene glycoside constituents of various *Siraitia* (especially *S. grosvenorii*) are the source of plant-derived sweeteners, which may become commercially important in the future.

Numerous species of Cucurbitaceae have economic importance, usually as vegetables. The cucurbit crops that are grown most commonly are cucumber, melon, and watermelon. The number of tons of pickling cucumbers, fresh-market cucumbers, muskmelons, honeydew melons, and watermelons produced in the U.S. alone is staggering (see U.S. Department of Agriculture, National Agricultural Statistics Service online). However, since cucumber, melon, and watermelon show almost no heterosis effects (Gusmini and Wehner 2008), increases in yield in the past 55 years are probably mostly due to improved agricultural practices, and less so to breeding of F1 hybrids. Indeed, yields in processing cucumber seem to have reached a plateau (Gusmini and Wehner 2008), and breeders now place their hopes in fully sequenced genomes, such as that of a Chinese fresh-market type of *C. sativus* (Huang et al. 2009), a North American pickling type, and an isogenic gynoecious breeding line. More locally important Cucurbitaceae crops include squash or pumpkin (*Cucurbita maxima*), zucchini (*C. pepo* subsp. *pepo*), bitter gourd (*Momordica charantia*), waxgourd (*Benincasa hispida*), chayote (*Sicyos* (*Sechium*) *edule*), casa banana or casbanan (*Sicana odorifera*), and *Coccinia grandis*. Medicinally used species are *Cayaponia racemosa*, *Fevillea cordifolia*, and species of *Bryonia* (see under these genera). *Luffa* are also used as sponges (see under that genus), and *Lagenaria siceraria*, the bottle gourd, as vessels in African and Asian cultures (Whitaker and Davis 1962; Erickson et al. 2005; Clarke et al. 2006). Finally, the leaves and shoots of many species are boiled and eaten as a vegetable in both Africa and Asia (e.g., Okoli 1984), and many species play a role in folk medicine.

Relationships to Other Cucurbitales and Within-family Relationships. Molecular data place the Cucurbitaceae in a polytomy with Begoniaceae, Datiscaceae, and Tetramelaceae (Zhang et al. 2006), a clade supported by shared inferior ovaries and parietal placentation. The precise family relationships at this writing (2010) are unresolved. Their tendrils readily distinguish Cucurbitaceae from their closest relatives, and the family's monophyly is well supported by molecular data (Zhang et al. 2006; Kocyan et al. 2007; Schaefer et al. 2009). Molecular phylogenies that include all genera (Fig. 22; except *Khmeriosicyos*) reveal five well-supported clades, namely, (1) a group of five to six Asian genera including *Alsomitra*, *Bayabusua*, and *Neoalsomitra*, which corresponds to tribe Gomphogyneae of Bentham & Hooker (1867); (2) a group of one African genus and five Neotropical genera, including *Fevillea* and *Sicydium*, which corresponds to tribe Triceratieae of A. Rich. (1845); (3) a group of four or five genera from Madagascar, continental Africa, Asia, and South America, corresponding to tribe Zanonieae of Bentham and Hooker (1867); (4) a clade consisting of the Asian *Actinostemma*; and (5) a group of c. 100 genera comprising our clades V–XV, traditionally ranked as subfamily Cucurbitoideae of Kosteletzky (1833). Earlier classification schemes for the family often allocated our clades II–V to a subfamily variously called Zanonioideae (Benth. & Hook.f.) Luerss. or Nhandiroboideae (Kosteletzky 1833; Jeffrey 1980, 1990, 2005). However, Nhandiroboideae is an illegitimate name (see under the genus *Fevillea*), and Zanonioideae (Benth. & Hook.f.) Luerss. is a taxonomic synonym of Fevilleoideae Burnett (the latter validly published by Burnett 1835, p. 756). Neither morphological nor molecular data support the division of Cucurbitaceae into more or less equivalent, large clades that might be ranked as subfamilies, and we are therefore not using this rank. 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 other clades of Cucurbitaceae, and molecular phylogenies clearly show that Zanonioideae were a paraphyletic assembly.

Fossils and Biogeography. The fossil record of Cucurbitaceae and indeed of the order Cucurbitales is sparse (Zhang et al. 2006 give a brief review). The oldest fossils are seeds from the Uppermost Paleocene and Lower Eocene London Clay (65 Ma) that, based on their shape and testa morphology, represent Cucurbitaceae (Chandler 1964; Collinson et al. 1993). The earliest pollen of Cucurbitaceae is *Hexacolpites echinatus* from the Oligocene of Cameroon (Salard-Cheboldaeff 1978; accepted by Muller 1985); these grains under the light microscope are hexacolpate or stephanocolpate, and resemble polycolpate pollen of New World Sicyoeae. Leaves from the North American Paleocene, described as *Vitis lobata* (Knowlton) Brown and mentioned as possibly

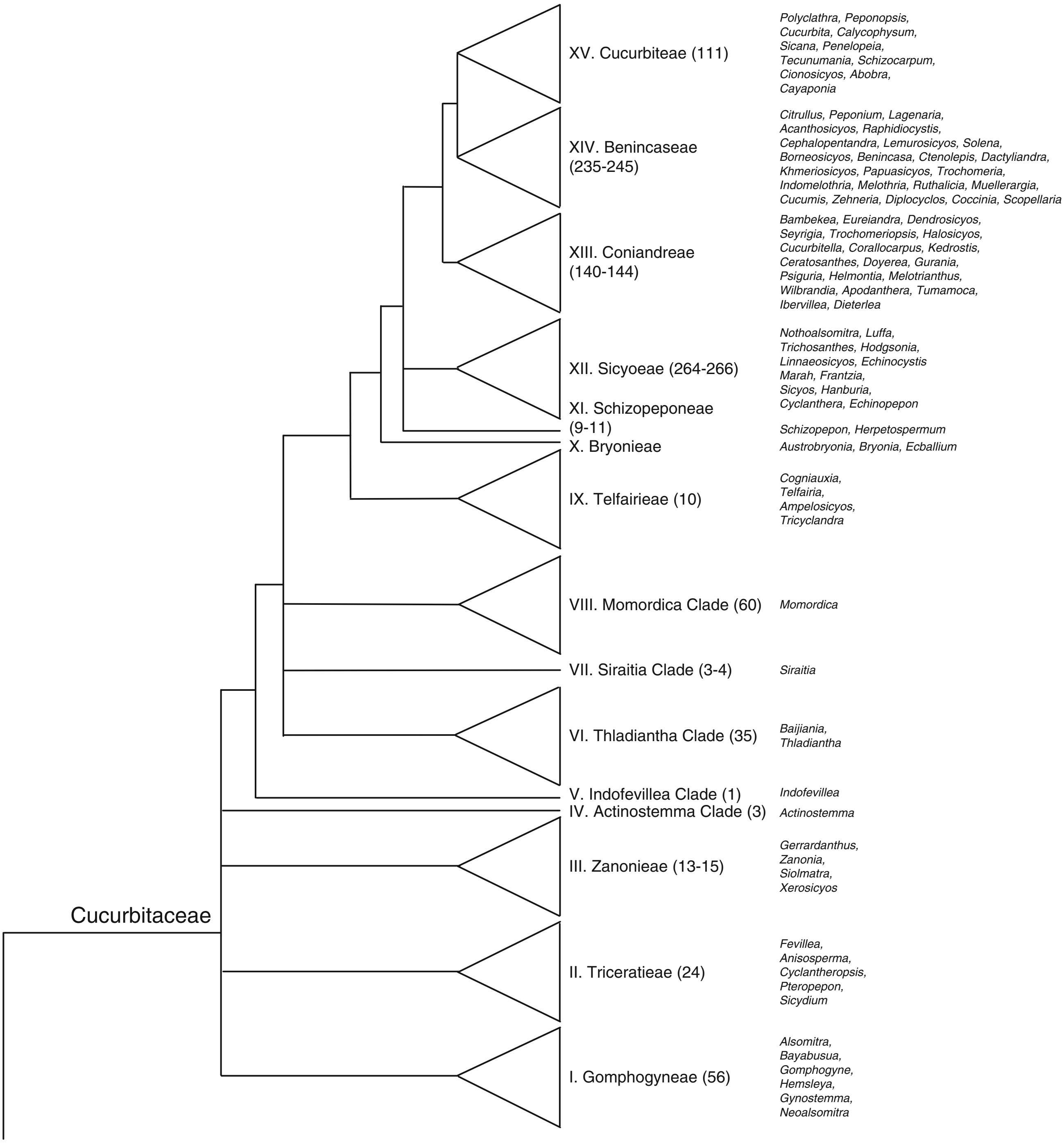

Fig. 22. Phylogenetic relationships among the genera and tribes of Cucurbitaceae as resolved by chloroplast and nuclear data (Kocyan et al. 2007; Schaefer et al. 2009). In parentheses, the respective species numbers. Formal names of all clades are proposed in Schaefer and Renner (in press)

cucurbitaceous in Raven and Axelrod (1974), probably represent Vitaceae, not Cucurbitaceae (R. Burnham and S. Renner, based on images of the type material, August 2005). Seeds of various species of *Cucurbitospermum* have been described from the Early Miocene (17.8 Ma) sites of Rusinga Island in Lake Victoria, Kenya (Chesters 1957; 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.

Subfossil records of *Cucurbita pepo* have been dated to 8,000–7,000 B.C. at Guilá Naquitz, and to about 7,000–6,500 B.C. at Ocampo Cave, Tamaulipas (Smith 1997), those of *C. moschata* in the northern Peruvian Andes to up to 9,200 B.P. (Dillehay et al. 2007), and phytoliths from Early Holocene domesticated *Cucurbita* are known from Southwest Ecuador (Piperno and Stothert 2003). *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 (Erickson et al. 2005).

Based on outgroup comparison, Cucurbitaceae 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 and the *Actinostemma* Clade) are now almost restricted to Asia. A third, the Triceratieae, is mainly Neotropical, except for a small African presence, *Cyclantheropsis*, with two species in Africa and one in Madagascar. The ancestors of the Triceratieae probably were more widely distributed in the Laurasian tropics and reached the American continent by dispersing across a still narrow Atlantic. *Cyclantheropsis* most likely results from a back dispersal from South America to Africa in the middle Eocene. The ancestors of the fourth early-diverging clade, the Zanonieae, 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 the *Siolmatra* lineage to America, and the *Zanonia* lineage back to tropical Asia. Clades V–XV, finally, diversified partly in Asia (e.g., *Thladiantha*, *Siraitia*, *Trichosanthes*), partly in Africa (e.g., *Momordica*, *Cucumis*, *Coccinia*, *Kedrostis*). Other examples of transoceanic dispersal are known from *Cayaponia* and *Luffa* (see under those genera). Dispersal from Africa to Asia occurred in *Coccinia*, *Corallocarpus*, *Kedrostis*, and *Momordica*.

The native European cucurbit flora belongs to a single clade, Bryonieae, comprising *Bryonia*, with 10 species, and its monotypic sister *Ecballium*. The sister group of both is the Australian genus *Austrobryonia*, with the split between the two clades dating to 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*). The native African Cucurbitaceae, most of which belong to clades V–XV, evolved from five successful dispersals from Asia to Africa, and two from America to Africa (in *Melothria* and *Cayaponia*). The famous cucumber tree, *Dendrosicyos socotranus*, endemic on Socotra some 350 km from the Arabian peninsula, diverged from its closest relative 34 (47–22) Ma, while the Socotra archipelago is only some 10 million years old. *Dendrosicyos* therefore seems to be an island relict of an old lineage of Coniandreae that went extinct on the mainland. Madagascar has 50 native species 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. Using Madagascar as a steppingstone, one of these clades, *Peponium*, later reached the Seychelles (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).

Key to the Genera

1. Tendrils absent 2
– Tendrils present 14
2. Trees or (sub)shrubs or erect herbs, not climbing or trailing 3
– Herbaceous trailers or creepers 11
3. Trees to 6 m tall with large trunks (to 1 m across). Socotra **45. *Dendrosicyos***
– Shrubs or subshrubs or erect herbs 4
4. Shrubs or subshrubs 5
– Erect or prostrate herbs 7
5. Plants not spiny. Africa, Madagascar, and Asia **50. *Corallocarpus***
– Plants spiny 6
6. Tendrils transformed into c. 1 cm long, straight spines; leaves reduced to small scale-like, ovate, c. 2 mm long bracts; thecae flexuous. Southern Africa **66. *Acanthosicyos***
– On older stems, the bases of the tendrils thickened and transformed into a pair of straight or curved, rather blunt, 0.4–3 cm long spines; leaves well-developed, petiolate, 2–7 by 2–5 cm, broadly ovate; thecae curved. East and Northeast Africa **21. *Momordica*** (*M. spinosa*, *M. macrocarpa*)
7. Fruit a small subglobose berry, to 2 cm long 8
– Fruit a large gourd-like pepo, >2 cm long, ripening green or yellow 9
8. Receptacle-tube cylindrical, 10–18 mm long with conical nectary; leaves entire or 3-lobed. South and East Africa **77. *Trochomeria*** (*T. polymorpha*)
– Receptacle-tube shallowly saucer-shaped, 0.5–1 mm long; leaves deeply palmately dissected. East Africa **82. *Cucumis*** (*C. messorius*)
9. Ripe fruit expelling seeds explosively. Mediterranean region and North Africa **28. *Ecballium***
– Fruit indehiscent 10
10. Fruit <10 cm; anthers distinct. Africa **82. *Cucumis*** (*C. canoxyi*, *C. reticulatus*, *C. rigidus*)
– Fruit >10 cm; anthers connate into a central head. America, introduced in Africa, Europe, Asia, Australia **89. *Cucurbita*** (*C. pepo* cultivars)
11. Plant spiny. Southern Africa **63. *Citrullus*** (*C. naudinianus*)
– Plant not spiny 12
12. Plant with long underground branches and subterranean fruits. Southern Africa **51. *Kedrostis*** (*K. psammophila*)
– Plant creeping and fruiting above ground 13
13. Thecae flexuous, glabrous. Southern Africa **63. *Citrullus*** (*C. ecirrhosus*)
– Thecae straight, fringed with hairs. Brazil **79. *Melothria*** (*M. campestre*)
14. Tendrils in groups of 5–8 per node, simple; fruit geocarpic, maturing below ground. Southern Africa **82. *Cucumis*** (*C. humifructus*)
– Tendrils solitary (1 or rarely 2 per node), simple or 2–8-fid with a basal, unbranched part; fruit usually maturing above ground (but see 45. *Echinopepon*) 15
15. Tendrils simple, not 2-fid or multi-fid with basal, unbranched part 16
– Tendrils 2–8-fid (often only at apex, which might be lost in herbarium material) 107
16. Thecae fringed with hairs 17
– Thecae glabrous (or hairs minute) 20
17. Stamens 3; anthers all 2-thecous. Africa, Asia, Australia, and Pacific Islands **83. *Zehneria***
– Stamens 3; two anthers 2-thecous, one 1-thecous 18
18. Testa covered by long appressed hairs. South and Central America (naturalized in Asia) **79. *Melothria***
– Testa glabrous 19
19. Fruit small, gourd-like, up to 2.5 cm long, ornamented with long, soft bristles. Madagascar, Indonesia, Northeastern Australia **81. *Muellerargia***
– Fruit a globose to ellipsoid, up to 20 cm long, smooth pepo. Tropical Africa and South/Central America **79. *Melothria***
20. Ovules few, pendent; pollen small to medium-sized, striate 21
– Ovules many, horizontal; pollen mostly medium-sized to large, reticulate, perforate, gemmate or echinate/baculate, very rarely striate-reticulate (*Dactyliandra, Papuasicyos*) 23
21. Fruit indehiscent, globose. South America **11. *Sicydium***
– Fruit dehiscent. Asia 22
22. Fruit dehiscing into 3 valves; seeds winged **13. *Zanonia***
– Fruit operculate; seeds winged or unwinged **16. *Actinostemma***
23. Petals fringed 24
– Petals not fringed 27
24. Thecae circular. Madagascar **25. *Tricyclandra***
– Thecae straight or folded, not circular 25
25. Stamens 5; anthers all 1-thecous; thecae triplicate. Madagascar **24. *Ampelosicyos***
– Stamens 3; two anthers 2-thecous, one 1-thecous 26
26. Anthers connate into a central head; filaments distinct. Hispaniola **35. *Linnaeosicyos***
– Anthers distinct. Asia **33. *Trichosanthes***
27. Pollen echinate or perforate 28
– Pollen reticulate or striate-reticulate 36
28. Filaments connate into a central column 29
– Filaments distinct, sometimes very short or absent 33
29. Thecae connate into a horizontal, ring-like structure. South and Central America **41. *Cyclanthera***
– Thecae distinct or connate into a central head-like structure 30
30. Fruits fleshy, unarmed, indehiscent, 1-seeded. Central America **39. *Sicyos***
– Fruit ± dry, seeds few to many 31

31. Fruit globose, smooth, 5–7 cm in diam., indehiscent. Hispaniola **92. *Penelopeia***
– Fruit dehiscent, ± setose or prickly. America 32
32. Fruit operculate; seeds relatively small, ± compressed **42. *Echinopepon***
– Fruit not operculate; seeds large, ± globose **37. *Marah***
33. Fruit a large, fleshy, indehiscent pepo 34
– Fruit a small dry or fleshy berry 35
34. Petals yellow. America, introduced in Africa, Europe, Asia, Australia **89. *Cucurbita***
– Petals greenish white. Central America **95. *Cionosicys***
35. Fruit a fleshy berry, ripening red. Argentina and Uruguay **96. *Abobra***
– Fruit a dry berry with a firm, thin wall, ripening green, red, brown or black; seeds in loose cellular pulp. America **97. *Cayaponia***
36. Pollen striate-reticulate 37
– Pollen reticulate or gemmate 38
37. Stigma 3-lobed. Africa and Asia **74. *Dactyliandra***
– Stigma-lobes feather-like divided. New Guinea **76. *Papuasicyos***
38. Stamens 5 39
– Stamens 2–3 45
39. Thecae triplicate/sinuate 40
– Thecae straight or ± curved 41
40. Sepals > petals. Indonesia **83. *Zehneria*** (*Z. macrosepala*)
– Sepals < petals. Africa and Socotra **44. *Eureiandra***
41. Plant densely black- or reddish-glandular hairy. Tropical Africa **20. *Siraitia*** (*S. africana*)
– Plant glabrous or hairy but not black- or reddish-glandular 42
42. Seeds pear-shaped to subglobose. Africa, Madagascar, Asia 43
– Seeds ovate-oblong, ± compressed. Asia 44
43. Fruit operculate, the basal part of the fruit green, expanded into a cup, the upper part red **50. *Corallocarpus***
– Fruit indehiscent or opening by valves, ripening entirely orange to red **51. *Kedrostis***
44. Petals small, to 5 mm long, cream-colored or white **19. *Baijiania***
– Petals >5 mm long, yellow **18. *Thladiantha***
45. Stamens 2 46
– Stamens 3 51
46. Adult plants usually leafless with green, succulent stems. Madagascar **46. *Seyrigia***
– Adult plants with well-developed leaves; stems not succulent 47
47. Sepals showy, orange to red, sepals > petals. Tropical America **54. *Gurania***
– Sepals green or dark-colored, sepals < petals 48
48. Flowers small; petals inconspicuous, c. 3 mm long, yellowish-green. Tropical America **56. *Helmontia***
– Flowers medium-sized; petals >5 mm long, yellow, orange or white 49
49. Male flowers often subtended by a ± orbicular bract, often 1–3 of the petals with an incurved basal scale. Africa and Asia, introduced in Australia and America **21. *Momordica***
– Male flowers not subtended by bracts; petal scales absent 50
50. Pollen often in tetrads; woody or less often herbaceous climber; petals orange, red or pink. Tropical and subtropical America **55. *Psiguria***
– Pollen in monads; herbaceous climber or trailer; petals greenish-white to yellow. Southern US to Argentina **59. *Apodanthera***
51. Pollen in tetrads. Indonesia **71. *Borneosicyos***
– Pollen in monads 52
52. Male flowers often subtended by a ± orbicular bract, often 1–3 of the petals with an incurved basal scale. Africa and Asia, introduced in Australia and America **21. *Momordica***
– Male flowers not subtended by an orbicular bract, petal scales absent 53
53. Petiole base with suborbicular ciliate bract 54
– Petiole base without ciliate bract 55
54. Thecae linear, straight; petals ± 1 mm long. Africa, Madagascar, and Asia **73. *Ctenolepis***
– Thecae triplicate; petals larger. Africa and Madagascar **77. *Trochomeria***
55. Thecae straight or slightly curved (sometimes apically hooked) 56
– Thecae strongly curved, duplicate, triplicate or flexuous 81
56. Petals 2-furcate to deeply 2-fid. Central and South America 57
– Petals entire 59
57. Filaments very short, distinct **52. *Ceratosanthes***
– Filaments longer, connate into a central column 58
58. Flowers small, opening during the day **61. *Ibervillea***
– Flowers medium-sized to large, fragrant, opening at night **62. *Dieterlea***
59. Fruit a large, hard-shelled pepo, to 20 cm long; thecae fringed with hairs. Tropical Africa and America **79. *Melothria***
– Fruit smaller, a fleshy berry or gourd; if large (*Cucumis melo*), then thecae not hairy 60
60. Fruit ornamented 61
– Fruit ± smooth 62
61. Fruit with long, soft bristles. Madagascar, Northern Australia, and Indonesia **81. *Muellerargia***
– Fruit with dense to scattered fleshy spines, pustules or tubercles that end in a hyaline bristle. Africa, Asia, naturalized in America, Australia, and the Pacific Islands **82. *Cucumis***
62. Stamens inserted near the base or halfway up the receptacle-tube 63
– Stamens inserted in the upper half or near the mouth of the receptacle-tube 64
63. Anthers all 2-thecous; leaves petiolate, triangular to ± ovate, entire to 3-lobed. Africa, Asia, Australia, and Pacific Islands **83. *Zehneria***

– Two anthers 2-thecous, one 1-thecous; leaves shortly petiolate to sessile, base cordate or hastate. Asia **70. *Solena***
64. Filaments connate into a central column. Mexico and Southern US 65
– Filaments distinct or very short to absent 66
65. Fruit a fusiform or ellipsoid berry, shortly rostrate, 6–15 cm long and 3–6 cm in diam. **62. *Dieterlea***
– Fruit a globose berry, c. 1 cm in diam., glabrous, with remains of flower **60. *Tumamoca***
66. Stigma 3-lobed, long-hairy. Southeast Asia **78. *Indomelothria***
– Stigmas 1–5, entire or lobed, if 3-lobed, then glabrous, papillose or short-hairy
67. Stigmas 2. Central and South America 68
– Stigmas 3–5 69
68. Fruit fleshy, indehiscent, ovoid to ellipsoid, ± rostrate, 1–7 cm long, ripening green or red to brown often with white stripes or spots **59. *Apodanthera***
– Fruit an ovoid-conical berry, c. 2 cm long and 1.5 cm in diam., sessile in the leaf axils, rostrate **58. *Wilbrandia***
69. Stigmas 4–5 70
– Stigmas 3 71
70. Testa smooth, chocolate-brown, often with distinct, ivory-colored margin. Southern US to Argentina **59. *Apodanthera***
– Testa smooth, margin ± distinct, not winged. South America **49. *Cucurbitella***
71. Two anthers 2-thecous, one 1-thecous 72
– All anthers 2-thecous 75
72. Testa covered by long appressed hairs. America, introduced in Asia **79. *Melothria***
– Testa glabrous or rarely puberulent 73
73. Testa light-colored, ± yellowish. Africa, Asia, Australia, introduced in America **82. *Cucumis***
– Testa brown 74
74. Testa finely sculptured, no distinct margin. Madagascar **47. *Trochomeriopsis***
– Testa smooth, often with distinct, ivory-colored margin. Southern US to Argentina **59. *Apodanthera***
75. Anthers 2 76
– Anthers 3 77
76. Testa chocolate-brown. Southern US to Argentina **59. *Apodanthera***
– Testa pale brown or yellowish. Africa, Asia, Australia **83. *Zehneria***
77. Seeds tumid to globose 78
– Seeds compressed 79
78. Disk in male flowers urceolate, ± connate with base of tube. New Guinea **76. *Papuasicyos***
– Disk in male flowers ± globose, distinct. Africa, Asia, Australia **83. *Zehneria***
79. Testa covered by long appressed hairs. America, introduced in Asia **79. *Melothria***
– Testa glabrous 80
80. Stigmas hairy. Southeast Asia **86. *Scopellaria***
– Stigmas glabrous or papillose but not hairy. Africa, Asia, Australia **83. *Zehneria***
81. Thecae strongly curved or duplicate 82
– Thecae triplicate or flexuous 91
82. Filaments inserted near the base or in the lower half of the receptacle-tube 83
– Filaments inserted halfway up or in the upper half of the tube 84
83. Leaves petiolate, triangular to ± ovate, entire to 3-lobed; disk in male flowers globose, entire or 3-parted. Africa, Asia, Australia, and Pacific Islands **83. *Zehneria***
– Leaves shortly petiolate to sessile, base cordate or hastate; disk in male flowers 3–4-lobed, conspicuous, carnose. Asia **70. *Solena***
84. Receptacle-tube elongate, tubular to cylindrical, often dilated at the apex. Asia, Australia, introduced in Africa and the Neotropics **33. *Trichosanthes***
– Receptacle-tube broadly campanulate or ± cylindrical but not elongated 85
85. Fruit laterally compressed, shortly rostrate. Argentina **48. *Halosicyos***
– Fruit ellipsoid to oblong or subglobose, not laterally compressed, sometimes rostrate 86
86. Seeds pear-shaped, slightly compressed, reddish brown, with distinct pale brown margin. Central America **53. *Doyerea***
– Seeds compressed, pale or dark-colored 87
87. Testa verrucous. Brazil **57. *Melothrianthus***
– Testa smooth or finely scrobiculate 88
88. Testa finely scrobiculate. New Guinea **76. *Papuasicyos***
– Testa smooth 89
89. Testa brown. Southern US to Argentina **59. *Apodanthera***
– Testa pale yellowish or cream-colored 90
90. Staminodes forming a ring; seeds with distinct margin. Madagascar **73. *Ctenolepis***
– Staminodes distinct; seeds without distinct margin or rarely margin thickened. Australia **26. *Austrobryonia***
91. Filaments inserted halfway up or in the upper half of the tube 92
– Filaments/stamens inserted near the base or in the lower half of the receptacle-tube 94
92. Seeds with broad, flattened margin; leaves pedately 3–7-lobed, drying black. Tropical West Africa **80. *Ruthalicia***
– Seeds without distinct margin or margin narrow; leaves unlobed or palmately 3–5-lobed, usually drying green 93
93. Seeds tumid, subglobose, or asymmetrically ovoid. Africa and Socotra **44. *Eureiandra***
– Seeds ovate or elliptic, small to medium-sized, globose or lenticular compressed. Africa, Asia, Australia, introduced in America **82. *Cucumis***
94. Fruit densely brown-setose. Tropical Africa and Madagascar **67. *Raphidiocystis***
– Fruit ± glabrous or sparsely setose or hairy or with prominent spines but not brown-setose 95

95. Fruit hairy 96
– Fruit ± glabrous 98
96. Testa blackish, smooth, not winged, no distinct margin. Africa and Madagascar **64. *Peponium***
– Testa brown or grayish-brown, without distinct margin or with dentate or narrow, corky margin 97
97. Testa brown; leaves petiolate, palmately 3–5-lobed, the lobes lobulate-dentate. Madagascar **69. *Lemurosicyos***
– Testa grayish-brown; leaves shortly petiolate to sessile, the blade ovate or elliptic, margin entire, base cordate or hastate. Asia **70. *Solena***
98. Leaves very shortly petiolate to sessile, ± amplexicaul 99
– Leaves with distinct petioles 102
99. Seeds slightly compressed to ± globose 100
– Seeds strongly compressed 101
100. Testa grayish-brown, sometimes with narrow, corky margin. Asia **70. *Solena***
– Testa whitish, without distinct margin. Africa and Madagascar **77. *Trochomeria***
101. Testa black, verrucous. Africa **68. *Cephalopentandra***
– Testa pale, smooth to fibrillose. Africa, Asia, introduced in Australia and America **85. *Coccinia***
102. Seeds subglobose, ovoid or ellipsoid, tumid; testa smooth, hard, whitish. Africa and Madagascar **77. *Trochomeria***
– Seeds compressed 103
103. Testa bright brown, finely grooved, with broad, grooved, crenulate-tuberculate margin. Cambodia **75. *Khmeriosicyos***
– Testa without distinct margin or margin not grooved, crenulate-tuberculate 104
104. Receptacle-tube elongated, ± cylindrical. Africa and Madagascar **64. *Peponium***
– Receptacle-tube campanulate or turbinate 105
105. Flowers small, in axillary, racemose panicles or sub-umbellate fascicles. Europe, Northern Africa, Canaries, Central Asia **27. *Bryonia***
– Flowers medium-sized to large, if small then solitary (rarely in few-flowered fascicles). Africa and Asia, introduced in Australia and America 106
106. Thecae triplicate; style filiform; fruit small and globose or cylindrical and to 30 cm long, baccate, usually glabrous **85. *Coccinia***
– Thecae flexuous; style short, columnar; fruit large, globose or oblong, glabrous or covered with prominent spines **63. *Citrullus***
107. Tendrils 2-fid 108
– Tendrils 3–8-fid 175
108. Basal part of the tendrils sensitive and thus tendrils coiling above and below the bifurcation 109
– Basal part of the tendrils insensitive, not coiling 127
109. Sepals and petals 4; leaves entire or 3-lobed, orbicular or flat, succulent or non-succulent, perennial or deciduous. Madagascar **15. *Xerosicyos***
– Sepals and petals 5, or sepals 3–4 and petals 5 110
110. Sepals 3–4 and petals 5 111
– Sepals and petals 5 113
111. Stamens 3, two anthers 2-thecous, one 1-thecous; thecae vertical; ovules many per locule; seeds with a butterfly-shaped wing, expanded laterally and divaricate. South East Asia to New Guinea **1. *Alsomitra***
– Stamens 5, distinct; thecae horizontal; ovules 2 per locule 112
112. Leaves entire; seeds with a chalazal wing. Indomalesia **13. *Zanonia***
– Leaves compound, palmate or pedate; seeds in the median position of an encircling wing expanded along the chalaza-micropyle axis. South America **14. *Siolmatra***
113. Filaments connate into a central column 114
– Filaments ± distinct 117
114. Thecae 2–3, horizontal; fruit a samara, indehiscent 115
– Thecae 5, vertical; fruit a dry achene, indehiscent or a subglobose capsule, dehiscent 116
115. Thecae 2, semicircular, forming together a split ring. Africa and Madagascar **9. *Cyclantheropsis***
– Thecae 3, straight, forming the sides of an equilateral triangle. South America **10. *Pteropepon***
116. Leaves cordate; ovule 1 per ovary; fruit dry, globose, indehiscent; seed subspherical. Mexico **11. *Sicydium***
– Leaves compound, pedate, 3–7-foliolate; stylodia 3; ovules more than 1 (usually 2–4) per ovary; fruit a subglobose capsule (3-valvate at the apex), dehiscent; seeds not compressed, unwinged or winged. Asia and Indomalesia **5. *Gynostemma***
117. Stamens 1, anther 2-thecous. South America **10. *Pteropepon***
– Stamens 2–5, all anthers 1-thecous, distinct or two anthers 2-thecous, one 1-thecous (sometimes the 1-thecous or one of the 2-thecous anthers reduced or aborted) 118
118. Stamens 3, two anthers 2-thecous, one 1-thecous; ovary 1-locular; ovule 1 per ovary; fruits indehiscent, baccate; seed subspherical 119
– Stamens 4 and 1 staminode or stamens 5 121
119. Fruit a cylindrical-clavate capsule, c. 20 cm long, opening with 3 valves; seeds with broad circular membraneous wing, c. 5 cm in diam., testa finely verrucous, dull brown, margin coarsely 8–9-spined. Malaysia **2. *Bayabusua***
– Fruit indehiscent, much smaller. South and Central America 120
120. Fruit a large, fibrous samara with 1 continuous, encircling wing or small, membranaceous, with two lateral wings **10. *Pteropepon***
– Fruit baccate, globose, fleshy or fibrous, not winged **11. *Sicydium***
121. Stamens 4 and 1 staminode 122
– Stamens 5 123
122. Corolla slightly to strongly zygomorphic; ovary 3-locular at the apex, 1-locular at the base; ovules many per locule; fruit a capsule (apically 3-valvate); seeds clearly winged, fusiform. Africa **12. *Gerrardanthus***
– Corolla actinomorphic; ovary 1-locular; ovules 1 per ovary; fruit a samara; seed compressed;

pericarp (wing included) fibrous or membranaceous. South America **10. *Pteropepon***

123. Petals lanceolate, long acuminate; corolla actinomorphic. Asia **16. *Actinostemma***
– Petals ovate or oblong, never long-acuminate; corolla not actinomorphic 124
124. Fruit operculate or capsule or opening by longitudinal splits. America 125
– Fruit not operculate. Asia or Africa 126
125. Fruit operculate (rarely a capsule); leaves pedately 3–7-lobed or 3–5-foliolate **7. *Fevillea***
– Fruit opening by longitudinal splits; leaves simple, entire **8. *Anisosperma***
126. Fruit fleshy 127
– Fruit dry 129
127. Petals fringed. Tropical Africa and Madagascar **23. *Telfairia***
– Petals entire 128
128. Plant glabrous or hairy but not glandular. Asia **19. *Baijiania***
– Plant ± glandular hairy. Tropical Africa or Asia **20. *Siraitia***
129. Fruit indehiscent, 20–30 cm long; seeds large, 3.5–4 cm long. Asia **17. *Indofevillea***
– Fruit apically 3-valvate, to 8 cm long; seeds small 130
130. Seeds with wing on the chalazal end; flowers actinomorphic. China, Indomalesia, and Australia **6. *Neoalsomitra***
– Seeds unwinged or wing encircling the seed, uniform in width or extended along the chalaza-micropyle axis. Asia 131
131. Annual, herbaceous climbers or trailers, to 5 m long with fibrous roots **3. *Gomphogyne***
– Mostly perennial and tuberous climbers or trailers **4. *Hemsleya***
132. Filaments connate into a central column 133
– Filaments distinct or connate to pairs only 140
133. Male flowers 4-merous, female flowers 3-merous. Central America **39. *Sicyos***
– All flowers 5-merous 134
134. Thecae connate into a horizontal, ring-like structure. South and Central America **41. *Cyclanthera***
– Thecae distinct or connate into a central head-like structure 135
135. Fruits fleshy, unarmed, indehiscent, 1-seeded. Central America **39. *Sicyos***
– Fruit ± dry, if fleshy, then seeds few to many 136
136. Fruit indehiscent, smooth. Hispaniola **92. *Penelopeia***
– Fruit dehiscent, ± setose or prickly 137
137. Fruit operculate; seeds relatively small, ± compressed. America **42. *Echinopepon***
– Fruit not operculate 138
138. Seeds large, ± globose. North and Central America **37. *Marah***
– Seeds small, ± compressed 139
139. Fruits dry, indehiscent. America, Pacific Islands, Australia, introduced in Africa **39. *Sicyos***
– Fruits ± fleshy, opening explosively, solitary. Tropical America **40. *Hanburia***
140. Pollen baculate or echinate 141
– Pollen reticulate or striate 148
141. Fruit indehiscent 142
– Fruit dehiscing 146
142. Fruit fleshy 143
– Fruit dry 145
143. Fruit a small red, ovoid to globose, fleshy berry, c. 1 cm long and 1 cm in diam. Argentina and Uruguay **96. *Abobra***
– Fruit a fleshy pepo, >5 cm long 144
144. Testa densely appressed hairy, pale yellowish-brown. Central America **93. *Tecunumania***
– Testa glabrous, smooth, cream-colored or black. America, introduced in Africa, Europe, Asia, Australia **89. *Cucurbita***
145. Stamens inserted in the center of the flower. Seeds compressed, ovoid or less often ± triangular or dagger-shaped and apically tricornute; tests not banded. Tropical and subtropical America **97. *Cayaponia***
– Stamens inserted near the mouth of the receptacle-tube. Seeds ovoid, compressed; testa brown or banded crosswise with light and dark stripes. Mexico and Guatemala **94. *Schizocarpum***
146. Fruit ± ribbed, 5–8 cm long, seeds 6, 12 or c. 48, oblong or obovate, compressed; testa smooth, margin obtuse, not winged. Asia **30. *Herpetospermum***
– Fruit ± rounded, ellipsoid to pear-shaped, rostrate or not, smooth 147
147. Seeds broadly ovate, compressed, contracted at base; testa brown, narrowly winged. Central America **87. *Polyclathra***
– Seeds ovoid, compressed, not contracted; testa brown or banded crosswise with light and dark stripes, margin with or without wing. Mexico and Guatemala **94. *Schizocarpum***
148. Petals fringed 149
– Petals not fringed 152
149. Seeds small. Asia to Australia **33. *Trichosanthes***
– Seeds large 150
150. Anthers connate into a central globose head. Asia **34. *Hodgsonia***
– Anthers distinct 151
151. Stamens 5, anthers all 1-thecous. Madagascar **24. *Ampelosicyos***
– Stamens 3–5, one or several anthers 2-thecous. Tropical Africa and Madagascar **23. *Telfairia***
152. Stamens 2 153
– Stamens 3 or 5 154
153. Male flowers often subtended by a ± orbicular bract, often 1–3 of the petals with an incurved basal scale; receptacle-tube broadly campanulate. Africa and Asia, introduced in Australia and America **21. *Momordica***
– Male flowers long pedunculate but without orbicular sheathing bract; receptacle-tube elongate-cylindrical. Peru **59. *Apodanthera***
154. Stamens 5 155
– Stamens 3 158

155. Seeds pear-shaped to subglobose. Africa, Madagascar, Asia 156
– Seeds ± compressed 157
156. Fruit operculate, the basal part green, expanded into a cup, the upper part red **50. *Corallocarpus***
– Fruit indehiscent or opening by valves, ripening entirely orange to red **51. *Kedrostis***
157. Fruit a ± fleshy berry. Asia **18. *Thladiantha***
– Fruit dry with seeds in fibrous tissue. Africa, Arabia, Asia, Australia, America **32. *Luffa***
158. Male flowers often subtended by a ± orbicular bract, often 1–3 of the petals with an incurved basal scale; receptacle-tube broadly campanulate. Africa and Asia, introduced in Australia and America **21. *Momordica***
– Male flowers without prominent, ± orbicular sheathing bract and without petal scales 159
159. Thecae straight or ± curved 160
– Thecae duplicate or triplicate or convoluted 162
160. Seeds 1–3, pendent, ovate, compressed; testa brown, ± sculptured, margin irregularly dentate, not winged. Asia **29. *Schizopepon***
– Seeds usually more than 3; testa yellowish or brown, ± smooth, margin sometimes distinct but not dentate 161
161. Stamens inserted near mouth of receptacle-tube; seeds often chocolate-brown with distinct ivory-colored margin. America **59. *Apodanthera***
– Stamens inserted halfway up the receptacle-tube; seeds yellowish or brown but not with distinct, ivory-colored margin. Africa, Asia, Australia, introduced in America **82. *Cucumis***
162. Thecae duplicate. Tropical Africa **22. *Cogniauxia***
– Thecae triplicate, flexuose or convoluted 163
163. Petioles with two, ± conspicuous apical glands. Africa, introduced in Asia and America **65. *Lagenaria***
– Petioles not with paired glands 164
164. Receptacle-tube elongate, tubular to cylindric 165
– Receptacle-tube short, broad, shallow 166
165. Stamens inserted halfway up the receptacle-tube. Asia, Australia, introduced in Africa and America **33. *Trichosanthes***
– Stamens inserted near the mouth of the tube. Africa and Madagascar **64. *Peponium***
166. Fruits in clusters or racemes 167
– Fruit solitary (rarely 2–3) 169
167. Fruits up to 8 in racemes, globose, c. 2.5 cm across, with strong gourd-like odor, style and calyx rests persistent on fruit. Tropical West Africa **43. *Bambekea***
– Fruits in clusters of 2–6, globose, ellipsoid or ovoid, usually <2 cm across, style and calyx not persistent on fruit 168
168. Stamens inserted near the mouth of the receptacle-tube; fruits ripening bright red with silvery white stripes or marks. Africa, Asia, Australia **84. *Diplocyclos***
– Stamens inserted halfway up the receptacle-tube; fruits ripening yellow, orange, red or greenish to brownish, often with longitudinal pale stripes. Africa, Asia, Australia, introduced in America **82. *Cucumis***
169. Fruit dry with seeds embedded in fibrous tissue. Africa, Asia, Australia, America **32. *Luffa***
– Fruit ± fleshy 170
170. Fruit a small, baccate, globose, ellipsoid or ovoid berry with white pulp, ripening bright red with silvery white stripes or marks. Africa, Asia, Australia **84. *Diplocyclos***
– Fruit a ± large pepo or gourd, if berry, then not with white pulp and bright red pericarp 171
171. Fruit at first hispid, later glabrous, dark green and covered with white wax; seeds many, compressed, smooth, white with thick margin. Asia, Australia, Pacific Islands, introduced in Africa **72. *Benincasa***
– Fruit not hispid when young, not covered with white wax when older 172
172. Stamens inserted near the mouth of the receptacle-tube. Australia **31. *Nothoalsomitra***
– Stamens inserted at the base of the tube or halfway up 173
173. Stamens inserted halfway up the tube. Africa, Asia, Australia, introduced in America **82. *Cucumis***
– Stamens inserted at the base of the tube. Africa, Asia, introduced in Australia and America 174
174. Style filiform; fruit small and globose or cylindrical and to 30 cm long, baccate, usually glabrous **85. *Coccinia***
– Style short, columnar; fruit large, globose or oblong, glabrous or covered with prominent spines **63. *Citrullus***
175. Petals fringed 176
– Petals not fringed 177
176. Seeds small. Asia, Australia, introduced in Africa and America **33. *Trichosanthes***
– Seeds large. Asia **34. *Hodgsonia***
177. Petals 6. North America **36. *Echinocystis***
– Petals 3–5 178
178. Male flowers 4-merous, female flowers 3-merous. Central America **39. *Sicyos***
– All flowers 5-merous 179
179. Pollen reticulate 180
– Pollen echinate, baculate or perforate 183
180. Receptacle-tube elongated, cylindrical 181
– Receptacle-tube (broadly) campanulate 182
181. Thecae triplicate; stamens inserted halfway up the tube. Asia **33. *Trichosanthes***
– Thecae straight or ± curved; stamens inserted near the mouth of the tube. America **59. *Apodanthera***
182. Fruit ± fleshy, indehiscent. Africa, Asia, introduced in Australia and America **63. *Citrullus***
– Fruit dry with fibrous tissue, operculate. Africa, Asia, Australia, America **32. *Luffa***
183. Filaments connate into a central column 184
– Filaments distinct 190

184. Thecae connate into a horizontal, ring-like structure. South and Central America **41. *Cyclanthera***
– Thecae distinct or connate into a central head-like structure 185
185. Fruit dry, globose, smooth, 5–7 cm in diam., indehiscent. Hispaniola **92. *Penelopeia***
– Fruit ± fleshy, if dry, then not globose 186
186. Fruit 1-seeded, fleshy, medium-sized to large. Central America 187
– Fruit few- to many-seeded, if 1-seeded, then fruit dry or small 188
187. Nectaries in open pouches. Mexico **39. *Sicyos***
– Nectaries often with umbrella-like covering (not in *F. tacaco* and *F. talamancensis*!). Costa Rica, Nicaragua, Panama **38. *Frantzia***
188. Fruit explosively dehiscent **40. *Hanburia***
– Fruit indehiscent or operculate 189
189. Fruits indehiscent, winged or 3–4-angled, small ovoid to fusiform, armed with retrorse barbs or unarmed, glabrous or villous, sometimes enclosed by a subtending leaf; seed solitary, ovoid or tumid to compressed. America, Pacific Islands, Australia, introduced in Africa **39. *Sicyos***
– Fruits operculate, echinate, rostrate, if indehiscent, then subterranean (to 3.5 cm deep), on 6–9 cm long peduncle (*E. arachoidea*); seeds solitary or few, quadrangular or angular-ovoid, compressed. America **42. *Echinopepon***
190. Fruit dehiscent, dry or fleshy 191
– Fruit indehiscent 193
191. Fruit a fleshy pepo, splitting into three carpellar segments at maturity **88. *Peponopsis***
– Fruit ± dry at maturity 192
192. Fruit splitting into several irregular segments. Central America **87. *Polyclathra***
– Fruit splitting into 3 valves. Asia **30. *Herpetospermum***
193. Fruit a dry berry 194
– Fruit a medium-sized to large, fleshy pepo 195
194. Flowers large, solitary in the axils; peduncle of male flowers to 30 cm long, to 15 cm in female; receptacle-tube campanulate to urceolate, ± inflated. South America **90. *Calycophysum***
– Flowers small, in racemes, panicles, pairs or solitary, male and female often coaxial; receptacle-tube campanulate, not inflated. America **97. *Cayaponia***
195. Stamens inserted close to the mouth of the receptacle-tube; fruit a globose, ellipsoid or cylindrical pepo, smooth, to 60 cm long. Central America **91. *Sicana***
– Stamens inserted near the base of the receptacle-tube 196
196. Receptacle-tube and corolla ± campanulate or funnel-shaped. America, introduced in Africa, Europe, Asia and Australia **89. *Cucurbita***
– Receptacle-tube flat, saucer-shaped, villous; corolla flat, villous outside, smooth inside. Asia **72. *Benincasa*** (*B. fistulosa*)

Genera of Cucurbitaceae

I. Tribe Gomphogyneae Benth. & Hook.f. (1867).

Tendrils apically 2-fid (rarely simple). Stamens 3 or 5. Fruit a capsule or berry. Seeds 1 to many, often winged.

1. *Alsomitra* (Blume) Spach

Alsomitra (Blume) Spach, Hist. Nat. Vég. Phan. 6: 187 (1838); Duyfjes & W.J. de Wilde, Proc. 4th Int. Flora Males. Symp. 1998, Kuala Lumpur: 101–105 (1998).
Macrozanonia Cogn. (1893).

Dioecious, perennial, woody liana, 30–50 m long, the stem up to 15 cm in diam. Leaves broadly ovate to rounded-ovate, entire, rarely 3-lobed, to 16 cm long; petiole with basal ring-shaped callus; young plants with c. 1 cm long, oblong, hastate, ± auriculate, distichous leaves; tendrils with elongated, not peltate adhesive pads. Male and female flowers in panicles or racemes; receptacle-tube campanulate; calyx first completely connate with minute 5-lobed orifice, at anthesis tearing into (2)3 (4) irregular parts; petals narrowly elliptic, acute, papillose at apex; stamens 3, inserted near the mouth of the tube; filaments short; all anthers 2-thecous or two anthers 2-thecous and one 1-thecous; thecae straight, vertical, papillose hairy; pollen small (polar axis 19–26 μm, equatorial axis c. 21 μm), 3-colporate, perforate to indistinctly rugulate (Khunwasi 1998; van der Ham 1999); pistillodes 3, minute; ovary ± ellipsoid; placentae 3, apical; ovules many; stylodia 3; stigmas fleshy, 2-lobed. Fruit a large, ovoid-globose to ovoid-cylindrical capsule, 20–25 cm in diam., dehiscent by an apical 3-radiate slit into 3 valves, ripening brown. Seeds many, compressed, suborbicular to elliptic, 25–30 by 20–23 mm; testa smooth, margin with large, membranous wing, laterally expanded, butterfly-like, 10–12 cm wide; cotyledons remaining in the seed during germination.

One species, *A. macrocarpa* (Blume) M. Roem., in Thailand, Malaysia, Indonesia, Philippines, and New Guinea; in tropical lowland riverine forests on rich clay soil; flowering Dec.–Jan., fruiting March–June (in Java).

2. *Bayabusua* W.J. de Wilde

Bayabusua W.J. de Wilde, Sandakania 13: 1 (1999).

Dioecious, perennial, woody lianas, 20–40 m long. Leaves broadly cordate-ovate, entire; young plants with 4-verticillate basal leaves; tendrils to 15 cm long, inserted axillary, always with circular, peltate adhesive pads. Male flowers in erect, axillary spikes or racemes; female flowers solitary or in small groups; receptacle-tube shallowly cup-shaped; sepals almost distinct, broadly obtuse-triangular; corolla rotate; petals broadly obovate, almost distinct, reflexed, purple-red, densely covered with multicellular hairs; stamens 3, inserted near the center of the tube; filaments distinct; two anthers 2-thecous (the thecae halfway connate), one 1-thecous, creamy white, somewhat fleshy; thecae straight, oblong; pollen medium-sized (polar axis c. 34 μm, equatorial axis c. 21 μm), 3-colporate or partly syncolporate, striate (van der Ham 1999); ovules many. Fruit a cylindrical-clavate capsule, c. 20 cm long, opening with 3 valves, ripening brown. Seeds many, compressed; testa finely verrucous, dull brown, margin coarsely 8–9-spined, with broad circular membraneous wing, c. 5 cm in diam.

One species, *Bayabusua clarkei* (King) W.J. de Wilde, endemic in Peninsular Malaysia; in lower montane forest (200–800 m a.s.l.), extremely rare; flowering in Feb., June, Aug.; fruiting Dec.–Feb.

3. ***Gomphogyne*** Griff.

Gomphogyne Griff., Account Bot. Coll. Cantor: 26 (1845); de Wilde, Duyfjes & van der Ham, Thai For. Bull. (Bot.) 35: 45–68 (2007).

Dioecious, annual, herbaceous climbers or trailers, to 5 m long; roots fibrous. Leaves simple or pedately 5–(7–9)-foliolate, petiolulate, ovate to subcircular. Male flowers in racemes or thyrses, female flowers in racemes or fascicles (rarely solitary), often with 1–2 small tendrils on the peduncle close to the flowers; receptacle-tube saucer-shaped, reduced; sepals long-triangular; corolla rotate; petals long-acuminate, white; stamens 5, inserted near the center of the tube; filaments short, distinct, diverging; anthers all 1-thecous; thecae straight or ± curved; pollen medium-sized (polar axis 33–40 μm, equatorial axis 21–32 μm), 3-colporate, striate (Khunwasi 1998; de Wilde et al. 2007a); ovary turbinate or subclavate, 3-locular at apex and 1-locular at base; ovules few; stylodia 3, short; stigmas 2-fid. Fruit foveolate. Seeds 1–9, (little) compressed, ellipsoid; testa thick, black, sparsely irregularly verrucose, unwinged. $n = 16$ (Thakur and Sinha 1973).

Two species, *G. cissiformis* Griff. and *G. nepalensis* W.J. de Wilde & Duyfjes, in Asia; mountain slopes, evergreen and deciduous forest, or open scrub.

4. ***Hemsleya*** Cogn. ex F. B. Forbes & Hemsl.

Hemsleya Cogn. ex F. B. Forbes & Hemsl., J. Linn. Soc. Bot. 23: 490 (1888); D.-Z. Li, Systematics and evolution of *Hemsleya* (Cucurbitaceae). Kunming: Yunnan Sc. Tech. Pr. (1993).

Dioecious, usually perennial and tuberous climbers or trailers. Leaves pedately (3–)5–9(–11)-foliolate, rarely simple. Male flowers in thyrses, female flowers in racemes; receptacle-tube rotate; sepals oblong or lanceolate; corolla very variable in form; petals membranaceous, oblong or ovate, white to deep orange-brown; stamens 5; filaments short, distinct; anthers all 1-thecous; pollen medium-sized (polar axis 33–40 μm, equatorial axis 21–29 μm), 3-colporate, (indistinctly) striate (Khunwasi 1998; de Wilde et al. 2007a); ovary 3-locular at apex and 1-locular at base; placentae 3; ovules many; stylodia 3, short; stigmas 2-lobed. Fruit a clavate-cylindrical to globose capsule, opening apically triradiately. Seeds compressed; testa hard with (or rarely without) an encircling woody (rarely membraneous) wing, uniform in width or expanded along the chalaza-micropyle axis. $n = 14$ (Samuel et al. 1995).

About 30 species mostly in China, a few in the Himalaya, Indochina, Eastern Malesia.

5. ***Gynostemma*** Blume

Gynostemma Blume, Bijdr.: 23 (1825); W.J. de Wilde & Duyfjes, Blumea 52: 263–280 (2007).
Pestalozzia Zoll. & Moritzi (1846).
Trirostellum Z. P. Wang & Q. Z. Xie (1981).

Dioecious or monoecious, small herbaceous or woody climbers with or without tuberous rootstock. Leaves 3–9-foliolate (rarely simple), leaflets petioluled, margin dentate. Male flowers in panicles, female flowers in fascicles; receptacle-tube reduced, saucer-shaped; sepals triangular; corolla rotate; petals long triangular, greenish white, subulate; stamens 5, inserted near the base of the tube; filaments connate into a central column; anthers 1-thecous, connate into a central head;

thecae straight, short-ellipsoid; pollen small to medium-sized (polar axis 20–35 μm, equatorial axis 15–23 μm), 3-colporate, striate (Khunwasi 1998; de Wilde et al. 2007a); ovary subglobose, (2)3–5-locular; ovules 2 per locule; stylodia (2)3 or 5, short; stigmas 2-fid. Fruit a dry berry or capsule, (sub)globose, to 10 mm in diam., opening apically triradiately. Seeds 1–5, ovoid or subtriangular; testa verrucous, not winged or with a narrow encircling wing. $n = 11$ (Gao et al. 1995).

About 10 species in India, Sri Lanka, China, Taiwan, Japan, Indomalesia, New Guinea; in moist forests, thickets, and meadows.

6. **Neoalsomitra** Hutch. Fig. 23

Neoalsomitra Hutch., Ann. Bot. (London) II, 6: 97 (1942); W.J. de Wilde & Duyfjes, Blumea 48: 99–121 (2003).

Dioecious (rarely monoecious), perennial (rarely annual), herbaceous to woody climbers, to 30 m long, with or without tuberous rootstock and in a few species with conspicuously swollen base (pachypodium); the lower parts of the stem in *N. schefferiana* (Cogn.)Hutch. ornamented with hard, green, 1–2(–4) cm long thorns. Leaves lobed or 3–5-foliolate, subcircular. Inflorescences many-flowered, paniculate. Flowers in panicles or racemes; receptacle-tube cup-shaped; sepals distinct; corolla rotate or cup-shaped; petals very short-connate at base, yellowish or greenish; stamens 5, inserted centrally; filaments distinct or ± connate; anthers all 1-thecous; thecae straight; pollen small to medium-sized (polar axis 17–36 μm, equatorial axis 17–35 μm), 3-colporate, striate (Khunwasi 1998; van der Ham 1999); ovary cylindrical-clavate, 3-locular at the apex and unilocular at the base; ovules 5(–10) per placenta; stylodia 3, short; stigmas reniform; staminodes 0 or 5. Fruit a cylindrical-clavate capsule, solitary or in groups, to 8 cm long, glabrous or pubescent, apex truncate, opening triradiately. Seeds compressed, mostly horned or star-shaped; testa finely tubercled or smooth with narrow or broad margin, with membranous translucent wing.

About 12 species, NE India, Malesia, S China, New Guinea, Australia, Fiji; in humid ravines, deciduous forest, lowland savannah and dry forest, primary evergreen forest, coastal rainforest, riverbanks.

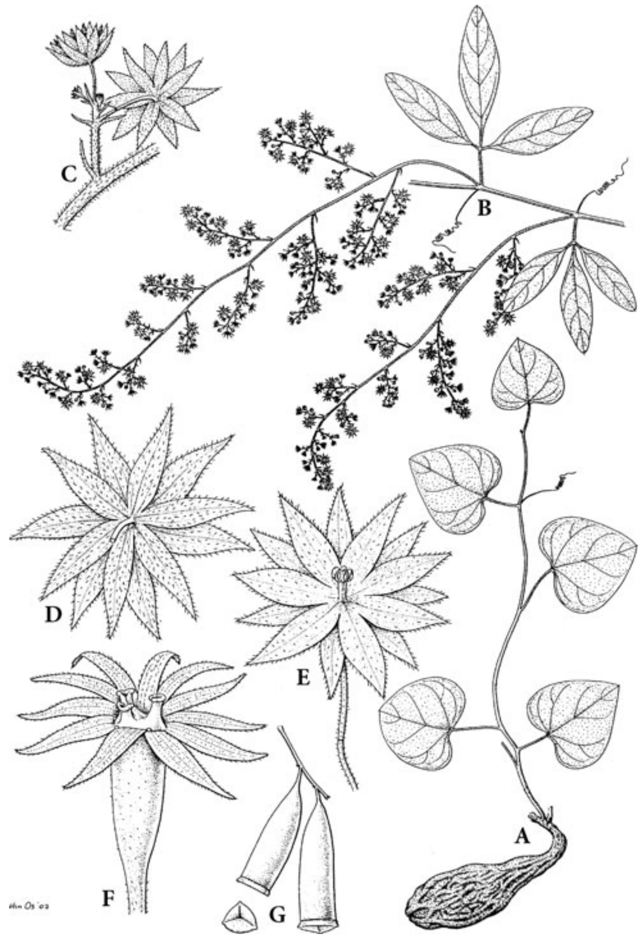

Fig. 23. Cucurbitaceae. *Neoalsomitra angustipetala*. **A** Sprouted tuber with simple eophylls. **B** Male inflorescence. **C** Portion of female inflorescence. **D, E** Male flower. **F** Female flower. **G** Fruits. (de Wilde and Duyfjes 2003; artist J. van Os)

II. Tribe Triceratieae A. Rich. (1845).

Fevilleeae Benth. & Hook.f. (1867).

Leaves simple. Tendrils simple or apically 2-fid. Stamens 1–5. Fruit a pepo, samara or achene. Seeds solitary or 10–15, often with narrow, wing-like margin.

7. ***Fevillea*** L

Fevillea L., Sp. Pl. 2: 1013 (1753) and Gen. Pl., ed. 5: 443 (1754); G.L. Robinson & R.P. Wunderlin, Sida 21: 1971–1996 (2005).
Nhandiroba Plum. ex Adans., nom. illegit.
Hypanthera Silva Manso (1836).

Dioecious, perennial, woody climbers, to several meters long. Leaves pedately 3–7-lobed or 3–5-foliolate, with 2 glands at the distal end of the petiole, or marginal glands at the tip of the main veins; tendrils short or very long, apically 2-fid. Male flowers in panicles or fascicles, female flowers solitary or in pairs; receptacle-tube saucer-shaped to cup-shaped; sepals ± 2 mm long, fused to the petals above; petals suborbicular or oblong-hastate, greenish, yellow, orange, or dull brown, ± 4 mm long, the lower margin fused with the sepals and extending a glandular protuberance, each petal with a median uncinate appendage; stamens 5, inserted near the center of the flower; filaments short, distinct; anthers all 2-thecous; thecae straight, vertical; pollen medium-sized (polar axis 27–33 μm, equatorial axis c. 21–34 μm), 3-colporate, (coarsely) striate (Khunwasi 1998); ovary obconical, subtrigonous, 3-locular at the apex and 1-locular at the base; placentae 3; ovules 4 per locule; stylodia 3; stigmas 2-fid; staminodes 5 or 0. Fruit a ± globose or ovate-oblong pepo or capsule, 3.5–16 cm long, 3–13 cm in diam., indehiscent or circumscissile dehiscent along calyx scar, ripening mottled green, brown or reddish. Seeds 10–17, orbicular, ± compressed, large, to 6×2 cm and 3–9 g dry weight, or much smaller (in *F. anomalosperma* M. Nee c. 1×1×0.2 cm), oil-rich; testa pale brown, smooth to striate-verrucous or pustulate, often with narrow, wing-like margin.

Eight species, from Southern Mexico to Northern Argentina, also in the Caribbean; canopy plant in moist or wet forests.

Fevillea cordifolia L. is widely cultivated for the oil-rich seeds, and this and *F. trilobata* L. have been used for centuries by indigenous South Americans as candles, purgative, and antidote for several kinds of poisoning (Gentry and Wettach 1986). Host of the fungus *Uromyces novissimus* Speg. (Monoson and Rogers 1978).

8. ***Anisosperma*** Silva Manso

Anisosperma Silva Manso, Enum. Subst. Brazil.: 38 (1836).

Dioecious, perennial, woody climber, to several meters long, with caudex to 5 cm in diam. Leaves unlobed, simple, narrowly ovate, acuminate; tendrils stout, long, apically 2-fid. Male flowers in axillary fascicles, female flowers solitary or in pairs; receptacle-tube saucer-shaped to cup-shaped; sepals ± 2 mm long, fused to the petals above; petals oblong-hastate, greenish-white, ± 4 mm long, the lower margin fused with the sepals, each petal with a median uncinate appendage; stamens 5, inserted near the centre of the flower; filaments short, distinct; anthers all 2-thecous; thecae straight, vertical; pollen medium-sized (polar axis 29 μm, equatorial axis 31 μm), 3-colporate, striate (Khunwasi 1998); ovary fully inferior. Fruit ovoid or oblong, subtrigonous, and shortly apiculate, dehiscent by longitudinal splits. Seeds c. 15–20, suborbicular, compressed, 3.5–3.5 cm long, 3–4 cm wide, and c. 1.5 cm thick; testa yellowish brown, striate-verrucous, with broad wing-like margin.

One species, *A. passiflora* (Vell.) Silva Manso, from gallery forest in Brazil.

Molecular phylogenetic data suggest that this monotypic genus is sister to *Fevillea* (Nee et al. 2010).

9. ***Cyclantheropsis*** Harms — Fig. 24

Cyclantheropsis Harms, Bot. Jahrb. Syst. 23: 167 (1896).

Dioecious, perennial, herbaceous to softly woody climber to 5 m long, with tuberous rootstock. Leaves entire or 3–5-lobed, the blade ovate, base cordate, apically acute; tendrils apically 2-fid. Flowers small; male flowers in axillary panicles, female flowers 3–6, in thyrses or monochasia; receptacle-tube saucer-shaped; sepals triangular, 0.5–1 mm; corolla regular; petals triangular, c. 1 mm, distinct, greenish-yellow; stamen 1, central; thecae 2, horizontal, semicircular, at the top of the column, forming a split ring; pollen medium-sized (polar axis 29–34 μm, equatorial axis 24–27 μm), 3-colporate, striate (Khunwasi 1998); ovary compressed; placenta 1, apical; ovule 1; stylodia 3, short; stigmas 2-fid; staminodes 3, small. Fruits 1–4, an elliptic compressed samara, to 55 by 22 mm, indehiscent, ripening brown. Seed solitary, elliptic and compressed, to 11 mm long; testa pale brown, slightly rough; germination hypogeal (Zimmermann 1922).

Three species, two in East and South tropical Africa, and one endemic in Madagascar; in lowland evergreen forest, deciduous forest, and bushland.

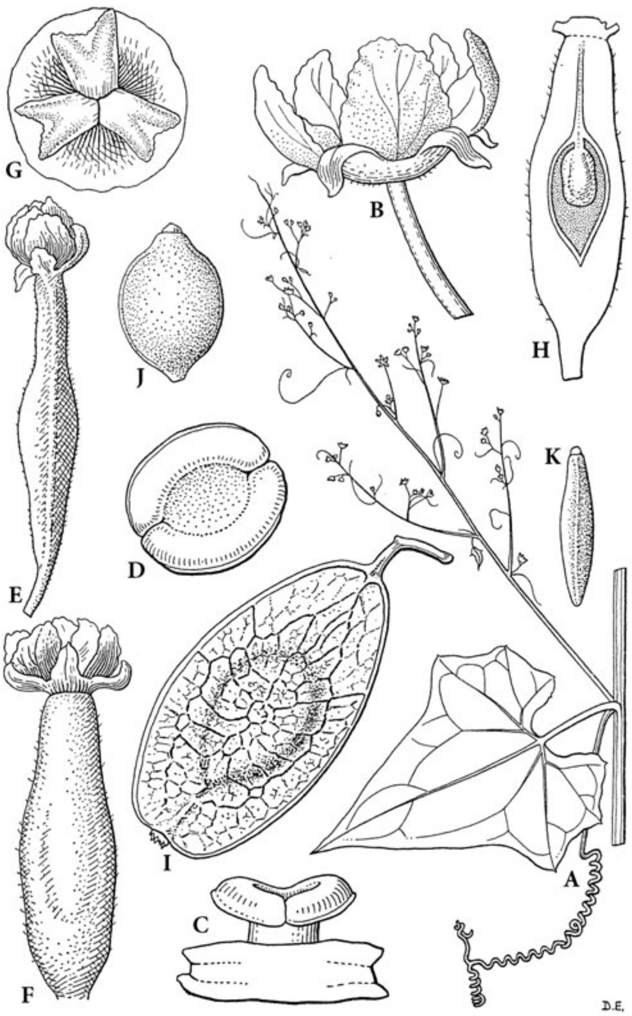

Fig. 24. Cucurbitaceae. *Cyclantheropsis parviflora*. **A** Node with branched tendril and inflorescence. **B** Male flower. **C** Staminal column and disk. **D** Anther thecae, in plan. **E** Female flowers, side view. **F** Same, face view. **G** Stylodia. **H** Ovary, median longitudinal section. **I** Fruit. **J** Seed, face view. **K** Same, side view. (Jeffrey 1967)

10. *Pteropepon* (Cogn.) Cogn.

Pteropepon (Cogn.) Cogn., Pflanzenreich IV. 275 (Heft 66): 260 (1916).
Sicydium sect. *Pteropepon* Cogn. (1878).
Pseudosicydium Harms (1927).

Monoecious or dioecious, perennial, herbaceous or woody climbers with tuberous roots. Leaves entire or 3–5-lobed, the blade subdeltoid, subcircular subcordate or subtruncate with 2 lateral punctate glands just above the insertion of the petiole at the base; tendrils apically 2-fid. Flowers small; male flowers in panicles or thyrses, female flowers solitary or few in monochasia or panicles; receptacle-tube saucer-shaped; sepals linear, or deltoid to lanceolate; corolla rotate; petals ovate-lanceolate, connate at the base, whitish, greenish or yellowish; stamens 1–3, inserted at the base of the tube; filaments short, recurved, distinct or absent or connate into a central column; anthers all 1-thecous or two anthers 2-thecous, one 1-thecous or one anther 2-thecous and one 1-thecous or only one 2-thecous anther; thecae straight, horizontal; pollen medium-sized (polar axis 33–35 μm, equatorial axis 27–32 μm), 3-colporate, striate (Khunwasi 1998); ovary oblong, strongly compressed subtrigonous, 1-locular with an apical placenta; ovule 1; stylodia 3; stigmas 3, 2-fid; staminodes reduced. Fruit a large, fibrous samara with 1 continuous, encircling wing or small, membranaceous, with 2 lateral wings, solitary or 2–3, compressed. Seed solitary, pendent, compressed; testa verrucous or scrobiculate.

Five species in South America, two of them endemic in Argentina (Martínez Crovetto 1952), one in Peru, and two in Brazil; in humid ravines close to rivers, primary rainforest, and secondary scrub.

11. *Sicydium* Schlechtend.

Sicydium Schlechtend., Linnaea 7: 388 (1832).
Triceratia A. Rich. (1845).
Chalema Dieterle (1980).

Dioecious or rarely monoecious, perennial or annual, herbaceous climber with tuberous or fibrous roots. Leaves (sub)cordate, tip acuminate; tendrils simple or apically 2-fid. Flowers small, in panicles; receptacle-tube saucer-shaped; corolla rotate; petals ovate-lanceolate to triangular, whitish-greenish; stamens 3 or 5, inserted near base of the tube; filaments very short, distinct or connate into a central column; anthers all 1-thecous or two anthers 2-thecous, one 1-thecous; thecae straight; pollen small to medium-sized (polar axis 17–37 μm, equatorial axis 17–29 μm), 3-colporate, striate (Khunwasi 1998; Lira Saade et al. 1998); staminodes 0 or 3; ovary ovoid, 1-locular; ovule 1; stylodia 3, linear; stigmas linear or punctiform. Fruit baccate, globose, indehiscent, fleshy or fibrous, ripening black or a dry, globose achene, c. 3 mm in diam. Seed solitary, brownish, (sub)globose or compressed; testa rugose-verrucous, no distinct margin.

About seven species in Central to tropical South America, and the Caribbean and Mexico (Lira Saade 1995, 2004a, b); in disturbed tropical and deciduous forest and along rivers, in dry forest and among shrubs of coastal lowlands; flowering and fruiting all year.

III. Tribe Zanonieae Benth. & Hook.f. (1867).

Tendrils 2-fid, rarely simple. Stamens 4–5. Fruit a dry capsule. Seeds few, winged.

12. *Gerrardanthus* Harv. ex Hook.f. Fig. 25

Gerrardanthus Harv. ex Hook.f. in Benth. & Hook.f., Gen. Pl. 1: 820, 840 (1867).
Atheranthera Masters (1871).

Herbaceous to softly woody climbers to 15 m long, with tuberous rootstocks, often as partly exposed pachypodia (to 1.8 m in diam.). Leaves petiolate, ovate-cordate, unlobed or palmately 3–5-lobed; tendrils apically 2-fid. Male flowers in axillary panicles, female flowers solitary or in small groups; receptacle-tube broad, saucer-shaped; sepals 5, small, ovate or triangular; corolla regular to strongly zygomorphic; petals 5, distinct, unequal, yellowish to orange or brown; stamens 5 (one often reduced to a staminode), inserted near the center of the tube; filaments distinct; anthers all 1-thecous, 2 pairs and 1 single; thecae straight, horizontal; pollen medium-sized (polar axis 42–50 μm, equatorial axis 41–52 μm), 3-colporate, reticulate (Khunwasi 1998); ovary 3-sided, 3-locular at the apex and 1-locular at the base; placentae 3; ovules several, pendent; stylodia 3, divergent; stigmas reniform, 2-lobed; staminodes 5. Fruit obconic-cylindric, 3-sided, dehiscing by an apical triradiate slit, ripening pale yellow. Seeds fusiform, the body to 2 cm long; testa (pale) brown, with distal, membranous, to 2 cm long wing; germination epigeal (Zimmermann 1922).

Three to five species in tropical Africa, and two species in South Africa; in lowland rainforest, deciduous bushland, and wooded grassland (Crouch et al. 1999).

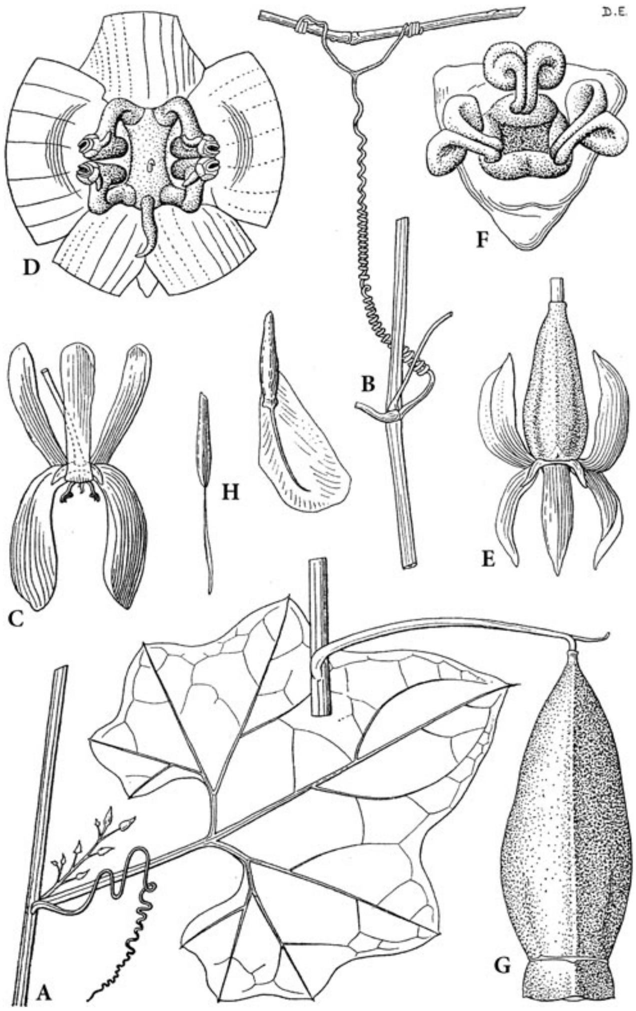

Fig. 25. Cucurbitaceae. *Gerrardanthus lobatus*. **A** Flowering node. **B** Apically bifid tendril. **C** Male flower. **D** Stamens, in plan. **E** Female flower. **F** Stylodia. **G** Fruit. **H** Seeds, side and face view. (Jeffrey 1967)

13. *Zanonia* L.

Zanonia L., Sp. Pl. 2: 1028 (1753) & Gen. Pl., ed. 5: 454 (1754); W.J. de Wilde & Duyfjes, Blumea 52: 281–290 (2007).

Woody climber to 15 m tall. Leaves simple, shortly petiolate, ovate-oblong, coriaceous; tendrils apically 2-fid (or rarely simple) in juvenile plants with apical adhesive pads of to 5 mm length. Male flowers in pendent, many-flowered, to 60 cm long panicles, female flowers in to 40 cm long racemes; receptacle-tube saucer-shaped; sepals 3–4 (but calyx morphologically 5-merous), c. 2 mm long; petals 5, distinct, fleshy, 2.5–7 mm long, cream-colored; stamens 5, inserted centrally; filaments distinct, short, thick; anthers all 1-thecous; thecae horizontal; pollen medium-sized (polar axis c. 40 µm, equatorial axis c. 29 µm), 3-colporate, striate (Khunwasi 1998); ovary clavate, 3-locular at the apex and 1-locular at base; placentae 3; ovules 2 per locule, pendent; stylodia 3, short; stigmas 2-fid; staminodes very small or absent. Fruit to 10×5 cm, elongate-cylindrical, claviform, apex truncate, pendent, dehiscent by a 3-radiate, apical slit into 3 valves. Seeds few, ovate, compressed; testa smooth, leathery winged, the wing to 8×2 cm.

One species, *Z. indica* L., with two subspecies in Cambodia, India, Sri Lanka, Bhutan, Indonesia, Laos, Thailand, Malesia, Myanmar, Vietnam, Southern China, Philippines, and New Guinea; forest edges, riversides, open forest on mountain slopes, 0–2,300 m; flowering and fruiting collections throughout the year.

14. ***Siolmatra*** Baill.

Siolmatra Baill., Bull. Mens. Soc. Linn. Paris 1: 458 (1885); Robinson & Wunderlin, Sida 21: 1961–1969 (2005).

Woody climbers. Leaves compound, petiolate, the petiole with a basal ring-shaped callus, the blade 3-palmate or 5-pedate, lateral leaflets asymmetrical; tendrils apically 2-fid. Flowers in panicles; receptacle-tube saucer-shaped; sepals 3; corolla contorted; petals 5, unguiculate, obovate, whitish; stamens 5, distinct, inserted at the base of the tube; filaments short; anthers all 1-thecous; thecae straight, horizontal; pollen small to medium-sized (polar axis 24–28 µm, equatorial axis 23–26 µm), 3-colporate, striate (Khunwasi 1998); staminodes absent; ovary obconical, subtrigonous, 3-locular at the apex and 1-locular at the base; placentae 3; ovules 2, pendent; stylodia 3; stigmas 2-lobed, reniform. Fruit nodding, obconical-subtrigonous, apex truncate, to 3 cm long, dehiscent by a 3-radiate, apical slit into 3 short teeth. Seeds strongly compressed, ellipsoid; testa yellowish brown, finely verrucous, margin with membranous wing, expanded along the chalaza-micropyle axis, c. 2 cm long.

Two species endemic in the Amazon basin (Brazil, Peru, Bolivia); in tropical rainforest.

15. ***Xerosicyos*** Humbert

Xerosicyos Humbert, Compt. Rend. Hebd. Séances Acad. Sci. 208: 220 (1939).
Zygosicyos Humbert (1945).

Herbaceous to woody climbers or shrubs (*X. danguyi* Humbert) with rootstock or large, partially exposed pachypodium, to 1 m in diam. and 1 m high (*X. pubescens* Keraudr.). Leaves simple, shortly petiolate, 3-lobed or 3-foliolate; tendrils apically 2-fid, glabrous or pubescent. Male flowers in sessile or pedunculate fascicle, female flowers solitary or in pedunculate fascicles; receptacle-tube reduced, flat; sepals 4, small, lanceolate-deltoid; corolla irregularly contorted, rotate or zygomorphic; petals 4, distinct, (long) lanceolate, yellow or yellowish-green; stamens 4, inserted near the mouth of the tube; filaments distinct or connate in pairs in the lower half or united into a central column but distinct at the tip; anthers 4, all 1-thecous; thecae reniform, horizontal; pollen small to medium-sized (polar axis 24–30 µm, equatorial axis 16–23 µm), 3-colporate, striate (Keraudren 1968); ovary obconical, 2-locular at the apex and 1-locular at the base; placentae 2; ovules 2 per locule, ± pendent; stylodia 2, straight, ± divergent; stigma ± 2-lobed or horse-shoe-shaped; staminodes 4. Fruit obconical, compressed, 2–3 cm long, apically dehiscent by the ventral carpellar suture, ripening yellow. Seeds 4, elliptical, compressed, c. 1 cm long; testa smooth, pale brown, narrowly winged.

Five species endemic in Madagascar; in xerophilous forest and bushland (Rauh 1996; Eggli 1998).

IV. Actinostemma Clade

Tendrils 2-fid, rarely simple. Stamens 5 or 6. Fruit a dry pyxidium. Seeds few.

16. ***Actinostemma*** Griff.

Actinostemma Griff., Account Bot. Coll. Cantor: 24 (1845).
Mitrosicyos Maximowicz (1859).
Pomasterion Miquel (1865).
Bolbostemma Franquet (1930).

Herbaceous climbers with fibrous roots or underground stolons bearing crowded scales at the tip.

Leaves hastate-cordate, entire or 3–5-lobed, base often with glands. Flowers unisexual or rarely bisexual; receptacle-tube cup -shaped; sepals linear-lanceolate; petals ovate-lanceolate or ovate, long caudate-acuminate; stamens 5 (rarely 6) or 2 pairs and a single stamen, inserted on the base of the tube; filaments distinct, short; anthers all 1-thecous; thecae straight; pollen small to medium-sized (polar axis c. 26–40 μm, equatorial axis c. 21–42 μm), 3-colporate, striate (Khunwasi 1998); ovary subglobose or ovoid, semi-inferior, verrucous; placentae 1 or 3; ovules 2–4; style 1, short; stigmas 2 or 3, reniform; staminodes 0–5. Fruit ovoid, conical, the upper part falling off at maturity, glabrous or echinate. Seeds ovate compressed; margin denticulate, with short chalazal wing or not winged. $n = 8$ (Probatova and Rudyka 1981).

Three species, two in China and one, *A. tenerum* Griff., widespread in Russia, India, China, Taiwan, Korea, Laos, Vietnam, Japan (Franquett 1930; Ali Khan 2002); in grassland and thickets near open water.

V. Indofevillea Clade

17. *Indofevillea* Chatterjee

Indofevillea Chatterjee, Nature 158: 345 (1946) & Kew Bull. 2: 119 (1947).

Woody climber, to several meters long. Leaves leathery, broadly ovate-cordate, entire, to 20 cm long; tendrils 2-fid, 20–30 cm long. Flowers in axillary panicles; sepals ovate-lanceolate, to 6 mm long; petals ovate-lanceolate, to 4 mm long; stamens 5, inserted near the base of the tube; filaments very short, four in pairs, one distinct; anthers all 1-thecous; thecae reniform, hairy; pollen medium-sized (polar axis c. 49 μm, equatorial axis c. 53 μm), 3-colporate, reticulate (Khunwasi 1998); ovary ellipsoid to oblong. Fruits 3–6 in clusters, c. 30 cm long, oblong, dry, indehiscent with thick woody pericarp. Seeds many, compressed, unwinged, ovoid, 3.5–4 cm long, c. 2 cm broad, 0.5 cm thick; testa yellowish, smooth, faintly winged.

One species, *I. khasiana* Chatterjee, in NE India, Bhutan, Tibet; in open forest on mountain slopes; flowering and fruiting in August.

VI. Thladiantha Clade

Tendrils simple or 2-fid. Stamens 5, inserted near the mouth of the tube; filaments short, two pairs connate at the base, one solitary; anthers all 1-thecous. Fruits fleshy, indehiscent. Seeds many, unwinged.

18. *Thladiantha* Bunge

Thladiantha Bunge, Enum. Pl. China Bor. 29. (1833).

Herbaceous climbers, with tuberous roots. Leaves entire or pedately 3–7-foliolate, the base cordate. Flowers medium-sized; receptacle-tube shortly campanulate or cup-shaped; sepals linear, lanceolate, ovate-lanceolate or oblong; corolla campanulate; petals yellow, entire, oblong, broadly ovate or obovate; thecae straight; pollen large (polar axis 52–79 μm, equatorial axis 64–71 μm), 3-colporate, reticulate (Khunwasi 1998); ovary ovate, oblong or fusiform, smooth or verrucous; stigmas 3, 2-lobed, reniform. Fruit smooth or verrucous, ribbed or not ribbed. Seeds horizontal; testa brown or blackish. $n = 9$ (Li et al. 1993).

About 30 species in China, Taiwan, Tibet, India, Korea, Japan, Thailand, Vietnam, Indonesia, Philippines, New Guinea, one species, *T. dubia* Bunge, naturalized in Europe and N America; in montane forest and bushland, tropical rainforest, riverine forest, on disturbed and cultivated ground. For floral biology and pollination, see Vogel (1990).

19. *Baijiania* A. M. Lu & J. Q. Li

Baijiania A. M. Lu & J. Q. Li in J. Q. Li, Acta Phytotax. Sin. 31: 50 (1993); W.J. de Wilde & Duyfjes, Blumea 48: 279–284 (2003).
Sinobaijiania C. Jeffrey & W.J. de Wilde; W.J. de Wilde & Duyfjes, Blumea 51: 494–498 (2006).

Woody or herbaceous climber to 6 m long, with small or very large spherical tubers, often as partly exposed pachypodia. Leaves ovate-cordate or ovate-oblong, unlobed or 2–3-lobed, to 30 cm long; tendrils apically 2-fid (rarely simple), to 25 cm long. Flowers small; receptacle-tube shallow, cup-shaped; sepals short, triangular-linear or triangular-ovate; petals elliptic, rounded, cream-colored or greenish white, to 5 mm long; thecae ± curved; pollen medium-sized (polar axis 24–25 μm, equatorial axis 26–27 μm), 3-colporate, reticulate (Zhang and Lu 1989); disk at the base of the tube conspicuous, 3-parted; ovary ellipsoid; style c. 2 mm long; stigma 3-lobed, the lobes notched; staminodes 5, 2 pairs and 1 solitary. Fruit solitary or 2–3, subglobose or cylindric, 3–4.5 cm in diam., soft hairy or ± glabrous, ripening orange. Seed ± ovate or ovate-oblong, rounded, c. 5 mm in diam. $n = 16$ (*B. yunnanensis* (A.M. Lu & Zhi Y. Zhang) A.M. Lu & J.Q. Li).

Five species, in China, Taiwan, Thailand, and Borneo (Sabah, SE Kalimantan, Sarawak); along forest margins, in primary or moderately disturbed forest.

VII. Siraitia Clade

20. *Siraitia* Merr.

Siraitia Merr., Pap. Michigan Acad. Sci. 19: 200 (1934); J.Q. Li, Acta Phytotax. Sin. 31: 45–55 (1993); J.W. de Wilde & Duyfjes, Blumea 51: 409–503 (2006).
Microlagenaria (C. Jeffrey) A.M. Lu & J.Q. Li (1993).

Herbaceous climbers to 7 m long, with spherical, enlarged tubers. Leaves entire and unlobed or palmately 3–5-lobed, blade ovate-cordate, sparsely dentate; plant covered with black, blackish-brown or yellowish glandular hairs; tendrils apically 2-fid. Male flowers to 50 in racemes or panicles, female flowers solitary or fasciculate; receptacle-tube short, campanulate; sepals entire, linear to lanceolate or triangular; petals distinct, rounded, lanceolate or obovate-lanceolate, cream-colored, 1–3 with an incurved basal scale; stamens 5, distinct or 2 pairs and one single, inserted near the base of the tube; filaments distinct; anthers all 1-thecous; thecae straight, curved or triplicate; pollen medium-sized (polar axis 35–51 μm, equatorial axis 36–54 μm), 3-colporate, reticulate (Zhang and Lu 1989; Khunwasi 1998); ovary ovoid, hairy; style stout, apex 3-lobed; stigma 2-lobed; ovules many, horizontal; staminodes 5. Fruit (sub)globose or cylindric, fleshy, indehiscent, tomentose, ripening yellow. Seeds few, ± compressed, subovoid or ovoid or oblong; testa pale brown or yellowish, rarely with 2 longitudinal parallel central ridges (*S. africana*) margin unwinged or with 2 or 3 corky wings. $n = 14$ (Li et al. 1993).

Three or four species in India, Indonesia, Peninsular Malaysia, Thailand, South and Southwest China; forest on mountain slopes, riversides or thickets.

Molecular phylogenetic data indicate that *S. africana* (C. Jeffrey) A. M. Lu & J. Q. Li in Southern Tanzania (2 localities) and Southeast Nigeria (1 locality) indeed is closely related to the Asian species; on lake shores and in thickets at low altitudes; not recollected since the 1960s. Locally used as a source of cucurbitane glycosides as a natural sweetener.

VIII. Momordica Clade

21. *Momordica* L.

Momordica L., Sp. Pl.: 1009 (1753).
Dimorphochlamys Hook.f. (1867).
Raphanocarpus Hook.f. (1871).
Raphanistrocarpus (Baill.) E.G.O. Müll. & Pax (1889).
Calpidosicyos Harms (1923).

Herbaceous or woody climber or trailer to 15 m long (rarely small shrubs) with fibrous or woody, sometimes tuberous and greatly enlarged root or rootstock. Leaves entire or pedately 3–7–15-foliolate, often with discoidal glands/nectaries; tendrils simple or apically 2-fid (rarely paired at the nodes and spinose); probract absent or sessile, orbicular (*M. calantha* Gilg). Male flowers solitary or in umbels, racemes, fascicles or pseudopanicles; female flowers solitary; receptacle-tube short, broad, ± campanulate; sepals entire; corolla rotate, campanulate-urceolate or zygomorphic; petals distinct, entire, white, yellow, cream-colored or greenish, usually with black center, 1–3 with an incurved scale inside; stamens 3 or 2, inserted in the lower half of the tube; filaments distinct; two anthers 2-thecous, one 1-thecous or one 3-thecous and one 2-thecous; thecae arcuate, duplicate or triplicate; pollen large (polar axis 65–73 μm, equatorial axis 68–79 μm), 3-colporate, reticulate (Keraudren 1968; Khunwasi 1998); ovary smooth, ribbed, tuberculate or papillose; ovules few to many, horizontal or pendent or erect; stigma 3-lobed; staminodes 5. Fruit small to large, fusiform or ovoid-ellipsoid or globose, usually spiny, tuberculate, winged or ridged, indehiscent or dehiscent by 3 valves or irregularly. Seeds few to several, yellow, brown or black, often with white, yellow or red arilloid, medium-sized to large, subglobose to compressed; testa smooth or variously sculptured, margin often grooved; germination epigeal or hypogeal (Zimmermann 1922; Schaefer, unpubl. data). $n = 11$ or 14 (Beevy and Kuriachan 1996).

About 60 species in tropical and subtropical Africa, Arabia, (sub)tropical Asia, Malesia and Northeastern Australia (Schaefer and Renner 2010a; H. Schaefer, monograph in preparation); two species, *M. charantia* L. and *M. balsamina* L., naturalized in the Americas and most of the Pacific islands; in tropical rainforest, deciduous forest and bushland, savannah and semi-deserts. Host of the fungi *Puccinia cucumeris* Henn., *P. vanderystii* Henn., and *P. momordicae* Kalchbr. and Cooke (Berndt 2007). For floral biology and pollination, see Vogel (1990).

IX. Tribe Telfairieae Arn. (1841).

Tendrils simple or 2-fid. Stamens 3 (rarely 5). Fruit fleshy, ellipsoid or pear-shaped. Seeds 5–200; testa unwinged.

22. *Cogniauxia* Baill.

Cogniauxia Baill., Bull. Mens. Soc. Linn. Paris 1: 423 (1884).
Cogniauxella Baill. (1884).

Dioecious, herbaceous climber or trailer, to several meters long. Leaves simple, the blade ovate-cordate, entire or 3–5-lobed, to 18 cm long; tendrils 2-fid. Flowers large, showy, 7–8 cm in diam.; male flowers in racemes, female flowers solitary; receptacle-tube elongated, dilated at the apex; sepals triangular; petals distinct, ± asymmetric, obovate, yellow to orange; stamens 3 (rarely 5), inserted near the mouth of the tube; filaments distinct; two anthers 2-thecous, one 1-thecous; thecae duplicate; pollen medium-sized to large (polar axis c. 60 μm, equatorial axis 48–51 μm), 3-colporate, irregularly reticulate (Khunwasi 1998); ovary narrowly oblong; placentae 3; ovules many, horizontal; style short, fleshy; stigmas 2-lobed; staminodes 5. Fruit ovoid, shortly rostrate, fleshy, smooth, to 15 cm long and 8 cm in diam., ripening red. Seeds compressed, to 2 cm long, with acuminate apex and almost 2-lobed base; testa brown, smooth.

Two species in tropical Africa (Gabon, Cameroon, Congo, Angola); along forest margins and roadsides, also in secondary forest.

23. *Telfairia* Hook. Fig. 26

Telfairia Hook., Bot. Mag.: 2751 (1827).
Joliffia Bojer ex Delile (1827).

Dioecious (rarely monoecious fide Akoroda et al. 1990), large, woody liana, to 30 m long, with strong, fleshy, ± tuberous roots. Leaves petiolate, pedately (3–)5–7-foliolate, leaflets ± elliptic; tendrils apically 2-fid; probracts tubular, with nectaries. Flowers large, showy, sweet-scented, diurnal; male flowers in racemes, female flowers solitary (rarely in pairs); receptacle-tube short, campanulate; sepals triangular-acuminate, dentate; petals c. 2 cm long, distinct, white, purplish or pink, fringed; stamens 5 or 3, inserted halfway up the tube; filaments distinct; anthers five, 2-thecous or three (two 4-thecous, one 2-thecous); thecae ± straight; pollen large (polar axis 60–82 μm, equatorial axis 50–70 μm), 3-colporate, reticulate (Keraudren 1968; Khunwasi 1998); ovary ribbed; ovules many, horizontal; stigmas 3. Fruit fleshy, ellipsoid, to 60 cm long and 25 cm in diam., weighing to 12 kg, ribbed, with or without an expanded, basal collar, with white waxy surface when young, dehiscing apically by 8–10 longitudinal valves. Seeds up to 200, large, broadly ovate, 3.5–5 cm in diam., ± compressed, in yellowish-white pulp, covered by fibrous sheath, containing edible oil; testa yellowish to pale or dark reddish brown, smooth or ± verrucous; germination hypogeal (Zimmermann 1922), seeds often germinate within the fruit (Akoroda et al. 1990). n=12 in *T. occidentalis* Hook.f. (Okoli 1987).

Three species in tropical Africa; in lowland rainforest, often cultivated in villages and nearby for the leaves and oily seeds (Okoli and Mgbeogu 1983).

24. *Ampelosicyos* A. Thouars

Ampelosicyos A. Thouars, Hist. Vég. Isles Austr. Afrique 68 (1808), as *Ampelosycios*.
Delognaea Cogn. (1884).

Monoecious (*A. meridionalis* Keraudren perhaps dioecious), herbaceous to woody climbers or trailers, some (or all) with partly exposed, tuberous rootstock of to 30 cm in diam. Leaves simple, petiolate, 3–5-foliolate, the leaflets oblong-lanceolate, entire or deeply lobed; tendrils simple or 2-fid, long, glabrous or (partly) pubescent.

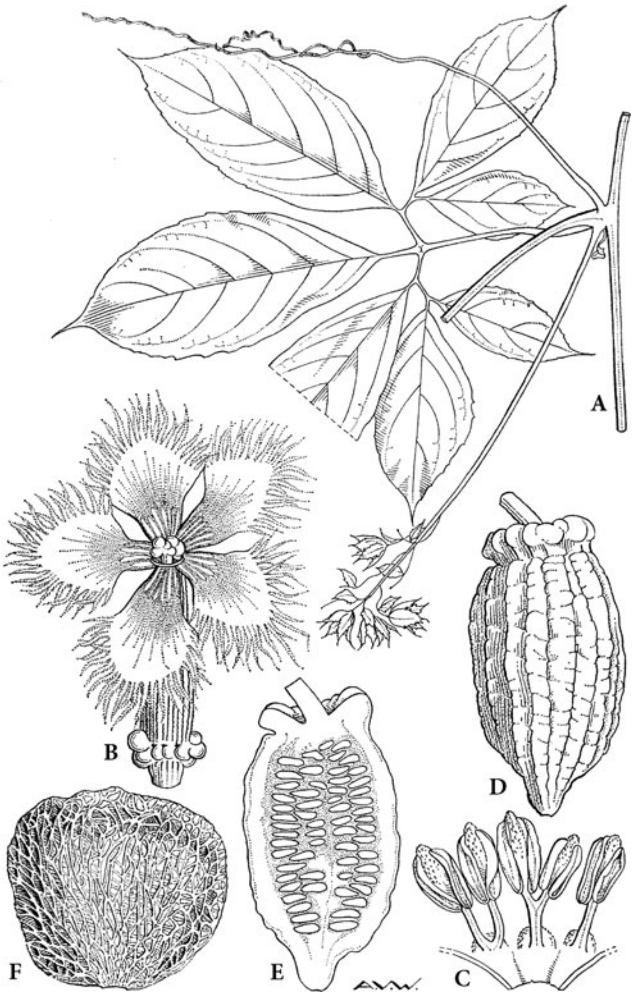

Fig. 26. Cucurbitaceae. *Telfairia pedata*. **A** Node with male inflorescence. **B** Female flower. **C** Stamens. **D** Fruit. **E** Fruit, longitudinally sectioned. **F** Seed with endocarpic fibrous sheath. (Jeffrey 1967)

Flowers medium-sized to large; male flowers in small racemes or solitary, female flowers solitary; receptacle-tube elongate, cylindrical, apically expanded, to 20 cm long and 2 mm in diam. near the base, apically expanded to to 12 mm; sepals triangular-dentiform, about 2 mm long; petals distinct, to 3 cm long, ± ellipsoidal, white to yellowish, margin with to 2 cm long fringes; stamens 5, inserted near the mouth of the tube; filaments very short; anthers all 1-thecous; thecae triplicate; pollen medium-sized to large (polar and equatorial axes c. 46–66 μm), 3-colporate, (micro)reticulate to striate-reticulate (Keraudren 1968); ovary smooth; placentae 3; ovules many, horizontal; stigmas 3, 2-lobed. Fruit ± pear-shaped, 7–15 cm long, fleshy, smooth, indehiscent, yellow with whitish pulp. Seeds horizontal, bean-shaped, large, to 3 cm long and 2 cm in diam., rich in oil; testa pale cream-colored, smooth, no distinct margin.

Three species endemic in Madagascar (Keraudren-Aymonin 1971); in forest remnants, highly endangered.

25. *Tricyclandra* Keraudren

Tricyclandra Keraudren, Bull. Soc. Bot. France 112: 327 (1966).
Odosicyos Keraudren (1981).

Dioecious, herbaceous climber or trailer to several meters long, with large tuberous root (weighing several kg) or subterranean, tuberous rootstock, 1 m or more in diam. Leaves simple, petiolate, the blade pedately 3–5-lobed; tendrils simple, long. Flowers medium-sized, opening at night, with light, pleasant fragrance; male flowers in pedunculate, elongated racemes, female flowers unknown; receptacle-tube funnel-shaped, elongate; sepals triangular, 1 mm long; petals ± connate, white to cream, apically divided into long fringes; stamens 3, inserted in the upper half of the tube; filaments distinct, very short; anthers all 1-thecous; thecae circular; pollen (*T. leandrii* Keraudr.) large (polar axis c. 55 μm, equatorial axis c. 55 μm), 3-porate, verrucate (Keraudren 1968). Fruit ± ellipsoid, fibrous pepo, 3 cm long, 2 cm in diam., or 12–15 cm long and 5–8 cm in diam., indehiscent, rostrate, smooth. Seeds 5–6 or 15–25, obovate, asymmetrical, compressed; testa pale brown, smooth.

Two species endemic in Madagascar; in dry bush and deciduous forest; highly endangered in their natural range but often cultivated in Europe as ornamental plants; flowering Sept.–Nov.

X. Tribe Bryonieae Dumort. (1827).

Tendrils simple or absent. Stamens 3. Fruit a small or oblong berry, indehiscent or watery and ejecting seeds by elastic contraction. Seeds few to many, compressed, unwinged.

26. *Austrobryonia* H. Schaef.

Austrobryonia H. Schaef. in Schaefer et al., Syst. Bot. 33: 126 (2008).

Monoecious, perennial or annual trailers with woody rootstock. Leaves ± ovate, unlobed or shallowly 3-, 5- or 7-lobed; tendrils simple. Flowers solitary or in fascicles; receptacle-tube broadly campanulate; sepals small, narrow-triangular; corolla ± rotate; petals ovate, yellow-green or yellow; stamens inserted halfway up the tube; filaments distinct, short; two anthers 2-thecous, one 1-thecous; thecae curved; pollen prolate, 3-colporate (Jeffrey 1969); ovary subglobose or ellipsoidal; ovules many, horizontal; disk annular; style very short or stigma ± sessile; stigma 2- or 5-lobed, the lobes capitate or linear, papillose; staminodes 3. Fruit a globose or ellipsoidal, 10–35 mm long berry, ripening green to yellow. Seeds few to several, ovate, compressed; testa smooth, pale, margins sometimes thickened.

Four species endemic in dry regions of Central and Western Australia (molecular phylogeny: Schaefer l.c.); on clay soils of river flood plains, waterhole and dam margins and swales in dunefields, grasslands on cracking clay, grassy woodlands on red earth.

27. *Bryonia* L.

Bryonia L., Sp. Pl.: 1012 (1753); Jeffrey, Kew Bull. 23: 441–461 (1969).

Monoecious or dioecious, perennial climbers or trailers with fleshy or woody rootstock. Leaves ovate-cordate to triangular, entire to 5-lobed; tendrils simple. Flowers small, in axillary, racemose panicles or sub-umbellate fascicles; receptacle-tube shortly campanulate; corolla almost rotate; petals connate at base, greenish-white; stamens inserted near the rim of the tube; filaments short, distinct; two anthers 2-thecous, one 1-thecous; thecae triplicate; pollen medium-sized to large (polar axis c. 42–60 μm, equatorial axis c. 35–52 μm), 3-colporate, reticulate (Khunwasi 1998); ovary globose; style elongate, 3-fid; stigmas 2-lobed; ovules many, horizontal; staminodes 3–5 or absent. Fruit a fleshy berry, smooth, ripening green with pale stripes, red or black, when mature separating from the peduncle and in *B. verrucosa* ejecting the seeds by elastic contraction. Seeds few, compressed, ellipsoid; testa brown, smooth, no distinct margin. Usually $n = 10$ (Volz and Renner 2008).

Ten species in Europe, North Africa, Canary Islands, Central Asia (Volz and Renner 2009); forest margins and disturbed ground, semi-deserts and dry bushland. Host of the fungus *Puccinia isiacae* Winter (Berndt 2007) and of the oligolectic sand bee *Andrena florea*.

Medicinal uses of *Bryonia* have been recorded for over two millennia (Renner et al. 2008). Today, there is a considerable market for *Bryonia* preparations, mostly for homeopathic medicine, although effectiveness remains contested.

28. *Ecballium* A. Rich.

Ecballium A. Rich. in Bory de St.-Vincent, Dict. Class. Hist. Nat. 6: 19 (1824), nom. cons.

Monoecious or dioecious, annual to perennial trailers. Leaves cordate; tendrils absent. Male inflorescence a raceme, female flowers solitary; receptacle-tube short-campanulate; sepals linear-lanceolate; corolla broadly campanulate or almost rotate; petals ovate-oblong, apex acute, yellow; stamens inserted near the center of the tube; filaments short, distinct; two anthers 2-thecous, one 1-thecous; thecae reflexed; pollen medium-sized to large (polar axis c. 67 μm, equatorial axis c. 38 μm), 3-colporate, reticulate (Khunwasi 1998); ovary oblong, hispid; style short; stigmas 3, 2-lobed; ovules many, horizontal; staminodes 3. Fruits oblong, hispid, scabrous, watery, when mature separating from the peduncle and contracting at the base, ejecting the seeds by elastic contraction. Seeds many, oblong, compressed; testa pale yellow to brown, smooth, narrowly marginate. $2n = 18$ (Slavik et al. 1993).

One species, *E. elaterium* (L.) A. Rich., with a monoecious and a dioecious subspecies (Costich and Galán 1988; Costich and Meagher 1992). Mediterranean to North Africa and Southwest Asia; on disturbed ground. Pollination biology: Dukas (1987) and Rust et al. (2003).

XI. Tribe Schizopeponeae C. Jeffrey (1964).

Herpetospermeae (C. Jeffrey) C. Jeffrey, Bot. Zhurn. 90: 333 (2005).

Tendrils 2 or 3-fid. Stamens 3. Fruit indehiscent or 3-valved. Seeds 1–48, unwinged.

29. *Schizopepon* Maxim.

Schizopepon Maxim., Mém. Sav. Étr. Acad. St. Pétersbourg 9: 110 (1859).

Dioecious or monoecious climbers; rarely flowers bisexual. Leaves ovate-cordate or hastate, usually 5–7-lobed; tendrils 2-fid. Flowers small; male flowers usually in racemes, female flowers solitary or few in a raceme; receptacle-tube cupular or campanulate; sepals lanceolate or subulate; petals white, ovate; stamens inserted at the base of the tube; filaments short, distinct or connate; two anthers 2-thecous, one 1-thecous; thecae straight; pollen (*S. longipes* Gagnep.) medium-sized (polar axis c. 43 μm, equatorial axis c. 47 μm), 3-colporate, reticulate (Khunwasi 1998); ovary ovate or conical, 3-locular; ovule pendent, one per locule; style short; stigmas 3(–5), slightly expanded, 2-lobed; hermaphrodite individuals produce solitary perfect flowers from leaf axils; each hermaphrodite flower has three stamens, a short style with a 3-lobed stigma, and a triangular hypogenous ovary. Fruits small, ovate or conical, smooth or punctate, apex acute or long-acuminate, 3-valved or indehiscent. Seeds 1–3, pendent, ovate, compressed; testa brown, ± sculptured, margin irregularly dentate. $n = 10$ (Nishikawa 1981).

Six to eight species in Russia, India, Myanmar, China, and Japan (Lu 1985); in river valleys, thickets, forests, on roadsides and mountain slopes up to 3,000 m; flowering and fruiting May–Nov. Details on floral biology: Akimoto et al. (1999) and Fukuhara and Akimoto (1999).

30. *Herpetospermum* Wall.

Herpetospermum Wall. ex Benth. & Hook.f., Gen. 1: 834 (1867).
Edgaria C.B. Clarke (1876).
Rampinia C.B. Clarke (1876), nom. illegit.
Warea C.B. Clarke (1876), nom. illegit.
Biswarea Cogn. (1882).

Dioecious climbers with spreading roots. Leaves ovate-cordate, to 15 cm long, 5–7-lobed or unlobed, margin entire or irregularly dentate; tendrils 2(–3)-fid. Flowers medium-sized, showy, fragrant; male flowers in racemes (rarely solitary), female flowers solitary; receptacle-tube narrowly tubular below, dilated above and broadly campanulate; sepals linear to subulate; corolla broadly campanulate to rotate; petals connate at the base, entire, elliptic, yellow; stamens inserted in the upper half of the tube; filaments distinct; two anthers 2-thecous, one 1-thecous; thecae straight, duplicate or triplicate; pollen very large (polar axis 108–110 μm, equatorial axis 111–134 μm), 3-porate, baculate/gemmate (Khunwasi 1998); ovary oblong to narrowly ovoid, 3-locular; ovules 1–6 or 16 per locule, pendent or ± horizontal; stigmas 3, dilated; staminodes 3 or absent. Fruit dry, fibrous, broadly oblong to ellipsoid-fusiform, ± ribbed, 5–8 cm long, apically dehiscing into 3 valves. Seeds 6, 12 or c. 48, oblong or obovate, compressed; testa smooth, margin obtuse. n=11 in *H. darjeelingensis* (Thakur and Sinha 1973).

Three species in India, Myanmar, Nepal, Tibet, China (Yunnan); among shrubs and on riverbanks; flowering July–October.

XII. Tribe Sicyoeae Schrad. (1838).

Tendrils simple or 2–8-fid. Stamens 2–5. Fruit fleshy or dry, indehiscent, explosively dehiscent or operculate. Seeds solitary or few to many.

31. *Nothoalsomitra* I. Telford

Nothoalsomitra I. Telford, Fl. Australia 8: 388, 172 (1982).

Dioecious, perennial, herbaceous climbers with woody base, to several meters long. Leaves pedately 3-foliolate, the leaflets ± equal, ovate to lanceolate, to 11 cm long; tendrils 2-fid. Flowers small; male flowers in racemes, female flowers solitary; receptacle-tube long and deeply campanulate; sepals 5, triangular, to 2 mm long; petals 5, to 6 mm long, white-tomentose outside, yellow inside; stamens 3, inserted near the mouth of the tube; filaments distinct, relatively long; two anthers 2-thecous, one 1-thecous, distinct but appressed into a central head; thecae flexuose, triplicate; pollen large (polar axis c. 60 μm, equatorial axis c. 63 μm), 3-colporate, reticulate (Khunwasi 1998); ovary ellipsoidal; ovules many, horizontal; style short, thick; stigmas 3, the lobes spreading, flexuose; staminodes 3.

Fruit fleshy, ellipsoidal, 8–12 cm long and 4–5 cm in diam., glabrous, indehiscent, ripening variegated green to yellowish. Seeds many, ovoid, 11–13 by 7–9 mm, ± tumid, truncate; testa brown, smooth, no distinct margin.

One species, *N. suberosa* (Bailey) I. Telford, endemic to subtropical E Australia; in rainforest and humid *Eucalyptus* forest.

32. *Luffa* Mill.

Luffa Mill., Gard. Dict. Abridg. ed. 4 (1754).
Trevouxia Scopoli (1777).
Turia Forssk. (1775), vide I. Friis, Taxon 33: 666 (1984).

Monoecious or dioecious (*L. echinata*), herbaceous climbers or trailers to 15 m long. Leaves simple, the blade ovate-cordate, palmately 3–5-lobed; tendrils apically 2–6-fid; probract small, lingulate. Flowers large; male flowers in racemes, female flowers solitary; receptacle-tube campanulate; sepals 3 or 5, entire; petals 5, distinct, entire, yellowish-white to golden yellow; stamens 5, inserted near the mouth of the tube; filaments distinct; anthers all 1-thecous or two 2-thecous and one 1-thecous; thecae convoluted; pollen (very) large (polar axis 70–110 μm, equatorial axis 70–110 μm), 3-colporate, perforate to reticulate (Khunwasi 1998); ovary smooth, ribbed, tuberculate or spiny; ovules many, horizontal; stigmas 3, 2-lobed; staminodes 5. Fruit dry with fibrous tissue, subglobose to cylindrical, beaked, smooth, ribbed or ± spiny, ripening brown, operculate (a pyxidium). Seeds many, oblong-elliptic, compressed; testa smooth, blackish, with or without a narrow, ± distinct membraneous border and 2 oblique bumps above hilum on each face. $n = 13$ in *L. acutangula* (L.) Roxb., *L. aegyptiaca* Mill. and *L. operculata* L. (Dutt and Roy 1971; Heiser and Schilling 1988; Heiser et al. 1988; Singh 1991; Beevy and Kuriachan 1996).

Five or seven species: four in Africa, Asia, Australia, and Polynesia, one or three in Central and South America; on riverbanks, along forest margins, and on disturbed ground.

Loofah sponges constitute an important biodegradable and renewable resource, and demand is rising, along with an interest in producing large acreages of *Luffa* in regions with a long growing season and warm temperatures, such as the southeastern United States.

33. *Trichosanthes* L.

Trichosanthes L., Sp. Pl.: 1008 (1753).
Anguina Mill. (1755).
Cucumeroides Gaertner (1791).
Involucraria Ser. (1825).
Gymnopetalum Arn. in R. Wight (1840).
Tripodanthera M. J. Roem. (1846).
Scotanthus Naudin (1862).
Eopepon Naudin (1866).
Platygonia Naudin (1866).

Dioecious or rarely monoecious, annual or perennial, herbaceous climbers, some with woody rootstock. Leaves simple, the blade entire or palmately 3–7(–9)-lobed, rarely compound, 3–5-foliate, margin usually denticulate; tendrils 2–5-fid (rarely simple), sometimes with apical adhesive pads; probract often present. Flowers medium-sized to large, mostly fragrant and opening at night; male flowers usually bracteate, in racemes, rarely solitary and coaxillary with a raceme, female flowers solitary (rarely in racemes); receptacle-tube elongate, tubular to cylindric, often dilated at the apex; sepals 5, entire, serrate or laciniate, triangular to lanceolate; petals 5, long-fimbriate less often entire, white, rarely pink or red; stamens 3, inserted halfway up the tube; filaments very short, distinct; two anthers 2-thecous, one 1-thecous; thecae triplicate; pollen medium-sized to (very) large (polar axis 32–98 μm, equatorial axis 34–125 μm), 3(4)(col)porate, psilate, perforate, rugulate, verrucate or (micro) reticulate (Khunwasi 1998; Pruesapan and van der Ham 2005); ovary ovoid or fusiform, glabrous to villous; placentae 3; ovules many, horizontal, ± pendent; style slender to filiform; stigmas 3, entire or 2-fid. Fruit fleshy, pulpy, globose, ovoid to ellipsoid or fusiform, indehiscent, usually glabrous and smooth, sometimes ribbed, ripening orange to red (rarely metallic blue). Seeds many, oblong or ovate, sagittate, or ± rounded, 1-loculed, compressed or 3-loculed, turgid, the two lateral locules empty; testa ± smooth, yellowish to white, black or dark brown, with or without distinct margin; germination epigeal. $n = 11$ or 12 (Beevy and Kuriachan 1996), up to $2n = 88$ in *T. kirilowii* Maxim.

About 100 species in India, China, Taiwan, Japan, Southeast Asia, New Guinea, Northeast Australia (de Wilde and Duyfjes 2004, 2006b); in humid forest; one species, *T. cucumerina* L. var. *anguina* (L.) Haines, cultivated in tropical regions of Africa, Asia, Central and South America. Host of the fungi *Puccinia gymnopetali-wightii* T.S. Ramakr., Srinivasan and Sundaram, and *Uredo trichosanthis* (Berndt 2007).

Molecular phylogenetic data indicate that *Gymnopetalum* is nested inside *Trichosanthes*, a genus that itself is polyphyletic (Schaefer et al. 2008a) and in need of re-evaluation.

34. ***Hodgsonia*** Hook.f. & Thomson

Hodgsonia Hook.f. & Thomson, Proc. Linn. Soc. London 2: 257 ('1853', 1854); W.J. de Wilde & Duyfjes, Blumea 46: 169–179 (2001).

Dioecious, perennial, woody liana, to 30 m long, stems to 7 mm in diam. Leave simple, petiolate (to 8 cm long), the blade subcircular, palmately 3–5-lobed, to 25 cm in diam.; tendrils 2–3-fid; probract thorn-like, c. 5 mm long. Flowers large, fragrant, opening at night; male flowers in bracteate, pedunculate racemes, female flowers solitary (rarely in short racemes); receptacle-tube elongate, to 12 cm long, apically dilated into a shallow cup; sepals 5, small (1–4 mm long); corolla rotate; petals 5, distinct, cuneate, to 5 cm long, white to yellowish, long-fimbriate with 5–15 cm long, spiraling or straight threads; stamens 3, inserted in the upper half of the tube; filaments distinct, short; two anthers 2-thecous, one 1-thecous, connate into a globose head; thecae duplicate; pollen (*H. macrocarpa* Cogn.) very large (polar axis c. 158 μm, equatorial axis 148 μm), 3-colporate, coarsely reticulate (Khunwasi 1998); disk 3-parted, free or joined to base of tube; ovary subglobose, secondarily 3-carpellate, secondarily 6-locular; placentae 6, parietal; ovules 6 or 12 in 6 collateral pairs, erect or pendent; style filiform; stigma large, obconical, 3-lobed; staminodes absent. Fruit a large, pulpy drupe, hard-walled, smooth or shallowly 6–12-grooved, depressed globose, to 25 cm in diam., with 6 large, simple or compound, ± ovoid, veined pyrenes. Seeds 1–3 per pyrene, compressed, large, corky, containing edible oil; testa thin. $n = 9$ (Chen 1993).

Two species in Northeast India, Bhutan, South China, Myanmar, Laos, Cambodia, Vietnam, Thailand, Malaysia, Indonesia; in lowland and lower montane forest, on riverbanks; sometimes cultivated for the seeds.

35. ***Linnaeosicyos*** H. Schaef. & Kocyan

Linnaeosicyos H. Schaef. & Kocyan in Schaefer et al., Syst. Bot. 33: 349–355 (2008).

Dioecious, perennial climber or trailer to 6 m long, with fleshy rootstock. Leaves simple, the blade reniform to suborbicular, entire to deeply 3-lobed, the upper side distinctly pustulate with short trichomes on whitish-gray, discoidal, multicellular, cystolith-bearing hairbases; tendrils simple, to 12 cm long. Flowers solitary; receptacle-tube broadly campanulate, in buds to 20 mm long, glabrous; sepals 5, narrow-triangular, c. 10 mm long; petals 5, ovate, 30 mm×12 mm, white with green veins, fimbriate; stamens 3, inserted 10 mm below the mouth of the receptacle-tube; filaments distinct, c. 1 mm long, glabrous; two anthers 2-thecous, one 1-thecous, connate into a head, c. 9 mm long; thecae triplicate; pollen reticulate, 4-colporate, c. 30 μm in diam. (Schaefer et al. 2008a); ovary ellipsoidal, c. 25 mm long; placentae 3; ovules numerous; stigma 3-lobed, the lobes capitate; staminodes minute. Fruit turbinate to ellipsoidal, green, pendent, 8–12 cm long, 3–4 cm diam. Seeds in soft, whitish pulp, many (several hundreds), linear-oblong, compressed; testa yellowish-brown, margin distinct, flat.

One species, *L. amara* (L.) H. Schaef. & Kocyan, endemic in Hispaniola (Dominican Republic); among cacti in dry thickets and in dry forests from sea level to 300–400 m; flowering December to May, ripe fruits in April, June, and October.

Molecular sequence data show that this species is the sister to all other New World Sicyoeae (Schaefer et al. 2008a).

36. ***Echinocystis*** Torr. & A. Gray

Echinocystis Torr. & A. Gray, Fl. N. Am. 1: 542 (1840), nom. cons.
Pseudoechinopepon (Cogn.) Cockerell (1897).

Monoecious, annual, herbaceous climber, to several meters long. Leaves simple, 5-lobed; tendrils 3–5-fid. Flowers small; male flowers in racemes, female flowers solitary (rarely pairs), coaxillary with the male raceme; receptacle-tube flat; sepals 6; corolla rotate; petals 6, white; stamens 3, inserted near the center of the tube; filaments very short; thecae triplicate; pollen large (polar axis c. 54 μm, equatorial axis c. 60 μm), 5-colporate, perforate-rugulate (Khunwasi 1998); ovary globose, echinate; placentae 2; style very short; stigma capitate. Fruit an ovoid, fleshy pepo, echinate with slender spines, apically dehiscent. Seeds 4, compressed; testa pale brown; germination epigeal. n=16 (Samuel et al. 1995; Gervais et al. 1999).

One species, *E. lobata* (Michx.) Torr. & A. Gray, in Eastern North America (Stocking 1955); in thickets, along roadsides, and in other disturbed areas.

37. ***Marah*** Kellogg

Marah Kellogg, Proc. Calif. Acad. Sci. 1: 38 (1854); l.c. ed. 2, 1: 37 (1873); S. T. Dunn, Bull. Misc. Inf. (Royal Gardens, Kew) 1913(4): 145–153.
Megarrhiza Torr. & A. Gray (1860–1861).

Monoecious (sometimes temporarily dioecious), perennial, herbaceous climber or trailer with (very) large tuberous rootstocks, often as partly exposed pachypodia. Leaves petiolate, the blade round, cordate, palmately 3–9-lobed; tendrils simple or 2–3-fid. Male flowers in racemes or panicles (or solitary), female flowers solitary, often coaxillary with male; receptacle-tube campanulate to saucer-shaped; sepals 5, filiform or absent; corolla 3–15 mm wide (wider in female), cup-shaped to rotate; petals 5, oblong to lanceolate, white or cream to yellowish green; stamens 3 (rarely 4), inserted near the center of the tube; filaments connate into a central column; anthers twisted together; thecae flexuose; pollen large (polar axis 61–92 μm, equatorial axis 54–88 μm), 4–5-colporate, perforate-rugulate (Khunwasi 1998); ovary ovoid to globose, rostrate, glabrous or setose; placentae 2–4; style short; stigma 1, ± hemispherical, 2–5-lobed; ovules 1–8 per locule, erect; staminodes 0–3. Fruit a dry, round, ovate, or oblong capsule, irregularly dehiscent, ± symmetric, 3–6 cm in diam., ± prickly or setose, sometimes rostrate, glabrous or tomentose. Seeds 4–30, ± globose, turgid, to 3.5 cm in diam.; testa smooth, yellowish to gray, margin not distinct; germination hypogeal; n=15 (Parfitt et al. 1990).

About seven species in the Western and Southeastern US (Washington to California, Arizona, New Mexico) and Mexico; in moist canyons and scrubland; flowering in February–June.

38. ***Frantzia*** Pittier

Frantzia Pittier, Contr. U.S. Natl. Herb. 13(4): 127–128 (1910).
Polakowskia Pittier (1910).

Monoecious, perennial, herbaceous climbers, to several meters long, with tuberous roots; tendrils 3- to 5-fid. Leaves simple, long-petiolate, the blade palmately lobed or angulate. Flowers small; male flowers in racemes, female flowers solitary or 2–5, often coaxillary with male inflorescence; receptacle-tube semi-globose, with 10 pouch-like nectaries at the base, some species with umbrella-like covering over the nectaries; sepals 5, triangular or thick and rounded; corolla rotate; petals 5, ovate-lanceolate, apex acute, white; stamens 3, inserted on the base of of the tube; filaments connate into a central column; two anthers 2-thecous, one 1-thecous or anthers connate into a subglobose head; thecae flexuous; pollen large (polar axis 74–77 μm, equatorial axis 85–88 μm), 7–10-colpate, echinate (Khunwasi 1998); ovary fusiform, setose; placenta 1; style 1, short; stigma 3–5-lobed, lobes reflexed; ovule 1, pendent. Fruit medium-sized, 3–6 cm long, fleshy, ovoid to fusiform, indehiscent, sulcate at the apex, sparsely spiny along the ridges or at the apices or glabrous, ripening green, yellowish or purple. Seed solitary, ovate, compressed, pendent, woody, germinating within the fruit. Chromosome numbers are $n = 12$ in *F. villosa* Wunderlin and $n = 14$ in *F. venosa* L. D. Gomez (Mercado and Lira Saade 1994).

About five species in Central America (Costa Rica, Nicaragua, Panama); in forest and secondary scrub (Wunderlin 1976); one species, *F. tacaco* (Pittier) Wunderlin, is a widely cultivated vegetable.

Molecular data (Sebastian et al. 2010 and unpubl. data) suggest that a monophyletic *Frantzia* minimally includes *F. pittieri* (Cogn.) Pittier, *F. tacaco*, *F. talamancensis* Wunderlin, *F. venosa* L. D. Gómez, and *F. villosa* Wunderlin.

39. ***Sicyos*** L.

Sicyos L., Sp. Pl. 2: 1013 (1753).
Sicyoides Mill. (1754).
Sechium P. Browne (1756), nom. cons.
Bryoniastrum Heist. ex Fabr. (1759).
Chayota Jacq. (1780).
Sicyosperma A. Gray (1853).
Microsechium Naudin (1866).

Sechiopsis Naudin (1866); D. M. Kearns. Syst. Bot. 17: 395–408 (1992), rev.
Pterosicyos Brandegee (1914).
Ahzolia Standl. & Steyerm. (1944).
Anomalosicyos Gentry (1946).
Sicyocaulis Wiggins (1970).
Skottsbergiliana H. St. John (1974).
Parasicyos Dieterle (1975).
Sicyocarya (A. Gray) H. St. John (1978).
Sarx H. St. John (1978).
Cladocarpa (H. St. John) H. St. John (1978).
Costarica L.D. Gómez (1983).

Monoecious, annual or perennial, herbaceous climbers or trailers, to 10 m long, with fibrous to tuberous roots or woody rootstocks. Leaves simple, petiolate (rarely sessile), blade angulate or lobed, rarely suborbicular; tendril (2)3–5(6)-fid, rarely simple, with long stout peduncle. Flowers small (even minute), white, greenish or yellow; male flowers in racemes or panicles, female flowers solitary, in small racemes, umbels or dense capitula of 3–40 (rarely solitary or pairs), usually coaxillary with the male flowers, sometimes enclosed in a pair of dentate bracts; receptacle-tube cup-shaped to broadly campanulate, sometimes pitted with nectariferous foveolae (pouches); sepals 5 (rarely 3–4), very small; corolla rotate; petals 5 (rarely 3–4), basally connate, white or yellowish-green; stamens (2)3(–5), inserted near the base of the tube; filaments more or less connate into a central column; anthers sessile; thecae sigmoid, flexuous, or straight; pollen medium-sized to large (polar axis 31–92 µm, equatorial axis 34–110 µm), 6–12-colpate, echinate (Khunwasi 1998); ovary ovoid, fusiform, angular, or rarely winged, ± pubescent; ovule 1, pendent, reflexed; style slender or fleshy; stigmas 2–3, ± dilated, often reflexed. Fruits fleshy or dry, indehiscent, clustered in capitula, sometimes enclosed by a subtending leaf or bracts, small or up to 20 cm long (*S. edulis*), ovoid to fusiform, armed with retrorse barbs or unarmed, occasionally a winged samara, glabrous or villous. Seed solitary, tumid to compressed; testa smooth, no distinct margin. $n = 12$ in *Sicyos angulatus* L. (Turala-Szybowska 1990) and *S. nihoaense* H. St. John (Carr 1985), $n = 12$, 13, or 14 in *S. edule* Jacq. (Beevy and Kuriachan 1996), $n = 14$ in *Microsechium compositum* Donn. Sm., $n = 14$ in *M. hintonii* (Paul G. Wilson) C. Jeffrey, and $n = 15$ in *Sechium chinantlense* (Mercado and Lira 1994).

About 75 species, mostly from Mexico to Argentina, Hawaii, North America (2 species), Australia, New Zealand, Norfolk and Lord Howe Islands, Galapagos (*Sicyocaulis pentagonus* Wiggins, Sta. Cruz, Isabela; *S. villosus* Hook.f., Floreana, known only from the type collection by Darwin and apparently extinct), *S. polyacanthus* Cogn. in Africa (introduced); forest margins, hillsides, clearings, roadsides, pastures, seabird colonies.

According to molecular phylogenetic results (Sebastian et al. 2010, and unpubl. data), all the above-listed monotypic or small genera are nested among species of *Sicyos*, including *Sechium* P. Browne, *Sechiopsis* Naudin (including *Pterosicyos* Brandegee, as suggested by Kearns 1992), *Sicyosperma* A. Gray, *Sicyocaulis* Wiggins, *Parasicyos* Dieterle, and *Costarica* L. D. Gómez, which we therefore synonymize here and with the required formal transfers in a forthcoming paper.

40. ***Hanburia*** Seem.

Hanburia Seem., Bonplandia 6: 293 (1858).
Elateriopsis A. Ernst (1873).
Nietoa Seem. ex Schaffner (1876).

Monoecious, perennial, herbaceous climber, to 15 m long. Leaves simple, the blade broadly ovate to cordate or pentagonal, entire or 3–7-lobed, some species with discoidal glands at the base of the leaf; tendrils 2–5-fid (rarely simple), sometimes with adhesive disks. Flowers medium-sized to large, some species with vanilla-scent; male flowers in pedunculate racemes, female flowers solitary; receptacle-tube short, urceolate-cylindrical or campanulate; sepals 5, short, ± triangular or linear to subulate; corolla campanulate; petals 5(6), triangular, 5–30 mm long, yellow or (greenish-)white; stamens 3–5, inserted near the base of the tube; filaments connate into a central column; anthers connate into a central, ± globose head, all 1-thecous; thecae triplicate or convolute; pollen (very) large (polar axis 88–122 µm, equatorial axis 82–130 µm), 4–7-colporate, perforate-rugulate (Khunwasi 1998); ovary ovoid to subglobose or oblique, mostly rostrate, hispid; ovules several, erect to ascendent; style elongate; stigma peltate. Fruit fleshy, 11–14 cm long, 7.5 cm in diam., setose, rostrate, ± asymmetrically marsupiform, explosively dehiscent. Seeds few, large, circular, to 2–4 cm in diam., or ovate to pear-shaped, compressed, angularly lobed, in white, spongy pulp; testa black to gray, smooth or minutely rugulate, margin distinct.

Seven species in Central to tropical South America; in primary and disturbed rainforest, deciduous forest, and cloud forest.

41. *Cyclanthera* Schrad.

Cyclanthera Schrad., Index Sem. Gött. 1831: 2 (1831).
Discanthera Torr. & A. Gray (1840).
Rytidostylis Hook. & Arn. (1840).
Pseudocyclanthera Mart. Crov. (1954).
Cremastopus Paul G. Wilson (1962).

Monoecious, annual or perennial, herbaceous climbers, to 10 m long, sometimes with woody base. Leaves simple or pedately 3–7-foliolate, the blade lanceolate to orbicular, entire or 3–9-lobed; tendrils simple or 2-fid (rarely to many-fid), to 30 cm long. Flowers small to medium-sized; male flowers in racemes or panicles, female flowers usually solitary (rarely in groups of 2–3), often coaxillary with the male inflorescence; receptacle-tube cup-shaped, cupular or elongate-tubular; sepals 5, subulate, dentiform to filiform or absent; corolla rotate; petals 5(–10), yellow, white or greenish, united at the base only, (ovate-)triangular to lanceolate, usually acute; stamens 3, fused, inserted in the center of the tube; filaments united into a short or elongate, bottle-shaped central column; anthers connate into a globose head; thecae united into a horizontal, flat or 10-folded ring, opening by a continuous split; pollen medium-sized to (very) large (polar axis 58–107 μm, equatorial axis 45–167 μm), 4–11-colporate, perforate-rugulate (Khunwasi 1998); ovary ovoid to oblique, hirsute, echinate or setose, ± rostrate, 1-locular; ovules few to several, ascendent; style very short or elongate, slender; stigma large, subglobose or spherical. Fruit (oblique) ovoid to triangular or reniform, ± fleshy, setose, setiform or echinate, rarely glabrous, explosively dehiscent, rarely indehiscent. Seeds solitary or many, compressed, angled, 2-lobed at apex and base, ± turtle-shaped; testa crustaceous, ± verrucouse. $n = 16$ (Samuel et al. 1995, Gervais et al. 1999).

About 40 species in Southwestern USA, Mexico, Central and South America, one species extending into the Galapagos archipelago; roadsides, forest clearings, on riverbanks and cultivated ground, hedges, tropical deciduous forest, in humid lowland forest, dry xeric forest, and montane cloud forest. *Cyclanthera pedata* (L.) Schrad. is cultivated in Asia.

Molecular phylogenetic data indicate that *Rytidostylis* and *Pseudocyclanthera* are nested inside *Cyclanthera*.

42. *Echinopepon* Naudin

Echinopepon Naudin, Ann. Sci. Nat. Bot. V, 6: 17 (1866).
Brandegea Cogn. (1890).
Vaseyanthus Cogn. (1891).
Apatzingania Dieterle (1974).

Monoecious, annual or perennial, herbaceous climbers, to 5 m long, with fibrous roots or woody rootstock. Leaves simple, the blade thin, angulate-cordate, often palmately 3–5(–9)-lobed or dissected, margin entire or denticulate; tendrils simple or 2–3-fid. Flowers small; male inflorescence a raceme or panicle, female flowers mostly solitary; receptacle-tube cup-shaped to urceolate or shallowly campanulate; sepals 5, small or minute, green; corolla rotate or campanulate; petals 5, ovate-triangular, white or cream-colored, sometimes knobby-glandular (*E. insularis*); stamens 3–5; filaments connate into a central column; anthers distinct, all 2-thecous; thecae straight, curved or duplicate; pollen (very) large (polar axis 58–168 μm, equatorial axis 78–168 μm), 5–14-colpate or colporate, some pantocolpate-inaperturate, sometimes the colpi with distinct margins, perforate (some weakly verrucate or micro-reticulate) (Khunwasi 1998); ovary conic to ovoid, ± rostrate; placentae 1–2; ovules 1–5 per locule, erect to ascending (rarely horizontal or pendent); style short; stigma fleshy, subglobose. Fruits ovoid or ellipsoid, operculate (a pyxidium), glabrous or hairy, often conspicuously echinate, rostrate, rarely dry, subterranean (to 3.5 cm deep), on 6–9 cm long peduncle (*E. arachnoideus*). Seeds solitary or few, quadrangular or angular-ovoid, compressed; testa smooth, rugose or sculptured, no distinct margin. $n = 12$ (Ward and Spellenberg 1988).

About 20 species, Southern United States to Northern Argentina (Gentry 1950; Dieterle 1974; Monro and Stafford 1998); in forest clearings, semi-deserts and ravines, on hillsides, roadsides, sand dunes and seaside gravel shores, some are weeds of cultivated ground.

XIII. Tribe Coniandreae Endl. ex M. Roem. (1846).

Tendrils simple or 2–3-fid, rarely absent. Stamens 2, 3 or 5. Fruit fleshy, indehiscent. Seeds few or many, unwinged.

43. *Bambekea* Cogn.

Bambekea Cogn., Bull. Jard. Bot. État 5: 115 (1916).

Dioecious, perennial, woody climber or trailer, to 15 m long, with large tuberous rootstock, to 25 cm in diam. and 1 m long. Leaves broadly ovate, entire to palmately 3–5(–7)-lobed; tendrils 2-fid, to 20 cm long. Flowers in racemes, often with a coaxillary solitary flower; receptacle-tube very short, broad, shallow; sepals small; corolla rotate; petals entire, distinct, yellowish to orange; male petals 6 mm long, 4.5 mm broad; stamens 5, inserted near the mouth of the tube; filaments distinct; anthers all 1-thecous; thecae triplicate; pollen medium-sized (polar axis c. 38 μm, equatorial axis c. 40 μm), 3-colporate, reticulate (Khunwasi 1998); female flowers with sepals to 7 mm long, petals to 12 mm long, 5 mm broad; ovary ellipsoid to cylindrical; ovules many, horizontal; style fleshy, 7–8 mm long; stigmas globular; staminodes 5. Fruits to 8 in racemes, globose, c. 2.5 cm across, with strong gourd-like odor, style and calyx rests persistent on fruit. Seeds many, c. 5 mm long; testa smooth.

One species, *B. racemosa* Cogn., in tropical Central and West Africa (Nigeria, Gabon, Ivory Coast, Cameroon, Congo); in lowland secondary rainforest.

44. *Eureiandra* Hook.f.

Eureiandra Hook.f., Gen. Pl. 1: 826 (1867).

Dioecious, perennial (rarely annual?), herbaceous to ± woody climbers with tuberous rootstocks (to 20 cm in diam.). Leaves entire or palmately 3–5-lobed; tendrils simple. Flowers medium-sized to large, often on leafless shoots; male flowers in short, pedunculate fascicles or solitary, female flowers solitary; receptacle-tube narrowly campanulate and apically dilated, short; sepals lanceolate, acute, often acuminate, finely pubescent; petals distinct, to 3.5 cm long, cream-colored to orange-yellow (rarely white), obovate, rounded, apiculate; stamens 5 or 3, inserted about halfway up the tube; filaments distinct or 2 pairs connate; anthers all 1-thecous or two 2-thecous and one 1-thecous; thecae triplicate, glabrous or minutely to conspicuously hairy; pollen large (polar axis 54–79 μm, equatorial axis 63–79 μm), 3-colporate, reticulate (Khunwasi 1998); ovary ellipsoid-cylindrical, ± rostrate; ovules many, horizontal; stigma 3-lobed; staminodes 3–5. Fruit to 13 cm long and 8 cm in diam., ellipsoid or cylindrical, rostrate, fleshy, indehiscent, ripening orange to red. Seeds ovate to ± globose; testa blackish, smooth or fibrillose, margin not distinct or narrow.

About eight species in tropical and subtropical Africa, one species, *E. balfourii* Cogn., endemic in Socotra; in woodland and wooded grassland, coastal forests.

45. *Dendrosicyos* I.B. Balfour Fig. 27

Dendrosicyos I.B. Balfour, Proc. R. Soc. Edinburgh 11: 513 (1882).

Monoecious, perennial tree with a bloated trunk, 3 (–6) m high and to 1 m in diam. and few, thick, pendent branches. Leaves ovate-cordate, deeply pedately 4–6-lobed, prickly, the margin serrate, with characteristic, unpleasant odor; tendrils

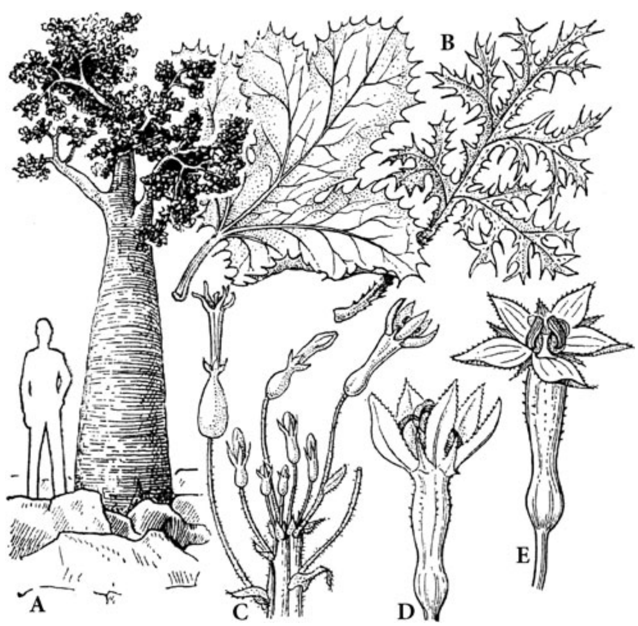

Fig. 27. Cucurbitaceae. *Dendrosicyos socratanus*. **A** Habit. **B** Lower (left) and upper (right) leaves. **C** Flowering shoot. **D** Male flower. **E** Female flower. (Takhtajan 1981)

absent. Flowers medium-sized (2.5 cm in diam.), in pendent axillary fascicles; receptacle-tube funnel-shaped; sepals lanceolate; petals linear-lanceolate, yellow, tomentose; stamens 3, inserted on mouth of the tube, exserted; thecae straight; pollen large (polar axis c. 69 μm, equatorial axis c. 71 μm), 3-colporate, reticulate (Khunwasi 1998); ovary ovoid, smooth, rostrate; style long, slender; stigmas 3, 2-lobed; staminodia 5. Fruit cylindric, to 4 cm long, rostrate, glandular setose, ripening orange. Seeds c. 6 mm long, compressed, in orange pulp.

One species, *D. socotranus* I. B. Balfour, endemic in Socotra; in shrubland communities. For morphology: Olson (2003), biogeography: Schaefer et al. (2009).

46. ***Seyrigia*** Keraudren

Seyrigia Keraudren, Bull. Soc. Bot. France 107: 299 (1961).

Dioecious, perennial climber with ± succulent, much-branched, (3–)5-angled stems, to 3 m high, the roots with potato-shaped tubers. Leaves mostly absent in adult plants or very small, caducuous, 3–5-lobed; tendrils simple, partly pubescent, to 20 cm long. Flowers small; male flowers in pedunculate, ± condensed racemes, female flowers solitary or in pairs; receptacle-tube cup- to funnel-shaped; sepals 2 mm long, triangular; petals elliptic-lanceolate, 1–3 mm long, yellowish-white; stamens 2, inserted near the mouth of the tube; filaments short, pubescent; anthers 2-thecous; thecae straight; pollen medium-sized (polar axis 42–46 μm, equatorial axis 25–31 μm), 3-colporate, (micro)reticulate (Keraudren 1968); pistillode cup-shaped; ovary ovate-oblong; placentae 2; ovules horizontal, 2 per locule; stigmas lobed; staminodes 2. Fruit fleshy, c. 2 cm long, ovoid, apiculate to rostrate, glabrous, indehiscent, ripening brilliant red. Seeds 2–4, 6–7 mm long, 4 mm large, in transparent arilloid and red pulp; testa brown, slightly sculptured, no distinct margin. $n = 13$ in *S. bosseri* Keraudren, *S. multiflora* Keraudren, *S. humbertii* Keraudren and *S. gracilis* Keraudren (Keraudren 1968).

Six species endemic in South and Southwest Madagascar; in xerothermic forest and bushland.

47. ***Trochomeriopsis*** Cogn.

Trochomeriopsis Cogn., Monogr. Phan. 3: 661 (1881).

Dioecious, perennial, herbaceous climber or trailer, to several meters long. Leaves entire, 5-lobed, or 3–5-foliolate; tendrils simple. Flowers medium-sized to large; male flowers in panicles, female flowers solitary, in pairs or racemes; receptacle-tube elongate; sepals small; petals sub-linear, 5–6 cm long, yellowish-green; stamens 3, sessile, inserted at the mouth of the tube; filaments very short or absent; two anthers 2-thecous, one 1-thecous; thecae straight; pollen medium-sized (polar axis c. 37 μm, equatorial axis c. 33 μm), 3-colporate, reticulate (Keraudren 1968) or medium-sized (polar axis c. 49 μm, equatorial axis c. 56 μm), 3-colporate, reticulate according to Khunwasi (1998); ovary subcylindrical; placentae 3; style short; stigmas 3; staminodes 3. Fruit a cylindrical, smooth, fleshy berry, to 12 cm long and 3.5 cm in diam., ripening red, tinged with yellow. Seeds 20–30, with red arilloid, triangular, to 8 mm long; testa pale brown or blackish, finely sculptured, no distinct margin. $n=12$, with diploid, triploid and tetraploid individuals (Keraudren 1968).

One species, *T. diversifolia* Cogn., endemic in Madagascar; in dry *Euphorbia* bushland and dry forest, on sand dunes; flowering and fruiting all year.

48. ***Halosicyos*** Mart. Crov.

Halosicyos Mart. Crov., Bol. Soc. Argent. Bot. 2: 84 (1947).

Dioecious, perennial, herbaceous climber or trailer with large woody rootstock. Leaves ± circular, finely dissected, the lobes 10 mm long and 2 mm broad; tendrils simple, filiform. Flowers small; male flowers in racemes, female flowers solitary; receptacle-tube subcylindrical, the throat long-hairy; sepals dentiform; corolla rotate; petals sub-spathulate, 3.5–4 mm long, green; stamens 3, inserted near the mouth of the tube; filaments distinct; two anthers 2-thecous, one 1-thecous, coherent; thecae curved; pollen 3-colporate, reticulate (Pozner 1998a); ovary oblong, compressed; placentae 2; style elongate, c. 4 mm long; stigmas 2; staminodes 5. Fruit 7–8 mm long, laterally compressed, glabrous, shortly rostrate, ripening red. Seeds 4–8, pyriform, 5–5.5 by ± 2 by ± 1.5 mm; testa sculptured or rugose, slightly winged.

One species, *H. ragonesei* Mart. Crov., endemic in Central Argentina; on sandy soil and in halophilous bushland on the border of salinas.

49. *Cucurbitella* Walp.

Curcubitella Walp., Repert. Bot. Syst. 6: 50 (1846) = *Cucurbitella* Walp. corr. Walpers (1847); R. Pozner, Ann. Missouri Bot. Gard. 85: 425–439 (1998).
Prasopepon Naudin (1866).

Monoecious or dioecious, perennial, herbaceous climbers or trailers, to several meters long, with tuberous roots. Leaves entire, dissected, or palmately 3–7-lobed; tendrils simple. Flowers small; male flowers in racemes (rarely solitary), female flowers solitary; receptacle-tube campanulate; corolla imbricate; petals connate in the lower half, orange to yellow; stamens 3, inserted near the mouth of the tube; two anthers 2-thecous, one 1-thecous; filaments distinct, short, hirsute; thecae straight; pollen large (polar axis 59–67 µm, equatorial axis 58–71 µm), 3-colporate, finely reticulate (Khunwasi 1998); ovary oblong, pubescent; placentae 5; ovules horizontal, many; style columnar; stigmas 5, 2-fid; staminodes 0. Fruit a globose berry, ripening greenish with white spots or lines. Seeds many, ovate, compressed, in green, sticky pulp (arilloid jacket); testa smooth, brown, margin ± distinct.

One variable species, *Cucurbitella asperata* (Gillies ex Hook. & Arn.) Walp., in Argentina, Bolivia, Brazil, Uruguay, Paraguay (Pozner 1998b); in dry bushland, along roadsides, and on disturbed ground.

50. *Corallocarpus* Welw. ex Hook.f.

Corallocarpus Welw. ex Hook.f., Gen. Pl. 1: 831 (1867); Jeffrey, Kew Bull. 30: 485–491 (1975).
Phialocarpus Deflers (1895), pro parte, vide *Kedrostis*
Gijefa (M. Roem.) O. Kuntze (1903 ('1904')).

Monoecious, perennial, herbaceous climbers or trailers with tuberous rootstock or small shrubs (*C. glomeruliflorus* Schweinf. ex Deflers). Leaves ovate to reniform-cordate, palmately 3–5-lobed to finely dissected; tendrils simple (rarely 2-fid or absent). Flowers small, greenish-yellow; male flowers in small, pedunculate racemes, female flowers solitary or fasciculate, often coaxillary with the male raceme; receptacle-tube campanulate; sepals small; corolla rotate; petals united at base; stamens 5, inserted in the mouth of the tube; filaments distinct, short; anthers all 1-thecous, sometimes in two pairs with one single, appearing as two 2-thecous and one 1-thecous; thecae straight; pollen medium-sized to large (polar axis 51–75 µm, equatorial axis 49–73 µm), 3-colporate, finely reticulate to microreticulate (Khunwasi 1998); ovary smooth; ovules few to many, horizontal; staminodes 5 or absent; stigmas 2(3)-lobed. Fruit a small berry, to 2 cm long, ovoid, ellipsoid, often rostrate, operculate, the basal part green, expanded into a cup, the upper part red, solitary or in small groups. Seeds few to several, small, pear-shaped (rarely subglobose). $n = 13$ in *C. epigaeus* (Rottler) Hook.f. (Beevy and Kuriachan 1996).

Thirteen species in mainland Africa, two endemic in Madagascar, two in Arabia, India, and Pakistan; rainforest margins, wooded grasslands, deciduous and evergreen bushland.

51. *Kedrostis* Medik.

Kedrostis Medik., Philos. Bot. 2: 69 (1791).
Coniandra Schrad. ex Eckl. & Zeyh. (1836).
Cyrtonema Schrad. ex Eckl. & Zeyh. (1836).
Rhynchocarpa Schrad. ex Endl. (1839).
Achmandra Arn. (1840). ('*Aechmandra*', 1841), as to type *Aechmandra rostrata* (Rottler) Arn. = *Kedrostis rostrata* (Rottler) Cogn.
Pisosperma Sonder (post 15 Oct. 1862).
Cerasiocarpum Hook.f. (1867).
Toxanthera Hook.f. (1883).
Phialocarpus Deflers (1895), pro parte, vide *Corallocarpus*

Monoecious or dioecious, perennial, herbaceous climbers or trailers to 2 m long with tuberous rootstock, or woody climbers or subshrubs to 12 m long, with thick basal stems and coral-like bark or tuberous herb creeping with white underground branches each with several subsidiary tubers and only very short, leaf-bearing aboveground twigs (*K. psammophila* P. Bruyns). Leaves entire (rarely 3-foliolate), ± ovate or hastate, ± palmately lobed to deeply dissected into lanceolate segments; tendrils simple or 2-fid or absent (*K. psammophila*). Flowers small to large; male flowers in pedunculate racemes, female flowers solitary, paired or in small fascicles, in *K. psammophila* arising from subterranean stems; receptacle-tube shortly campanulate, in female *K. psammophila* initially horizontal then erect, narrowly cylindrical and solid, 35–70 mm long and 2–3 mm in diam., mostly subterranean; sepals small, ± lanceolate; corolla rotate; petals ± ovate, 1.5–8 mm long, in female *K. psammophila* 10–12 mm long, united at base, greenish to yellow; stamens 5, inserted near the mouth of the tube; filaments short; anthers all 1-thecous, two in pairs and one solitary or the pairs connate (two 2-thecous and one 1-thecous); thecae ± straight; pollen medium-sized (polar axis 53–91 μm, equatorial axis 48–95 μm), 3-colporate, perforate to (striate) reticulate (Khunwasi 1998); ovary ovoid, smooth or finely papillate; ovules horizontal; style slender; stigmas 2(3)-fid; staminodes (3–)5. Fruits solitary or in clusters, baccate, fleshy, subglobose, ovoid-rostrate, conical or fusiform, to 9 cm long and 3 cm in diam., indehiscent or opening by valves, ripening orange to red, rarely subterranean and ripening white (in *K. psammophila*). Seeds 1–10, small, tumid, asymmetrically pear-shaped to subglobose; testa smooth. $n = 12$ in *K. elongata* Keraudren (Keraudren 1968) and $n = 13$ in *K. foetidissima* (Jacq.) Cogn. (Beevy and Kuriachan 1996).

About 20 species in tropical and subtropical Africa and Arabia, six species in Madagascar, and four species in Asia (India, Sri Lanka, W Malesia); in deciduous bushland, thickets, woodland, lowland rainforest, and semi-desert grassland. Host of the fungus *Puccinia arbor-miraculensis* R. Berndt (Berndt 2007).

52. ***Ceratosanthes*** Adans.

Ceratosanthes Adans., Fam. Pl. 2: 139, 535 (1763).

Dioecious or monoecious (*C. hilariana* Cogn.), perennial, herbaceous climber, to 5 m long, with large tuberous rootstock. Leaves ovate, pentagonal to reniform, palmately 3–5-lobed, in flower, sometimes reduced or caducous; tendrils simple, filiform, short. Flowers small, opening at night; male flowers in long pedunculate racemes, female flowers solitary or in fascicles of 2–4; receptacle-tube elongate, cylindrical, apically expanded; sepals lanceolate, ± 2 mm long; petals cream-colored, 2-fid in the apical half, ± 10 mm, usually involute; stamens 3, inserted near the mouth of the tube; filaments very short, distinct; two anthers 2-thecous, one 1-thecous; thecae straight; pollen medium-sized (polar axis 50–60 μm, equatorial axis 53–63 μm), (3)4-colporate, irregularly reticulate (Khunwasi 1998); ovary globose to fusiform; placentae 2; ovules many, horizontal; stigmas 2, 2-fid. Fruit an ovoid-oblong berry, to 4 cm long and 2 cm in diam., rostrate, smooth, glabrous, indehiscent, ripening green or red, often with white spots. Seeds many, ovoid to subglobose, tumid; testa smooth, pale, with distinct margin.

Four species, Central America to northern Argentina; semi-arid plains and mountain slopes, roadsides, cultivated ground.

53. ***Doyerea*** Grosourdy

Doyerea Grosourdy, Med. Bot. Criollo 1(2): 338 (1864).
Anguriopsis J.R. Johnst. (1905).

Dioecious, perennial, woody climber to 6 m long, with thick, trunk-like base, to 15 cm high. Stems scandent, zigzag and conspicuously compressed. Leaves rounded-cordate, unlobed or 3-lobed (sometimes to almost 3-foliolate), often with prominent, marginal callosities; tendrils simple, woody, with thickened base that persists as conical spur-like structure. Inflorescence in short, sessile, few- to 40-flowered racemes, to 3 per axil; flowers small, in dense clusters; receptacle-tube turbinate-campanulate; sepals valvate, acute, to 1 mm long; corolla rotate; petals yellowish-green; stamens 3, inserted near the mouth of the tube; filaments short or absent; two anthers 2-thecous, one 1-thecous; thecae curved; pollen small (polar axis c. 43 μm, equatorial axis c. 41 μm), 3-colporate, reticulate (Khunwasi 1998); ovary ellipsoidal; placentae 2; ovules 4–6 per locule; style thick, simple, apically shortly 2-fid; stigmas penicillate-fringed, 2-lobed; staminodes 3. Fruits ellipsoid or oblong, fleshy, rostrate, 1–3 cm long, indehiscent, thin-walled, ripening red with white spots. Seeds 8–15, pear-shaped, slightly compressed, to 3–4 mm long; testa reddish brown, with distinct pale brown margin.

One species, *D. emetocathartica* Grosourdy, Caribbean, Central America, Venezuela, Guyanas, Brazil; at low altitudes in dry thickets and woodlands or on rocky slopes; flowering and fruiting Jun.–Dec. Host of the fungus *Uromyces corallocarpi* Dale (Monoson and Rogers 1978).

54. ***Gurania*** (Schltdl.) Cogn. Fig. 28

Gurania (Schltdl.) Cogn., Bull. Soc. R. Bot. Belg. 14: 239 (1875).
Dieudonnaea Cogn. (1875).
Ranugia (Schltdl.) T. Post & O. Kuntze (1903 ('1904')).

Appearing dioecious, but almost certainly monoecious, with plants first male, then female, perennial, herbaceous or woody climber, to 15 m or more in length. Leaves ovate-cordate, simple, unlobed or palmately lobed or 3-foliolate; tendrils simple. Flowers small or medium-sized; male flowers in fascicles or racemes (to 120 per raceme), female flowers solitary, in small groups or pendulous racemes; receptacle-tube urceolate to cylindrical, bright orange to red; sepals mostly prominent, fleshy, often enlarged, shiny orange to red, sometimes with green or yellow tip, rarely small, ± triangular, reflexed; petals inconspicuous, lanceolate, erect, fleshy, orange or yellowish-green; stamens usually 2, inserted halfway up or near the mouth of the tube; filaments short, distinct; anthers 2-thecous; thecae straight or curved to ± convolute; pollen mostly in tetrads (these 149–174 μm in diam.), the monads medium-sized to large (polar axis 51–88 μm, equatorial axis 62–111 μm), 3-porate, perforate, reticulate or psilate and baculate (Khunwasi 1998); ovary cylindrical, smooth; placentae 2; ovules many, horizontal; stigmas 2. Fruits fleshy, to 7 cm long and 2–3 cm in diam., cylindrical to pear-shaped, indehiscent, ripening (yellowish-)green. Seeds many, in yellow pulp, oblong-elliptic, ± compressed; testa smooth, gray to blackish, sometimes slightly marginate.

About 37 species in Central to tropical South America; in tropical forest. Host of the fungi *Passalora guraniae* R. Kirschner and *Stenella praelonga* (Syd.) U. Braun (Kirschner and Piepenbring 2006). For sexual strategy, see Condon and Gilbert (1988).

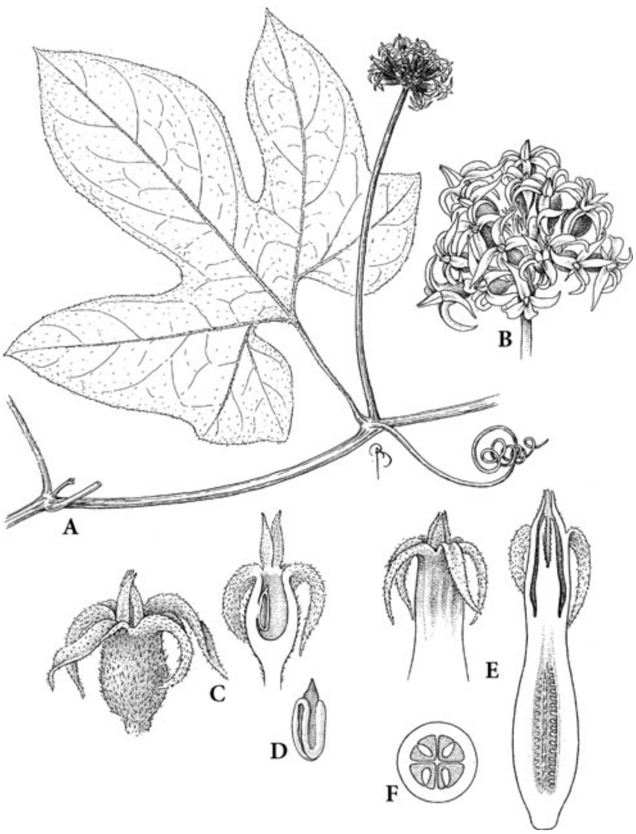

Fig. 28. Cucurbitaceae. *Gurania subumbellata*. **A** Node with female inflorescence and tendril. **B** Male inflorescence; calyx more conspicuous than corolla. **C** Male flowers. **D** Anther with connective. **E** Female flowers. **F** Transverse section of ovary showing locules and placentation. (Reproduced with permission of the artist Bobbi Angell)

55. *Psiguria* Neck. ex Arn.

Psiguria Neck. ex Arn., J. Bot. (Hooker) 3: 274–275 (1841).
Anguria Jacq. (1760), nom. illegit.

Appearing dioecious, but almost certainly monoecious, with plants first male, then female, perennial, herbaceous or woody climber, to 10 m or more in length. Leaves simple or 3-foliolate, entire or palmately 3–5-lobed; tendrils simple. Flowers small to large; male flowers in racemes or axillary spikes, female flowers solitary or in groups of 2–5; receptacle-tube urceolate to cylindrical, green; sepals small, ± triangular, green; petals broad, spreading, red, orange, or pink; stamens 2, inserted halfway up the tube; filaments distinct; anthers 2-thecous; thecae duplicate or rarely straight; pollen in monads or tetrads (152–185 μm in diam.), the monads medium-sized to large (polar axis 77–80 μm, equatorial axis 98–126 μm), 3–6-porate, verrucate, perforate or psilate (Khunwasi 1998); ovary oblong, smooth; placentae 2; ovules many, horizontal; stigmas 2. Fruits fleshy, 3–8 cm long and 2–3 cm in diam., ellipsoid to oblong, smooth, indehiscent, ripening yellowish-green or black, sometimes striped. Seeds many, to 11 mm long, oblong-elliptic, ± compressed; testa smooth, gray, no distinct margin.

About 6–12 species in Central to tropical South America; in tropical forest. Host of the fungi *Uromyces poliotelis* Syd. and *U. anguriae* H.S. Jack. and Holw. (Monoson and Rogers 1978). For a molecular phylogeny, see Steele et al. (2010).

56. *Helmontia* Cogn.

Helmontia Cogn., Bull. Soc. R. Bot. Belg. 14: 239 (1875).

Appearing dioecious, but almost certainly monoecious, with plants first male, then female, perennial, herbaceous or woody climbers, to several meters long. Leaves simple or 3-foliolate, unlobed or palmately lobed; tendrils simple. Flowers small; male flowers many (to 120 per raceme), in racemes or umbels, female flowers in pendulous racemes; receptacle-tube obconic to cylindrical; sepals small, ± triangular, reflexed; petals distinct, c. 3 mm long, yellowish-green; stamens 2, inserted near the mouth of the tube; filaments distinct; anthers 2-thecous; thecae straight; pollen simple (not in tetrads), medium-sized (polar axis 51–69 μm, equatorial axis 62–74 μm), 3-porate, perforate or reticulate (Khunwasi 1998). Fruits fleshy, ovoid to ellipsoid, indehiscent, ripening yellowish-green. Seeds many, seeds oblong-elliptic, ± compressed; testa smooth.

Two to four species in Guyana, Venezuela, and Brazil; in tropical forest.

Molecular data suggest eventual inclusion in *Psiguria/Gurania* (Kocyan et al. 2007).

57. ***Melothrianthus*** Mart. Crov.

Melothrianthus Mart. Crov., Notul. Syst. (Paris) 15: 58 (1954).

Dioecious, herbaceous climber or trailer. Leaves unlobed, lanceolate with subcordate to sagittate base; tendrils simple. Flowers small; male flowers in corymbs, bracteate, female flowers solitary; receptacle-tube narrowly campanulate; sepals lanceolate; petals connate at base, oblong-lanceolate, entire; stamens 3, inserted near the mouth of the tube; filaments absent; two anthers 2-thecous, one 1-thecous; thecae curved; pollen medium-sized (polar axis c. 43 μm, equatorial axis c. 45 μm), 3-colporate, perforate (Khunwasi 1998); ovary lanceolate; placentae 2; ovules many, horizontal; style robust, inserted in the center of a circular disk; stigma solitary, 2-lobed, fleshy. Fruit oblong, slightly pubescent. Seeds compressed, oblong; testa verrucous, no distinct margin.

One species, *M. smilacifolius* (Cogn.) Mart. Crov., endemic in Brazil; growing in humid places. Possibly 2–3 additional as yet undescribed species.

58. ***Wilbrandia*** Silva Manso

Wilbrandia Silva Manso, Enum. Subst. Brazil.: 30 (1836).

Monoecious or dioecious, perennial climber or trailer with woody rootstock. Leaves entire to palmately 3–7-lobed; tendrils simple, circinate. Flowers small; male flowers in racemes or spikes, female flowers solitary or in dense axillary clusters; petals oblong to lanceolate, papillose, white; stamens 3, inserted in the upper third of the tube; filaments very short, distinct; two anthers 2-thecous, one 1-thecous, coherent into a central head; thecae straight; pollen medium-sized (polar axis c. 52–53 μm, equatorial axis c. 54–56 μm), 3-colporate, reticulate (Khunwasi 1998); ovary ovoid-oblong, rostrate; placentae 2 or 3; ovules many, horizontal; style 2–3 mm long; stigmas 2 or 3, entire or 2-fid. Fruit an ovoid-conical berry, c. 2 cm long and 1.5 cm in diam., sessile in the leaf axils, rostrate. Seeds many, ovate to oblong, compressed, c. 5 mm long; testa with distinct margin.

Five species in South America (Brazil, Paraguay, Argentina; Martínez Crovetto 1946); in rainforest and secondary scrub.

59. ***Apodanthera*** Arn.

Apodanthera Arn., J. Bot. (Hooker) 3(21): 274 (1841).
Guraniopsis Cogn. (1908).

Monoecious or dioecious (*A. congestiflora*?, *A. hatschbachii*?, *A. succulenta*?, *A. villosa*?), herbaceous climbers or trailers to 5 m long, some with succulent stems, with perennial rootstock (to 1 m long and 10 cm in diam.). Leaves simple or 5-foliolate (*A. fasciculata* Cogn.), often 3–5 (–9)-lobed, often undulate and with nasty odor; tendrils simple or 2–3-fid. Flowers small to medium-sized; male inflorescence a pedunculate raceme, female flowers usually solitary, in some species long-pedunculate; receptacle-tube elongated, cylindrical; sepals linear; corolla to 6 cm across; petals (almost) distinct, greenish-white or yellow; stamens 2–3, inserted halfway up or near the mouth of the tube; filaments short and distinct or absent; two anthers 2-thecous, one 1-thecous or two 2-thecous; thecae straight or ± curved; pollen medium-sized to large (polar axis 47–103 μm, equatorial axis 52–104 μm), 3-colporate, reticulate (Khunwasi 1998); ovary ovoid or oblong; ovules numerous, horizontal; style columnar; stigmas (2–)3(–5), U-shaped. Fruit fleshy, indehiscent, ovoid to ellipsoid, ± rostrate, 1–7 cm long, ripening green or red to brown often with white stripes or spots, edible. Seeds few to many, ovoid, compressed; testa smooth, chocolate-brown (all species?), often with distinct, ivory-colored margin. n = 14 (Ward 1984).

About 16 species in America (Texas to Argentina); on roadsides and cultivated ground, in bushland and Andean grasslands (Martínez Crovetto 1956).

The seeds of *A. aspera* Cogn. have been used as oil-rich food in Mexico since pre-colonial times; remains have been found in the caves of Tehuacán, Puebla and Guilá Naquitz, Oaxaca, Mexico (Lira Saade 2004a, b). *Apodanthera sagittifolia* (Griseb.) Mart. Crov. differs from the rest of the genus in the presence of long hairs at the base of the filaments (Jeffrey 1978a, b), and does not group with *A. mandonii* Cogn. in molecular phylogenetic analyses (Schaefer et al. 2009). The genus is in need of revision.

60. *Tumamoca* Rose

Tumamoca Rose, Contr. U.S. Natl. Herb. 16: 21 (1912); D. M. Kearns, Madroño 41: 23–29 (1994).

Monoecious, perennial, herbaceous to ± woody climber or trailer with a bundle of tuberous roots (each to 15 cm in diam.). Leaves pedately 3-lobed, the lobes 2–4 cm long, divided into narrow, obtuse segments; tendrils simple, short. Flowers small, opening at night; male flowers in racemes, female flowers solitary; receptacle-tube elongate, narrowly cylindrical, c. 1 cm long; sepals triangular, minute; corolla rotate; petals narrowly linear, 4–6 mm long, pale yellow; stamens 3, inserted in the upper half of the tube; two anthers 2-thecous, one 1-thecous; pollen unknown; ovary globose to fusiform; ovules many, horizontal; staminodes 3. Fruit a globose berry, c. 1 cm in diam., glabrous, with remains of flower, ripening red (rarely yellow). Seeds 2–several, obovoid, 7–8 mm long, truncate at the apex; testa black, tuberculate-rugose, no distinct margin.

Two species in Arizona (near Tucson) and Mexico (Sonora); in semi-desert and xeric bushland; extremely rare; flowering June–September.

61. *Ibervillea* Greene

Ibervillea Greene, Erythea 3(5): 75 (1895).
Maximowiczia Cogn. (1881), nom. illegit.

Dioecious, annual or perennial climbers, to 3 m long, with large tuberous rootstocks, partly exposed as fleshy pachypodia. Leaves sublobate to 3–5-lobed, the lobes often dissected, to 10 cm long and 6 cm broad; tendrils simple. Flowers small, opening during the day; male flowers in racemes or fascicles (rarely solitary), female flowers solitary; receptacle-tube narrowly campanulate; sepals small, acute; corolla narrowly campanulate; petals 4–5 mm long, emarginate to 2-furcate, united near base, yellowish; stamens 3, inserted near the mouth of the tube; filaments connate into a central column; two anthers 2-thecous, one 1-thecous; thecae straight; pollen medium-sized (polar axis 56–68 µm, equatorial axis 56–67 µm), 3-colporate, reticulate (Khunwasi 1998); ovary ovoid to fusiform; placentae 3(–5); ovules many, horizontal; style columnar; stigmas 3–5; staminodes 3–5 (or 0). Fruit a fleshy, indehiscent, globose, ovoid or ellipsoid berry, 1.5 to 4 cm in diam., ripening orange to red. Seeds many, irregularly ovoid, scarcely compressed, in orange-red pulp; testa verrucous, transversely ridged or ± smooth, the margins raised.

Seven to eight species, Texas to Guatemala; semi-deserts, grassy plains, swampy woodlands, thorn-forest, margins of cultivated land; flowering June–Nov. For detailed morphological work, see Kearns (1994).

62. *Dieterlea* E. J. Lott

Dieterlea E. J. Lott, Brittonia 38: 407 (1986).

Dioecious, perennial, woody climber to 12 m long, with very large, tuberous rootstock. Leaves ovate-cordate to reniform, unlobed or ± 3–5-lobed; tendrils simple. Flowers large, in *D. fusiformis* E.J. Lott strongly fragrant and opening at night; male flowers in racemes, female flowers solitary; receptacle-tube narrowly cylindrical, 2–4.5 cm long; sepals distinct or united at base; petals distinct, 1.5–2.5 cm long, entire or apically 2-fid, white or pale yellow; stamens 3, inserted on mouth of the tube; filaments distinct; two anthers 2-thecous, one 1-thecous; thecae straight; pollen (*D. fusiformis*) large (polar axis c. 67 µm, equatorial axis c. 62 µm), 4-colporate, reticulate (Khunwasi 1998); ovary cylindrical, glabrous, 4-to 5-locular; ovules many, horizontal; stigmas 4–5, 2-lobed; staminodes 5 (rarely 3–4). Fruit fusiform or ellipsoid, shortly rostrate, 6–15 cm long and 3–6 cm in diam., indehiscent, ripening yellow to red. Seeds many, turgid, in red pulp; testa smooth, dark gray, margins raised, convex.

Three species in Mexico; tropical deciduous forest, dry rocky slopes.

Molecular data (Kocyan et al. 2007) suggest inclusion in *Ibervillea* but a broader analysis is needed.

XIV. Tribe Benincaseae Ser. (1825).

Dioecious or monoecious, annual or perennial, herbaceous or woody climbers or trailers, rarely shrubs. Leaves simple or 3–7-lobed, rarely absent; tendrils simple, 2–5-fid or absent. Sepals 5; petals 5; stamens (2)3–(5), two anthers 2-thecous, one 1-thecous, less often all 2-thecous or all 1-thecous; pollen mostly 3-colpate, reticulate. Fruit usually indehiscent, fleshy, medium-sized to large.

63. ***Citrullus*** Schrad. ex Eckl. & Zeyh.

Citrullus Schrad. ex Eckl. & Zeyh., Enum. Pl. Afr. Austral: 279 (1836), nom. cons., *Cucurbita citrullus* L., typ. cons.

Monoecious or dioecious, annual or perennial, herbaceous trailers to 6 m long, some with tuberous root to 1 m long. Leaves simple, petiolate, the blade rounded or broadly to triangular-ovate, palmately 3–5-lobed, the segments lobulate or dissected; tendrils 2–3-fid, simple or absent, in *C. naudinianus* Hook.f. spiniform. Flowers solitary (rarely fasciculate), axillary; receptacle-tube broadly campanulate; sepals 5, narrow; corolla rotate or broadly campanulate, medium-sized; petals 5, yellow to white, ovate-oblong, united at base; stamens 3, inserted near the base of the tube; filaments distinct, short; two anthers 2-thecous, one 1-thecous, distinct or slightly coherent; thecae flexuous; pollen medium-sized (polar axis 43–59 µm, equatorial axis 41–56 µm), 3-colporate, irregularly reticulate (Khunwasi 1998); ovary ovoid; placentae 3; style short, columnar; stigmas 3, thick, reniform, ± 3-lobed; ovules many, horizontal; staminodes 3, setiform or ligulate. Fruit large, globose or oblong, fleshy or dry, indehiscent, glabrous or covered with prominent spines. Seeds many, oblong, compressed; testa pale yellowish, blackish or brown, smooth, with or without distinct margin. $n = 11$ in *C. lanatus* (Thunb.) Mansf. and *C. colocynthis* Pangalo (Beevy and Kuriachan 1996).

Four species in the eastern Mediterranean region, North and tropical Africa, and western Asia (Fursa 1972a, b); in semi-deserts and xeric bushlands, on sand dunes and other disturbed ground; one species, *C. lanatus*, widely cultivated and a casual or locally naturalized in many parts of the tropics and subtropics. Host of the fungi *Puccinia citrulli* Syd., P. Syd. & Butler and *P. citrullina* Ragunathan & K. Ramakr. (Berndt 2007).

64. ***Peponium*** Engl.

Peponium Engl. in Engler & Prantl, Nat. Pflanzenfam., Nachtr.: 318 (1897).
Peponiella O. Kuntze (1898).

Dioecious, perennial, herbaceous climbers or trailers to 8 m long, some with tuberous rootstock. Leaves simple, petiolate, blade ± ovate-cordate, unlobed or palmately 3–5-lobed; tendrils 2-fid (rarely simple); probract oblanceolate to obovate, to 18 mm long. Flowers to 8 cm in diam., some or all species sweet-scented and opening in the evening (Zimmermann 1922); male flowers in pedunculate racemes or solitary, often raceme and solitary flower in the same axil, female flowers solitary; receptacle-tube elongated, ± cylindrical; sepals 5, linear-lanceolate; petals 5, entire, distinct, obovate, to 50 mm long and 40 mm broad, white or yellow; stamens 3, inserted near the mouth of the tube; filaments distinct; anthers all 2-thecous or two 2-thecous and one 1-thecous, connate into a central head; thecae triplicate; pollen large in continental African species (polar axis 90–98 µm, equatorial axis 92–102 µm), 3-colporate, striate (Page and Jeffrey 1975; Khunwasi 1998), in the nine Madagascan endemics medium-sized to large (polar and equatorial axis 38–82 µm), 3-colporate with very short narrow colpi, reticulate-rugulate, rugulate or striate-rugulate (Keraudren 1968); ovary ellipsoid, ± hairy; ovules many, horizontal; stigma 3-lobed; staminodes 3. Fruit fleshy, indehiscent, subglobose to ellipsoid, ± rostrate, ripening orange or red. Seeds many, elliptic, compressed; testa blackish, smooth, no distinct margin; germination epigeal (Zimmermann 1922). $n = 12$ in *P. betsiliense* Keraudr. (Keraudren 1968).

About 20 species, ten in Madagascar, one in the Seychelles and Aldabra, six in tropical Africa, and three in South Africa; in rainforest, wood-, bush- and grassland, often near open water.

65. *Lagenaria* Ser.

Lagenaria Ser., Mém. Soc. Phys. Genève 3: 26 (1825).
Adenopus Benth. (1849).
Sphaerosicyos Hook.f. (1867).

Monoecious, annual or perennial, herbaceous climbers. Leaves simple, petiolate, petioles with a pair of glands near the apex; leaf-blade ovate-cordate or reniform; probracts and bracts absent or small, tubular (*L. sphaerica* E. Mey.); tendrils 2-fid. Flowers large, solitary, sweet-scented and opening in the evening or in the morning (Zimmermann 1922), pollinated by hawkmoths (e.g., *Agrius convolvuli*, *Hippotion celerio*), moths (Noctuidae), butterflies (e.g., *Gorgyra johnstoni*), and honeybees (Morimoto et al. 2004); receptacle-tube narrowly campanulate or funnel-shaped (male flower) or cupular (female flower); sepals 5; petals 5, oblong-obovate, apex retuse, white; stamens 3, inserted on the receptacle-tube; filaments distinct; two anthers 2-thecous, one 1-thecous; thecae triplicate or much convoluted; pollen large (polar axis 62–77 μm, equatorial axis 69–81 μm), 3-colporate, perforate (Khunwasi 1998), in *L. sphaerica* smaller (polar axis 60 μm, equatorial axis 60 μm), 3-colporate, reticulate (Keraudren 1968); ovary ovate or cylindric; placentae 3; ovules numerous, horizontal; stylodia short; stigmas 3, 2-lobed; staminodes 3. Fruits fleshy, medium-sized to large, globose, bottle-shaped or ellipsoid, indehiscent, ripening green, often flecked with white, woody when mature. Seeds numerous, obovate, compressed; testa with distinct margin; germination epigeal (Zimmermann 1922). $n = 11$ in *L. siceraria* (Molina) Standl. (Keraudren 1968; Beevy and Kuriachan 1996).

Six species in tropical Africa and Madagascar; along forest margins and on disturbed ground, usually near water; one species, *L. siceraria*, is cultivated throughout the tropics and subtropics and in warm temperate regions.

DNA sequence analysis of archaeological bottle gourd specimens and comparison with modern Asian and African landraces reveal detailed patterns of natural and anthropogenic dispersal (Erickson et al. 2005; Clarke et al. 2006).

66. *Acanthosicyos* Welw. ex Hook.f. Fig. 29

Acanthosicyos Welw. ex Hook.f., Gen. Pl. 1: 824 (1867).

Dioecious, perennial shrub, to 1 m high with woody, robust, angled branches. Leaves reduced to small scale-like ovate, c. 2 mm long, bracts; tendrils transformed into c. 10 mm long, straight spines. Flowers medium-sized, tomentose, ± sessile; male flowers solitary or in small fascicles, female flowers solitary; receptacle-tube turbinate; sepals 5, short, unequal (2 suborbicular to obcordate, 3 ovate); petals 5, connate at the base, broadly ovate, entire, yellow; stamens 3, inserted near the mouth of the tube; filaments distinct, very short, fleshy; two anthers 2-thecous, one 1-thecous; thecae flexuous; pollen large (polar axis c. 68 μm, equatorial axis c. 70 μm), 3-colporate, reticulate (Khunwasi 1998). Fruit globose, verrucous, indehiscent, edible, ripening orange. Seeds many, oblong, tumid, 14–15 mm long and 9–11 mm broad; testa cream-colored, crustaceous, no distinct margin.

One species, *A. horridus* Welw., in Angola, Namibia, Botswana, and Republic of South Africa; in sandy places like dunes and riverbanks, where it forms stands of several meters in diam.

Citrullus naudinianus (Sond.) Hook.f. was transferred to *Acanthosicyos* by Jeffrey (1962) based on biochemical and seed coat characters, a view not accepted by Fernandes et al. (1986), Marticorena (1963), and Fursa (1972a, b), and also contradicted by molecular data (Schaefer et al. 2009).

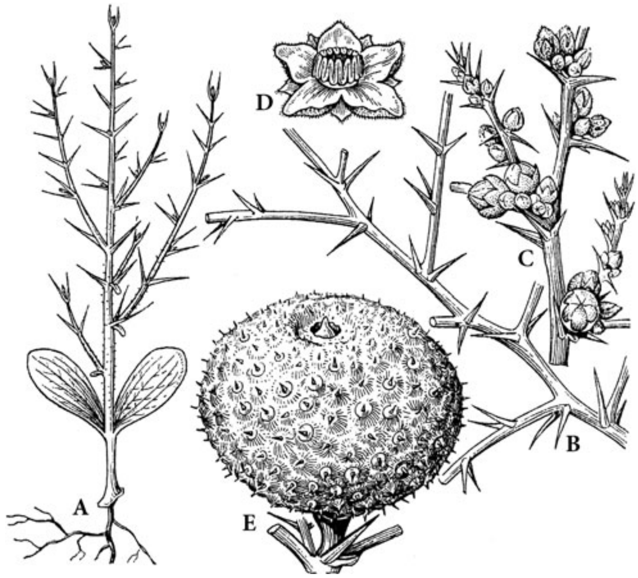

Fig. 29. Cucurbitaceae. *Acanthosicyos horridus.* **A** Seedling. **B** Branch of adult plant. **C** Branch with flower buds. **D** Male flower. **E** Fruit. (Takhtajan 1981)

67. ***Raphidiocystis*** Hook.f

Raphidiocystis Hook.f. in Benth. & Hook., Gen. 1: 828 (1867); Keraudren & Jeffrey, Bull. Jard. Bot. Nat. Belg. 37: 319–328 (1967), rev.

Monoecious, perennial, herbaceous climbers to 6 m long. Leaves simple, blade ovate-cordate, margin entire or sinuate; tendrils simple; probract elliptic, hooded. Flowers in racemes, often male and female coaxillary or solitary; receptacle-tube short, obconic or cylindrical; sepals 5, triangular-lanceolate, in some species pinnately divided and convoluted, to 10 mm long and broad; corolla campanulate to urceolate; petals 5, entire, reflexed, yellow to orange; stamens 3, inserted in the lower half of the tube; filaments long; anthers all 2-thecous; thecae triplicate; pollen large (polar axis 56–73 μm, equatorial axis 44–70 μm), 3-colporate, reticulate (Keraudren 1968; Khunwasi 1998); ovary ellipsoid, densely bristly; ovules many, horizontal; style columnar; stigmas 3, lobed; staminodes 3. Fruits fleshy, ellipsoid to spherical, to 7 cm long, densely brown-setose, ripening reddish, dehiscing into 10 longitudinal valves and extruding the seeds in red pulp at the apex (Zimmermann 1922). Seeds many, broadly ovate, c. 5 mm long and 4 mm broad, compressed; testa smooth.

Five species, four throughout tropical Africa and one, *R. brachypoda* Baker, endemic in Madagascar; in lowland rainforest, often in clearings or along rivers.

68. ***Cephalopentandra*** Chiov.

Cephalopentandra Chiov., Fl. Somalia 1: 187 (1929).

Dioecious (rarely monoecious?), perennial, herbaceous climber to 2 m long, with tuberous, partly above-ground rootstock, to 20 cm in diam. Leaves simple, subsessile, semi-amplexicaul, crisp, the blade elliptic-cordate, (slightly) pinnately or palmately 5–7-lobed (often *Quercus*-like), to 9 cm long; tendrils simple. Flowers medium-sized; male flowers solitary or paired, female flowers solitary; receptacle-tube cylindrical to campanulate; sepals 5, triangular-lanceolate, 2–3 mm long; petals 5, partly connate, yellow or cream-colored with green veins; stamens 3, all 2-thecous; filaments distinct, inserted in the lower half of the tube; thecae triplicate; pollen large (polar axis 82–84 μm, equatorial axis 79–80 μm), 3-porate, (baculate?)/gemmate (Aloyshina 1971); ovary ellipsoid, smooth, hairy; ovules many, horizontal. Fruit ellipsoid, attenuate at the ends, baccate, smooth, to 8 cm long, 4 cm in diam., ripening red. Seeds many, compressed, pear-shaped; testa black, verrucous.

One species, *C. ecirrhosa* (Cogn.) C. Jeffrey, in Northeastern tropical Africa (Kenya, Uganda, Somalia, Ethiopia); deciduous *Acacia* woodland and bushland of lowland semi-deserts to 1,000 m.

69. ***Lemurosicyos*** Keraudren

Lemurosicyos Keraudren, Bull. Soc. Bot. France 110: 405 (1964).

Monoecious, annual, herbaceous climber or trailer, to 5 m long. Leaves simple, petiolate, palmately 3–5-lobed, the lobes lobulate-dentate to 7 cm long; tendrils simple. Male flowers in racemes, female flowers solitary or in pairs, often coaxillary with the male raceme; receptacle-tube campanulate; sepals 5, small; petals 5, 3–5 mm long, oblong-lanceolate, white; stamens 3, inserted in the lower half of the tube; filaments distinct; two anthers 2-thecous, one 1-thecous, coherent, forming a central globose head; thecae triplicate; pollen large (polar axis 65–70 μm, equatorial axis 52 μm), 3-colporate, reticulate (Keraudren 1968); ovary oblong, pubescent; placentae 3; ovules many, horizontal; style slender; stigmas 3; staminodes 3. Fruit a fleshy berry, oblong to pear-shaped, hairy, ripening scarlet. Seeds many (c. 25–30), oblong, c. 10 mm long and 5 mm broad, in yellow pulp; testa brown, with dentate margin. $n = 12$ (Keraudren 1968).

One species, *L. variegata* (Cogn.) Keraudren, endemic in Madagascar.

70. ***Solena*** Lour.

Solena Lour., Fl. Cochinch. 477, 514 (1790), nom. cons.; W.J.J.O. de Wilde & Duyfjes, Blumea 49: 69–81 (2004), rev.
Karivia Arn. (1840).
Melothria sect. *Solena* (Lour.) Cogn. (1881) p.p.

Monoecious or dioecious, perennial, herbaceous or ± woody climber or trailer, 2–6 m long, with tuberous roots. Leaves simple, shortly petiolate to sessile, the blade ovate or elliptic, very variable, base cordate or hastate, to 22 cm long; tendrils simple, glabrous; probract very small, linear or absent. Flowers small; male flowers in condensed racemes, female flowers solitary, sometimes coaxillary with male raceme; receptacle-tube campanulate; sepals 5, ± subulate, minute; petals 5, distinct, triangular, yellow or yellowish-white; stamens 3, inserted near the base of the tube; filaments distinct, long; two anthers 2-thecous, one 1-thecous; thecae straight, duplicate or triplicate; pollen medium-sized to large (polar axis c. 63 μm, equatorial axis c. 49 μm), 3-colporate, (perforate-)verrucate (*S. heterophylla* Lour., *S. umbellata* (Klein ex Willd.) W.J. de Wilde & Duyfjes) or reticulate (*S. amplexicaulis* (Lam.) Ghandi) (van der Ham, pers. comm.); disk 3–4-lobed, conspicuous, carnose; ovary oblong, glabrous or hairy; ovules few to several, horizontal; staminodes 3 (rarely 4). Fruit fleshy, oblong or ovoid, attenuate at both ends, glabrous or hairy, indehiscent, ripening yellow or red. Seeds few to 20, slightly compressed to ± globose; testa smooth, grayish-brown, sometimes with narrow, corky margin. n=12 or 24 in *S. amplexicaulis* (Beevy and Kuriachan 1996).

Three species in Afghanistan, India, Myanmar, Sri Lanka, Malesia, Vietnam, Cambodia, and China; in thickets, on roadside slopes; flowering and fruiting all year. Host of the fungus *Pseudocercospora solenae-heterophyllae* (R.K. Verma and Kamal) U. Braun (Kirschner and Piepenbring 2006).

71. ***Borneosicyos*** W.J. de Wilde

Borneosicyos W.J. de Wilde, Reinwardtia 11: 224 (1998).

Dioecious, perennial, herbaceous climber, to 12 m long and stems to 1 cm in diam., roots unknown. Leaves simple, petiolate, the blade ovate-oblong, entire; probract oblong, small; tendrils simple; receptacle-tube shallow. Flowers small; male flowers in racemes or panicles, female flowers solitary or in racemes coaxillary with a single female flower; sepals 5, triangular, minute; petals 5, elliptic, entire, distinct, pale yellow; stamens 3, inserted toward the base of the tube; filaments distinct, short; two anthers 2-thecous, one 1- or 1.5-thecous, distinct but appressed into a central head; thecae triplicate; pollen in tetrads, these c. 85 μm in diam., the monads medium-sized (polar axis c. 44 μm, equatorial axis c. 59 μm), 3-colporate, micro-reticulate-gemmate (van der Ham and van Heuven 2003); ovary cylindrical-oblong; ovules few, horizontal; style cylindrical 9–10 mm long; stigmas 3, heart-shaped, papillose; staminodes 4–5. Fruit solitary, oblong, 8–10 cm long and 4–4.5 cm in diam., glabrous, indehiscent, ripening red. Seeds few, subglobose, c. 10 by 8–9 by c. 4 mm; testa smooth, faintly winged.

One species, *B. simplex* W.J. de Wilde (and possibly another undescribed species; de Wilde et al. 2003), endemic in Borneo (Sarawak, Sabah); in tropical montane primary forest, 1,000–1,800 m a.s.l.; flowering Jul., Dec., fruiting Jul., Oct.

72. ***Benincasa*** Savi

Benincasa Savi, Biblioth. Ital. 9: 158 (1818).
Camolenga T. Post & O. Kuntze (1903 ('1904')).
Praecitrullus Pangalo (1944).

Monoecious, annual, herbaceous climber or trailer with hollow stems. Leaves simple, petiolate, reniform-ovate, 5–11-lobed or -angled, deeply cordate; tendrils 2-fid or 3–4(5)-fid. Flowers solitary, medium-sized; receptacle-tube broadly campanulate or flat, saucer-shaped, villous; sepals 5 (rarely 6), short, triangular; corolla rotate, flat, villous outside, smooth inside; petals 5 (rarely 6), connate at base, obovate, entire, (sulfur-)yellow; stamens 3, inserted at the base of the tube; filaments short, distinct; two anthers 2-thecous, one 1-thecous (rarely three 2-thecous); thecae triplicate; pollen large (polar axis 51–64 μm, equatorial axis 58–70 μm), 3-colporate, reticulate in *B. hispida* (Thunb.) Cogn., baculate in *B. fistulosa* (Khunwasi 1998); ovary globose to ovoid; placentae 3; ovules many, horizontal; style short, thick; stigmas 1–3, undulate; staminodes 3. Fruit baccate, indehiscent, oblong-terete, at first hispid, later glabrous, ripening light or dark green, in *B. hispida* covered with white wax. Seeds many, oblong, compressed; testa smooth, black or white, with thick margin. n = 12 (Beevy and Kuriachan 1996).

Two species: *Benincasa hispida*, native to New Caledonia, New Ireland, New Guinea, tropical NE Australia; along forest margins and in secondary scrub; cultivated throughout the tropics (Marr et al. 2007). A second species, *B. fistulosa* (= *Praecitrullus fistulosus*), in India and Pakistan is apparently known in cultivation only.

Nicolson and Fosberg (2004: 382–383) have documented that the name *Benincasa hispida* (Thunb.) Cogn. does not need to be replaced by *Cucurbita pruriens* Solander in ms because its basionym (*Cucurbita hispida*) was first validly published by Thunberg in July 1784.

73. ***Ctenolepis*** Hook.f. Fig. 30

Ctenolepis Hook.f., Gen. Pl. 1: 832 (1867).
Blastania Kotschy & Peyritsch (1867).
Zombitsia Keraudren (1963).

Monoecious or dioecious, perennial, herbaceous or woody climber or trailer. Leaves simple, petiolate, entire to palmately 3–5-lobed; probract stipuliform, fimbriate; tendrils simple, to 30 cm long. Flowers small, greenish or yellow; male flowers in pedunculate racemes, female flowers solitary or in groups of 4–6, often coaxillary with male raceme; receptacle-tube obconic or campanulate; sepals 5, narrowly triangular, to 3 mm long; corolla rotate; petals 5, ± 1 mm long, united at base, yellowish, reflexed or not; stamens 3, inserted in lower half or near mouth of the tube; filaments distinct; two anthers 2-thecous, one 1-thecous, distinct, exserted or all 2-thecous (*C. lucorum*); thecae short, straight or duplicate and coherent in the center of the flower (*C. lucorum*); pollen medium-sized (polar axis 45–52 μm, equatorial axis 45–53 μm), 3-colporate, (irregularly) reticulate (Khunwasi 1998); ovary ellipsoid, smooth; ovules few or many, horizontal; style cylindric; stigma 2- or 3-lobed. Fruit a berry, small or to 5 cm in diam., ± globose, smooth, ripening red. Seeds mostly 2 or many (*C. lucorum*), ovoid, plano-convex or compressed with distinct margin; testa smooth, cream-colored. $n = 12$ in *C. garcinii* (Burm. f.) C. B. Clarke (Beevy and Kuriachan 1996). Three species: *C. cerasiformis* (Stocks) Hook.f., widespread from tropical and subtropical Africa to India and Pakistan, *C. garcinii*, endemic in India and Sri Lanka; on lake shores and river margins, in wood- and grassland, mostly at low altitudes.

One species, *C. lucorum*, endemic in Madagascar; in lowland forest. Host of the fungus *Puccinia ctenolepidis* Ramachar and Bagyanar (Berndt 2007).

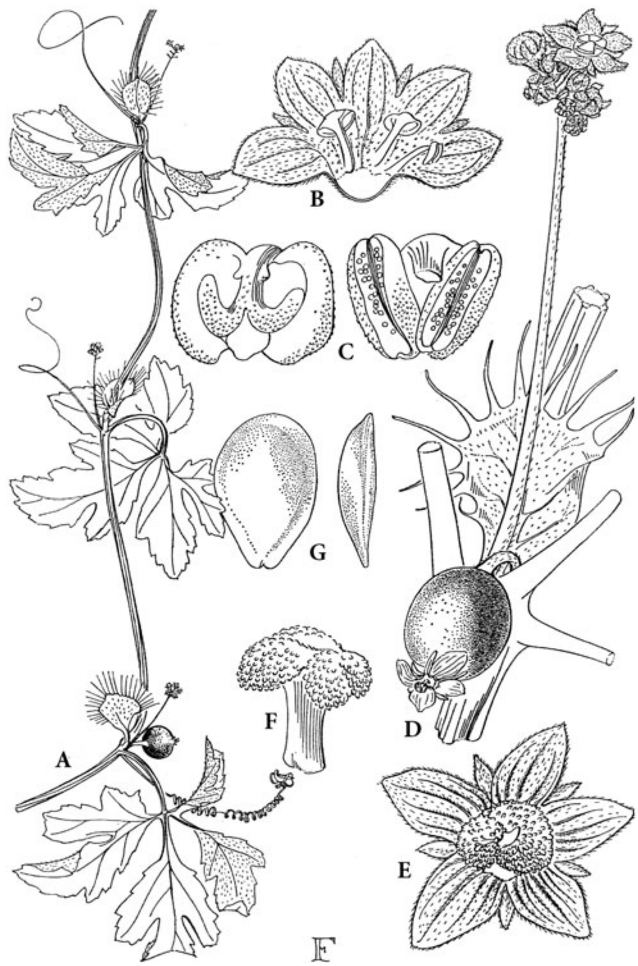

Fig. 30. Cucurbitaceae. *Ctenolepis cerasiformis*. **A** Habit. **B** Male flower. **C** Bithecate anther, ventral and dorsal view. **D** Flowering node with male inflorescence, young fruit, and stipuliform probract. **E** Female flower in plan. **F** Style with stigmas. **G** Seed, face and lateral views. (Jeffrey 1978b)

74. ***Dactyliandra*** (Hook.f.) Hook.f.

Dactyliandra (Hook.f.) Hook.f., Fl. Trop. Afr. 2: 557 (1871).

Monoecious or dioecious, perennial, herbaceous climbers or trailers. Leaves simple, petiolate, unlobed to palmately 5-lobed, with stipuliform bract at petiole base; tendrils simple. Flowers small, yellow; male flowers in pedunculate racemes, female flowers mostly solitary; receptacle-tube campanulate; sepals 5, triangular, small; corolla rotate; petals 5, distinct, ± 2 mm long; stamens 3, inserted near base of the tube; filaments distinct; two anthers 2-thecous, one 1-thecous, distinct; thecae duplicate; pollen large (polar axis 59–73 μm, equatorial axis 62–65 μm), 3-colporate, striate-reticulate (Khunwasi 1998); ovary ovoid; placentae 3; ovules many, horizontal; style 1; stigma 3-lobed; staminodes absent. Fruit a globose berry, ripening red. Seeds few, compressed, oblong to pear-shaped, ± angular; testa smooth, thick.

Two species: *D. welwitschii* Hook.f. in the Namib desert (Namibia, Angola) and the Thar desert (India and Pakistan), and *D. nigrescens* C. Jeffrey, endemic in Kenya; in dry bushland. Host of the fungus *Puccinia antennata* R. Berndt & A. Rössel (Berndt 2007).

75. ***Khmeriosicyos*** W.J. de Wilde & Duyfjes

Fig. 31

Khmeriosicyos W.J. de Wilde & Duyfjes, Blumea 49: 441 (2004).

Monoecious, herbaceous climber or trailer, possibly with tuberous root. Leaves simple, petiolate, the blade pentagonal, deeply 3(–5)-lobed, to 7 cm long; tendrils simple; probract conspicuous, 2–5 mm long, with several glands. Flowers small; male flowers in long-pedunculate racemes, female flowers solitary, often coaxillary with male raceme but flowering earlier; receptacle-tube shallow, cup-shaped, 5-ribbed; sepals 5, small, linear; petals 5, ovate-elliptic, 6–8 mm long; stamens 3, inserted halfway up the tube; filaments very short, distinct; two anthers 2-thecous, triplicate, one 1-thecous, distinct but appressed into a central head; pollen medium-sized (polar axis 52 μm, equatorial axis 51 μm), 3-colporate, reticulate (de Wilde et al. 2004). Fruit an ovoid, scabrous berry, c. 3 cm long and 2 cm in diam., pulpy. Seeds many, 8.5–9 mm long and 4.5–5 mm broad, strongly compressed; testa bright brown, finely grooved, with broad, grooved crenulate-tuberculate margin.

One species, *K. harmandii* W.J. de Wilde & Duyfjes, endemic in Northern Cambodia, known only from the type collection; in Dipterocarp forest.

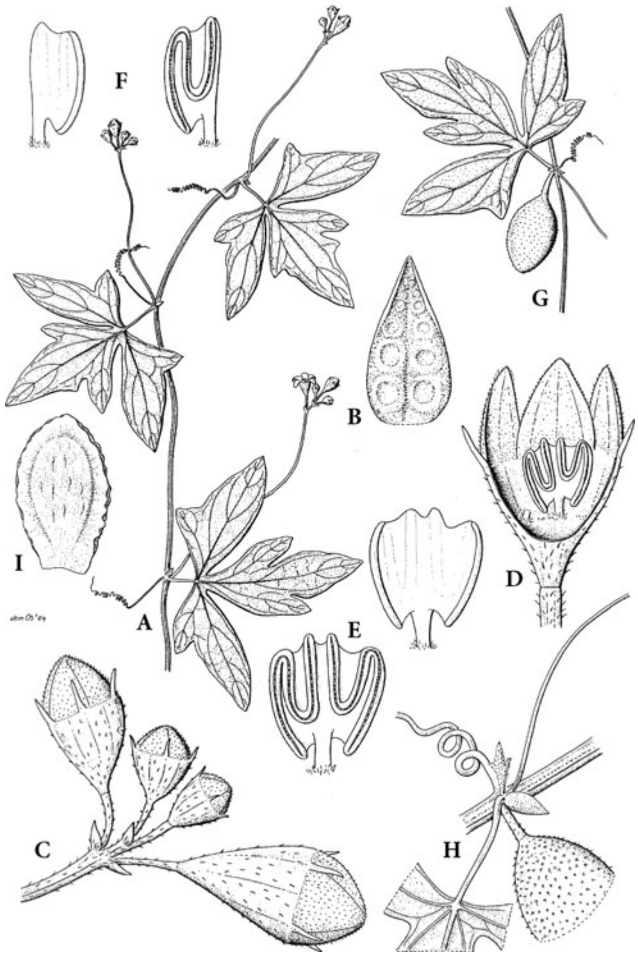

Fig. 31. Cucurbitaceae. *Khmeriosicyos harmandii*. **A** Branch with male inflorescences. **B** Glandular probract. **C** Tip of male inflorescence. **D** Opened male bud. **E** Bithecate stamen, ventral and dorsal view. **F** Monothecate stamen, dorsal and ventral view. **G** Node with fruit. **H** Ditto, enlarged, showing persistent probract. **I** Seed. (de Wilde et al. 2004; drawn by J. van Os)

76. ***Papuasicyos*** Duyfjes

Papuasicyos Duyfjes in Duyfjes, van der Ham & de Wilde, Blumea 48: 123–128 (2003).
Urceodiscus W.J. de Wilde & Duyfjes (2006).

Monoecious, annual to perennial, herbaceous climbers, to 6 m long. Leaves simple, petiolate, the blade entire or lobed, elliptic to hastate; tendrils simple. Flowers small to medium-sized, to 20 mm in diam.; male flowers in pedunculate racemes and solitary, female flowers solitary; often a single male or female flower coaxillary with a male raceme; receptacle-tube shallow, cup-shaped or urceolate to campanulate; corolla 10–15 mm in diam.; sepals 5, minute; petals 5, distinct, entire, cream-colored, yellow or orange, aestivation imbricate; stamens 3, distinct, inserted halfway up the tube; filaments long, slender, rarely short; anthers all 2-thecous, distinct but often appressed into a subglobose head; thecae straight, curved or sigmoid; pollen [*P. papuana* (Cogn.) Duyfjes, *P. belensis*] medium-sized (polar axis 31–38 μm, equatorial axis 32–38 μm), 3-colporate, striate-reticulate (Duyfjes et al. 2003; van der Ham and Pruesapan 2006); ovary subglobose or ellipsoid to fusiform; ovules many, horizontal; style 3-lobed, papillose-hairy or with forked and feather-like divided stigma-lobes; staminodes 3, inserted near the mouth of the tube. Fruit an edible, juicy berry, globose to ellipsoid-oblong, to 3 cm long and 1.5 cm in diam., glabrous, ripening scarlet to glossy red. Seeds many, tumid to globose, ovoid; testa cream-colored to pale brown, finely scrobiculate or foveolate, margin narrow or not distinct.

About eight species endemic in New Guinea; in (disturbed) montane *Nothofagus* forest, along forest margins, among tree ferns, in low scrub, in lowland swamp forest, and on river banks.

77. ***Trochomeria*** Hook.f.

Trochomeria Hook.f. in Benth. & Hook., Gen. 1: 822 (1867).
Heterosicyos Welw. ex Benth. & Hook. (1867).

Dioecious, perennial, herbaceous climbers or trailers to 2.5 m long or erect herb without tendrils, with tuberous (edible?) rootstock. Leaves simple, subsessile to petiolate, linear, elliptic, ovate-cordate, or sagittate, 3-lobed or palmately 3–5-lobed, often with ciliate stipuliform bract at petiole base; tendrils simple or absent. Flowers medium-sized, often on leafless stems, opening in the evening (Zimmermann 1922), exceptionally flowers bisexual (Jeffrey 1967: 89); male flowers in pedunculate clusters (rarely simple), female flowers solitary (rarely paired); receptacle-tube cylindrical, elongated; sepals 5, minute; corolla rotate; petals 5, ± distinct, often 10 mm long, triangular to linear, spreading, greenish or lemon-yellow sometimes with yellow papillae; stamens 3, inserted in the upper half of the tube; filaments distinct; two anthers 2-thecous, one 1-thecous, united into an oblong head; thecae triplicate; pollen large (polar axis 62–83 μm, equatorial axis 62–83 μm), 3-colporate, perforate or reticulate (Khunwasi 1998); ovary ovoid to subglobose, rostrate; ovules horizontal; stigma 3-lobed; staminodes 3. Fruit a fleshy, ellipsoid to subglobose, ± beaked, small to medium-sized berry, indehiscent, ripening scarlet. Seeds few, subglobose, ovoid or ellipsoid, tumid; testa smooth, hard, whitish (rarely pitted); germination hypogeal (Zimmermann 1922).

Eight species in tropical and subtropical Africa; in deciduous forest and ± dry bushland. Host of the fungus *Puccinia trochomeriae* Cooke (Berndt 2007).

78. ***Indomelothria*** W.J. de Wilde & Duyfjes

Indomelothria W.J. de Wilde & Duyfjes, Blumea 51: 5–9 (2006).

Monoecious, perennial, herbaceous climber, to 5 m long. Leaves simple, entire or shallowly lobed; probract absent; tendrils simple. Male flowers in pedunculate racemes; receptacle-tube campanulate to urceolate; sepals 5, minute, linear; corolla to 10 mm in diam.; petals 5, small, white (or yellow?), aestivation valvate; stamens 3, inserted in the upper half of the tube; filaments distinct, short, thick; two anthers 2-thecous, one 1-thecous; thecae straight (or slightly curved); pollen (*I. chlorocarpa* W.J. de Wilde & Duyfjes) medium-sized (polar axis c. 42 μm, equatorial axis c. 39 μm), 3-colporate, reticulate (van der Ham and Pruesapan 2006); disk free, ± 3-parted. Female flowers solitary, often coaxillary with male raceme; ovary narrowly ellipsoid; stigma 3-lobed, long-hairy; staminodes 0; disk annular, slightly 3-lobed. Fruit solitary, narrowly ellipsoid to fusiform, to 7 cm long on short pedicel, glabrous, smooth, ripening green. Seeds many, in pulp, compressed, ovate-elliptic, with dense appressed hairs, no distinct margin.

Two species in Southeast Asia (Myanmar, Thailand, Malesia (Sumatra, Borneo, Java)); forest margins, marshland, disturbed ground.

79. ***Melothria*** L.

Melothria L., Sp. Pl.: 35 (1753).
Diclidostigma Kunze (1844).
Landersia Macfadyen (1850).
Melancium Naudin (1862).
Cucumeropsis Naudin (1866).
Posadaea Cogn. (1890).

Monoecious, annual or perennial, herbaceous climbers or trailers to 10 m long, often with perennial rootstock. Leaves simple, petiolate, entire or palmately lobed, often with unpleasant odor; tendrils simple, rarely 2-fid, solitary, rarely 2 per node; probract absent. Flowers small; male flowers in pedunculate racemes or umbels, female flowers solitary (rarely in groups of 2–3), usually coaxillary with male; receptacle-tube campanulate to cylindrical; sepals 5, short, dentiform; corolla rotate; petals 5, entire, connate at the base, yellow, less often white (*M. dulcis* Wunderlin, *M. warmingii* Cogn.); stamens 3, inserted in the upper half of the tube; filaments distinct, short, slender; two anthers 2-thecous, one 1-thecous (rarely all 2-thecous); thecae ± straight, fringed with hairs; pollen medium-sized to large (polar axis 36–67 μm, equatorial axis 36–69 μm), 3-colporate, (micro)reticulate (Khunwasi 1998); disk globose or depressed, entire or 3-lobed; ovary smooth, ovoid to fusiform; style short, surrounded at base by an annular disk; placentae 3; ovules many, horizontal; stigmas 3, 2-lobed or 1, 3-lobed; staminodes 3 or absent. Fruit a small or up to 20 cm long berry, on long pedicel, fleshy, indehiscent, smooth, globose or ellipsoid, ripening cream with green stripes, yellow, orange, reddish or purple-blackish, edible. Seeds many, compressed, ovoid, with or without arilloid; testa smooth, ivory-colored, covered by long appressed hairs, no distinct margin. $n=12$ in *M. sphaerocarpa* (= *Cucumeropsis mannii*) (Osuji et al. 2006).

Melothria has about 12 species in tropical Central and South America, one species, *M. mannii*, in West tropical Africa and in Central and tropical South America, one species, *M. pendula* L., naturalized in Asia; roadsides and cultivated ground, arid plains, clearings, forest margins, grass- or woodlands. Host of the fungus *Uromyces novissimus* Speg. (Monoson and Rogers 1978).

Molecular data from plastid and nuclear loci indicate that *Melancium*, *Cucumeropsis*, and *Posadaea* are nested inside *Melothria*, and that there is next to no genetic difference between South American and African individuals (Schaefer and Renner 2010b).

80. *Ruthalicia* C. Jeffrey

Ruthalicia C. Jeffrey, Kew Bull. 15: 360 (1962).

Dioecious, perennial, herbaceous climber. Leaves simple, petiolate, the blade broadly ovate, pedately 3–7-lobed; tendrils simple. Flowers large, showy; male flowers in racemes, female flowers axillary, solitary or in pairs or few-flowered fascicles; receptacle-tube funnel-shaped, apically broadened; sepals 5, triangular; corolla rotate; petals 5, distinct or connate at the base, to 1.5 cm long, yellow; stamens 3, inserted near the mouth of the tube; filaments distinct. 2 anthers 2-thecous, one 1-thecous; thecae triplicate; pollen large (polar axis 52–80 μm, equatorial axis 53–78 μm), 3-colporate, reticulate (Khunwasi 1998); ovary ellipsoid; style fleshy, c. 8 mm long; ovules many, horizontal; stigmas 3; staminodes 3. Fruit globular to ellipsoid, to 4 cm long and 2.5 cm in diam., smooth, ripening red. Seeds many, in yellowish pulp, compressed, ellipsoid to oblong; testa slightly sculptured, with broad, flattened margin; germination epigeal (Zimmermann 1922).

Two species in tropical West Africa; along forest margins, in secondary forest and bushland.

81. *Muellerargia* Cogn.

Muellerargia Cogn., Monogr. Phan. 3: 630 (1881).

Monoecious, perennial?, herbaceous climber or trailer, to 2 m long. Leaves simple, petiolate; blade entire, ovate, triangular, or 3–5-lobed; tendrils simple; probract reniform or suborbicular. Male flowers in (umbellate) racemes, female flowers solitary, coaxillary with the male raceme; receptacle-tube campanulate, 2.5 mm long; sepals 5, triangular, small; corolla rotate; petals 5, (ob) ovate, 0.7 mm long; stamens 3, inserted near base or halfway up the tube; filaments very short to absent; two anthers 2-thecous, one 1-thecous; thecae straight and apically hooked; pollen (*M. jeffreyana* Keraudr.) medium-sized (polar axis 50 μm, equatorial axis 46–48 μm), 3-colporate, finely reticulate (Keraudren 1968); ovary ovoid or ellipsoid, setose; placentae 2–3; ovules many, horizontal; style short; stigmas ± 2-lobed, forming a central globular body; staminodes 3 or 0. Fruit fleshy, ovoid, to 2.5 cm long and 1–2 cm in diam., ± rostrate, ornamented with long, soft bristles, indehiscent or dehiscing through ruptured attachment of pedicel. Seeds many, oblong, compressed, 8–10 mm long; testa smooth or finely pitted, pale whitish, margin slightly thickened.

Two species, one endemic in Madagascar, and one collected a few times in tropical northern Australia and Timor, and the Lesser Sunda islands (Telford 1989); in forest remnants; highly endangered; flowering Feb. to May.

This ancient clade, with a highly disjunct range and just two surviving species, is the sister group to *Cucumis* (Renner and Schaefer 2008).

82. *Cucumis* L.

Cucumis L., Sp. Pl.: 1011 (1753); H. Schaefer, Blumea 52: 165–177 (2007).
Melo Mill. (1754).
Mukia Arn. (1840).
Oreosyce Hook. (1871).
Dicoelospermum C.B. Clarke (1879). ('*Dicaelospermum*', correction T. Post and O. Kuntze (1903 ('1904')).
Hymenosicyos Chiov. (1911).
Cucumella Chiov. (1929).
Myrmecosicyos C. Jeffrey (1962).

Monoecious or dioecious, annual or perennial, small to medium-sized, herbaceous or woody climbers or trailers, with fibrous roots or perennial rootstock (rarely tubers). Leaves simple, petiolate, the blade unlobed or palmately lobed; tendrils solitary or rarely in groups of 5–8, simple, rarely absent (exceptionally 2-fid). Male flowers solitary or in few-flowered groups, female flowers solitary or in fascicles of 2–6, usually separate from male flowers; flowers small to medium-sized; receptacle-tube funnel-shaped to campanulate or shallowly saucer-shaped; sepals 5 (rarely 4), small, long-triangular to filiform; petals 5, elliptic or (ob)ovate, distinct or united at base, yellow; stamens 3, inserted halfway up the tube; filaments short, glabrous; two anthers 2-thecous, one 1-thecous; thecae lateral, straight (sometimes apically hooked) or triplicate, rarely horizontal, arcuate and slightly coherent [*C. messorius* (C. Jeffr.) Ghebret. & Thulin], glabrous or fringed with minute hairs; pollen medium-sized to large (polar axis 22–61 μm, equatorial axis 49–80 μm), 3-(col) porate, (micro)reticulate-perforate (Khunwasi 1998); disk obconic or depressed globose, basal, free from the tube, rarely indistinct; ovary hairy, globose to oblong; ovules several to many, horizontal; style terete, thick, glabrous; stigma entire, sublobate or 3-lobed, the lobes carnose, papillose, often with 1–9 finger-like projections on the margin; staminodes 3 or 0. Fruit solitary or clusters of 2–6, fleshy, (sub)globose or ellipsoid, cylindrical, (ob)ovoid, or spindle-shaped, smooth and glabrous or pubescent or with dense to scattered fleshy spines, pustules or tubercles, sometimes beaked or fusiform, ripening yellow, orange, red or greenish to brownish, often with longitudinal pale stripes (rarely maturing underground), indehiscent (rarely expelling seeds explosively). Seeds few to many, ovate or elliptic, small to medium-sized, globose or lenticular compressed; testa light-colored, smooth or ornamented, glabrous or rarely puberulent, margin often distinct, usually not winged; germination epigeal. $n = 7$ or 12, with polyploids and aneuploids also reported (Beevy and Kuriachan 1996).

About 55 species in Africa, Asia and Australia; in semi-deserts and savannas, dry bushland and along forest margins, often on disturbed or cultivated ground. Host of the fungus *Puccinia cucumeris* Henn. (Berndt 2007).

Cucumis melo L. and *C. sativus* L. are among the World's most important vegetable crops, and there are three fully sequenced *C. sativus* genomes, namely, that of a Chinese fresh market cucumber (Huang et al. 2009), a North American pickling type, and an isogenic gynoecious breeding line, making the cucumber the sixth flowering plant to have been completely sequenced. The genus has also been the study system for one of the first biosystematic studies ever, that of Charles Naudin (1859), who over many years performed controlled crossings among species he had in cultivation in Paris. Molecular data have revealed that the former genus *Mukia* (de Wilde and Duyfjes 2007c) comprised a mix of species not closely related to each other (P. Sebastian, H. Schaefer, I. Telford, and S. S. Renner, unpubl. data).

83. *Zehneria* Endl.

Zehneria Endl., Prodr. Fl. Norfolk.: 69 (1833).
Pilogyne Eckl. ex Schrad. (1835).
Anangia W.J. de Wilde & Duyfjes, Reinwardtia 12(3): 219 (2006).
Neoachmandra W.J. de Wilde & Duyfjes, Blumea 51(1): 12 (2-3, 13; figs. 1c,2c) (2006).

Dioecious or monoecious, annual or perennial, herbaceous climbers or trailers, to 10 m long, some with tuberous roots. Leaves simple, petiolate, triangular to ± ovate, entire to 3–5-lobed, rarely 5-foliolate; tendrils simple; probract linear, minute, caducous or absent. Flowers small (rarely medium-sized), mostly unisexual but in one species bisexual (*Z. hermaphrodita* W.J. de Wilde & Duyfjes); male flowers solitary or 2–8 per node or in pedunculate, crowded racemes, female flowers solitary or in small groups. In monoecious species, female flowers coaxillary with male raceme or mixed racemes with flowers of both sexes; sepals 5, minute, triangular to narrowly elliptic, rarely much longer than the petals (*Z. macrosepala*); petals 5, distinct, white or cream-colored (rarely yellow?); stamens 3 or 5 (rarely 2), inserted near the base or in the upper half of the tube; filaments distinct, long and slender or short; anthers all 1-thecous or 2-thecous; thecae lateral, straight or curved to sinuate, often fringed with hairs; pollen medium-sized to large (polar axis 28–73 µm, equatorial axis 29–73 µm), 3-colporate, (micro)reticulate (rarely micro-reticulate-perforate) (Khunwasi 1998; van der Ham and Pruesapan 2006); disk globose, entire or 3-lobed; ovary globose to ellipsoid; stigma 3-lobed or style 3-parted with 2-lobed stigmas, ± hairy; staminodes 3 or 0. Fruit a pulpy berry, solitary or in fascicles on short pedicel, globose to ellipsoid or fusiform, with pitted pericarp, to 7 cm long, ripening green, white, pale yellowish, orange, red or blackish. Seeds few to many, compressed (rarely globose), ovate to elliptic; testa pale, smooth, glabrous or sometimes hairy (at the ends or throughout), margin narrow or indistinct; germination epigeal (Zimmermann 1922). $2n = 48$ in *Z. maysorensis* Arn. (Beevy and Kuriachan 1996).

About 60 species in tropical and subtropical Africa, five endemic in Madagascar, the rest from India and China to Northern Australia and the Pacific Islands; on disturbed ground, along forest margins, and in clearings, scrubland, grassland, on riverbanks, and in mangroves. Host of the fungi *Puccinia arisanensis* Hirats.f. and Hashioka, *P. melothriicola* (*Uredo melothriae* (Henn.) R. Berndt), *P. hieroglyphica*, *P. rhytidioderma* R. Berndt (*Uromyces zehneriae*), and *Uromyces cantonensis* (Berndt 2007).

Molecular data show that the type species of the recently described genera *Anangia* and *Neoachmandra* are nested within *Zehneria* (Schaefer et al. 2009). *Zehneria peneyana* (Naudin) Schweinf. & Asch. (*Pilogyne peneyana* Naudin) with 6-porate or 6-brevicolporate pollen (Keraudren 1968), which has not yet been sequenced for any locus, may represent a separate lineage. The generic name *Pilogyne* (type species *Pilogyne suavis* Schrad. from South Africa) has recently been taken up for about 20 species until now placed in *Zehneria* (de Wilde and Duyfjes 2009).

84. ***Diplocyclos*** (Endl.) T. Post & O. Kuntze

Diplocyclos (Endl.) T. Post & O. Kuntze, Lex.: 178 (‘*Diplocyclus*’). (1903 (‘1904’)).
Ilocania Merr. (1918).

Monoecious, herbaceous climbers, to 6 m long. Leaves simple, petiolate, broadly ovate, palmately 5-lobed; tendrils 2-fid; probract c. 3 mm long, with nectaries. Flowers small, fasciculate, often male and female together in the axils; receptacle-tube broadly campanulate; sepals 5, triangular-dentiform, to 2 mm long; corolla broadly campanulate; petals 5, ovate, white to greenish-yellow; stamens 3, inserted near the mouth of the tube; filaments distinct, short; two anthers 2-thecous, one 1-thecous; thecae triplicate; pollen large (polar axis 57–107 µm, equatorial axis 63–104 µm), 3-(col)porate, echinate and reticuloid (Khunwasi 1998); ovary globose or ovate; placentae 3; ovules few, horizontal; style slender; stigmas 3, 2-lobed; staminodes 3. Fruit solitary or in clusters of 2–5, baccate, globose or ovoid, ripening bright red with silvery white stripes or marks. Seeds to 6 mm long; testa slightly scorbiculate, strongly winged; germination epigeal (Zimmermann 1922). $n = 12$ in *D. palmatus* (L.) C. Jeffrey (Beevy and Kuriachan 1996).

Four species in tropical and subtropical Africa, Asia, Australia; rainforest clearings and margins, secondary growth.

85. ***Coccinia*** Wight & Arn.

Coccinia Wight & Arn., Prodr. Fl. Ind. Orient. 1: 347–348 (1834).
Cephalandra Eckl. & Zeyh. (1836).
Physedra Hook.f. (1867).
Staphylosyce Hook.f. (1867).

Dioecious, perennial, herbaceous to woody climbers or trailers to 10 m long, with tuberous roots reaching up to 10 kg. Leaves simple, blade angled, cordate, or deeply lobed; tendrils simple or 2-fid; probracts and bracts variable, often with nectaries. Flowers with petals 1.4–5.5 cm long; male flowers solitary, clustered or in racemes, female flowers solitary or in racemes; receptacle-tube short, campanulate or turbinate; sepals 5, entire, usually small and dentiform; corolla short-tubulate, to 8 cm in diam.; petals 5, connate, white, salmon, yellow or orange; stamens 3, inserted at the base of the tube; filaments connate apically or completely into a central column, rarely distinct; anthers all 2-thecous, less often two 2-thecous, one 1-thecous and forming a central head; thecae triplicate; pollen large (polar axis 58–92 μm, equatorial axis 35–92 μm), 3-colporate, reticulate (Khunwasi 1998); ovary ovoid, oblong or linear, smooth; placentae 3; ovules many, horizontal; style filiform; stigmas 3, 2-lobed; staminodes 3, oblong or subulate. Fruit fleshy, small and globose, ovoid, or cylindrical and up to 30 cm long, baccate, indehiscent, ripening orange to red, sometimes with green and white spots. Seeds many, ovate to pear-shaped, compressed; testa fibrillose, marginate; germination epigeal (Zimmermann 1922). $2n = 22 + XY$ sex chromosomes in *Coccinia grandis* (L.) Voigt (Bhaduri and Bose 1947; Bhar and Datta 1982).

About 30 species in tropical and subtropical Africa, one species, *C. grandis* (L.) Voigt, also in Asia and naturalized on the American and Australian continents; in rainforest, cloud forest, deciduous bushland, riverine forests, and semi-desert shrubland/bushland, rarely on sand dunes. Host of several fungi, including *Puccinia windhoekensis* Mennicken, Maier & Oberw., *P. cucumeris* Henn., *P. physedrae* Syd., *P. cephalandrea* Thümen, and *P. cephalandrae-indicae* Syd. & P. Syd. (Berndt 2007).

The tubers, leaves, and fruits of several species are edible, but *C. trilobata* fruits appear to be poisonous. Male individuals of *C. grandis* have a pair of different-sized chromosomes, interpreted as an X- and a Y-chromosome (Bhaduri and Bose 1947; N. Holstein and S. Renner, pers. obs.).

86. *Scopellaria* W.J. de Wilde & Duyfjes

Scopellaria W.J. de Wilde & Duyfjes, Blumea 51: 297 (2006).
Scopella W.J. de Wilde & Duyfjes (2006).

Monoecious, annual, biennial or perennial, herbaceous climbers or trailers, to 6 m long. Leaves simple, ovate, angular, or 3–5-lobed; tendrils simple, hairy throughout their length; probract absent. Flowers small to medium-sized, to 10 mm in diam.; sepals 5, minute, linear; petals 5, distinct, ovate-elliptic, yellow, aestivation imbricate; receptacle-tube campanulate; male flowers in short, pedunculate, crowded racemes, female flowers solitary (or pairs), coaxillary with male racemes; stamens 3, inserted near the mouth of the tube; filaments distinct, long, slender; anthers all 2-thecous; thecae lateral, straight; pollen [*S. marginata* (Blume) W.J. de Wilde & Duyfjes] medium-sized (polar axis c. 40 μm, equatorial axis c. 47 μm), 3-(brevi)colporate, irregularly striate-reticulate (van der Ham and Pruesapan 2006); disk free, globose; ovary globose to ellipsoid; stigma 3-lobed, hairy; staminodes 3; disk annular, free. Fruit a smooth berry, solitary (or in pairs) on ± long pedicel, juicy or pulpy, globose or ellipsoid to fusiform, to 3 cm long, ripening red. Seeds 1–40, to 6 mm long, compressed, ovate-elliptic; testa scorbiculate, pale, with distinct margin.

Two species from Southern China to Indonesia and the Philippines; in thickets, along forest margins and roadsides.

XV. Tribe Cucurbiteae Dumort. (1827).

Tendrils simple or 2–7-fid. Stamens (2)3(4). Fruits small, dry, indehiscent, or medium-sized to large pepos, or dry and splitting into several valves. Seeds one to many, unwinged, less often narrowly winged.

87. *Polyclathra* Bertol.

Polyclathra Bertol., Novi Comment. Acad. Sci. Inst. Bononiensis 4: 438 (1840); Jeffrey, Kew Bull. 25: 196–198 (1971).
Pentaclathra Endl. (1842).
Pittiera Cogn. (1891 ('1892')).
Roseanthus Cogn. (1896).

Monoecious, annual, herbaceous climbers or trailers, to several meters long. Leaves cordate, entire or ± 3–5-lobed; tendrils (2–)4(–6)-fid, to 20 cm long, with stout peduncle and (not only apically) adhesive pads. Flowers large, showy, solitary, axillary, the male on very long, the female on short stalks, opening at night; receptacle-tube campanulate to obconic-cylindric, much shorter in the female than in the male flowers; sepals triangular, narrower in the female flowers then in the male; petals white, broadly rounded; stamens inserted halfway up the tube; filaments long, distinct; two anthers 2-thecous, one 1-thecous, connate into a central head; thecae triplicate; pollen very large (polar axis 176–180 μm, equatorial axis 176–180 μm), pantoporate, echinate (Khunwasi 1998); ovary ellipsoid; ovules many, horizontal; style slender, elongated; stigmas 3, deeply 2-lobed. Fruit a dry berry, medium-sized, ellipsoid to oblong, rounded at the apex, green with white or yellow marks, the pericarp splitting into several irregular segments at maturity, exposing the seeds. Seeds many, broadly ovate, contracted at base, compressed; testa brown, narrowly winged.

Fide Kearns (1992), six species in Mexico, Costa Rica, Guatemala, Panama, and Nicaragua but only one formally described; in tropical or oak-pine forests; flowering and fruiting I–IV. Host of the fungus *Uromyces novissimus* Speg. (Monoson and Rogers 1978).

88. *Peponopsis* Naudin

Peponopsis Naudin, Ann. Sci. Nat., Bot. IV, 12: 88 (1859); Jeffrey, Kew Bull. 25: 194–196 (1971).

Dioecious, perennial, ± woody climber, 8–10 m long. Leaves broadly ovate-cordate, unlobed to 3–5-lobed, 10–18 cm long, usually with a few disk glands near the leaf base; tendrils multifid, densely short-villous, with apical adhesive pads. Flowers medium-sized, solitary, axillary; receptacle-tube obconic-tubular, apically expanded; sepals of male flowers ovate-lanceolate and to 2 cm long, of female flowers triangular-lanceolate, acute, 6–7 mm long; corolla broadly campanulate; petals connate halfway, broadly obovate-oblong, rounded, to 4 cm long, white to greenish-white; stamens inserted near the base of the tube; filaments distinct, 5 mm long; two anthers 2-thecous, one 1-thecous; thecae much convoluted; pollen large (polar axis and equatorial diameter 78–82 μm), 3-porate, echinate (R. van der Ham, pers. comm., 9 Dec. 2009); ovary ovoid, ± glabrous; placentae 3; ovules many, horizontal; style 12–14 mm long; stigmas 3, papillose, oblong to ovate-oblong; staminodes 3–4. Fruit a fleshy, subglobose pepo, 8–10 cm in diam., splitting into three carpellar segments at maturity, exposing the seeds. Seeds many (c. 200 per fruit), ovate-oblong, 4–9 by 2–5 mm, compressed; testa greenish to gray, finely perforate, margin narrowly winged.

One species, *P. adhaerens* Naudin, endemic in Mexico (Querétaro, Hidalgo, Puebla, and Veracruz); extremely rare, in pine forest 800–1,500 m a.s.l.; flowering and fruiting Jun.–Oct.

Molecular data indicate that this is the sister species to *Cucurbita* (Schaefer et al. 2009).

89. *Cucurbita* L.

Cucurbita L., Sp. Pl.: 1010 (1753), nom. cons.
Melopepo Mill. (1754).
Pepo Mill. (1754).
Ozodycus Raf. (1832).
Sphenantha Schrad. (1838).
Mellonia Gasp. (1847).

Monoecious, annual or perennial, herbaceous climbers or trailers to 6 m long, with hollow stems and fibrous or fleshy roots. Leaves ovate-cordate to suborbicular, pedately 3–5(–7)-lobed, sometimes with a nasty odor; tendrils 2- to 7-fid, rarely simple (absent in some cultivars). Flowers large, solitary in axils, some fragrant; male flowers with campanulate or elongated receptacle-tube; sepals lanceolate or foliaceous at the apex; corolla campanulate; petals ± connate, yellow; stamens inserted at the base of the tube; filaments usually distinct, short and fleshy; two anthers 2-thecous, one 1-thecous, connate into a central head; thecae reflexed; pollen very large (124–154 μm in diam.), pantoporate, echinate (Khunwasi 1998); ovary oblong, globose, cylindric or pear-shaped, constricted at apex; placentae 3–5; ovules many, horizontal; stylodia short, thick, united into a column; stigmas usually 3, 2-fid; staminodes 3, short-triangular. Fruit a large, fleshy, indehiscent pepo of variable form and color, with woody or corky peduncle, smooth or ribbed, interior tissue soft, fibrous, white, yellow or orange, sweet or bitter. Seeds many, ovate to elliptic, strongly compressed; testa smooth, cream-colored or black, with or without distinct margin. $n = 20$ in *C. maxima*, *C. digitata* A. Gray, *C. foetidissima* H.B. & K., and *C. palmata* S. Wats. (McKay 1931; Beevy and Kuriachan 1996).

About 15 wild species in tropical and subtropical America (Sanjur et al. 2002; M. Nee, pers. comm., Feb. 2010) and five domesticated ones cultivated worldwide. Whether the domesticated species should continue to be ranked as species or as forms of their wild progenitors is a matter of opinion. Disturbed places, humid ravines, floodplains, tropical deciduous forest, grasslands, deserts, rocky hillsides, oak- and pine-oak forests.

Subfossil records of *Cucurbita pepo* L. and *C. moschata* Duchesne ex Poir. from Central

America and the northern Andes indicate that squashes are among the oldest neotropical domesticated plants (Smith 1997; Piperno and Stothert 2003; Dillehay et al. 2007).

90. *Calycophysum* Triana

Calycophysum Triana, Nuev. Jen. Esp. 20 (1854 [1855]). [as "*Calycophisum*"]; Pittier, H. Contr. US. Natl. Herb. 20: 487–490 (1922); Jeffrey, Kew Bull. 25: 192–194 (1971).
Edmondia Cogn. (1881) (non Cassini 1818), nom. illegit.
Bisedmondia J. Hutch. (1967).

Monoecious, herbaceous (or woody) climber, root not tuberous, to 10 m long. Leaves ovate-cordate, entire or palmately 3–5–7-lobed; tendrils 3–6-fid, with apical, adhesive pads. Flowers bat-pollinated, large, solitary in the axils; peduncle of male flowers to 30 cm long, to 15 cm in female; receptacle-tube campanulate to urceolate, ± inflated; sepals large, ovate-lanceolate; corolla rotate to tubular-campanulate; petals white or yellowish-green; stamens inserted in the upper half of the tube; filaments distinct; anthers ± distinct, two 2-thecous, one 1-thecous; thecae duplicate; pollen (very) large (polar axis 90–168 μm, equatorial axis 91–169 μm), 3-porate, echinate (Khunwasi 1998); ovary ellipsoid; placentae 3; ovules horizontal, numerous; staminodes 3; stylodia fleshy; stigmas 3. Fruit a smooth, elliptic pepo, green with darker green stripes, ripening yellow to orange. Seeds many, compressed, irregularly elliptical, with arilloid; testa dark brown, irregularly structured.

Five species from Venezuela, Colombia, Ecuador, Peru, Bolivia; in Andean cloud forests and lowland rainforest.

91. *Sicana* Naudin

Sicana Naudin, Ann. Sci. Nat., Bot. IV, 18: 180 (1862).

Monoecious, annual or perennial, herbaceous climber, to 15 m long. Leaves ovate to sub-orbiculate, palmately 3–9-lobed, often with diskoidal glands at the leaf base, to 24 cm long; tendrils 3–5-fid, with apical adhesive pads. Flowers solitary, medium-sized to large, showy; receptacle-tube obconical or campanulate; sepals triangular-lanceolate, reflexed or less often ascendent; corolla campanulate, divided in the upper ¼; petals yellow; stamens inserted close to the mouth of the tube; filaments short, distinct or ± connate; two anthers 2-thecous, one 1-thecous; thecae duplicate; pollen large (polar and equatorial axes 79–98(120?) μm), (3?)6–8-pantoporate, echinate (Marticorena 1963; Ayala-Nieto et al. 1988); ovary elliptical; placentae 3; ovules many, horizontal; style short; stigmas 3; staminodes 0, 3 or 5. Fruit a globose, ellipsoid or cylindrical pepo, smooth, to 60 cm long. Seeds many, compressed, ovate, with distinct margin, sometimes narrowly winged. $n = 20$ in *S. odorifera* (Vell.) Naudin (Mercado and Lira Saade 1994).

About four species in the Caribbean Islands and Central America (Lira Saade 1991); in rainforest and secondary scrub; one species, *S. odorifera* Naudin, widely cultivated as a vegetable.

Sicana sphaerica Hook.f. may belong in a different genus (C. Jeffrey, pers. comm., 2008).

92. *Penelopeia* Urb.

Penelopeia Urb., Repert. Spec. Nov. Regni Veg. 17: 8 (1921).
Anacaona A. H. Liogier (1980).

Monoecious or dioecious, perennial, herbaceous to woody climber, to 10 m long. Leaves triangular, pedately 3–5-lobed; tendrils simple or 2–3-fid. Flowers small to medium-sized. Male flowers solitary or in axillary fascicles, female flowers solitary; receptacle-tube shortly cup-shaped to campanulate; sepals triangular, 4–10 mm long, connate in the lower half or distinct; corolla ± cylindrical; petals 5 (rarely 4), connate in lower half or distinct, yellow or pale green; filaments connate into a central column; anthers connate into a central head; thecae triplicate; pollen large (polar axis and equatorial diameter 65–75 μm in *P. sphaerica*), 3(4)-porate, echinate (R. van der Ham, pers. comm., 9 Dec. 2009); ovary ovoid; stigmas 3; placentae 3; ovules many, horizontal. Fruit globose, smooth, 5–7 cm in diam., indehiscent, ripening yellowish. Seeds many, elliptical.

Two species endemic in Hispaniola; in humid montane forest.

Molecular data (Kocyan et al. 2007) show that the two species are each others' closest relative, arguing for placing them in a single genus, rather than two genera, since this creates a more informative classification.

93. *Tecunumania* Standl. & Steyerm.

Tecunumania Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. 23(2): 96–97 (1944).

Dioecious, herbaceous climber. Leaves ovate-cordate and palmately 3–7-lobed, to 17×16 cm, often with tuft of hair and patelliform glands at leaf base; tendrils 2-(4-)fid. Flowers large, solitary; receptacle-tube campanulate; sepals linear, to 2 cm long; corolla rotate; petals obovate, connate at base, yellow; stamens inserted near the base of the tube; filaments distinct but closely appressed; anthers 2-thecous, connate into a globose head; thecae triplicate; pollen large (polar axis c. 97 μm, equatorial axis c. 102 μm), 3-porate, echinate (Khunwasi 1998); ovules many, horizontal; style elongated; stigmas 3, 2-lobed; staminodes 3. Fruit fleshy, subglobose, 7–8 cm long, indehiscent, ripening dark green. Seeds many, 6–7 mm long and 4–5 mm broad, compressed; testa pale yellowish-brown, densely appressed hairy, no distinct margin.

One species, *T. quetzalteca* Standl. & Steyerm., in Costa Rica, Mexico, Guatemala; in wet montane forest.

Molecular data do not yet firmly resolve the placement of the genus relative to *Schizocarpum*.

94. *Schizocarpum* Schrad.

Schizocarpum Schrad., Index Sem. Gött. 1830: 4 (1830); Jeffrey, Kew Bull. 25: 198–200 (1971).

Monoecious, annual or perennial, herbaceous climbers, to 7 m long. Leaves entire or 3–5-lobed; tendrils 2-fid. Flowers solitary, large, showy; receptacle-tube elongated, subcylindric at base, expanded distally; sepals reflexed or ascending, linear, ovate or triangular; corolla campanulate; petals connate in the lower half, triangular, yellow with dark central spot inside; stamens (2–)3(–4), inserted near the mouth of the tube; filaments distinct; anthers connate into a central ovoid head; thecae triplicate; pollen very large (polar axis 119–125 μm, equatorial axis 119–125 μm), pantoporate, echinate (Khunwasi 1998); ovary ovoid to fusiform, often rostrate; placentae 3; ovules 12 to many, ascending; style slender; stigmas 3, fleshy; staminodes 3. Fruit a dry, ± woody capsule, ellipsoid to pear-shaped, smooth, rostrate, indehiscent or dehiscing into three lobes from the apex downward, each with two rows of seed chambers, followed by the abscission of the pericarp. Seeds ovoid, compressed, 8–10 mm long; testa smooth, brown or banded crosswise with light and dark stripes, margin with or without wing.

Eleven species in Mexico and Guatemala; in oak or pine forest, tropical deciduous forest, disturbed ground, coastal plains; flowering and fruiting Jun.–Nov.

95. *Cionosicys* Griseb.

Cionosicys Griseb. Fl. Brit. W. I.: 288 (1860); *Cionosicyos* [orth. var.] Hook.f. (1867); Jeffrey, *Cionosicyos*, Kew Bull. 25: 200–201 (1971).

Monoecious, perennial herbaceous or woody climber, to several meters long. Leaves large, coriaceous, ovate to roundish, entire or 3-lobed; tendrils simple, stout. Flowers large, solitary, axillary; receptacle-tube turbinate (male) or cup-shaped (female); sepals ovate-lanceolate; corolla funnel-shaped to rotate; petals ovate-oblong, connate at the base, greenish-white; stamens inserted at the base of the tube; filaments distinct; anthers connate into a central column; thecae triplicate; pollen very large (polar axis 103–144 μm, equatorial axis c. 105–146 μm), 3-porate, echinate (Khunwasi 1998); placentae 3; ovules many, ascending to horizontal; stigmas strongly papillose. Fruit a large, ovoid, fleshy, hard-shelled pepo, to 10 cm long, glabrous, ripening yellowish. Seeds many, elliptic, tumid, 1–1.8 cm long; testa dark brown to black.

Four (or five) species in Central America, Cuba, and Jamaica; along forest margins and in montane forest.

96. *Abobra* Naudin

Abobra Naudin, Rev. Hort. 1862: 111 (1862).

Dioecious, perennial, herbaceous trailer, to 7 m long, with fleshy rootstock. Leaves small, palmately 5-lobed to dissected, to 12 cm long and broad; petioles 1–4 cm long; tendrils simple or 2-fid. Flowers small with strong odor; male flowers solitary or in pedunculate racemes, female flowers solitary; receptacle-tube cup-shaped; sepals short; corolla rotate; petals ovate-lanceolate, greenish-white; stamens inserted near the mouth of the tube; filaments short, distinct; two anthers 2-thecous, one 1-thecous; thecae triplicate; pollen large (polar axis c. 68 μm, equatorial axis c. 71 μm), 3-porate, margin distinct, echinate (Khunwasi 1998); ovary globose; placentae 3; ovules 6, erect; style slender; stigmas 3 (rarely 4), linear; staminodes 3. Fruit a fibrous red berry, with a firm, thin wall, c. 1 cm in diam. Seeds 3–6, 7–8 by 2–3 by ± 1.5 mm, slightly compressed (falcate); testa smooth, green or brownish.

One species, *A. tenuifolia* (Gillies in Hook.) Cogn., in Brazil, Argentina, and Uruguay; in xeric bushland and on dry soil. Host of the fungus *Uromyces novissimus* Speg. (Monoson and Rogers 1978).

Molecular data indicate that this is the closest relative of *Cayaponia*.

97. *Cayaponia* Silva Manso

Cayaponia Silva Manso, Enum. Subst. Braz.: 31 (1836), nom. cons.; Jeffrey, Kew Bull. 25: 201–234 (1971).
Alternasemina Silva Manso (1836).
Dermophylla Silva Manso (1836).
Perianthopodus Silva Manso (1836).
Arkezostis Raf. (1836 [1838]).
Trianosperma (Torr. & A. Gray) Mart. (1843).
Allagosperma M. Roem. (1846).
Cionandra Griseb. (1860).
Antagonia Griseb. (1874).
Selysia Cogn. (1881); Jeffrey, Kew Bull. 25: 234–236 (1971).

Monoecious or rarely dioecious, herbaceous or suffrutescent, often much-branched climbers or creepers, to 20 m long, with perennial roots. Leaves ovate-cordate, simple, palmately 3–7-lobed or entire, less often 3–5-foliolate, the blade often decurrent on the petiole, often with disk-shaped glands on the abaxial side; tendrils 2–7-fid (rarely simple), sometimes with apical adhesive pads. Flowers small, in racemes, panicles, pairs or solitary, male and female often coaxial, opening at night; receptacle-tube shortly campanulate to cylindrical; petals yellow, white or light green; stamens inserted near the base of the tube; filaments distinct; two anthers 2-thecous, one 1-thecous or all 2-thecous, usually coherent in a head; thecae duplicate or triplicate; pollen large to very large (polar axis 61–208 μm, equatorial axis 68–196 μm), 3–6-porate to 4–10-pantoporate, echinate with short pila between the spines (Khunwasi 1998; Barth et al. 2005); ovary globose, ovoid or oblong or ellipsoid-rostrate; placentae 1–3; ovules 2–30, ascending; style erect, linear, inserted on a basal nectary; stigmas 3, dilated, reflexed, strongly papillose or smooth; staminodes 3, minute; disk 3-lobed or ring-like. Fruits small, dry, indehiscent, smooth, with a firm, thin wall, ripening green, red, brown or black, often with very bitter taste. Seeds 1–30, in loose cellular pulp, erect, irregularly ovate or oblong, ± compressed, sometimes ± triangular or dagger-shaped, truncate and apically tricornute; testa brown, rigid and smooth, woody, no distinct margin.

About 50–59 species, most of them in tropical South America, few in Central America, Mexico and Southern US; one species endemic in Fernando de Noronha Island; one species, *C. africana* (Hook.f.) Exell, in West and Central Africa (São Tomé, Senegal, Guinea Bissau, Ivory Coast, Ghana, Cameroon, Gabon, Congo) and on Madagascar; one species, *C. martiana* (Cogn.) Cogn., introduced to Indonesia (Java); along forest margins, in clearings, and riverine forest. Host of the fungi *Uromyces pentastriatus* Viegas, *U. novissimus* Speg., *U. ratus* H. S. Jack. & Holw. (Monoson and Rogers 1978), *Passalora cayaponiae* (F. Stevens & Solheim) U. Braun & Crous, and *Stenella praelonga* (Syd.) U. Braun (Kirschner and Piepenbring 2006).

The genus appears to have repeatedly switched from ancestral pollination by bats to pollination by bees (Duchen and Renner 2010).

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