Synopsis of *Trichosanthes* (Cucurbitaceae) based on recent molecular phylogenetic data

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Abstract

The snake gourd genus, *Trichosanthes*, is the largest genus in the Cucurbitaceae family, with over 90 species. Recent molecular phylogenetic data have indicated that the genus *Gymnopetalum* is to be merged with *Trichosanthes* to maintain monophyly. A revised infrageneric classification of *Trichosanthes* including *Gymnopetalum* is proposed with two subgenera, (I) subg. *Scotanthus* comb. nov. and (II) subg. *Trichosanthes*, eleven sections, (i) sect. *Asterospermae*, (ii) sect. *Cucumeroides*, (iii) sect. *Edulis*, (iv) sect. *F oliobracteola*, (v) sect. *Gymnopetalum*, (vi) sect. *Involucraria*, (vii) sect. *Pseudovariifera* sect. nov., (viii) sect. *Villosae* stat. nov., (ix) sect. *Trichosanthes*, (x) sect. *Tripodanthera*, and (xi) sect. *Truncata*. A synopsis of *Trichosanthes* with the 91 species recognized here is presented, including four new combinations, *Trichosanthes orientalis*, *Trichosanthes subiflora*, *Trichosanthes scabra* var. *pectinata*, *Trichosanthes scabra* var. *penicaudii*, and a clarified nomenclature of *Trichosanthes costata* and *Trichosanthes scabra*.

Keywords

Cucurbitaceae, *Trichosanthes*, *Gymnopetalum*, infrageneric classification, new combinations

Introduction

Background

*Trichosanthes* L. is the largest genus in the Cucurbitaceae family, with over 90 species. The genus has its center of diversity in Southeast Asia, but ranges from India throughout Asia east to Taiwan, the Philippines and Japan, and southeast to New Guinea, Australia, Fiji and Vanuatu (de Wilde and Duyfjes 2010). The snake gourd (*Trichosanthes cucumerina* L.) is a popular vegetable in South and Southeast Asian cuisine and...
cultivated in tropical and subtropical regions around the globe. *Gymnopetalum* Arn. includes four species (de Wilde and Duyfjes 2006) and ranges from India through China and Southeast Asia into the Malay archipelago, but does not occur in New Guinea and Australia (de Wilde and Duyfjes 2010).

**Morphology and classification**

*Trichosanthes* are mostly stout perennial climbers, 3–30 m long, dioecious, less frequently monoecious, with branched tendrils, distinctly fringed petals, and often eggsized brightly colored fruits. Dioecy, variation in vegetative morphology (esp. in juvenile plants), and incomplete herbarium collections, complicate taxonomical studies and have contributed to the description of nearly 300 taxa (de Wilde and Duyfjes 2010; IPNI 2011).

No full taxonomic treatment of the genus exists, but in recent years regional revisions have been published for most of its distribution: India (Chakravarty 1959; Jeffrey 1980a; Jeffrey 1982), China (Lu et al. 2011; Yueh and Cheng 1974; Yueh and Cheng 1980), Thailand (Duyfjes and Pruesapan 2004), Cambodia, Laos and Vietnam (Keraudren-Aymonin 1975), Malaysia, Indonesia, the Philippines and Papua New Guinea (Rugayah and de Wilde 1997; Rugayah and de Wilde 1999; de Wilde and Duyfjes 2004; de Wilde and Duyfjes 2010), Australia (Telford 1982; Cooper and de Boer 2011) and Japan (Ohba 1984).

Infrageneric classifications of the genus *Trichosanthes* have been proposed by various authors (Yueh and Cheng 1974; Jeffrey 1980b; Chen 1985; Huang et al. 1997; Rugayah and de Wilde 1999; de Wilde and Duyfjes 2004). The most recent classifications of the genus (Rugayah and de Wilde 1999; de Wilde and Duyfjes 2004) propose six sections: (i) sect. *Trichosanthes*, (ii) sect. *Cucumeroides* (Gaertn.) Kitam. including subsect. *Cucumeroides* (Gaertn.) Kitam. and subsect. *Tetragonosperma* (C.Y.Cheng & Yueh) Rugayah, (iii) sect. *Edulis* Rugayah, (iv) sect. *Foliobracteola* C.Y.Cheng & Yueh, (v) sect. *Involucraria* (Ser.) Wight including subsect. *Bracteatae* C.Jeffrey ex S.K.Chen and subsect. *Pedatea* (C.Y.Cheng & Yueh) C.Jeffrey ex S.K.Chen, and (vi) sect. *Asterosperma* W.J.de Wilde & Duyfjes. However, both Rugayah and de Wilde (1999) and de Wilde and Duyfjes (2004; 2010) are reserved in their infrageneric classifications, and mention a need for further investigation.

Pollen morphology has also been used for infrageneric classification in the genus (Khunwasi 1998; Pruesapan and Van Der Ham 2005; Huang et al. 1997), but as a character is very variable in Cucurbitaceae, and its taxonomic value is not clear (Schaefer and Renner 2011). Palynological studies (Pruesapan and Van Der Ham 2005) have indicated that a variety of pollen types exist in *Trichosanthes* including 3(-4)-porate and 3(-4)-colporate pollen with psilate, perforate, verrucate, reticulate, and regulate ornamentation. Their study of pollen from 37 species distinguishes five pollen types, two of which are further divided into subtypes, and categorized these using exine ornamentation patterns for the major types and ectoaperture characters for the subtypes.
Gymnopetalum strongly resembles certain Trichosanthes species, but lack thread-like fringes on the petals, and the overall shape of the folded petals in the mature bud is elongate (short and rounded in Trichosanthes) (de Wilde and Duyfjes 2006). A revision of the genus was published by de Wilde and Dufyjes (2006), with minor nomenclatural changes published later (de Wilde and Duyfjes 2008). Cogniaux (1881) divided Gymnopetalum into two sections, (i) sect. Gymnopetalum containing the type G. tubiflorum (Wight & Arn.) Cogn. from southern India and Sri Lanka, and (ii) sect. Tripodanthera (M.Roem.) Cogn. containing the Southeast Asian and Malesian species. Later authors did not follow this classification (Jeffrey 1980a; Philcox 1997; de Wilde and Duyfjes 2006).

Recent molecular phylogenetic studies

The molecular phylogenetic study of Trichosanthes by de Boer et al. (Submitted) shows that Trichosanthes and Gymnopetalum are both non-monophyletic, but together form a clade with high support in the Bayesian tree and weak support in the ML tree (0.99/62). This indicates that Gymnopetalum should be merged with Trichosanthes, and that a revised infrageneric classification is necessary. Some previously recognized sections in Trichosanthes and Gymnopetalum are well supported, but others need to be described or redefined.

Results and discussion

Molecular phylogeny

The molecular phylogeny of Trichosanthes and Gymnopetalum by de Boer et al. (Submitted) has nomenclatural implications for the species in Gymnopetalum and the infrageneric classification of Trichosanthes. The species of Gymnopetalum are placed in different clades within Trichosanthes, with the sect. Gymnopetalum, including the type G. tubiflorum, grouping in a well-supported clade (1.00/84) together with species of sect. Trichosanthes and sect. Cucumeroides. The sect. Tripodanthera, consisting of the three other species in the genus, G. orientale W.J.de Wilde & Duyfjes, G. chinense (Lour.) Merr., and G. scabrum (Lour.) W.J.de Wilde & Duyfjes, forms a well-supported clade (1.00/86) together with the taxa in Trichosanthes sect. Edulis.

Within Trichosanthes the support for the two clades here defined as subgenera Trichosanthes (1.00/94) and Scotanthus (1.00/97) is high. However, splitting the genus into two genera corresponding to subg. Scotanthus and subg. Trichosanthes would not improve clarity, as both would consist of species with fringed and fringeless corollas. Maintaining a large Trichosanthes is in accordance with the recent taxonomic revisions of the genus (de Wilde and Duyfjes 2010; Chakravarty 1959; Lu et al. 2011; Duyfjes and Pruesapan 2004; Keraudren-Aymonin 1975; Cooper and de Boer 2011; Ohba 1984), and is the alternative that best provides taxonomic stability.
Some proposed sections in *Trichosanthes* and *Gymnopetalum* are well supported: (i) sect. *Cucumeroides* (1.00/93), including subsect. *Cucumeroides* (0.99/-) and subsect. *Tetragonosperma* (0.99/69), (ii) sect. *Edulis* (1.00/75), and (iii) sect. *Asterosperma* (1.00/100). The subsections of sect. *Cucumeroides* are statistically supported, but subsect. *Cucumeroides* consists solely of accessions of *Trichosanthes pilosa* Lour. and species that have been reduced to its synonymy (Cooper and de Boer 2011). Sect. *Involucraria* is only weakly supported (0.83/65), primarily due to the low support for inclusion of its type, *T. wallichiana* (Ser.) Wight. The subsections of *Involucraria* are not supported, and taxa belonging to subsect. *Pedatae* are nested in different locations within subsect. *Bracteatae*. Sect. *Tripodanthera* is not supported by the analysis, and could possibly form a grade at the base of sect. *Edulis*. However, morphological support for this section is strong as all taxa share characters of flower morphology, i.e. fringeless corollas. Sect. *Foliobracteola* Cheng & Yueh, which in its original sense included the species related to *T. kirilowii* Maxim. and *T. villosa* Blume (Yueh and Cheng 1974; Rugayah and de Wilde 1999; de Wilde and Duyfjes 2004), is not supported. However, a clade consisting of *T. kirilowii* Maxim., *T. miyagii* Hayata, *T. homophylla* Hayata, *T. hylonoma* Hand.-Mazz., *T. rosthornii* Harms, and *T. multiflora* Miq. is strongly supported (1.00/99). Section *Truncata*, in its original sense including *Trichosanthes truncata* C.B.Clarke, *T. kerrii* Craib, *T. homophylla* Hayata (Yueh and Cheng 1980), and *T. smilacifolia* C.Y.Wu (Jeffrey 1980b), is not supported, as the three latter species all end up elsewhere in the phylogenetic tree.

*Trichosanthes villosa* was placed in sect. *Involucraria* by Yueh and Cheng (1974), and later in subsect. *Involucraria* by Jeffrey (1980b), but subsequently moved to sect. *Foliobracteola* by Rugayah and de Wilde (1999). In the protologue of *T. phonsenae* Duyfjes and Pruesapan (2004), the authors stated that the three species *T. kerrii*, *T. phonsenae* and *T. villosa* form a coherent, distinct group based on presence of white fruit pulp, male flowers with the stamens inserted low in the receptacle tube, and a pseudo-ovary. The molecular evidence shows that all accessions of these species in this study form a well-supported monophyletic group, confirming the observations by Duyfjes and Pruesapan (2004) and warranting placement of these taxa in a new section, sect. *Pseudovariifera* H.J.de Boer.

Cooper and Ford (2010) and Cooper and de Boer (2011) placed *Trichosanthes subvelutina* F.Muell. ex Cogn. in section *Foliobracteola* as it has obovate seeds with an entire broad marginal band similar to those found in Malesian species of section *Foliobracteola*. However, Huang et al (1997) proposed to place it in section *Foliobracteola* subsect. *Villosae* based on it pollen morphology. The current phylogenetic data place the accessions of *T. subvelutina* as sister (1.00/91) to a well-supported clade (1.00/84) consisting of sections *Gymnopetalum*, *Trichosanthes*, and *Cucumeroides*, and the species is here placed in a separate section, sect. *Villosae* (Yueh & L.Q.Huang) H.J.de Boer.
Pollen

Species with colporate ectoaperturate pollen form two monophyletic groups in *Trichosanthes* subg. *Trichosanthes*, one including sections *Asterosperma, Pseudovariifera, Foliobracteola*, and *Truncata*, and the other including sect. *Villosae*, with *T. subvelutina* (data from R. van der Ham 2011, pers. comm.). The latter clade is sister to the clade consisting of sections *Trichosanthes, Gymnopetalum* and *Cucumeroides* (1.00/84). The remaining sections in subg. *Trichosanthes* have porate ectoapertures, and varying exine ornamentation including psilate, (micro-)reticulate, perforate, verrucate, and rugulate pollen (Huang et al. 1997; Pruesapan and Van Der Ham 2005). *G. scabrum* in sect. *Tripodanthera* has 3-colporate, rugulate-reticulate pollen (Khunwasi 1998; van der Ham et al. 2010), whereas in *G. tubiflorum* in sect. *Gymnopetalum* the pollen is 3-porate and microreticulate (R. van der Ham 2010, pers. comm.).

The other genera in the tribe Sicyoeae have colpate-colporate pollen, similar to that in many other distantly related groups in Cucurbitaceae (Schaefer and Renner 2011). In the light of the molecular data and the phylogenetic analysis (de Boer et al. Submitted), a transition from colporate to porate apertures has taken place three times in the evolutionary history of *Trichosanthes*, in the common ancestors of: 1) sect. *Involucraria*; 2) sect. *Edulis*; and 3) sections *Trichosanthes, Gymnopetalum* and *Cucumeroides*.

**Taxonomy and classification**

A revision of the infrageneric classifications suggested by previous authors on the basis of morphological studies (Yueh and Cheng 1974; Jeffrey 1980b; Huang et al. 1997; Rugayah and de Wilde 1999; de Wilde and Duyfjes 2004) is here proposed on the basis of the molecular phylogenetic data (de Boer et al. Submitted). A synopsis is presented in which we attempt to assign all 91 species recognized here to sections using the clades recovered in the phylogenetic analysis as a framework, along with a plenitude of data from macromorphological studies of herbarium vouchers (Chakravarty 1959; Jeffrey 1980a; Jeffrey 1980b; Jeffrey 1982; Telford 1982; Ohba 1984; Rugayah and de Wilde 1997; Rugayah and de Wilde 1999; Duyfjes and Pruesapan 2004; de Wilde and Duyfjes 2004; de Wilde and Duyfjes 2006; Cooper and Ford 2010; de Wilde and Duyfjes 2010; Lu et al. 2011; Cooper and de Boer 2011) and palynological work (Huang et al. 1997; Pruesapan and Van Der Ham 2005; van der Ham et al. 2010). Synonyms are only included if these are new or relevant for this paper. Names that have been placed in synonymy by previous authors can be found in the above-cited morphological studies.
**Trichosanthes** L. (1753) Sp. Pl. 2: 1008 – Type: *Trichosanthes anguina* L. [= *T. cucumerina* L.]

**T. subg. Scotanthus** (Kurz) H.J.de Boer, comb. nov. – *Gymnopetalum* subg. *Scotanthus* Kurz (1877) J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 46: 99. – Lectotype, designated here: *Bryonia cochinchinensis* Lour. [= *Trichosanthes costata* Blume]

*Scotanthus* Naud., nom. illeg. (1862) Ann. Sci. Nat., Bot. sér. 4, 16: 172. – Type: *Momordica tubiflora* Roxb. [= *Trichosanthes costata* Blume]

**T. sect. Edulis** Rugayah (1999) Reinwardtia 11: 232. – Type: *Trichosanthes edulis* Rugayah.

*T. densiflora* Rugayah (1999) Reinwardtia 11: 252

*T. dentifera* Rugayah (1999) Reinwardtia 11: 253

*T. dienensis* Merr. & L.M.Perry (1949) J. Arnold Arbor. 30: 59

*T. edulis* Rugayah (1999) Reinwardtia 11: 254

*T. bastata* Harms (1925) Bot. Jahrb. Syst. 60: 160

*T. laeoeica* C.Y.Cheng & Lu Q.Huang (1996) Bull. Bot. Res., Harbin 16: 503

*T. odontosperma* W.E.Cooper & A.J.Ford (2010) Austrobaileyia 8: 126

*T. pulleanea* Harms (1925) Bot. Jahrb. Syst. 60: 160

*T. schlechteri* Harms (1925) Bot. Jahrb. Syst. 60: 159

**T. sect. Involucraria** (Ser.) Wight (1840) Madras J. Lit. Sci. 12: 52. – *Involucraria* Ser. (1825) Mém. Soc. Phys. Genève 3: 27, t. 5. – Type: *Involucraria wallichiana* Ser. [= *Trichosanthes wallichiana* (Ser.) Wight]

*T. anamalaiensis* Bedd. (1864) Madras J. Lit. Sci. III, 1: 47

*T. borneensis* Cogn. (1881) Monogr. Phan. [A.DC. & C.DC.] 3: 369

*T. bracteata* (Lam.) Voigt (1845) Hort. Suburb. Calcutt. 58

*T. celebica* Cogn. (1881) Monogr. Phan. [A.DC. & C.DC.] 3: 385

*T. cordata* Roxb. (1832) Fl. Ind. 3: 703

*T. coriacea* Blume (1826) Bijdr. Fl. Ned. Ind. 15: 935

*T. dolichosperma* Duyfjes & Pruesapan (2004) Thai Forest Bull., Bot. 32: 84

*T. dunniana* H. Lév. (1911) Repert. Spec. Nov. Regni Veg. 10: 148

*T. ellipsoides* Merr. (1918) Philipp. J. Sci., C 13: 332

*T. elmeri* Merr. (1929) Univ. Calif. Publ. Bot. 15: 299

*T. emarginata* Rugayah (1999) Reinwardtia 11: 258

*T. eroa* Duyfjes & Pruesapan (2004) Thai Forest Bull., Bot. 32: 85

*T. fissibracteata* C.Y.Wu ex C.Y.Cheng & C.H.Yueh (1974) Acta Phytotax. Sin. 12: 438

*T. floresana* Rugayah (1999) Reinwardtia 11: 260

*T. globosa* Blume (1826) Bijdr. Fl. Ned. Ind. 15: 936

*T. intermedia* W.J.de Wilde & Duyfjes (2004) Sandakania 14: 19

*T. inthanonensis* Duyfjes & Pruesapan (2004) Thai Forest Bull., Bot. 32: 86

*T. khasiana* Kundu (1939) J. Bot. 77: 11

*T. kinabaluensis* Rugayah (2000) Reinwardtia 11: 419

*T. kostermansii* Duyfjes & Pruesapan (2004) Thai Forest Bull., Bot. 32: 89
T. laceribractea Hayata (1911) J. Coll. Sci. Imp. Univ. Tokyo 30. Art. 1: 117
T. lepiniana (Naud.) Cogn. (1881) Monogr. Phan. [A.DC. & C.DC.] 3: 377
T. leuserensis Rugayah (1999) Reinwardtia 11: 265
T. longispicata Rugayah (1999) Reinwardtia 11: 266
T. montana Rugayah (1998) Reinwardtia 11: 218
T. morrisii W.E.Cooper (2011) Austrobaileya 8: 381
T. obscura Rugayah (1999) Reinwardtia 11: 269
T. pallida Duyfjes & Pruesapan (2004) Thai Forest Bull., Bot. 32: 90
T. papuana F.M.Bailey (1900) Queensland Agric. J. 7: 349
T. pentaphylla F.Muell. in Benth. (1867) Fl. Austral. 3: 314
T. philippinensis Rugayah (1999) Reinwardtia 11: 271
T. planiglans Rugayah (1999) Reinwardtia 11: 273
T. pubera Blume (1826) Bijdr. Fl. Ned. Ind. 15: 936
T. quinquangularata A. Gray (1854) U.S. Expl. Exped., Phan. 15: 645
T. quinquefolia C.Y.Wu ex C.Y.Cheng & C.H.Yueh (1980) Acta Phytotax. Sin. 18: 351
T. refracta C.H.Yueh (1996) Bull. Bot. Res., Harbin 10: 500
T. rugatisemina C.Y.Cheng & C.H.Yueh (1974) Acta Phytotax. Sin. 12: 440
T. sepilokensis Rugayah (1999) Reinwardtia 11: 275
T. subrosa C.Y.Cheng & C.H.Yueh (1980) Acta Phytotax. Sin. 18: 349
T. tricuspidata Lour. (1790) Fl. Cochinch. 2: 589
T. valida Rugayah (1999) Reinwardtia 11: 277
T. wallichiana (Ser.) Wight (1840) Madras J. Lit. Sci. 12: 52
T. wawrae Cogn. (1881) Monogr. Phan. [A.DC. & C.DC.] 3: 384

T. sect. Tripodanthera (M.Roem.) H.J.de Boer, comb. nov. – Tripodanthera M.Roem. (1846) Fam. Nat. Syn. Monogr. 2: 48. – Gymnopetalum sect. Tripodanthera (M.Roem.) Cogn. (1881) Monogr. Phan. [A.DC. & C.DC.] 3: 390. – Type: Bryonia cochinchinensis Lour. [= Trichosanthes costata Blume]

T. costata Blume (1826) Bijdr. Fl. Ned. Ind. 15: 933. — Type: Blume s.n. barcode L0589632, (lectotype L, designated by de Wilde and Duyfjes (2006); 2 isotypes L), Java, Indonesia. Heterotypic synonyms: Evonymus chinensis Lour. (1790) Fl. Cochinch. 1: 156. – Gymnopetalum chinense (Lour.) Merr. (1919) Philipp. J. Sci. 15: 256 – Type: Loureiro †. Bryonia cochinchinensis Lour. (1790) Fl. Cochinch. 1: 595. – Gymnopetalum cochinchinense (Lour.) Kurz (1871) J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 40: 57 –Type: Loureiro s.n. (BM), Vietnam. Momordica tubiflora Roxb. (1832) Fl. Ind. 3: 711 – Type: Wallich Cat. 6749 (holotype? K-W), Dacca, Bangladesh. Note: The existence of Trichosanthes chinensis Ser. (1828) Prodr. [A.P. de Candolle] 3: 315 blocks the transfer of Gymnopetalum chinense, based on the basionym Evonymus chinensis, to Trichosanthes. The second name in line of priority would be Gymnopetalum cochinchinensis, based on the basionym Bryonia cochinchinensis. However, the combination Trichosanthes cochinchinensis M.Roem. (1846) Fam. Nat. Syn. Monogr. 2: 96, based on Trichosanthes cucumerina Lour.
blocks the transfer. The third name in line of priority is *Trichosanthes costata* Blume (1826) Bijdr. Fl. Ned. Ind. 15: 933, and this name is available for *Gymnopetalum chinense*.

**T. scabra** Lour. (1790) Fl. Cochinch. 2: 589. – *Gymnopetalum scabrum* (Lour.) W.J.de Wilde & Duyfjes (2008) Reinwardtia 12: 268. – Type: *Poilane 11322* (neotype P; isoneotype L, designated by de Wilde and Duyfjes (2008)), Annam. Heterotypic synonym: *Cucumis integrifolius* (’integrifolia’) Roxb. (1832) Fl. Ind. 3: 724. – *Gymnopetalum integrifolium* (Roxb.) Kurz (1871) J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 40: 58. – Type: *Wallich Cat. 6730* (holotype? K-W), Burma.

*var. scabra*

*var. pectinata* (W.J.de Wilde & Duyfjes) H.J.de Boer, *comb. nov. – Gymnopetalum scabrum* (Lour.) W.J.de Wilde & Duyfjes var. *pectinatum* (W.J. de Wilde & Duyfjes) W.J.de Wilde & Duyfjes (2008) Reinwardtia 12: 268 – *Gymnopetalum integrifolium* (Roxb.) Kurz var. *pectinatum* W.J.de Wilde & Duyfjes (2006), Blumea 51: 287. – Type: *W.J. de Wilde and Duyfjes 21692* (holotype L), Java, Indonesia.

*var. penicaudii* (Gagnep.) H.J.de Boer, *comb. nov. – Gymnopetalum penicaudii* Gagnep. (1918) Bull. Mus. Natl. Hist. Nat. 24: 374. – *Gymnopetalum scabrum* (Lour.) W.J.de Wilde & Duyfjes var. *penicaudii* (Gagnep.) W.J.de Wilde & Duyfjes (2008) Reinwardtia 12: 268 – Type: *Penicaud 43* (lectotype P), Hainan, China.

**T. orientalis** (W.J.de Wilde & Duyfjes) H.J.de Boer, *comb. nov. – Gymnopetalum orientale* W.J.de Wilde & Duyfjes (2006) Blumea 51: 290. – Type: *De Wilde and Duyfjes 21937* (holotype L), Lombok, Indonesia.

**T. subg. Trichosanthes**

Unresolved placement within this subgenus:

*T. reticulineris* C.Y.Wu ex S.K.Chen (1985) Bull. Bot. Res., Harbin 5(2): 114
*T. smilacifolia* C.Y.Wu ex C.H.Yueh & C.Y.Cheng (1980) Acta Phytotax. Sin. 18: 347

**T. sect. Asterosperma** W.J.de Wilde & Duyfjes (2004) Sandakania 14: 6. – Type: *Trichosanthes postarii* W.J.de Wilde & Duyfjes.

*T. auriculata* Rugayah (1998) Reinwardtia 11: 216
*T. fisca* W.J.de Wilde & Duyfjes (2004) Sandakania 14: 17
*T. postarii* W.J.de Wilde & Duyfjes (2004) Sandakania 14: 26
*T. rotundifolia* Rugayah (1998) Reinwardtia 11: 223

**T. sect. Cucumeroides** (Gaertn.) Kitam. (1943) J. Jap. Bot. 19: 35. – *Cucumeroides* Gaertn. (1791) Fruct. Sem. Pl. 2: 485, t. 180, t. 4. – Type: *Trichosanthes cucumeroides* (Ser.) Maxim. [ = *Trichosanthes pilosa* Lour.].

*T. adhaerens* W.J.de Wilde & Duyfjes (2004) Sandakania 14: 11
*T. beccariana* Cogn. (1881) Monogr. Phan. [A.DC. & C.DC.] 3: 380
*T. mucronata* Rugayah (1999) Reinwardtia 11: 268
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*T. pendula* Rugayah (1998) Reinwardtia 11 (3): 219
*T. pilosa* Lour. (1790) Fl. Cochinch. 2: 588. Heterotypic synonyms according to Coop-er and de Boer (2011): *T. baviensis* Gagnep. (1918) Bull. Mus. Natl. Hist. Nat. 24: 379; *T. trichocarpa* C.Y.Wu ex C.Y.Cheng & C.H.Yueh (1980) Acta Phytotax. Sin. 18: 340; *T. holzzei* F.Muell. (1886) Australas. Journ. Pharm. 1: 447.
*T. siamensis* Duyfjes & Pruesapan (2004) Thai Forest Bull., Bot. 32: 97
*T. tetragonosperma* C.Y.Cheng & C.H.Yueh (1974) Acta Phytotax. Sin. 12: 425

*T. sect. Foliobracteola* C.Y.Cheng & C.H.Yueh (1974) Acta Phytotax. Sin. 12: 427.
– Type: *Trichosanthes kirilowii* Maxim.
*T. homophylla* Hayata (1921) Icon. Pl. Formosan. 10: 8
*T. hylonomaha* Hand.-Mazz. (1936) Symb. Sin. Pt. 7: 1066
*T. isbigakiensis* E.Walker (1971) J. Jap. Bot. 46: 71
*T. jinggangshanica* C.H.Yueh (1980) Acta Phytotax. Sin. 18: 342
*T. kirilowii* Maxim. (1859) Prim. Fl. Amur. 482
*T. mianyangensis* C.H.Yueh & R.G.Liao (1992) Bull. Bot. Res., Harbin 2: 115
*T. miyagii* Hayata (1921) Icon. Pl. Formosan. 10: 11
*T. multiloba* Miq. (1865) Ann. Mus. Bot. Lugd.-Bat. 2: 82
*T. rosthornii* Harms (1901) Bot. Jahrb. Syst. 29: 603

*T. sect. Gymnopetalum* (Arn.) H.J.de Boer, *comb. et stat. nov.* – *Gymnopetalum* Arn. (1840) Madras J. Lit. Sci. 12: 52. – Type: *Bryonia tubiflora* Wight & Arn. [= *Trichosanthes tubiflora* (Wight & Arn.) H.J.de Boer].
*T. tubiflora* (Wight & Arn.) H.J.de Boer, *comb. nov.* – *Bryonia tubiflora* Wight & Arn. (1834) Prodr. Fl. Ind. Orient. 1: 347. – *Gymnopetalum tubiflorum* (Wight & Arn.) Cogn. (1881) Monogr. Phan. [A.DC. & C.DC.] 3: 388 – Type: *Rottler s.n.* ex Herb. Klein in Herb. Wight Cat. 1118, February 1796 (holotype K; isotypes E, several duplicates), Trincomalee, Ceylon.

*T. sect. Pseudovariifera* H.J.de Boer, *sect. nov.* Diagnosis: Similar to sect. *Foliobracteola*, but male flowers with stamens inserted low in receptacle tube, with pseudo-ovary (a thick-walled basal part of the receptacle tube, without staminodes), and fruit with white pulp. Type: *Trichosanthes villosa* Blume.
*T. kerrii* Craib (1914) Bull. Misc. Inform. Kew: 7
*T. phonsenae* Duyfjes & Pruesapan (2004) Thai Forest Bull., Bot. 32: 9
*T. sericeifolia* C.Y.Cheng & C.H.Yueh (1980) Acta Phytotax. Sin. 18: 346
*T. villosa* Blume (1826) Bijdr. Fl. Ned. Ind. 15: 934

*T. sect. Trichosanthes*
*T. cucumerina* L. (1753) Sp. Pl.: 1008
*T. dafangensis* N.G.Ye & S.J.Li (1989) Acta Phytotax. Sin. 27: 153
*T. dioica* Roxb. (1832) Fl. Ind. 3: 701
*T. integrifolia* Thwaites (1859) Enum. Pl. Zeyl. [Thwaites]: 127
**T. lobata** Roxb. (1832) Fl. Ind. 3: 703. – Heterotypic synonyms: *T. perrotetiana* Cogn. (1881) Monogr. Phan. [A.DC. & C.DC.] 3: 362; *T. vilosula* Cogn. (1881) Monogr. Phan. [A.DC. & C.DC.] 3: 342

*T. nervifolia* L. (1753) Sp. Pl.: 1008

**T. sect. Truncata** C.Y.Cheng & C.H.Yueh (1974) Acta Phytotax. Sin. 12: 427. – Type: *T. truncata* C.B.Clarke

*T. truncata* C.B.Clarke (1879) Fl. Brit. India [J.D. Hooker] 2: 608. – Heterotypic synonym: *T. ovata* Cogn. (1881) Monogr. Phan. [A.DC. & C.DC.] 3: 365

**T. sect. Villosae** (Yueh & L.Q.Huang) H.J.de Boer, stat. nov. – *Trichosanthes* subsect. *Villosae* Yueh & L.Q.Huang (1997) Act. Phytotax. Sinica 35: 127. – Type: *Trichosanthes subvelutina* F.Muell. ex Cogn.

*Trichosanthes subvelutina* F.Muell. ex Cogn. (1881) Monogr. Phan. [A.DC. & C.DC.] 3: 366

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**References**

de Boer HJ, Schaefer H, Thulin M, Renner SS [Submitted] Evolution and loss of long-fringed petals: A case study using a dated phylogeny of the snake gourds, *Trichosanthes* (Cucurbitaceae). BMC Evolutionary Biology.

Chakravarty HL (1959) Monograph on Indian Cucurbitaceae (Taxonomy and Distribution). Records of the Botanical Survey of India 27: 28–56.

Chen SK (1985) New taxa of the genus *Trichosanthes* L. (Cucurbitaceae) from China. Bulletin of Botanical Research, Harbin 5: 113–121.

Cogniaux CA (1881) Cucurbitaceae. In: Monographiae Phanerogamarum Prodromi nunc Continuato, nunc Revisio Auctoribus Alphonso et Casimir de Candolle Aliisque Botanicis Ultra Memoratis. Paris, France, 325–951.

Cooper WE, de Boer HJ (2011) A taxonomic revision of *Trichosanthes* L. (Cucurbitaceae) in Australia, including one new species from the Northern Territory. Austrobaileya 8: 364–386.

Cooper WE, Ford AJ (2010) *Trichosanthes odontosperma* (Cucurbitaceae), a new species from Queensland’s Wet Tropics. Austrobaileya 8: 125–131.

Duyfjes BEE, Pruesapan K (2004) The genus *Trichosanthes* L. (Cucurbitaceae) in Thailand. Thai Forest Bulletin (Botany) 32: 76–109.

van der Ham R, Mennes C, van Heuven BJ (2010) Fevilleoideae pollen (Cucurbitaceae): a study in striate ornamentation. Grana 49: 157–169. doi: 10.1080/00173134.2010.490336
Synopsis of *Trichosanthes* (Cucurbitaceae) based on recent molecular phylogenetic data

Huang L, Yang B, Yue C (1997) Pollen morphology of *Trichosanthes* and its taxonomic significance. Acta Phytotaxonomica Sinica 35: 125–135.

IPNI (2011) International Plant Names Index. Available at: http://www.ipni.org/

Jeffrey C (1980a) Further Notes on Cucurbitaceae: V: The Cucurbitaceae of the Indian Subcontinent. Kew Bulletin 34: 789–809. doi: 10.2307/4119071

Jeffrey C (1980b) The Cucurbitaceae of Eastern Asia. Royal Botanic Gardens Kew, Richmond, UK: 1–60.

Jeffrey C (1982) Further Notes on Cucurbitaceae: VI Cucurbitaceae of the Indian Subcontinent: Corrigenda and Addenda. Kew Bulletin 36: 737–740. doi: 10.2307/4117916

Keraudren-Aymonin M (1975) Cucurbitacées, Vol 15. In: Muséum National D’Histoire Naturelle (Eds) Flore de du Cambodge, du Laos et du Vietnam. Paris, France: 1–192.

Khunwasi C (1998) Palynology of the Cucurbitaceae. Doctoral Dissertation, University of Innsbruck, Austria.

Lu A, Huang L, Chen SK, Jeffrey C (2011) Cucurbitaceae. In: Wu ZY, Raven PH, Hong DY (Eds) Flora of China. Vol. 19. Missouri Botanical Garden Press, St. Louis, MO:

Ohba H (1984) Cucurbitaceae. In: Ohwi J, Meyer FG, Walker EH (Eds) Flora of Japan. Washington, D.C., USA, Smithsonian Institution, 196–199.

Philcox D (1997) Cucurbitaceae. In: Dassanayake MD, Clayton WD (Eds) A revised handbook to the flora of Ceylon. Vol. 11. Balkema, Rotterdam: 8–46.

Pruesapan K, Van Der Ham R (2005) Pollen morphology of *Trichosanthes* (Cucurbitaceae). Grana 44: 75–90. doi: 10.1080/00173130510010512

Rugayah, de Wilde WJJJO (1999) Conspectus of *Trichosanthes* (Cucurbitaceae) in Malesia. Reinwardtia 11: 227–280.

Rugayah, de Wilde WJJJO (1997) *Trichosanthes* L. (Cucurbitaceae) in Java. Blumea 42: 471–482.

Schaefer H, Renner SS (2011) Cucurbitaceae. In: Kubitzki K (Ed) Families and genera of flowering plants. Vol. 10. Springer, Berlin, 112–174.

Telford IR (1982) Cucurbitaceae. In: Flora of Australia, Vol. 8. Australian Govt. Pub. Service, 194–198.

de Wilde WJJJO, Duyfjes BEE (2004) The genus *Trichosanthes* (Cucurbitaceae) in Sabah. Sandakania 14: 5–32.

de Wilde WJJJO, Duyfjes BEE (2006) Review of the Genus *Gymnopetalum* (Cucurbitaceae). Blumea 51: 281–296. doi: 10.3767/000651906X622229

de Wilde WJJJO, Duyfjes BEE (2008) Miscellaneous South East Asian cucurbit news. Reinwardtia 12: 267–274.

de Wilde WJJJO, Duyfjes BEE (2010) Cucurbitaceae. In: Nooteboom HP (Ed) Flora Malesiana Vol. 19. Leiden, The Netherlands, Foundation Flora Malesiana, 1–342

Yueh CH, Cheng CY (1974) A preliminary study of the Chinese medicinal species of genus *Trichosanthes* L. Acta Phytotaxonomica Sinica 12: 415–458.

Yueh CH, Cheng CY (1980) The Chinese medicinal species of the genus *Trichosanthes* L. Acta Phytotaxonomica Sinica 18: 333–352.