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Phylogeny and circumscription of Antillean *Anemotrochus*, gen. nov., and *Tylodontia* (Apocynaceae: Asclepiadoideae: Gonolobinae)

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Abstract: Combined molecular and morphological analyses demonstrate that a number of small-flowered Caribbean *Asclepiadoideae* of hitherto uncertain affiliation form two independent lineages in *Asclepiadeae*–*Gonolobinae*, and not, as previously assumed, in the *Metastelmatinae*. One lineage is described as the new genus *Anemotrochus*, which includes the widespread Caribbean *A. eggersii*, a species originally described under *Metastelma*; *A. yamanigüeyensis*, a new species discovered by the authors in E Cuba; and *A. viridivenius*, a plant from Hispaniola formerly assigned to *Matelea*. The second lineage, *Tylodontia*, is a small genus restricted to Cuba. Besides its type species, *T. cubensis*, the genus comprises *T. fuscula*, a species formerly assigned to *Metastelma*; *T. stipitata*, a new species described here; and *T. urceolata*, a species formerly assigned to *Astephanus*. *Anemotrochus* and *Tylodontia* belong to the wider *Matelea* alliance, but they form endemic Antillean, mainly Cuban lineages independent from *Matelea*. All species, except for *A. viridivenius*, are fully described and illustrated, and distribution maps are provided. The names *Metastelma eggersii* and *Astephanus schlechterianus* (a synonym of *T. fuscula*) are lectotypified here.

Key words: Apocynaceae, Asclepiadoideae, Asclepiadeae, Gonolobinae, Metastelmatinae, Anemotrochus, Matelea, Tylodontia, Caribbean, Antilles, Cuba, endemism, molecular phylogeny, taxonomic revision

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Introduction

The *Gonolobinae* are a subtribe of the *Asclepiadeae* (*Asclepiadoideae*–*Apocynaceae*), comprising c. 400 species with almost exclusively American distribution (Krings & Morillo 2015). A single species, *Gonolobus rostratus* (Vahl) R. Br. ex Schult. has been introduced recently in W Africa (D. Goyder, according to Krings 2008). Woodson (1941) reduced the 46 genera described in this subtribe to three genera, *Fischeria* DC., *Gonolobus* Michx. and *Matelea* Aubl. Krings & al. (2008) demonstrated that this subtribe falls into two lineages, of which one comprises

Gonolobus, while the other one includes numerous genera synonymized under *Fischeria* and *Matelea* by Woodson (1941). Current publications tend to reassess several of these genera or even describe new ones (e.g. Stevens 2001; Goyder 2006; Stevens & Morales 2009; Morillo 2012, 2013; Morillo & Krings 2014). A recent phylogenetic study in *Metastelma* R. Br. (*Metastelmatinae*; Liede-Schumann & al. 2014) showed that the Caribbean species *M. eggersii* Schltr. falls into the *Gonolobinae*.

Grisebach (1866: 175) described *Tylodontia* Griseb., based on *T. cubensis* Griseb., as “juxta *Microloma* in-serendum” with shoots possessing recurved eglandular

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trichomes, an urceolate corolla, with the gynostegium inserted at the base and the small corona lobes in the middle of the tube. Bentham (1876) treated *Tylodontia* as a synonym of *Astephanus* R. Br. without making the necessary combination for the described species. Schumann (1895) also listed *Tylodontia* as a synonym of *Astephanus* without putting the combination into effect. Following Schumann (1895), *Astephanus* was defined by a gynostegium lacking a corona, whereas Grisebach (1866: 175) stated that *Tylodontia* has a “Corona parva, 5phylla”. This would have excluded *Tylodontia* from *Astephanus*. Gómez de la Maza (1895) combined *T. cubensis* into *Astephanus* with a new epithet, as *A. grisebachii*, because the name *A. cubensis* was blocked by Kunth (1819: 206), a taxon placed in *Metastelma* by Liede & Meve (1997). Based on the free anthers and the odd inflorescence, Schlechter (1899: 237) kept *Tylodontia* separate from *Astephanus*. Woodson (1941) combined *Tylodontia* into *Cynanchum* L. at the rank of a subgenus. He stated that the presence of a corona excluded it from *Astephanus*. Liede (1997: 176) included *Tylodontia* and *Astephanus urceolatus* in *Cynanchum* sect. *Macbridea* (Raf.) Liede. The characters she gave for this section are: “Plants herbaceous, twining, leaves lanceolate to linear, inflorescences extra-axillary, sciadioidal (umbel-shaped panicle; Liede & Weberling 1995), corolla abaxially glabrous, corona absent or consisting of basally fused staminal and interstaminal parts, with only staminal lobes differentiated, but these exceeding the gynostegium...”. However, as *T. cubensis* and *A. urceolatus* have thyrsoidal inflorescences, coronas consisting (also) of differentiated interstaminal parts and apically flattened style-heads, they cannot be included in *C. sect. Macbridea*. Further, Liede (1997: 176) noted that these taxa cannot be included in *Metastelma*: “...and all species lack the most reliable character of *Metastelma*, the bearded corolla lobes”. As *T. cubensis* has adaxially densely bearded corollas, this feature does not suit for excluding it from *Metastelma*, but the possession of interstaminal corona elements and furrowed pollinia, as well as the shoots, which are uniformly and densely covered with recurved trichomes, separate the species well from *Metastelma*. Later, Liede & Meve (2003: 587) tentatively included *T. cubensis* and *A. urceolatus* in “*Cynanchum*” with an ambiguous position until more material would become available, but remarking that *Tylodontia* might be resurrected. Their main arguments were that the *Astephaninae* are confined to the Old World and that Schlechter (1899: 240) argued “Die Gestalt der Corolla erinnert an *Tylodontia cubensis* Griseb.” (the shape of the corolla [of *A. urceolatus*] is reminiscent of *T. cubensis*). Considering the historically uncertain position of these taxa, in addition to recent morphological evidence that the mainly Cuban alliance of the *Metastelma*-like species *Astephanus urceolatus* Griseb., *Metastelma eggersii*, *M. fuscum* C. Wright, and *Tylodontia cubensis* Griseb. display characters typical of *Gonolobinae* (Mangelsdorff 2004), the present study aims to take a closer look at the Carib-

bean small-flowered *Metastelma*-like taxa in order to (1) clarify their systematic position, (2) test their monophyly and (3) revise these groups taxonomically, taking into account the results of the phylogenetic study.

Material and methods

Phylogeny

Taxon sampling — The datasets of Rapini & al. (2007) and Krings & al. (2008) were used as a starting point, because these two datasets combine a broad general sampling in New World *Asclepiadeae* (Rapini & al. 2007) with the largest sampling so far available in *Gonolobinae* (Krings & al. 2008). In both datasets, samples completely lacking one of the regions studied (*trnT-F*, *rps16* or *LEAFY*) were pruned. Finally, representatives of all hitherto known Caribbean (mainly Cuban) small-flowered *Metastelma*-like taxa were added, resulting in eleven samples representing seven species.

Duplicate samples were added for three Cuban species of *Matelea*, namely *M. bicolor* (Britton & P. Wilson) Woodson (Liede & Meve LM 3583), *M. nipensis* (Urb.) Woodson (Mangelsdorff RMC 318) and *M. taminifolia* (Griseb.) Woodson (Mangelsdorff RMC 125), and the Central American *Gonolobus ophioglossa* Woodson (Mangelsdorff RMP 1286). For three species of *Gonolobinae* (*G. barbatus* Kunth, *G. suberosus* (L.) R. Br. and *M. cyclophylla* (Standl.) Woodson) not all partial sequences could be obtained from the same specimen, so that the sequences of two different accessions had to be combined (see Appendix for all vouchers under their names as accepted here, including GenBank accession numbers). Preliminary analysis adding the eleven small-flowered *Metastelma*-like taxa to the complete dataset of Rapini & al. (2007) had placed all samples with full support in the New World Clade of *Asclepiadeae*. Therefore, only samples of the New World *Asclepiadeae* subtribes *Diplolepineae*, *Gonolobinae*, *Metastelmatinae*, *Orthosiniinae*, *Oxypetalinae*, *Pentacyphinae* and *Tassadiinae* were included in the main analysis (see Appendix). The two samples of *Pentacyphus* were considered as the outgroup following Liede-Schumann & al. (2014). The total matrix comprises 156 accessions, 67 of which are considered as *Gonolobinae*.

DNA extraction, amplification and sequencing — DNA was extracted from silica-gel-dried leaves (vouchers deposited at FR or UBT). Total DNA was extracted using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) following the manufacturer’s instructions. PCR primers and protocols for the plastid *trnT-trnL* and *trnL-trnF* spacers and the *trnL* intron are those described in Taberlet & al. (1991). The *trnL* intron and *trnL-trnF* intergenic spacer were amplified either as one fragment, using primers c and f, or as two separate fragments, using primers c and d, and e and f, respectively. The two segments were kept

Table 1. Sequence characteristics (156 terminals).

	<i>trnT-L</i>	<i>trnL</i>	<i>trnL-F</i>	<i>rps16</i>	<i>LEAFY</i>
Length (bp)	763–1027	489–547	197–387	812–849	79–138 (intron) 404–475 (intron+exon)
Median length (bp)	798	513	370	833	103.5 (intron) 464 (intron+exon)
Aligned length (bp)	1264	592	455	944	545
New sequences	13	13	13	13	16
Missing partial sequences	46	46	0	1	93
Missing data cells (total)	58 537 (29.7 %)	27 370 (29.6 %)	381 (0.5 %)	1610 (1.1 %)	68 030 (80.0 %)
Missing data cells (in available partial sequences)	393 (0.3 %)	138 (0.2 %)	381 (0.5 %)	666 (0.5 %)	17 345 (50.5 %)
Variable characters	221	82	118	273	145
Parsimony-informative characters	109	30	42	153	70

separate for alignment because most of the samples were amplified separately and the matrix of Krings contains only the *trnL-trnF* intergenic spacer. The *rps16* intron was amplified as in Liede-Schumann & al. (2005) using the primer pair *rps16-1F* and *rps16-2R*. *LEAFY* was amplified using the primers and PCR conditions described in Krings & al. (2008). All accessions were sequenced directly from the PCR product. In cases in which PCR yielded more than one band, the major band was excised, purified with the QIAquick gel extraction kit (Qiagen) and then sequenced directly. For one accession of the Caribbean small-flowered *Metastelma*-like taxa (Liede & Meve 3593), no PCR product for *LEAFY* could be obtained (see Appendix). For seven species of *Gonolobinae*, Krings & al. (2008) had recovered 2–7 *LEAFY* sequences by cloning. In these cases, the majority rule consensus of all sequences of the same species was calculated using CodonCode Aligner, v.3.0.3 (CodonCode Corp., Dedham, Massachusetts, U.S.A.), and inserted in the final matrix.

For all five markers, forward and reverse sequences were aligned with CodonCode Aligner, v.3.0.3, and the consensus was exported in fasta format. The fasta files of all markers except *LEAFY* were aligned manually in Mesquite (Maddison & Maddison 2011). For *LEAFY*, the fasta files were prealigned with the OPAL package inside Mesquite (Wheeler & Kececioglu 2007) and the resulting alignment was corrected manually. A total of 67 partial sequences was obtained newly for this study. Because the two datasets integrated here are only partially congruent in terms of marker selection, the matrix has a high number of missing partial sequences (see Table 1 and Appendix).

Phylogenetic analysis — Congruency of the partitions was assessed using the ILD (Incongruence Length Difference; Farris & al. 1994) test as implemented in PAUP 4.0b10 (Swofford 2003). We conducted 1000 replicates using random addition (10 addition sequences), keeping a maximum of 100 trees in each repetition. Taxa miss-

ing a partial sequence in the set under investigation were excluded. Only values of $p < 0.01$ were considered as significantly incongruent (Cunningham 1997).

Following the recommendation by Huelsenbeck & Rannala (2004), the most complex model GTR + G + I was implemented for each partition and model parameters were allowed to be optimized independently. Test runs implementing the models of Krings & al. (2008) did not result in a different tree topology (results not shown).

For Maximum Likelihood (ML) reconstructions, all analyses were implemented in GARLI 2.0 (Zwickl 2006), with general settings left at default. Five independent runs were conducted to find the best tree. Support for individual relationships was evaluated using likelihood bootstrap, 100 replicates and two search replicates each, and the resulting trees summarized with sumtrees (Sukumaran & Holder 2010).

Bayesian inference (BI) relied on MrBayes 3.2 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003). The five partitions (*trnT-L*, *trnL*, *trnL-F*, *rps6*, and *LEAFY*) were considered unlinked, parameters estimated independently, and four simultaneous independent runs were conducted with default temperatures and prior distributions, saving one tree every 1000 generations. The analysis was run for 4 million generations, when constancy was reached at an average standard deviation of split frequencies ≤ 0.015 . Burn-in and run convergence were assessed by examination of the split frequencies diagnostic and the first 50 % of the trees were excluded from the construction of the 50 % majority rule consensus tree. All matrices and trees are available in Treebase (Piel & al. 2002; study number 16299).

Taxonomic revision

The treatment is based on the critical study of c. 150 herbarium specimens obtained from A, B, GH, GOET, HAC, HAJB, HBG, JBSD, JE, NY, P, S and US (herbarium codes follow Thiers [continuously updated]). The abbreviation “HFC” is used throughout for the collections of

the “Herbario de la Flora de Cuba” in addition to the individually named collectors. Additional material was provided by fieldwork conducted by R.D.M. during three excursions to Cuba in collaboration with Dr Jorge Gutiérrez (HAJB) and the late Dr Armando J. Urquiola (Pinar del Río) and by S.L.-S. and U.M. on one excursion to Cuba.

Results

Phylogeny

Partition homogeneity tests resulted in *p* values of 0.59 for *trnL-F* / *LEAFY*, 0.23 for *rps16* / *LEAFY* and 0.35 for *trnL-F* / *rps16*. All *p* values were above the threshold at which phylogenetic accuracy has been shown to suffer by combining gene partitions (i.e. *p* < 0.01; Cunningham 1997). Therefore, only the combined dataset was considered further.

All analyses recover a very highly supported ($BS_{ML} = 0.92$, $PP = 1.0$) monophyletic *Gonolobinae* (Fig. 1). In *Gonolobinae*, however, basal resolution is low, only a few clades are well supported. These are the *Fischeria* clade ($BS_{ML} = 0.73$, $PP = 0.99$), the *Macroscopis* Kunth-Schubertia Mart. clade ($BS_{ML} = 0.92$, $PP = 1.0$), the core *Gonolobus* clade ($BS_{ML} = 0.6$, $PP = 1.0$) and a small Caribbean (incl. Cuba) clade comprising *Matelea correllii* Spellman, *M. nipensis*, *M. oblongata* (Griseb.) Woodson and *M. phainops* Krings, while a clade comprising Central American species of *Matelea* is only poorly supported ($PP_{ML} = 0.81$).

In all analyses, the small-flowered *Metastelma*-like taxa fall into two separate, well-supported clades (labelled *Anemotrochus* and *Tylodontia*, Fig. 1). One clade ($BS_{ML} = 1.0$, $PP = 1.0$) comprises taxa hitherto known as *Metastelma eggersii* Schltr. [Liede & Meve 3592, Mangelsdorff RMC 387, Neil 270], *Matelea viridivenia* Alain [Clase & al 5609, Veloz & al. 836], and a so-far undescribed species [Mangelsdorff RMC 222a, 222b, RMC 357]. *Matelea viridivenia* from Hispaniola is sister to the widespread *Metastelma eggersii* and the undescribed species from Cuba. This clade is sister to a clade comprising Cuban *Matelea* species, *M. bicolor* and *M. ekmanii* (Urb.) Woodson, albeit with no support in the ML analysis and little support in the Bayesian analysis ($PP = 0.93$). In *Metastelma eggersii*, the sample from the Caicos Islands is sister to the two Cuban samples.

The other clade ($BS_{ML} = 0.52$, $PP = 0.97$) comprises *Tylodontia* cf. *cubensis* [Liede & Meve LM 3593], as well as taxa hitherto known as *Astephanus urceolatus* [Mangelsdorff RMC 233], *Metastelma fuscum* [RMC 327], and a so-far undescribed species [Mangelsdorff RMC 332, RMC 333]. This clade is sister to the Cuban *Matelea tamnifolia*, the type of *Poicilla* Griseb., but the relationship receives support only in the Bayesian analysis ($PP = 0.96$).

Based on the results of the phylogenetic analysis detailed here, we propose to recognize the clade including

Metastelma eggersii, *Matelea viridivenia* and a hitherto undescribed species (Mangelsdorff RMC 222a, 222b, RMC 357) as a new genus: *Anemotrochus* Mangelsdorff, Meve & Liede. For the clade including *Astephanus urceolatus*, *Metastelma fuscum*, *Tylodontia* cf. *cubensis* and a hitherto undescribed species (Mangelsdorff RMC 332, RMC 333), we propose to reinstall *Tylodontia* Griseb.

Macro- and micromorphology

Morphological circumscription of Anemotrochus and Tylodontia — All seven taxa accepted share a dense indumentum of shoots, petioles, peduncles, and pedicels consisting of eglandular, retrorse, antrorse or spreading multicellular trichomes. *Tylodontia* has ovate to ovate-lanceolate leaf blades with obtuse to slightly cordate bases, acute apices, and straight margins, while *Anemotrochus* has much smaller, usually ovate to broadly lanceolate leaf blades with rounded or cuneate bases, rounded, often minutely apiculate apices and more or less revolute margins.

The corollas of *Tylodontia* and most species of *Anemotrochus* are fused for more than half the total length with a tubular to urceolate basic shape (Fig. 2). Only in *A. viridivenia* is the corolla radiate and only basally fused. The corolla lobes are pronouncedly dextrorsely imbricate in bud and asymmetric in outline when unfolded. *Anemotrochus* possesses papillose or pilose corolla lobes with the right side of the lobes being completely glabrous, laminar-solid staminal corona lobes, reduced or absent interstaminal corona elements, and an expanded basal mouth of the anther wings.

All currently known species of *Tylodontia* have a non-annular corolline corona (cf. also Kunze 1995) consisting of a complicated system of ridges and bulges (Fig. 3A, 3B, 8F), whereas *Anemotrochus* lacks such corolline outgrowths. The anther wings of *Tylodontia* consist of two separate structures, the basal one almost as long (*T. cubensis*) or longer than the apical one, with more or less expanded margins and the upper one being the structure where the pollinia are inserted (Fig. 9C, 10H), *Anemotrochus* lacks a longer expanded basal part (Fig. 3A). All species of *Tylodontia* have more or less pronounced interstaminal coronal elements (Fig. 10H), whereas in *Anemotrochus* only an almost invisible ridge connects the staminal lobes at their bases (Fig. 3A).

Morphological characteristics grouping Anemotrochus and Tylodontia in the Gonolobinae — Because character evolution in *Gonolobinae* has not yet been studied in detail and is beyond the scope of the present analysis, an evaluation of a particular character as apomorphic or as plesiomorphic is still not possible. Of the characters listed as typical for the subtribe (Liede 1997, following, e.g., Stevens 1988, Kunze 1995 and Swarupnandan & al. 1996), all species possess the broad, flat style-head and strongly divergent pollen sacs. *Tylodontia* furthermore possesses the annular corona [sensu Kunze

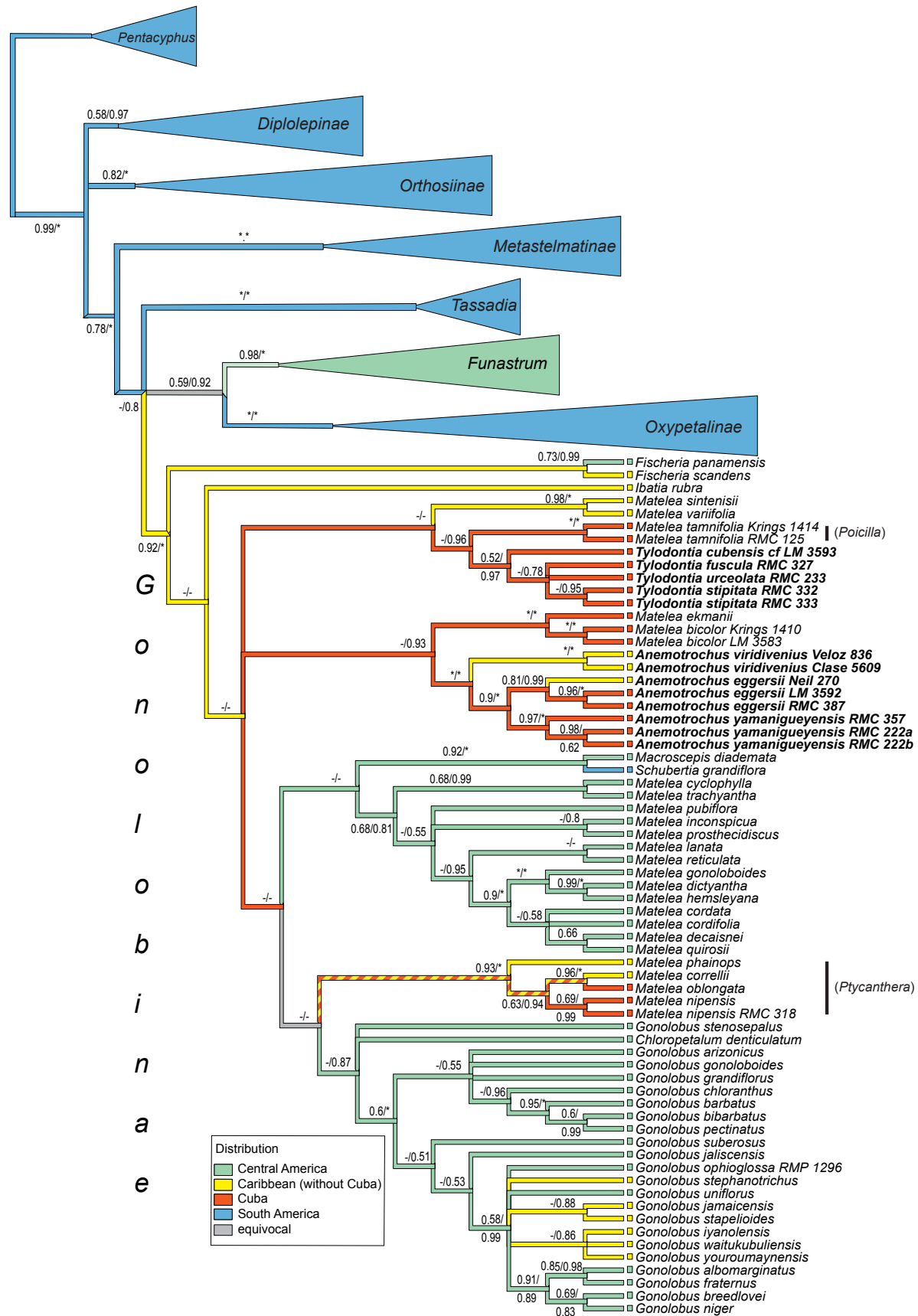


Fig. 1. Maximum Likelihood tree showing position of *Tylodontia* and *Anemotrochus* in *Gonolobinae*. Distribution plotted on tree using “Trace all characters” function of Mesquite (Maddison & Maddison 2011). Numbers indicate Maximum Likelihood bootstrap support (BS_{ML}) / Bayesian Posterior Probability (PP); $BS_{ML} = 100$ and PP = 1.0 indicated by asterisks.

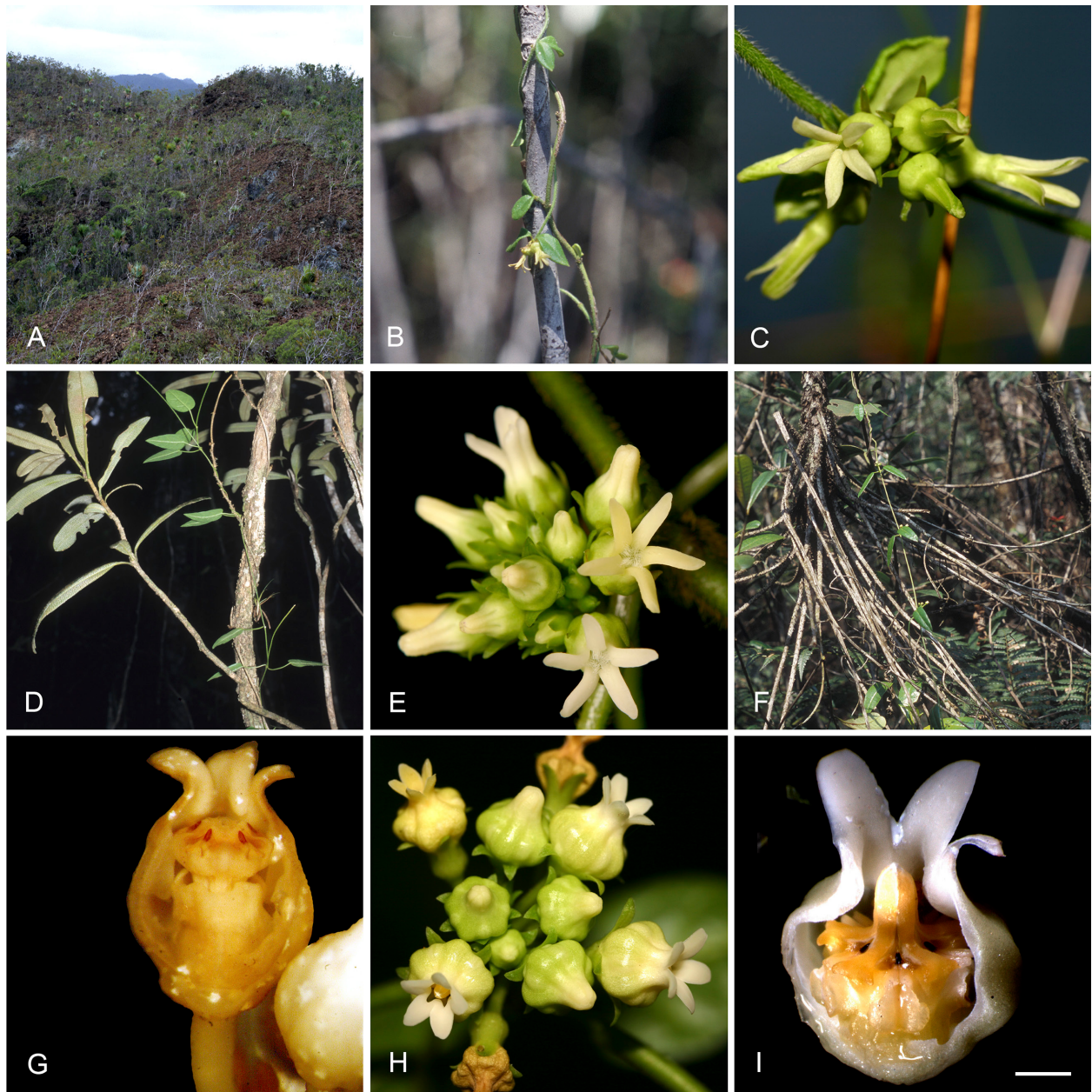


Fig. 2. A: Charrascales E of Yamanigüey, type locality of *Anemotrochus yamanigüeyensis*; B: *A. yamanigüeyensis* climbing at type locality, 6 Mar 2006; C: *A. yamanigüeyensis* flowering in cultivation; D: *Tylodontia fuscula* above banks of Río Palmarito, Piedra la Vela, Guantánamo, 29 Mar 2003; E: *T. fuscula* inflorescence in cultivation; F: *T. stipitata* climbing on *Cyathea* sp. close to entrance of Parque Nacional Alejandro de Humboldt, 3 Mar 2006; G: *T. stipitata* flower, frontside of corolla removed, note prominent corolline corona on left side of corolla, stipitate gynostegium and ringlike corona of fused interstaminal and staminal parts; H: *T. urceolata* inflorescence in cultivation; I: *T. urceolata* flower, frontside of corolla removed, note prominent lower anther wings and connivent-erect connective appendages; scale bar = 1 mm. – Origin: A, C: RMC 222; B: Liede & Meve 3569; D, E: RMC 327; F, G: Liede & Meve 3568; H, I: RMC 233. – Photographs: all by R. Mangelsdorff except B, F by U. Meve.

(1995); but here, sensu Endress & Bruyns (2000), named corolline corona], which, in *Asclepiadeae*, is found only in *Gonolobinae* (Liede & Kunze 1993), though not in all members of the subtribe, including *Anemotrochus*. *Tylodontia urceolata*, in addition, possesses “dorsal anther appendages” (sensu Kunze 1995), an additional appendage exactly on the back of the fertile parts of the anther (cf. Fig. 10H) but not below as is typical for staminal corona formations. The pollinia conform to the definition of Woodson (Woodson 1941: 198) that “the faces of

the pollinium are more or less dissimilar: one convex or rounded and the other flattened or somewhat excavated”, and “in some cases both sides are deeply furrowed or excavated”. In both genera, the anther wings possess additional guiding structures (sensu Kunze 1995). Neither genus possesses glandular hairs, but the shoots of all species are covered over the whole surface by an indumentum composed of multicellular, eglandular, whitish to slightly coloured trichomes, a character frequently found in *Gonolobinae* (and *Oxypetalinae*).

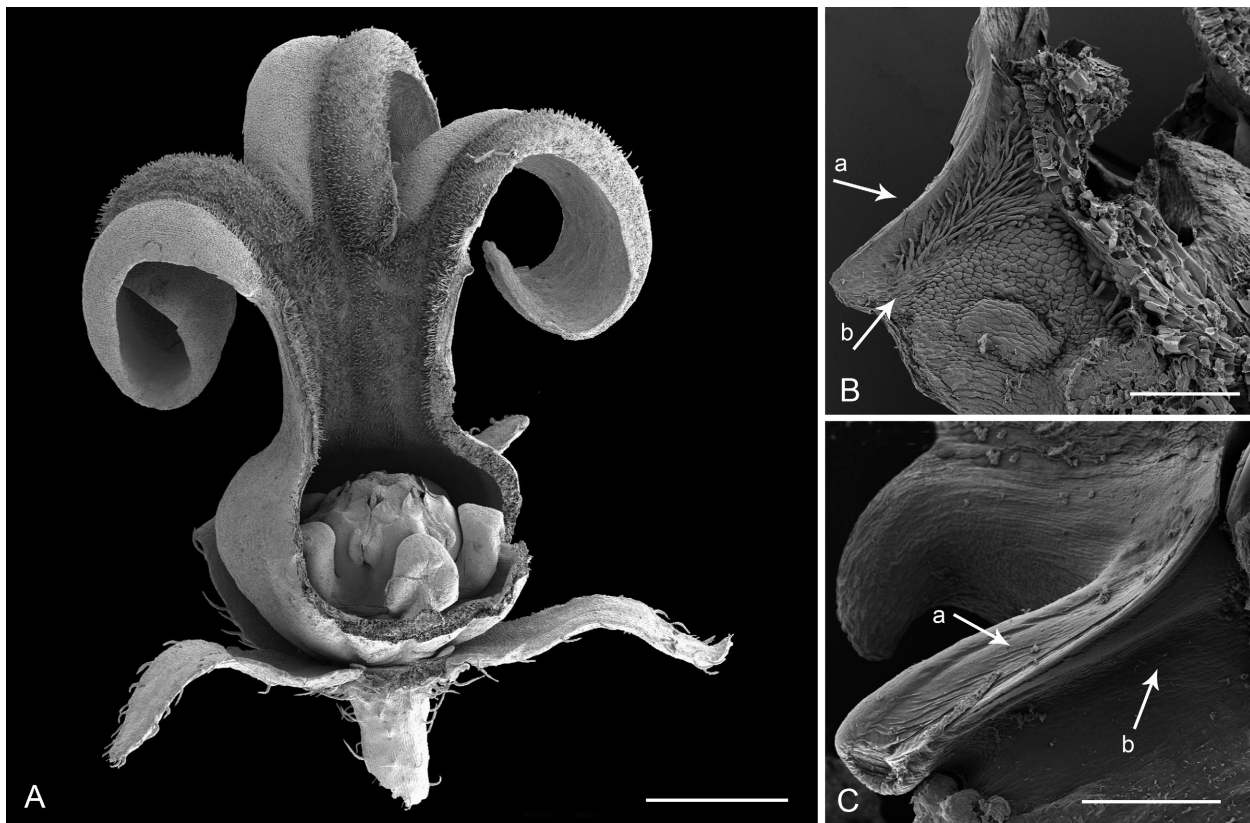


Fig. 3. A: *Anemotrochus yamanigueyensis*, flower with parts of the corolla removed to expose gynostegium with its 5 flattened ovoid corona lobes (note corolla lobe indumentum restricted to right half of lobes); B: *A. yamanigueyensis*, inner side of anther wing with bristles on guide rail section, a: distal, b: proximal ridge; C: *Tyloedontia urceolata*, anther wing including guide rail section without bristles, a: distal, b: proximal ridge. – Scale bars: A = 1 mm; B = 100 μ m; C = 200 μ m. – A, B: RMC 222; C: RMC 233. – SEM photographs: R. Mangelsdorff & M. Ruppel, Goethe-Universität Frankfurt am Main.

Delimitation of Anemotrochus and Tyloedontia from Matelea s.str. — The two genera delimited here can be distinguished from *Matelea* s.str. by a number of characters. Pubescence is ubiquitous on the stems in all species, in contrast to being mostly in one or two lines in *Matelea* s.str. Furthermore, indumentum consists only of non-glandular trichomes of more or less equal length, while *Matelea* s.str. is characterized by a mixed indumentum comprising long and short eglandular trichomes as well as glandular ones. Leaf shape (see above) distinguishes both *Anemotrochus* and *Tyloedontia* from *Matelea* s.str., which is characterized by much larger, narrowly elliptic to lanceolate leaves with cuneate to rounded bases (Krings & Morillo 2015). *Anemotrochus* has distinct laminar-solid staminal coronas, whereas evident interstaminal corona elements are absent. Distinct staminal corona elements are also found in *T. cubensis*; they are more reduced in *T. fuscula*, separating the latter and *Anemotrochus* from *Matelea* s.str. as currently circumscribed by Morillo (2012) and Morillo & Krings (2014). Further characters possibly segregating the new genera from *Matelea* s.str. are the serrate seed margins and the absence of a coma, but as fruits and seeds are not known from all species, these characters might not hold up to future inquisition.

Tyloedontia stipitata possesses, next to a complicated system of corolline corona structures, a gynostegial corona

composed of dominant interstaminal and minor staminal parts that encircle the stipe of the gynostegium, resulting in a structure superficially similar to *Matelea annulata* Alain, where instead the ring-like corona is formed by complete fusion of staminal and interstaminal elements with ligules in the interstaminal position. *Tyloedontia urceolata* has a lobulate interstaminal corona and a vestigial corona in staminal position, a combination of structures also not found in *Matelea* s.str. Below the guiding structure into which the pollinium is to be inserted, another significant structure is present in *Tyloedontia* consisting of bead-like swollen anther wing margins that are almost as long or longer and more prominent than the guide rails themselves (Fig. 10H; cf. also Kunze 1994). These structures presumably function as nectar-exuding structures. Similar structures, but less prominent, can also be found in *Anemotrochus*. Krings (2011) named them “hooked” anther wings when describing *Anemotrochus (Matelea) viridivenius*. Within the *Gonolobinae*, dorsal anther appendages are known only in *Fischeria* and *Gonolobus* (Krings & al. 2008). While *Fischeria* possesses vesicular dorsal appendages, those of *Gonolobus* are laminar (Krings & al. 2008). The architecture of the solid bifurcate dorsal appendage of *T. urceolata* is unique within this subtribe. Finally, nectar chambers that are not known in *Matelea* s.str. can be observed in *Anemotrochus eggersii* and *A. yamanigueyensis*.

Discussion

The present study was conducted to clarify the position of several unusual Caribbean taxa and had therefore restricted sampling of the species-rich *Gonolobinae* as a whole (South American taxa especially are widely missing). Nevertheless, our phylogenetic tree, which is largely in agreement with the one shown by Krings & al. (2008), allows some preliminary conclusions. Similar to *Metastelma* (Liede-Schumann & al. 2014), *Gonolobinae* show a strong geographical pattern. Both Central America and the Caribbean (including Cuba) apparently have been settled more than once, leading to the extreme species richness observed today. In contrast to the results of Krings & al. (2008), the species-poor genus *Fischeria* is retrieved in the ML analysis as unsupported sister to all other *Gonolobinae*, but *Macroscelis* and *Schubertia* are retrieved amid *Matelea* s.l. Core *Gonolobus* remains monophyletic with high support, corroborating the results of Krings & al. (2008). While *Anemotrochus* is very well supported, support for *Tylodontia* is lower. However, this is most likely the result of the missing *LEAFY* sequence of the first-branching *T. cubensis*.

According to Krings (2011), the *Gonolobinae* comprise at least two major lineages, the one including *Gonolobus* s.l., the other one *Fischeria* DC., and a diverse array of taxa largely synonymized with *Matelea* by Woodson (1941). *Matelea* sensu Woodson comprises at least 260 species, and several attempts have been made to describe smaller natural genera (e.g. Stevens 2001; Morillo 2012, 2013, 2015; Morillo & Krings 2014). However, as Krings (2011: 730) stated, “The synorganization of androecium and gynoecium appears to have facilitated such a myriad of gynostegial structural variation ... that it is at times difficult to discern relationships, much less morphological synapomorphies, in the absence of a resolved phylogeny”. *Ibatia* Decne. and *Chloropetalum* Morillo are well separated from the rest of “*Matelea*”, which falls into a number of well-supported clades whose relationships among each other are not yet understood, a result corresponding to the findings of Krings & al. (2008) and Morillo (2015). The small-flowered Caribbean taxa studied here form two such clades, opening two possibilities for integrating these taxa into the existing *Asclepiadoideae* systematics. First, these species could be treated as *Matelea* s.l., adding floral types not yet found in the genus, no matter how widely it is understood. To add *Anemotrochus* and *Tylodontia* to *Matelea* s.l. would most likely also necessitate the inclusion of *Gonolobus*, *Macroscelis* and *Schubertia* in order to establish a monophyletic unit, based on the position of the type species, *M. palustris* Aubl., in Krings & al. (2008), even though this was based only on a single partial sequence (*trnL-F*, 370 bp). The other option is to circumscribe the two lineages as independent genera, following the pattern started by Stevens (2001), and continued by Morillo (2012, 2013, 2015) and Morillo & Krings (2014), who separated sev-

eral genera from the large pool of *Matelea* mostly based on morphological criteria. While the recognition of small segregate genera in *Matelea* counters the general trend in *Asclepiadoideae* to amalgamate small genera into large ones (Goyder 2004; Liede-Schumann & al. 2012; Liede-Schumann & Meve 2015; Khanum & al. 2016), the two genera proposed here are well supported, *Tylodontia* by both morphological and molecular data, and *Anemotrochus* by molecular data and vegetative morphological characters.

The overall similarity between flowers of *Tylodontia* and two of the three *Anemotrochus* species presumably constitutes a parallelism due to adaptation to similar habitats and pollination syndromes, as can be inferred from the phylogenetic analysis. This corresponds with the floral similarity of the two genera with several species of *Metastelma* occurring in the Caribbean, which has caused such taxonomic confusion (this paper; Liede-Schumann & al. 2014; Liede-Schumann & Meve 2015). An apparent problem seems to be that often non-homologous structures have been compared, whereas additional important structures were not investigated thoroughly enough. Longitudinal sections through flowers seem especially promising for character analysis. Also, thorough comparison of vegetative characteristics can lead to natural groupings in *Gonolobinae*; in particular, details of leaf shape and indumentum structure are promising candidates.

Molecular analysis suggests that *Anemotrochus eggersii* and *A. yamanigüeyensis*, both with urceolate to tubular flowers, form a clade with *A. viridivenius* (*Matelea viridivenia*) with rotate, adaxially pubescent flowers of whitish basic colour patterned with green. No flowers could be investigated by ourselves, so that all data are derived from Krings & al. (2008) and Krings (2011). The gynostegium of *A. viridivenius* has a basally ligulate laminar staminal corona, almost completely reduced interstaminal corona parts, an expanded basal part of the anther wings, as known from *Tylodontia*, and shares a similar growth form with *A. eggersii* and *A. yamanigüeyensis*.

Krings (2011) states that *Matelea alainii* Woodson, a Cuban endemic, is more similar to *M. viridivenia* than to any other species of *Matelea* s.l., considering the small leaves, indumentum type, gynostegial and follicle morphology. Unfortunately, despite considerable efforts, no material of *M. alainii* was available for our molecular study; the only extant material are the type (with several isotypes), and one additional poor specimen, all dating from 1956. While a transfer of *M. alainii* to *Anemotrochus* seems not advisable under these conditions, the delimitation of the genus is not affected. If *M. alainii* is really the closest relative of *A. viridivenius*, it will either be retrieved as sister to it or it will be inserted between *A. viridivenius* and the *A. eggersii*-*A. yamanigüeyensis* clade. In either case, *M. alainii* can be included in *Anemotrochus*. The decision not to describe a separate genus for *M. viridivenius* (and *M. alainii*) is independent of the

number of species possibly contained in the group and is a consequence of recent results in *Asclepiadoideae*, which have shown that open and closed flower types, while conspicuously different, have obviously arisen several times inside well-supported lineages; e.g. Bruyns & al. (2015), who have shown that the open-flowered genus *Brachystelma* Sims has evolved several times from inside *Ceropegia* L. with tubular flowers. Therefore, we weigh the full molecular support for the genus and the vegetative similarities of the species higher than the more obvious character of open versus closed flowers.

Taxonomic treatment

Preliminary key to the genera of the *Gonolobinae* in the Antilles (by Gilberto Morillo)

1. Stems, leaves and inflorescences sparsely to $\pm$ densely indumented with whitish multicellular eglandular trichomes, no glandular capitate trichomes present, or these few and inconspicuous **2**
 - Stems, leaves and/or inflorescences sparsely to $\pm$ densely indumented with whitish, yellowish or light brown multicellular eglandular and glandular capitate trichomes **6**
2. Leaf blades oblong-lanceolate, basally sagittate; staminal corona segments prominent-convex and cucullate (hooded), not ligulate (Cuba) **Poicilla** (*P. tamnifolia*)
 - Leaf blades ovate, oblong-ovate to narrowly elliptic, basally cuneate, rounded, obtuse, truncate or slightly cordate (in *Tylodontia cubensis* and *T. urceolata*); staminal corona segments not cucullate, ligulate or not **3**
3. Corolla campanulate, lobes glabrous, basally incurved with an ocellus-like concavity, and with a large white ocellus at apex; staminal corona a costate ridge adnate to stipe in most of its length, apically ligulate; follicles ovoid, 5-ridged (Jamaica) **Jacaima**
 - Corolla rotate-subcampanulate or urceolate, lobes pubescent at least on adaxial face, spreading or somewhat curved, without a basal concavity and without ocelli; staminal corona laminate or thick-laminate, adnate to stipe only at base, not ligulate; follicles fusiform, 10-ridged, smooth or with some isolated protuberances, strongly beaked in some species **4**
4. Corolla rotate, lobes reticulate, pubescent on both faces; staminal corona lobes oblong, extending c. 0.5 mm beyond style-head; corolline corona a protuberance at base of staminal corona; follicles oblong-fusiform, with coarse and prominent protuberances (Hispaniola) **Anemotrochus** (*A. viridivenius*)
 - Corolla urceolate, lobes not reticulate, abaxially glabrous; staminal corona lobes well differentiated, or part of a highly complex system of fused staminal-interstaminal coronas which are folded into corolline corona, shorter or as long as gynostegium, sometimes apparently absent; corolline corona absent or forming a complicated system of ridges and bulges mostly in fused part of corolla; follicles smooth or with some isolated protuberances **5**
5. Leaf blades tapering and without colleters at base; corolline corona absent; follicles fusiform, with some isolated protuberances, and with sparse trichomes (West Indies) **Anemotrochus**
 - Leaf blades basally rounded or slightly cordate, with 2–4 colleters at base; corolline corona part of a complicated system of ridges and bulges mostly in fused part of corolla, or apparently absent or reduced; follicles, as far as known, smooth and glabrous (Cuba) **Tylodontia**
6. Mature leaf blades 2–6 $\times$ 1–3 cm, basally rounded, obtuse or truncate, with glabrous or nearly glabrous surface, pubescent on veins **7**
 - Mature leaf blades usually from 6–20 $\times$ 4–15 cm or larger, basally cordate or subcordate (truncate to cuneate in few *Gonolobus* species, where dorsal laminar anther appendages and corolline coronas occur), usually with pubescent surface and veins **8**
7. Corolla lobes ovate, adaxially pubescent; staminal corona lobes obovate to suborbicular, rounded to emarginate at apex, with a small internal ligule, as long as gynostegium; style-head flat, anther wings thick, slightly incurved; follicles subcylindric-fusiform, not winged (Cuba) **Poicillopsis** (*P. ovatifolia*)
 - Corolla lobes linear-lanceolate, glabrous; staminal corona lobes swollen at base, subtriangular in front view, ridged, rising vertically and then connecting to stipe below anthers, shorter than gynostegium; style-head conical or convex with a slightly raised protuberance; anther wings thin, with divergent apices; follicles fusiform, with 5 undulating wings (follicles unknown for one species) (Hispaniola) **Ptycanthera**
8. Mature stems with thick fissured cork in lower internodes; latex with unpleasant smell; pollinia pendent from caudicles **9**
 - Mature stems lenticellate or with thin layer of cork in lower internodes; latex with or without an unpleasant smell; pollinia horizontal or slightly bent down from caudicles **10**
9. Inflorescence an umbelliform cyme; corolla urceolate or tubular; gynostegium generally included; staminal corona segments fleshy, basally adnate to corolla tube over at least $\frac{1}{2}$ of its length, free at apex and frequently concealing corolla throat; corolline corona present; follicles (5–)7-winged, 2 wings incomplete (Neotropics) **Macroscepis**
 - Inflorescence a racemiform cyme; corolla subcampanulate or campanulate, gynostegium generally exerted; staminal corona segments usually laminar, adnate to base of corolla tube, not concealing corolla throat; corolline corona absent; follicles muricate (Neotropics) **Ibatia**

10. Mature stems 5–10 mm thick or thicker, with light brown pubescence of eglandular spreading long trichomes (1.5–6 mm) and glandular capitate trichomes (0.15–0.4 mm), these turning black when dried; corolla lobes conspicuously crisped in one or both margins; gynostegial corona usually forming an annular structure adnate to stipe, apically 5-lobed in some species; anthers inflated dorsally, vesicular, frequently pear-shaped; corolline corona absent; follicles broadly ovoid to fusiform, smooth or with some small protuberances, neither muricate nor winged (Neotropics) **Fischeria**
- Mature stems generally 1.5–4(–5) mm thick, usually with whitish or yellowish pubescence, eglandular trichomes spreading or retrorse (0.4–2(–2.5) mm), glandular capitate trichomes (0.1–0.4 mm) translucent to light brown when dried; corolla lobes planar, sometimes somewhat concave or marginally undulate, but not crisped; gynostegial corona of staminal and interstaminal segments; staminal corona lobes adnate to base of corolla tube, usually ridge-like and raised, not ligulate, interstaminal segments flabellate, oblong-sulcate or cup-like; corolline corona present, annular but sometimes interrupted or discontinuous, or represented by pubescent mounts of tissue subopposite to anthers; laminar dorsal anther appendages present or absent; follicles 3–5-winged, wings sometimes discontinuous or reduced, absent in one species **11**
11. Laminar dorsal anther appendages present; mature stems conspicuously lenticellate (Neotropics and temperate North America) **Gonolobus**
- Laminar dorsal anther appendages absent; mature stems with a thinly suberized layer, not lenticellate (Neotropics) **Chloropetalum** (*C. denticulatum*)

1. *Anemotrochus* Mangelsdorff, Meve & Liede, gen. nov.

Type: *Anemotrochus eggersii* (Schltr.) Mangelsdorff, Meve & Liede

Diagnosis — Differing from *Matelea* by shoots densely covered throughout with eglandular, retrorse, and multicellular trichomes, small subsessile to very shortly petiolate leaves with tapering bases, a gynostegium with prominent staminal corona parts, and only slightly furrowed pollinia.

Description — Prostrate to ascending vines with white latex. Shoots often differentiated in long and short shoots, often intertwining, surfaces densely and uniformly indumented with eglandular, multicellular, whitish, retrorse trichomes. Bark on older shoots light brown to beige, slightly corky. Leaves opposite, small, not exceeding 15 × 5 mm, subsessile or shortly petiolate; blade ovate or ovate-lanceolate, rarely widely circular, elliptic-lanceolate or obovate, membranous, bases rounded, obtuse to cuneate, margins entire, often revolute. Inflorescences

extra-axillary, mostly on short shoots with up to 6 flowers, subsessile. Flowers small (corolla lobes 2–4.5 mm long), on pedicels to 6 mm long. Corolla broadly urceolate fused for c. ½ of total length, or basally subcampanulate with expanded lobes, white, cream, yellowish-greenish, and whitish with greenish reticulation intensifying to centre; lobes ovate to linear, often twisted, adaxially on left side pubescent with needle-like or short and blunt trichomes (exact pattern for *A. viridivenius* not known). Corolline corona a protuberance at base of staminal corona (*A. viridivenius*) or absent (*A. eggersii* and *A. yamanigueyensis*). Staminal corona laminar to rather solid, c. ½ as long to as long as gynostegium. Interstaminal corona appearing as inconspicuous sinus between staminal corona segments (*A. viridivenius*) to almost invisible. Anther wings separated in a basal, basally centripetal part and an apical, basally centrifugal part (Fig. 4E). Pollinaria with pendulous, slightly furrowed pollinia. Follicles 1 or 2 per flower, fusiform with protuberances on surface, with c. 15 seeds (*A. eggersii*). Seeds ovate to obovate, winged, comose.

Number of species — Three. One species widely distributed in mainly littoral habitats in the Bahamas, Cuba, Jamaica, Hispaniola and numerous small islands, one species a Cuban endemic and one a Hispaniolan endemic. *Matelea alainii* Woodson, also from Cuba, is vegetatively very similar, while the flowers possess no evident staminal corona lobes. However, in the absence of molecular data, it seems premature to transfer this taxon to *Anemotrochus*.

Etymology — The name is derived from Greek άνεμος (ánemos, wind) and τροχός (trochós, wheel), i.e. a windmill, after the appearance of the corolla when viewed from the top.

Key to the species of *Anemotrochus*

1. Corolla rotate to subcampanulate, whitish, with reticulate greenish pattern (Hispaniola) **3. *A. viridivenius***
- Corolla subglobose to urceolate, white, cream, yellowish-greenish or brownish, occasionally with reddish tinge, but without pattern **2**
2. Corolla adaxially strigose; staminal corona laminar, lobes basally connate (Caribbean) . . . **1. *A. eggersii***
- Corolla adaxially with short papillose emergences; staminal corona solid, lobes separated (E Cuba) **2. *A. yamanigueyensis***

1. *Anemotrochus eggersii* (Schltr.) Mangelsdorff, Meve & Liede, comb. nov. ≡ *Metastelma eggersii* Schltr. in Urban, Symb. Antill. 1: 258. 1899 ≡ *Cynanchum eggersii* (Schltr.) Alain in Mem. Soc. Cub. Hist. Nat. “Felipe Poey” 22: 119. 1955. – Holotype: Bahamas, Fortune Island, Feb 1888, H. F. A. Eggers 3869 (B [destroyed];

lectotype, designated here: HBG 117/1921!; isoelectotypes: G 00176944!, GOET 19/2002/8!, HBG 125/1921!, K 000196954!, MPU 019147 [photo!], NY 00111026!, P 00190920!, WU [n.v.]. – Fig. 4.

= *Metastelma jamaicense* Schltr. in Urban, Symb. Antill. 5: 469. 1908 = *Cynanchum rendlei* Stearn in Phytologia 21: 138. 1971 [non *Cynanchum jamaicense* (Griseb.) Woodson in Ann. Missouri Bot. Gard. 28: 210. 1941]. – Holotype: Jamaica, in Long Mountain, West near Kingston, 260 m, 7 Nov 1904, W. Harris 8866 (NY 00111034!; isotypes: BM 000952916!, NY 00111035!, P!, S [photo!]).

Description — Plants herbaceous, ascending, to 2 m high, pronouncedly differentiated in long- and short shoots. *Long shoots* sparsely and irregularly branched, *short shoots* mostly from both sides of a node. *Shoots* perennial, ± lignified, basally corky, bark light brownish or greyish, densely covered over whole surface with multicellular, recurved, 20–300(–500) µm-long trichomes. *Internodes* of long shoots 0.5–2.5 cm long, 0.6–1 mm in diam., short shoots extremely condensed, 1.4–3.2 mm in diam. *Leaves* with 0.2–1.2 mm-long petiole; *blade* 1.5–12(–15) × 1.2–3(–5) mm (largest on Bahamas), broadly circular, elliptic-lanceolate or obovate, basally rounded to cuneate, without colleters, apically mostly emarginate, apiculus 0.2–0.3 mm long, marginally slightly revolute and thickened, adaxially glabrous, abaxially occasionally on veins, margins and apex with scattered recurved trichomes 100–200(–300) µm long. *Inflorescences* normally on short shoots, 1–3-flowered. *Inflorescence bracts* ovate-lanceolate, 0.3–0.6 × 0.2–0.3 mm, pilose. *Pedicels* 0.8–1.8 mm long, sparsely to densely pilose over whole surface or along a single line with recurved, 100–300 µm-long trichomes. *Floral buds* elongated conical, c. 4 × 2 mm, with imbricate, contorted aestivation. *Flowers* fragrant (fide Gillis & al. 12196, Proctor & al. 33196). *Calyx* free to basally fused, abaxially glabrous or with some trichomes at central base, lobes ovate-lanceolate, 1–1.4 × 0.6–0.8 mm, apically obtuse to acuminate. *Corolla* broadly urceolate, fused for c. ½ of total length, 2.5–3.5 mm long, white, cream, yellowish-greenish or brownish (darkening with age); lobes oblong, 1–1.6 × 0.5–1 mm, apically obtuse, reflexed expanded, slightly contorted, adaxially on left side of lobes and on mouth of tube villose with needle-like, 200–400 µm-long trichomes. *Gynostegial corona* with staminal and interstaminal parts, shorter or equalling gynostegium, staminal parts laminar, broadly deltate, 0.3–0.55 × 0.25–0.5 mm, erect, margins occasionally slightly revolute, sometimes slightly tuberculate; interstaminal parts consisting of inconspicuous ridges connecting basal margins of staminal corona. *Gynostegium* 0.5–0.6 mm long, c. 1 mm in diam., sessile. *Anthers* broader than long, trapezoidal. *Anther wings* spreading at an angle of 60–70° relative to flower axis, 0.3–0.6 mm long, basally forming a distinct mouth projecting out of plane of gynostegium. *Connective append-*

ages ovate, c. 0.25 × 0.2 mm, adnate to top of style-head, narrower than stamen. *Pollinarium*: *Pollinia* apically attached to caudicle, liberated at an angle of 45° relative to corpuscular axis, c. 0.15 × 0.6–0.7 mm, narrowly ellipsoid, flattened in cross-section, with a distinct fold relative to corpusculum on inner side; *caudicles* c. 40 µm long, toward corpusculum more cylindric, toward pollinium more flattened; *corpusculum* narrowly ovoid, c. 150 × 70 µm. *Style-head* 0.2–0.25 mm long, 0.6–0.7 mm in diam., green, with mushroom-shaped upper part forming an inconspicuous ring-like structure above corpusculi (“noses” above corpusculi inconspicuous). *Follicles* (seen only on material from the Bahamas) 1 or 2 per flower, angle between them 180° or more, 25–35 × 4–6 mm, obclavate, beaked, light to dark brown, occasionally with isolated, 0.4–1.4 mm-long protuberances, with scattered trichomes. *Seeds* c. 15 per follicle, ovoid to obscurely pyriform, 2.8–3.2 × 1.6–1.7 mm, seta side tuberculate, aseta side smooth; marginally with 0.16–0.32 mm-wide wing with dentate margins; coma 19–22 mm long, white.

Phenology — Flowering presumably over the whole year; flowering specimens were collected in January, March–July, August and October–December.

Distribution — Bahamas, Cuba, Jamaica, Hispaniola (one sterile specimen seen) and numerous small islands (Fig. 6).

Ecology — Coastal habitats on sand and boulders.

Conservation status — As this taxon has a wide distribution and occurs in localities that are of low value for land utilization, the category Least Concern (LC) is appropriate (IUCN 2012, 2016).

Etymology — Named after Henrik Fr. A. Baron von Eggers (1844–1903), Danish soldier and botanist.

Remarks — In overall appearance, the specimens from the Bahamas are more coarse than the ones from Cuba. This might be the result of collection artifacts, as the Cuban specimens were fewer and less well preserved.

Additional specimens investigated — BAHAMAS: 29 Feb. 1980, L. J. K. Brace 344 (NY); Andros: North Andros, beach area on Evans Bay, 13 Dec 1974, D. S. Correll & D. Evans 43938 (NY); Atwood Cay: 3 Dec 1907, P. Wilson 7399 (NY); Berry Islands [N Andros]: Whale Cay, on sand, 29 Jan 1905, N. L. Britton & C. F. Millspaugh 2191 (NY); Castle Island: 22 Dec 1907, P. Wilson 7799 (NY); Cat Island: the Bight and vicinity, rocky rail, 6 Mar 1907, N. L. Britton & C. F. Millspaugh 5879 (NY); Crooked Island: Pitts Town, 9 Jan 1906, L. J. K. Brace 4613 (NY); Long Cay (formerly Fortune Island): between Long Cay Village and boat landing, in whitelands along road, 7 Jun 1977, D. S. Correll & G. R. Proctor 48839 (NY); Fortune

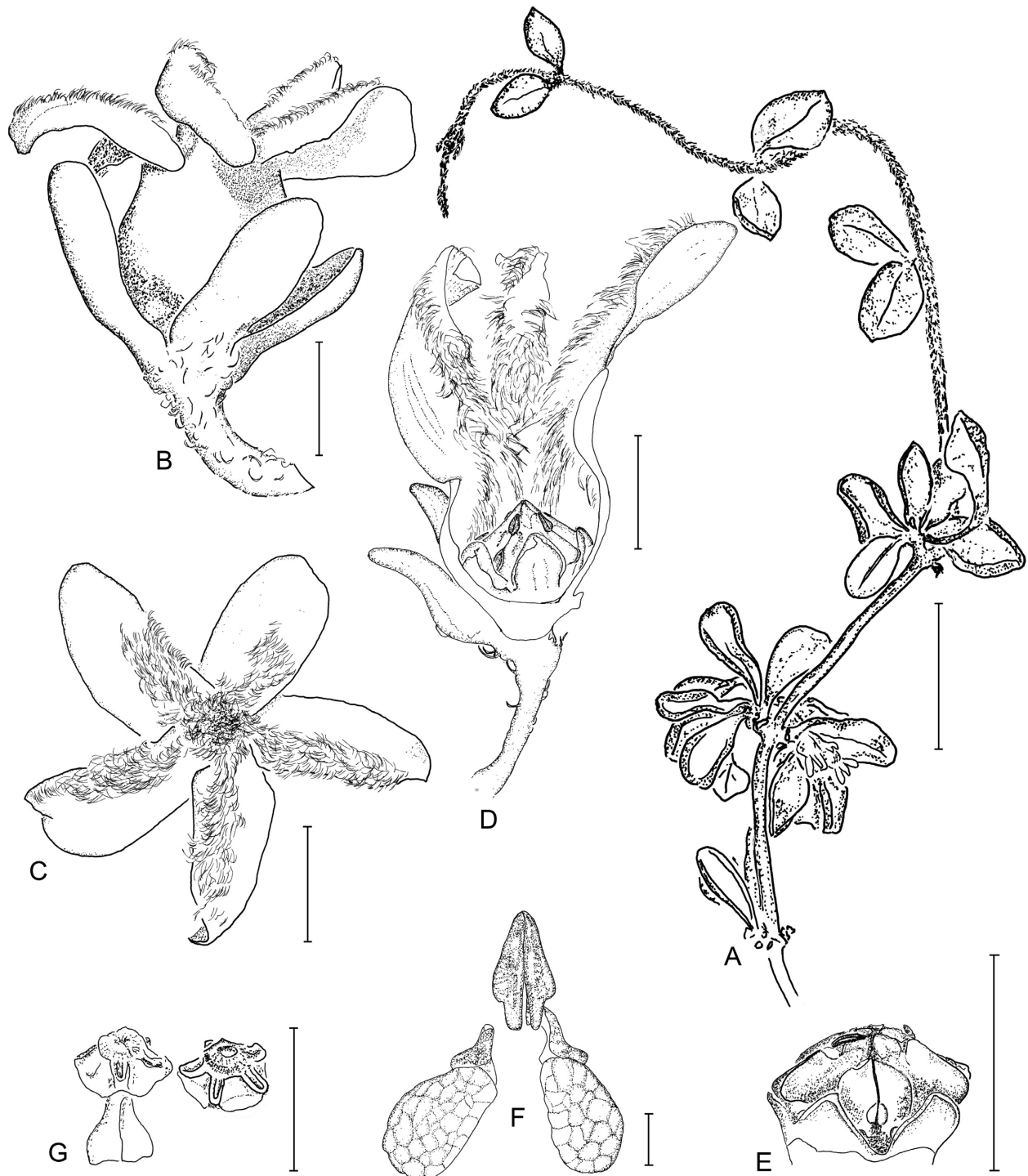


Fig. 4. *Anemotrochus eggersii* – A: section of mature plant with long and short shoots; B: flower; C: corolla, top view; D: flower, longitudinal section; E: gynostegium; F: pollinarium (broken); G: style-head, carpels. – Scale bars: A = 1 cm; B–E, G = 1 mm; F = 0.1 mm. – Origin: A: Ekman 15757; B, C, G: Ekman 15759; D, F: Harris 8866 (type of *Metastelma jamaicense*). – Drawn by R. D. Mangelsdorff.

Island: 5 Feb 1888, *H. F. A. Eggers* 3869 (B, GOET, HBG [2 sheets] NY); Eleuthera: rock sound and vicinity, shell point opposite settlement, 21 Feb 1907, *N. L. Britton* & *C. F. Millspaugh* 5552 (NY); Inagua: Tenados, 14 Oct 1904, *G. V. Nash* & *N. Taylor* 1031 (NY [2 sheets]); Tenados, 28 Oct 1904, *G. V. Nash* & *N. Taylor* 1349 (NY); South Beach, in sandy thickets, 14 Feb 1973, *G. R. Proctor* & *W.*

T. Gillis 33272 (A); Great Inagua, across causeway along South Side Road, about 2 miles E of Matthew Town, in dry coppice, 1 Mar 1974, *D. S. Correll* 41697 (NY); Marguana: 10 miles W of Abraham Bay, 5–6 Dec 1907, *P. Wilson* 7433 (GH, NY); Mayaguana, Pirates Well Up-the-Bay, dunes and whitelands, 9 Feb 1973, *W. T. Gillis* & *G. R. Proctor* 11598 (A, B); Mayaguana, East of Pirate

Wells, 9 Feb 1973, *G. R. Proctor & W. T. Gillis* 33196 (A); Ragged Island: along dirt road near Duncan Town airstrip, in open coppice, 16 Apr 1977, *D. S. Correll* 48349 (NY); Great Ragged Island, 24 Dec 1907, *P. Wilson* 7808 (NY). — CUBA: Prov. Guantánamo: Baracoa, Llano de Maisi, 30 Dec 1959, *Hno. Alain, Al. Lopez-Figueiras* 7068 (HAC); Guantánamo Bay, coastal cliffs, 17–30 Mar 1909, *N. L. Britton* 2195 (NY); Guantánamo, Cainanero, in wild cliffs facing sea, 23 Nov 1922, *E. L. Ekman* 15757 (S); Guantánamo, in wild cliffs facing sea, 23 Nov 1922, *E. L. Ekman* 15755 (NY); Guantánamo-Baitiquirí, 18 Jan 1981, *P. Herrera & al.* 0036109 (HAC); Guantánamo-Manigua, costera cerca de Playa Baitiguiri, May 1968, *J. Bisse & E. Köhler* HFC 8309 (HAJB, JE [2 sheets]); Guantánamo-Cerca de Playa Baitiguiri, 8 Feb 1972, *J. Bisse* HFC 21394 (HAJB [2 sheets], JE); Guantánamo alrededores de Tortuguilla, 12 Apr 1972, *J. Bisse & R. Berazaín* HFC 21826 (HAJB [3 sheets], JE). Prov. Holguín: Bahía de Naranjo, 5 Apr. 2003, *Mangelsdorff* RMC 387 (FR). Prov. Las Villas: Villa Clara, Corralillo, Motembo, cuabales 3 km al suroeste del pueblo, 28 Jan 1981, *R. Berazaín & al.* HFC 43624 (HAJB). Prov. Pinar del Río: Pan de Guijabón, 19 Mar 2006, *Liede & Meve* 3592 (UTB). — TURKS AND CAICOS ISLANDS: CAICOS ISLANDS: Providenciales, at S tip of Five Cays, 16 Dec 1975, *D. S. Correll* 46424 (NY); Pine Cay, 25 Aug 1974, *D. S. Correll* 43128 (NY); North Caicos, open area behind dune near Whitby, 10 Jun 1974, *W. T. Gillis & G. R. Proctor* 12196 (A); North Caicos, Whitby, in coastal coppice, 12 Feb 1978, *D. S. Correll & al.* 49477 (NY); in sandy pine yard, 4 Mar 1911, *C. F. Millspaugh & C. M. Millspaugh* 9212 (GH, NY); South Caicos, 14 Dec 1907, *P. Wilson* 7670 (NY). — TURKS ISLANDS: Grand Turk, 27 Aug 1905, *G. V. Nash & N. Taylor* 3765 (NY); Long Cay [additional no. 9367 mounted on sheet, same locality but different collection date: 22 Mar 1911], rocky plain, 20 Mar 1911, *C. F. Millspaugh & C. M. Millspaugh* 9350 (GH, NY); Eastern Cay [additional no. 9350 mounted on sheet, same collector but different collection date: 20 Mar 1911], Whitelands, 22 Mar 1911, *C. F. Millspaugh & C. M. Millspaugh* 9367 (GH, NY). — HAITI: Presqu'île du Nord-Ouest, Jean Robel, first terrace, east of Bord-de Mer, 7 Jul 1925, *E. L. Ekman* 4011 (B).

2. *Anemotrochus yamanigüeyensis* Mangelsdorff, Meve & Liede, **sp. nov.** – Fig. 2B, C, 3A, B, 5.

Holotype: Cuba, Prov. Holguín, Yamanigüey, 20 m, in low and dry Charrascales, 6 Mar 2006, *Liede & Meve* 3569 (FR!; isotypes: HAJB!, UTB! [in alcohol]).

Diagnosis — Differing from *Anemotrochus eggersii* by the more slender and tender habit, always remaining climbing, instead of the more robust and slightly shrubby habit of *A. eggersii*, only rarely forming short shoots, flowers formed only on long shoots; by corolla lobes that possess short and warty trichomes instead of long, acicular ones as in *A. eggersii* and solid staminal corona lobes instead of laminar ones with revolute margin as in *A. eggersii*.

Description — Plants herbaceous, basally lignified with age, prostrate or twining to c. 1.5 m high, irregularly branched, partially creeping over ground and sending off runners, which emerge some distance from mother plant. Shoots perennial, basally corky, bark light brownish, densely covered over whole surface with multicellular, recurved, 150–750 µm-long trichomes. Internodes 1.5–5 cm long, 0.75–2 mm in diam., slightly thinner and less densely pubescent than nodes. Leaves with 1.2–1.4 mm-long petiole on slightly raised bases; blade 7–8 × c. 4.8 mm, slightly coriaceous, ovate, basally cuneate, without colleters, apically acuminate, apiculus 0.2–0.4 mm long, marginally slightly revolute, thickened, adaxially sparsely covered with recurved, 120–260 µm-long trichomes sitting on slightly lifted pads, abaxially isolatedly covered with recurved, c. 200 µm-long trichomes. Inflorescences on long shoots only, sessile, ± horizontal when in anthesis, sciadioid, up to 6-flowered, up to 3 flowers open synchronously. Inflorescence bracts caducous, narrowly triangular to linear, 0.35–0.9 × c. 0.18 mm, ciliate. Pedicels 10–16 mm long, densely covered over whole surface with recurved, 100–300 µm-long trichomes on slightly lifted pads. Floral buds elongated conical, c. 5.5 × 2.5 mm, with basally imbricate to apically contorted aestivation. Flowers spreading to pendulous, heavily and sweetly fragrant, nectariferous. Calyx basally fused, abaxial bases with trichomes; lobes triangular to narrowly deltate, c. 2 × 0.6 mm, apically acute to acuminate, occasionally ciliate. Corolla urceolate to tubular, slightly thick, whitish-greenish to cream, occasionally with reddish tinge; lobes linear-oblong, 4–4.5 × 0.7–0.8 mm, acute, recurved toward tip, slightly twisted, pronouncedly overlapping, basally and on mouth of tube papillate and with 5 more densely pigmented nerves, apically slightly rugose to warty, adaxially pilose only on left side with warty, 70–520 µm-long trichomes. Gynostegial corona of staminal parts attached directly underneath anthers, shorter than gynostegium, yellowish green; lobes flattened ovoid, c. 0.4 mm long (measured from point at which lobe is adaxially fused with stamen), c. 0.6 mm long, erect to inflexed. Gynostegium c. 0.9 mm long in total (from mouth of guide rails to top of gynostegium c. 0.5 mm), c. 1 mm in diam., atop a bulge c. 0.4 mm long (this is region below mouth of guide rails). Anthers about as long as broad, pentagonal to hexagonal, abaxially convex. Anther wings of adjacent anthers separated into 3 different parts, basal part (“pseudostipe”) c. 0.11 mm long, guide rail part centrifugal, spreading at an angle of c. 45° relative to flower axis, 0.23–0.25 mm long with an additional basal guiding structure almost in same plane as anther and widening at base into a presumable nectar-exuding part; guide rails differentiated into a distal and proximal ridge, which is bristly in between (Fig. 3B). Connective appendages ovate (with acuminate apices), c. 0.35 × 0.2 mm, slightly inflexed and adnate to top of style-head. Pollinarium: pollinia apically attached to caudicle, c. 320 × 120 µm, clavate, ovate in cross-section, caudicles c. 200 µm long, cylindric, slightly convexly recurved; corpusculum elliptic,

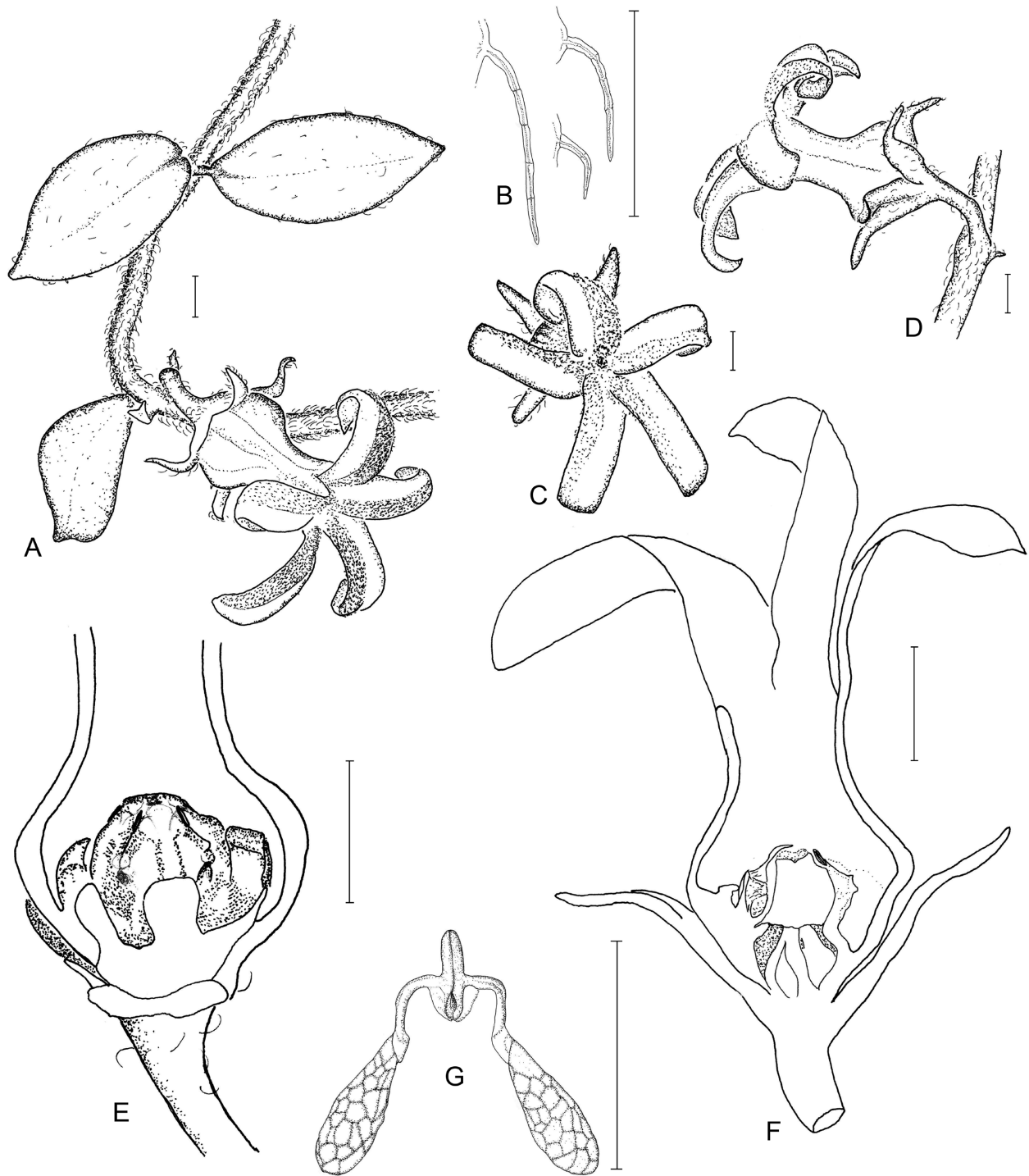


Fig. 5. *Anemotrochus yamanigueyensis* – A: flowering shoot; B: trichomes on shoot; C: flower, top view; D: flower, side view; E: gynostegium; F: flower, longitudinal section; G: pollinarium. – Scale bars: A, C–F = 1 mm; B, G = 0.5 mm. – Origin: A–G: RMC 222. – Drawn by R. D. Mangelsdorff.

basally spreading into arm-like structures, c. 170 μ m long. *Style-head* c. 0.65 mm long, c. 0.55 mm in diam., white, with depressed-conical upper part with prominent central depression. *Fruits* and *seeds* unknown.

Phenology — The type specimen flowered in March. One plant in cultivation (in Germany) flowered regularly from September to January.

Distribution — E Cuba: Holguín Province (Fig. 6).

Ecology — Coastal habitats on ultramafic soil (Fig. 2A). In microphyllous evergreen shrubwoods with bixeric tropical climate (Borhidi 1991).

Conservation status — This taxon, so far as is known, has a very local distribution in an area of low value for

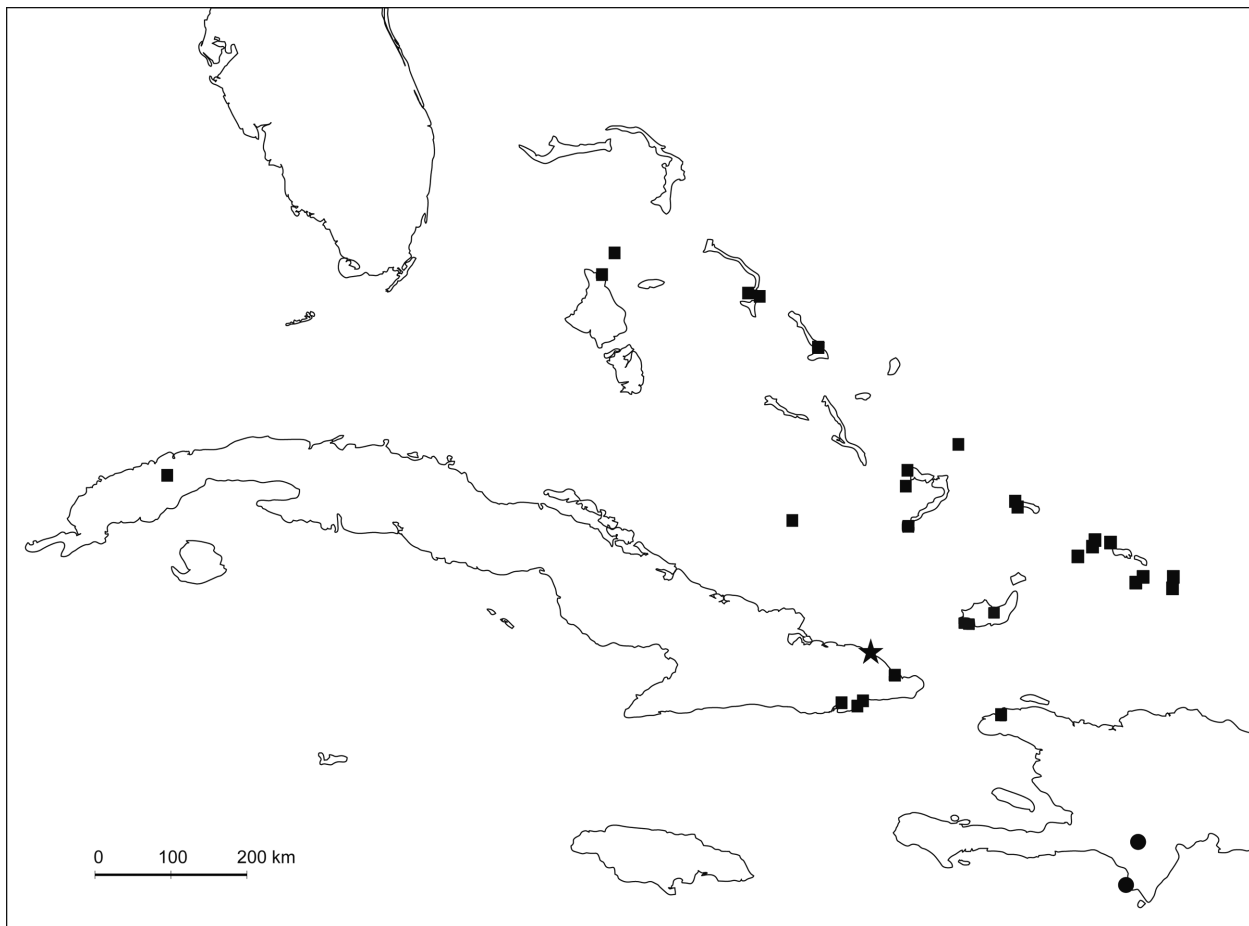


Fig. 6. Distribution of the species of *Anemotrochus* – *A. eggersii* (■); *A. viridivenius* (●); *A. yamanigüeyensis* (★).

land utilization, but it grows on ultramafic soils that might be of interest for mining in the future. The category Vulnerable VU B1ab(iii) is appropriate (IUCN 2012, 2016).

Etymology — Named after the type locality, Yamanigüey, Cuba.

Remarks — The bristly zone between distal and proximal ridge of guide rail was observed only in this species. Possibly it occurs in *Anemotrochus eggersii* as well, but the material analysed was too badly preserved for thorough study.

Additional specimens investigated (paratypes) — CUBA: Prov. Holguín: Minoraea Moa, E of Yamanigüey, 74°44'47"W, 20°34'23"N, 0–10 m, Charrascales (shrub vegetation) on serpentine, near coastline, 5 Mar 2002, *R. Mangelsdorff* RMC 222 (FR, specimen prepared from cultivated material, Bot. Gard. Frankfurt am Main, 11 Dec 2003); Moa, Breñales de Playa Vaca, 9 Nov 1945, *J. Acuña* 13316 (HAC).

3. *Anemotrochus viridivenius* (Alain) Mangelsdorff, Meve & Liede, **comb. nov.** $\equiv$ *Matelea viridivenia* Alain

in *Phytologia* 22: 169. 1971. – Holotype: Dominican Republic, Prov. Pedernales, Cabo Rojo, 4 Nov 1969 (fl.), *A. Liogier* 16637 (NY [photo!]).

Description and illustration — See Krings (2011).

Phenology — Fide Krings (2011) flowering specimens were collected in April, November and December.

Distribution and ecology — Endemic to Hispaniola, xerophytic thickets in the south, from sea level to c. 150 m (Fig. 6).

Etymology — The epithet is derived from Latin *viridis* (green) and *vena* (vein), because of the green-veined corolla.

Additional specimen investigated — DOMINICAN REPUBLIC: Prov. Independencia: Municipio Duverge, La Zursa, part above seabath on hillside, 2036097 N, 022897 E, 15 m, dry spiny forest, very arid, accompanied by *Capparis* sp., *Croton* sp., *Maytenus buxifolia* (A. Rich.) Griseb., *Melocactus lemairei* (Monv. ex Lem.) Miq. ex Lem. and *Prosopis juliflora* (Sw.) DC., 6 Jun 2009, *T. Clase & al.* (JBSD [sub no. 5609]).

2. *Tylodontia* Griseb., Cat. Pl. Cub.: 175. 1866. – Type: *Tylodontia cubensis* Griseb.

Description — Plants climbing to c. 3 m high, sparsely and irregularly branched, with white latex. Shoots, petioles, peduncles and pedicels $\pm$ densely covered by eglandular, retrorse multicellular, basally slightly thickened and variably sized trichomes to 2 mm long; unicellular or glandular trichomes absent. *Stipules* present. *Leaf blade* ovate-lanceolate, basally rounded or slightly cordate. *Inflorescences* extra-axillary, bostrychoid with mostly geminiflorous partial inflorescences, sciadioid-thyrsoïdal, or, more commonly, with a $\pm$ lengthened rachis that can form flowers for an extended period. *Corolla* $\pm$ white, fused for at least $\frac{1}{2}$ of total length, subglobose-urceolate, adaxially pilose or glabrous. *Corolla lobes* carnosae, dextrorsely imbricate in bud, pronouncedly asymmetric with left side basally extended and covering neighbouring lobe, basally often grooved, margins of grooves often continued as ridges in tube. *Corolline corona* a $\pm$ prominent system of epipetal elevations or lobe-like structures at base or in middle of tube. *Gynostegial corona* consisting of staminal and interstaminal parts. *Outer corona* with interstaminal parts often larger (pseudolobes), inserted at base of gynostegium, mostly apically and laterally involute. *Staminal (inner) corona elements* mostly inconspicuous (laminar in *T. cubensis*). *Anther wings* separated in 2 different structures, basal one conspicuous, mostly longer and more prominent than upper one, vertically oriented, upper one (where pollinia are inserted) almost horizontal (basally centrifugal) and seemingly an extension of hyaline membrane covering pollinia. Zone between distal and proximal ridge of guide rail not bristly (Fig. 3C). *Connective appendages* laminar, $\pm$ appressed to style-head (linear and erect in *T. urceolata*). *Gynostegium* $\pm$ stipitate (subsessile in *T. cubensis*). *Pollinarium*: *Pollinia* pendulous, flattened in cross-section, obliquely ovate-kidney-shaped with a more flattened zone at upper median margin relative to anther; *caudicles* basally inserted, cylindric, distally flattened, geniculate; *corpusculum* ovate-elliptic. *Style-head* roughly mushroom-shaped, broader than long, centrally pitted. *Follicles* 1 per flower, fusiform to obclavate, 6–7 cm long, rostrate.

Number of species — Four. Endemic in Cuba, rare.

Etymology — The name is derived from Greek τύλος (*týlos*, wheal or callosity) and οδοῦς (*odoús*, genitive οδόντος, *odóntos*, tooth), presumably because of the swollen, short anthers.

Remarks — The four species are highly variable with regard to their gynostegial corona structures. *Tylodontia cubensis* has broad staminal corona lobes that are basally adjacent but more or less free. In contrast, *T. urceolata* has free interstaminal corona lobes, no visible staminal corona lobes, but bifurcate dorsal anther appendages. *Tylodontia fuscata* has a highly complex system of fused staminal and

interstaminal coronal parts that are folded into the corolline corona lobes, while *T. stipitata* has a ring-like corona consisting of fused staminal and interstaminal parts.

From *Matelea* s.l., *Tylodontia* is easily distinguished by the tiny flowers with an urceolate whitish corolla, more or less laminar (or collar-like) staminal and often rather prominent interstaminal corona parts and anther wings that are separated into two different structures, of which the basal one is much more prominent than the apical one.

Key to the species of *Tylodontia*

1. Corolla to 1.8 mm long, lobes reflexed to touching tube; basal anther wings inconspicuous (W Cuba) **1. *T. cubensis***
- Corolla 2.3–6 mm long, lobes not reflexed; basal anther wings conspicuous with vaulted margins (E Cuba) **2**
2. Corolla adaxially densely tomentose . . . **2. *T. fuscata***
- Corolla adaxially glabrous to isolatedly pilose . . . **3**
3. Corolla 2.4–2.6 mm long, stipe distinctly narrower than gynostegium, connective appendages inconspicuous, inflexed, laminar **3. *T. stipitata***
- Corolla 3–6 mm long, stipe of approximately same width as gynostegium; connective appendages conspicuous, erect, solid, plano-convex in cross-section **4. *T. urceolata***

1. *Tylodontia cubensis* Griseb., Cat. Pl. Cub.: 175. 1866 $\equiv$ *Astephanus grisebachii* M. Gómez in Anales Soc. Esp. Hist. Nat. 23: 276. 1895 [non *Astephanus cubensis* Kunth in Humboldt & al., Nov. Gen. Sp. 3: 206. 1819] $\equiv$ *Cynanchum grisebachii* (M. Gómez) Woodson in Ann. Missouri Bot. Gard. 28: 214. 1941 [non *Cynanchum cubense* (A. Rich.) Woodson in Ann. Missouri Bot. Gard. 28: 213. 1941]. – Holotype: Cuba, Pinar del Río, “Vuelta abajo”, tobacco area from Artemisa to Pinar del Río and south, 1 Aug 1862 [cf. Howard 1988: App. 1 & 9], C. Wright 2964 (GOET 19/2007/71; isotypes: GH 00076855!, K 000196685!, P 00106955!, YU 001845!). – Fig. 7.

Description — Plants ascending twining, to c. 2 m high, sparsely and irregularly branched. *Shoots* herbaceous, basally slightly lignified, densely covered with multicellular, recurved, 70–650 μ m-long trichomes. *Internodes* in fertile part 3–10.5 cm long, 0.7–1 mm in diam. *Stipules* narrowly triangular, c. 0.14 $\times$ 0.06 mm. *Leaves* with 9–15 mm-long petiole; *blade* 18–35 $\times$ 8–25 mm, ovate, basally rounded to obtuse to cordate, with 2–4 colleters at adaxial base, apically acuminate, apiculus 0.4–0.7 mm long, adaxially on veins and margins sparsely and on blade and toward margin isolatedly covered with multicellular, recurved, 70–300 μ m-long trichomes, abaxially mainly on veins and margins sparsely covered with recurved (on living plants presumably erect), 70–500 μ m-long trichomes; marginally sparsely covered with appressed to recurved, 120–500 μ m-long trichomes. *Inflorescences* presumably

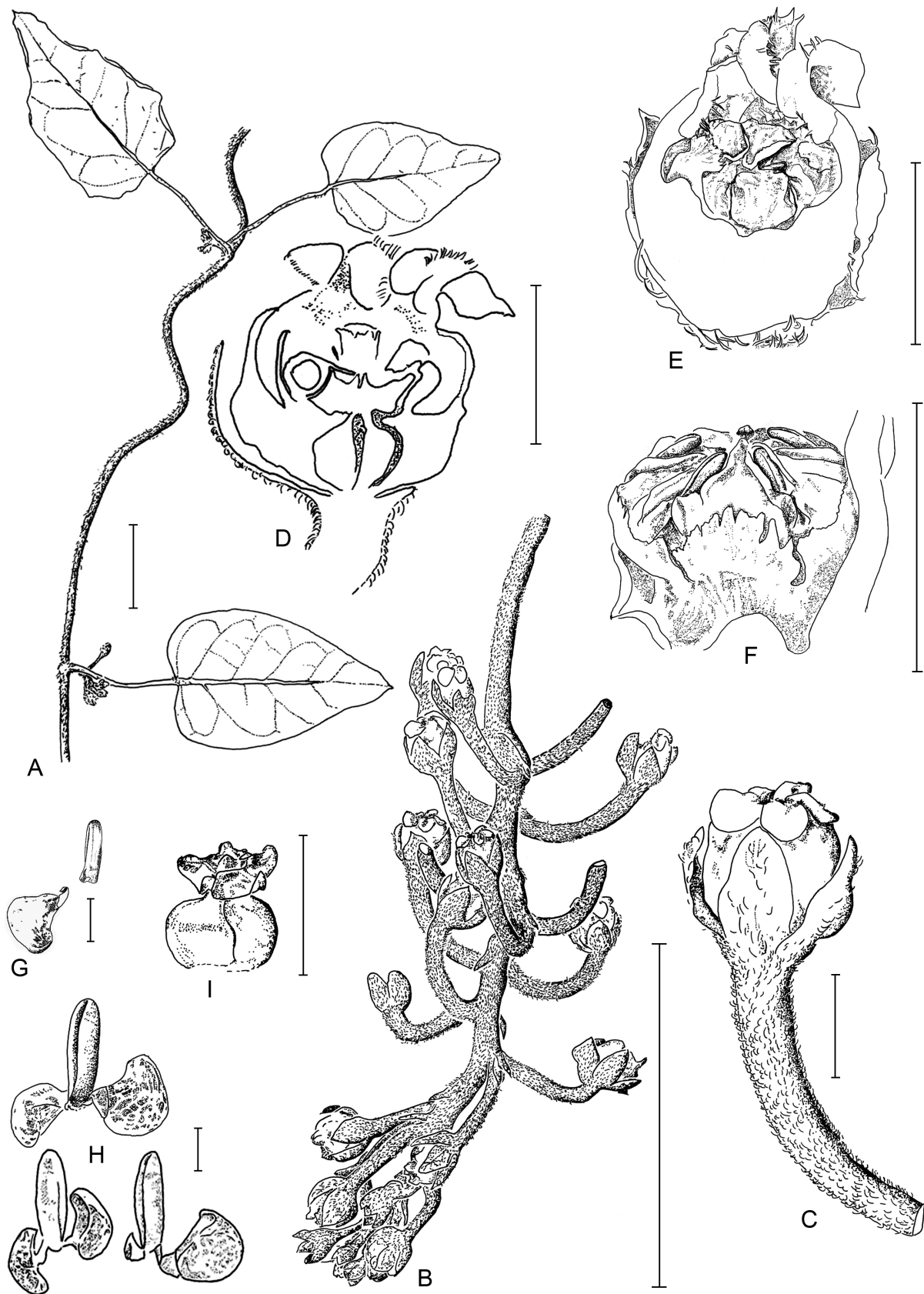


Fig. 7. *Tylodontia cubensis* – A: flowering stem; B: inflorescence; C: flower, side view; D: longitudinal section of flower; E: gynostegium, front of staminal corona removed; F: gynostegium; G: pollinium; H: pollinarium; I: style-head, carpels. – Scale bars: A, B = 1 cm; C–F, I = 1 mm; G, H = 0.1 mm. – Origin: A, F, H: HFC 32315; B, C, E, G, I: Wright 2964; D: HFC 10895. – Drawn by R. D. Mangelsdorff.

pendent, thyrsoïdal, >70-flowered, up to 17 flowers open synchronously. *Peduncles* 2–10 mm long, densely covered with recurved, 70–300 µm-long trichomes. *Rhachis* straight, to 28 mm long. *Floral bracts* lanceolate to linear, 0.25–1 × 0.06–0.25 mm, with trichomes on surface. *Pedicels* 2.5–4 mm long, very densely covered with recurved, 50–220 µm-long trichomes. *Floral buds* globose to conical, 1.2–1.6 × c. 1.2 mm, with imbricate aestivation. *Flowers* presumably erect. *Calyx* free to basally fused; lobes ovate to deltate, 0.8–1.1 × 0.45–0.72 mm, apically obtuse to acute, abaxially pubescent. *Corolla* subglobose, fused for c. ¾ of total length, basal ¼ adnate to gynostegium, 1.4–1.8 mm long (–2.5 mm, *HFC* 32515); lobes lanceolate to ovate, 0.35–0.45 mm wide, apically obtuse, recurved to declinate, twisted, basally asymmetric with left side extended and covering ½ of neighbouring lobe, on adaxial surface basally grooved with ridge into fused part down to base of interstaminal parts of gynostegium (corolline corona), verrucose, usually with sparse, verrucose, 45–95 µm-long trichomes on inner margins, rarely glabrous (*HFC* 32415); corolla cells with radial cuticular ridges, resulting in an intensely verrucose surface. *Corolline corona* system of V-shaped bulges on bases of corolla lobes. *Gynostegial corona* of basally fused lobes differentiated in staminal position, rounded to transversely rectangular, 0.4–0.7 mm long, c. 0.8 mm wide, apically lacinate with up to 7 blunt indentations, appressed to back of anther, shorter (*HFC* 32515) to slightly longer than gynostegium, then apically inflexed (*Wright* 2964, *HFC* 10895). *Gynostegium* c. 0.3 mm long, c. 0.95 mm in diam., sessile to atop a bulge c. 0.15 mm long. *Anthers* slightly wider than long, pentagonal, abaxially convex; *anther wings* extending along whole length of anther, separated into basal part (sensu Kunze 1995), c. 0.15 mm long, centripetal, and upper part (guide rail), c. 0.12 mm long, centrifugal, consisting of distal ridge alone, wings smooth. *Connective appendages* ovate, c. 0.08 mm long, appressed to top of style-head, margins revolute, flanking corpusculi. *Pollinaria*: *pollinia* apically attached to caudicles, 140–270 × 100–160 µm, ovoid, obliquely elliptic in cross-section, with proximal sterile, hyaline region; *caudicles* inserted at base of corpusculum at an angle of c. 140° to corpuscular axis, c. 38–75 µm long, triangular in outline; *corpusculum* narrowly ellipsoid, 140–270 × 40–90 µm. *Style-head* c. 0.75 mm long, c. 0.15 mm in diam., colour unknown, pentagonal, flat, centrally umbonate. *Fruits* and *seeds* unknown.

Phenology — Flowering specimens were collected in October and November.

Distribution — W Cuba: Pinar del Río Province (Fig. 11A).

Ecology — Fide *Bisse & Lippold HFC* 10895: “pinars”.

Conservation status — This taxon has a local distribu-

tion in areas of low value for land utilization and seems to be extremely rare there. The category Vulnerable VU B2ab(ii,iii) is appropriate (IUCN 2012, 2016).

Etymology — Named after Cuba.

Remarks — *Wright* 2964 (GOET) was identified by Howard (1988, App. 1: 159) as the holotype of *T. cubensis*, although Grisebach did not clearly designate this specimen in the protologue. However, Howard is undoubtedly right as Grisebach was domiciled in Göttingen and this sample is the only one annotated by Grisebach.

Because rarely collected and with small, often badly preserved flowers, *Tylodontia cubensis* is one of the enigmatic Cuban *Asclepiadeae*. The flimsy flowers are easily damaged when prepared, as the anthers dislocate. The axes of symmetry are difficult to understand because the corolla lobes overlap each other for almost one-half and are partially twisted.

Pollinaria sizes are rather variable in this species, with the smallest sizes measured in *Wright* 2964 and the largest ones in *HFC* 32515. As can be noted from the description, the specimen from the Pan de Guajaibón (*HFC* 32515) deviates in several aspects from the type. More material is necessary to decide whether these characteristics are of taxonomic value.

Additional specimens investigated — CUBA: Prov. Pinar del Río: Viñales, pinares al sur del pueblo, Nov 1968, *J. Bisse & H. Lippold HFC* 10895 (JE); Bahía Honda, Pan de Guajaibón, 200–670 m, 14 Oct 1976, *A. Álvarez & al. HFC* 32515 (HAJB, JE); Pan de Guajaibón, below top, at bottom of stairs, 22°47'N, 83°22'W, 650 m, 19 Mar 2006, *Liede & Meve* 3593 (UBT).

2. *Tylodontia fuscula* (C. Wright) Mangelsdorff, Meve & Liede, **comb. nov.** = *Metastelma fuscum* C. Wright in *Anales Real Acad. Ci. Méd. Habana* 7: 105. 1870 [and in Sauvalle, *Fl. Cub.*: 120. 1873] = *Astephanus fuscus* (C. Wright) Schltr. in *Urban, Symb. Antill.* 1: 242. 1899 = *Cynanchum fuscum* (C. Wright) Alain in *Mem. Soc. Cub. Hist. Nat.* “Felipe Poey” 22: 118. 1955. – Holotype: Cuba, Prov. Holguín, “En selvas densas, Monteverde”, 29 Oct 1865, *C. Wright s.n.* (GH 00076544!). – Fig. 2D, E, 8.

= *Astephanus schlechterianus* Urb., *Symb. Antill.* 9: 419. 1925 = *Cynanchum ekmanii* Alain in *Mem. Soc. Cub. Hist. Nat.* “Felipe Poey” 22: 118. 1955 [non *Cynanchum schlechterianum* Warb. in Perkins, *Fragm. Fl. Philipp.* 1: 121. 1904]. – Holotype: Cuba, Prov. Holguín, “Prov. Oriente in Sierra de Nipe in cacumine Loma Mensura cr. 1000 m, m. Oct. flor.”, *E. L. Ekman* 3175 (B [destroyed]; **lectotype, designated here: S!**).

Description — Plants ascending, twining, to 2 m high, sparsely and irregularly branched. Shoots herbaceous, ba-

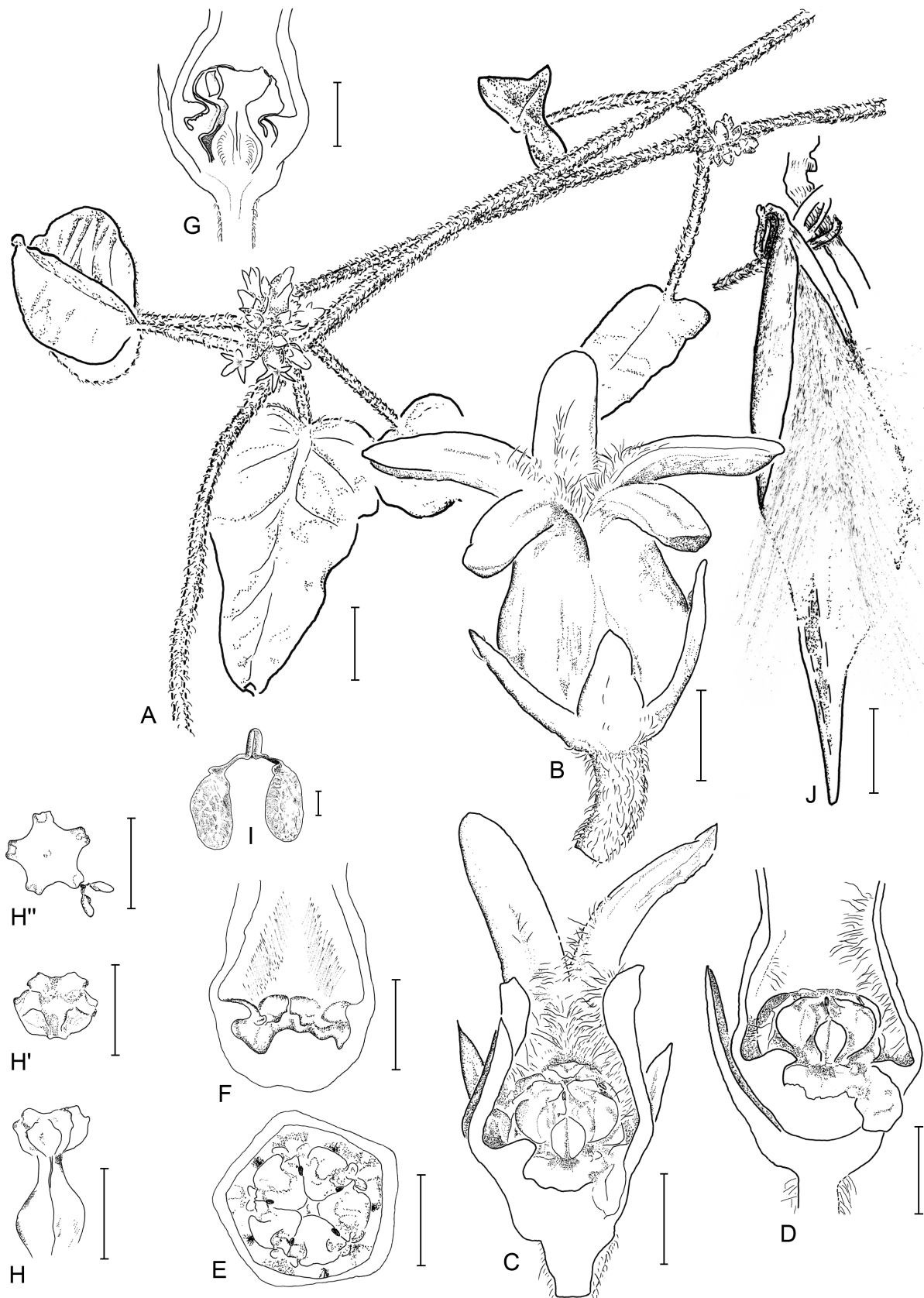


Fig. 8. *Tylodontia fuscula* – A: flowering stem; B: flower, side view; C: longitudinal section of flower; D: longitudinal section of flower, front part of corolline corona bent away; E: gynostegium, top view; F: corolla base, adaxial view, corolline corona; G: longitudinal section of flower; H: style-head, carpels; H': style-head oblique top view; H'': style-head, top view with pollinium attached; I: pollinarium; J: follicle. – Scale bars: A, J = 1 cm; B–H'' = 1 mm; I = 0.1 mm. – Origin: A–H'': RMC 327; I: Wright s.n. (29 Oct 1865); J: Shafer 4051. – Drawn by R. D. Mangelsdorff.

sally lignified to slightly corky, bark greyish to brownish, densely covered over whole surface with multicellular, recurved, 200–1000(–1800) μm -long trichomes. *Internodes* 3–14 cm long, 0.6–1 mm in diam. *Stipules* deltate, 0.14–0.2 $\times$ c. 1 mm. *Leaves* with 1–18(–20) mm-long petiole; *blade* 11–42 $\times$ 2–14(–20) mm, herbaceous, ovate-lanceolate, basally slightly cordate to obtuse or rounded, with 2 or 3 colleters at adaxial base, apically acuminate to apiculate, apiculus c. 0.6 mm long, densely pilose; lamina isolatedly to sparsely covered on veins and margins with recurved trichomes, adaxially 270–500 μm , abaxially 470–1200 μm and marginally 280–800 μm long. *Inflorescences* pendent, sciadioidal, later thyrsoidal, 10–50-flowered, up to 15 flowers open synchronously, partial inflorescences mostly geminiflorous. *Peduncles* 1–3(–5) mm long, densely covered over whole surface with recurved, 120–800 μm -long trichomes. *Rhachis* to 15 mm long. *Floral bracts* linear-lanceolate, 0.8–2 $\times$ 0.2–0.4 mm, pilose and ciliate. *Pedicels* 1–4 mm long, densely covered with recurved, 100–400 μm -long trichomes. *Floral buds* conical, c. 2.7 $\times$ 1.2 mm. *Flowers* spreading to pendulous, with faint jasmine-like fragrance in morning, nectariferous. *Calyx* basally fused; lobes narrowly triangular to ovate, c. 1.4 $\times$ 0.7 mm, apically acute to acuminate, glabrous. *Corolla* elongated urceolate, fused for c. $\frac{1}{2}$ of total length, 3.2–4.5 mm long, white, basally greenish; lobes lanceolate, solid, coriaceous, c. 0.6 mm wide, apically obtuse, in cross-section shallowly triangular, slightly twisted, erect to spreading, abaxially slightly warty, adaxially on central bases and on epipetalous parts of tube with multicellular, 200–360 μm -long trichomes. *Corolline corona* white, solid, $\pm$ horizontally bulging, 0.27–0.38 mm long, consisting of epipetalous, inflexed, V-shaped lobes with slightly denticulate, rounded margins, notched in middle, forming a ring-like structure encircling base of gynostegium, and projecting parts of gynostegial corona. *Gynostegial corona* consisting of staminal and interstaminal parts; staminal parts composed of 2 or 3 small projections on back of anther bases; interstaminal parts lobulate, bluntly deltoid, apically and marginally inflexed, c. 0.1–0.18 mm long, free part in middle to 0.3 $\times$ 0.3 mm, greenish. *Gynostegium* c. 1 mm long, c. 1.3 mm in diam., slightly lifted for c. 0.5 mm. *Anthers* almost square, abaxially convex; *anther wings* separated into basal part c. 0.4 mm long, centrifugal to almost perpendicular at an angle of c. 20° relative to flower axis, prominently bulging and secreting nectar; upper guide rail part c. 0.23 mm long, oriented at an angle of c. 40° relative to flower axis, parallel and basally widened; centrifugal over whole length. *Connective appendages* bluntly triangular, 0.2–0.25 $\times$ 0.37–0.45 mm, inflexed, appressed to top of style-head, white. *Pollinarium*: *pollinia* apically attached to caudicles, 300–350 $\times$ 150–160 μm , ovoid to reniform, narrowly elliptic in cross-section, with proximal sterile hyaline region; *caudicles* c. 170 μm long, flattened to cylindrical; *corpusculum* ellipsoid, c. 150 $\times$ 60 μm . *Style-head* 0.38–0.45 mm long, 0.79–0.86 mm in diam., green, pen-

tagonal, flat. *Follicles* 1 per flower, 9–12 $\times$ 0.6–0.75 cm, obclavate to fusiform, ovate in cross-section, apically strongly beaked, light brown, glabrous; fruit stalks curved at an angle of 90°. *Seeds* light brown, pyriform, 3.5–3.8 $\times$ 1.5–2.5 mm, seta side faintly sculptured with longitudinal ridges, a seta side additionally with tubercles; marginally with c. 0.4 mm-wide wing; coma c. 2.5 cm long, white.

Phenology — Flowering specimens were collected in August and October. In cultivation in Germany the species flowered in December and April–August.

Distribution — Cuba: mountainous regions in the east (Fig. 11B).

Ecology — From higher regions on ultramafic soils. The first author found the species (*RMC* 327) growing amid dense undergrowth on the steep and shady forested banks of the Río Palenque (Fig. 2D). The plant was rooted in thick humus layers covered by mosses and next to *Odontosoria aculeata* (L.) J. Sm. (*Lindsaeaceae*), *Pilea* sp. (*Urticaceae*) and *Poaceae* spp.

Conservation status — This taxon has a local distribution in areas of low value for land utilization. As the political situation in Cuba might change in the future, currently unexploited or protected areas might be in danger of change of land use. The category Vulnerable VU B1ab(ii,iii) is appropriate (IUCN 2012, 2016).

Etymology — The epithet is derived from Latin *fuscus* (brown), presumably because of the brownish indumentum of dried specimens.

Remarks — The two specimens cited below, collected and determined by Shafer as *Tylodontia fuscula*, are the only known collections of fruits in this genus.

Additional specimens investigated — CUBA: Prov. Holguín: Sierra de Cristal, Pico de Cristal, 25 Aug 1959, *M. Lopez Figueiras s.n.* (HAC); Piedra la Vela, above banks of río Palmarito, 500 m, 29 Mar 2003, *R. D. Mangelsdorff RMC 327* (FR).

Tylodontia cf. *fuscula* with fruits: CUBA: Prov. Holguín: S of Sierra Moa, Camp la Gloria, N of Río Jaguaní, plain with “monte mala” over deep iron ore, exposed serpentines, 24–30 Dec 1910, *J. A. Shafer 8070* (A, NY); vicinity of Camp la Benito Oriente, Troea, N of camp, 900 m, 24 Feb 1910, *J. A. Shafer 4051* (NY).

3. *Tylodontia stipitata* Mangelsdorff, Meve & Liede, sp. nov. — Fig. 2F, G, 9.

Holotype: Cuba, Prov. Guantánamo, Mun. Imías, Sierra del Purial, loma al noreste de Alto de la Yamagua (c. 3 km N de Los Lechugos), 800–900 m, Charrasco, suelo laterita, 18 Apr 1984, *I. Arias & al. HFC 53422* (JE!); isotypes: B [n.v.], HAJB [n.v.].

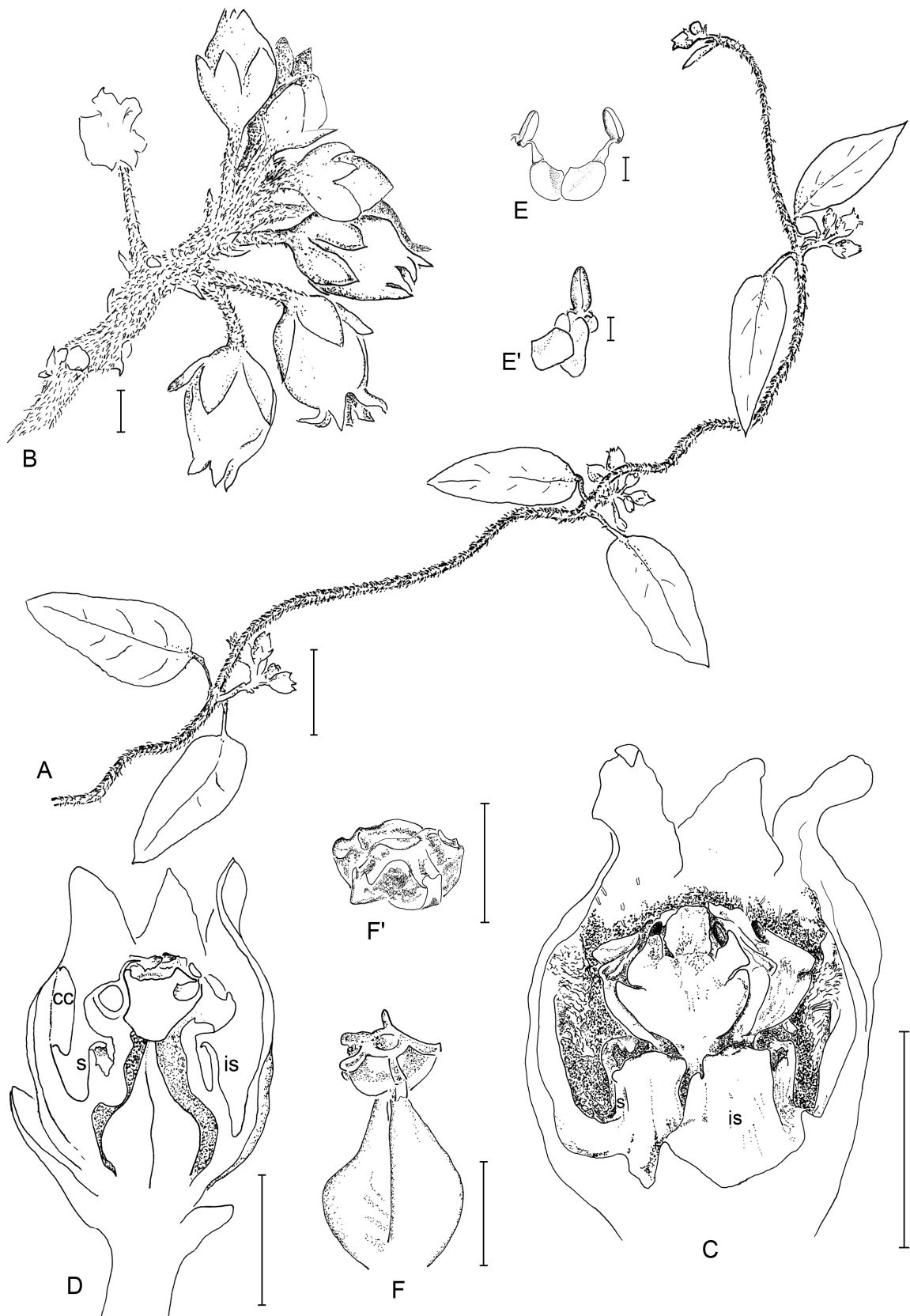


Fig. 9. *Tyloedontia stipitata* – A: flowering stem; B: inflorescence; C: flower, side view, front part of corolla removed, s: staminal part of corona, is: interstaminal part of corona; D: longitudinal section of flower, cc: corolline corona, s: staminal part of corona, is: interstaminal part of corona; E, E': pollinaria; F: style-head, carpels; F': style-head, oblique top view. – Scale bars: A = 1 cm; B–D, F, F' = 1 mm; E, E' = 0.1 mm. – Origin: A, B, D, E, F: HFC 53422; C, E: HFC 44947; F: HFC 42177. – Drawn by R. D. Mangelsdorff.

Diagnosis — Differing from *Tylodontia cubensis* by less floriferous inflorescences, much larger flowers, a stipitate gynostegium ensheathed by a ring-like corona, and lower anther wing parts that are much more prominent than the guide rails.

Description — *Plants* ascending, twining, to 2 m high, sparsely to irregularly branched. *Shoots* basally slightly woody with brownish-greyish bark, subglabrous to strigose over whole surface with multicellular, recurved, 200–1000 µm-long trichomes. *Internodes* 5–10 cm long, c. 1 mm in diam. *Stipules* narrowly triangular to deltate, c. 0.2 × 0.18 mm. *Leaves* with 1–18 mm-long petiole; *blade* 7–40 × 3–19 mm, ovate-lanceolate, basally cordate to rounded or cuneate, with 2 colleters at adaxial base, apically acuminate, apiculus c. 0.2 mm long, densely pilose; lamina glabrous, adaxially on veins and margins sparsely covered with appressed to recurved or flexuous, 100–450 µm-long trichomes, abaxially with erect to recurved, 200–600 µm-long trichomes; main vein adaxially often sunken in fold. *Inflorescences* thyrsoidal, to 17-flowered with up to 7 flowers open synchronously. *Peduncles* 4–13 mm long, glabrous to densely covered over whole surface with recurved, flexuous or inflexed, 100–600 µm-long trichomes. *Rhachis* to 11 mm long. *Floral bracts* deltoid to lanceolate, 0.4–1 × 0.1–0.6 mm, pilose and ciliate. *Pedicels* 3–6 mm long, glabrous or sparsely to densely covered over whole surface or along a single line with flexuous to inflexed trichomes. *Floral buds* conical to ovoid, c. 1.8 × 1.7 mm. *Flowers* oriented at an angle of c. 60°, secund. *Calyx* basally fused; lobes ovate, 1.2–1.6 × 0.6–0.8 mm, apically acute, abaxially glabrous or nearly so. *Corolla* urceolate, fused for c. 4/5 of total length, 2.4–2.6 mm long, subcarinose, yellowish white, abaxially glabrous, glossy, adaxially with a few isolated, papillose trichomes; lobes triangular, c. 0.6 × 0.5 mm, slightly coriaceous, apically acute, left side larger than right side, twisted, spreading. *Corolline corona lobes* V-shaped, 0.15–0.2 mm long, epipetalous in middle of tube, separated from each other in petal sinuses, thereby forming a conspicuous system of ridges separating interstaminal sections, solid, surface slightly warty. *Gynostegial corona* with staminal and interstaminal parts, basally connate, encircling stipe of gynostegium like a collar; staminal parts shorter and more slender than interstaminal parts, erect, apically inflexed, slightly crenulate, on adaxial side connate to stipe by a ridge and here lower as in interstaminal position, abaxially basally fused with corolla tube and forming ridges that separate interstaminal cavities, interstaminal parts more prominent, free sections c. 0.3 mm long, laminar, forming a cavity below lower guide rail. *Gynostegium* 0.55–0.6 long, c. 1.1 mm in diam., stipitate; free stipe 0.2–0.85 mm long from base of staminal corona, 0.42–0.48 mm from adaxial and 0.72–0.86 mm from abaxial base of interstaminal corona parts. *Anthers* broader than long, broadly rhombic, abaxially prominently convex; *anther wings* separated into basal part c. 0.4 mm long, centripetal, prominently bulging and spreading, up-

per guide rail part 0.25–0.3 mm long, centrifugal, consisting of proximal and distal ridge. *Connective appendages* triangular to ovate, 0.25–0.3 × 0.15–0.32 mm, inflexed, appressed to style-head. *Pollinaria: pollinia* (sub-)apically attached to caudicles, 200–240 × 120–140 µm, obliquely obovoid-rectangular, elliptic in cross-section, with an upper, prominent, deltoid protrusion; *caudicles* c. 80 µm long, sub-basally inserted at corpusculum, convexly recurved; *corpusculum* narrowly ellipsoid, c. 160 µm long. *Style-head* c. 0.4 mm long, c. 1.1 mm in diam., colour unknown, pentagonal, with discoid, centrally depressed upper part. *Fruits* and *seeds* unknown.

Phenology — Flowering specimens were collected in April, May and October.

Distribution — Cuba: mountainous regions in the east, rare (Fig. 11C).

Ecology — Typically found in regions with high precipitation and in Charrascos on ultramafic soils. Liede-Schumann and Meve (LM 3568, UBT) found this species in the Sierra de Moa climbing on shrubs and low tree ferns (Fig. 2F).

Conservation status — This taxon has a local distribution in areas of low value for land utilization and partly within the protected lands of the Parque Nacional Alejandro de Humboldt. As the political situation in Cuba might change in the future, currently unexploited or protected areas might be in danger of change of land use. The category Vulnerable VU B1ab(ii,iii) is appropriate (IUCN 2012, 2016).

Etymology — The epithet is derived from Latin *stipes* (stalk), because of the stipitate gynostegium.

Remarks — This new species has been found several times since 1980.

Additional specimens investigated (paratypes) — CUBA: Prov. Holguín: Alrededores del Aserrío La Melba, 450–500 m, Charrascos con *Bonnetia cubensis* [(Britton) R. A. Howard], 28 Apr 1980, A. Álvarez & al. HFC 42177 (HAJB [2 sheets]); Moa, subida al Alto de Galinga por el camino del norte, 800–1000 m, Charrascos de altura, 4 May 1980, A. Álvarez & al. HFC 42790 (HAJB, JE); Moa, cerca del Aserrío La Melba, 400–500 m, Charrascos, 25 Apr 1981, G. Arnold & al. HFC 44947 (B [n.v.], HAJB, JE); Moa, Camino de la mina Delta, Jul 1949, Clemente 6827, Hno. Alain 927, *Chrysogone* s.n. (HAC); along road to La Melba, outside entrance of Humboldt National Park, 350 m, 3 Mar 2006, Liede & Meve 3568 (UBT). Prov. Guantánamo: Baracoa, Alto entre la Loma al Mirador y la Loma Buena Vista en el camino desde el río Baez, hasta el río Los Naranjos, 500 m, 6 Aug 1975, A. Álvarez & al. HFC 26941 (HAJB).

4. *Tylodontia urceolata* (Griseb.) Mangelsdorff, Meve & Liede, **comb. nov.** $\equiv$ *Astephanus urceolatus* Griseb., Cat. Pl. Cub. 173. 1866 $\equiv$ *Cynanchum wrightianum* Alain in Mem. Soc. Cub. Hist. Nat. “Felipe Poey” 22: 118. 1955 [non *Cynanchum urceolatum* (E. Fourn.) K. Schum. in Engler & Prantl, Nat. Pflanzenfam. 4(2): 253. 1895]. – Holotype: Cuba, Prov. Guantánamo, “in monte Toro pr. S. Anna”, *C. Wright s.n.* (GOET id. 9547, reg. no. 9514!). – Fig. 2H, I, 3C, 10.

Description — Plants ascending, twining to 2 m high, sparsely irregularly branched. Shoots densely covered over whole surface with multicellular, recurved and straight 80–900 μ m-long trichomes, basally woody, with greyish bark. Internodes 8–10 cm long, 0.5–1 mm in diam. Stipules narrowly triangular to deltate, c. 0.14 $\times$ 0.1 mm. Leaves with 4–17 mm-long petiole; blade 17–35 $\times$ 7–18 mm, herbaceous, ovate, basally cordate, with 0–2 colleters at adaxial base, apically acuminate, apiculus 0.2–0.6 mm long, lamina on both surfaces isolated to sparsely covered over whole surface to mainly on veins and margins with erect to recurved, 100–800 μ m-long trichomes, margins sparsely to densely ciliate with appressed to recurved, 100–700 μ m-long trichomes. Inflorescences horizontal, thyrsoidal to sciadioidal, spreading to horizontal, 3–6(–11)-flowered, 2–4 flowers open synchronously. Peduncles 3–6 mm long, densely covered over whole surface with recurved or inflexed, 50–300 μ m-long trichomes. Rhachis straight, c. 2.4 mm long. Floral bracts lanceolate to linear, 0.5–1.8 $\times$ 0.3–0.7 mm, abaxially with trichomes, ciliate. Pedicels 2–4.5 mm long, sparsely to densely covered over whole surface with recurved or inflexed, 50–250 μ m-long trichomes. Floral buds conical, c. 4 $\times$ 3.5 mm, with 5 bulges in interstaminal and 5 smaller ones in staminal position (Fig. 10C, E). Flowers spreading to horizontal, no scent noted by collectors, nectariferous. Calyx almost free; lobes linear to ovate, c. 2.7 $\times$ 0.7–0.8 mm, apically obtuse to acute, glabrous or nearly so. Corolla urceolate, fused for c. $\frac{2}{3}$ of total length, 4–5 mm long, white, basally greenish; lobes lanceolate to triangular, c. 1.25 $\times$ 0.9–1.3 mm, coriaceous, adaxially rugose, apically obtuse to acute, recurved. Corolline corona forming low ridges in interstaminal position, slightly verrucose, glabrous. Gynostegial corona separated in almost free staminal and interstaminal parts, staminal parts inconspicuously lifted zones on base of anthers, c. 0.1 mm high, interstaminal parts whitish-greenish, c. 0.8 mm long, lobules triangular, apices slightly involute, enclosing a cavity below lower anther wings, basally emarginate. Dorsal anther appendage a bifurcate, solid crest on dorsal top of anther with lateral tips diverging outward. Gynostegium c. 2 mm long, c. 2.7 mm in diam., atop a stipe c. 0.8 mm long. Anthers about as long as broad, almost square, with longitudinal ridges at both sides; anther wings separated into basal part c. 0.8 mm long, to c. 0.2 mm in diam., prominently bulging over whole length, resembling spreading wings, almost paral-

lel to floral axis, secreting nectar; apical part (guide rail) c. 0.65 mm long, forming an angle of slightly more than 90° to floral axis, basally centrifugal, forming a distinct “mouth” with basal parts resulting in “lips” projecting beyond plane of anthers, consisting of a distal and proximal ridge. Connective appendages narrowly ligulate, c. 1.4 $\times$ 0.35 mm, erect, apically connivent, narrower than stamens, yellowish. Pollinarium: pollinia apically attached to caudicles, c. 450 $\times$ 260 μ m, obliquely ovoid, elliptic in cross-section, without hyaline zone; caudicles cylindric to flattened (toward pollinium), 130–140 μ m long, geniculate; corpusculum narrowly ellipsoid, c. 230 $\times$ 120 μ m. Style-head c. 1.3 mm long, c. 0.75 mm in diam., whitish-greenish, pentagonal, roughly barrel-shaped, centrally depressed. Fruits and seeds unknown.

Phenology — Flowering specimens were collected in October. In cultivation in Germany the species flowered October–December.

Distribution — Cuba: mountainous regions in the east, rare (Fig. 11D).

Ecology — Regions with high precipitation, typically on ultramafic soils (R. Mangelsdorff, pers. obs.).

Conservation status — This taxon has a local distribution in areas of low value for land utilization. As the political situation in Cuba might change in the future, currently unexploited or protected areas might be in danger of change of land use. The category Vulnerable VU B2ab(ii,iii) is appropriate (IUCN 2012, 2016).

Etymology — The epithet is derived from Latin *urceolus* (a small urn), because of the urn-shaped (urceolate) corolla.

Remarks — The type locality given in the protologue and by Schlechter (1899: 240), Monte Toro near Santa Ana, deviates from the one given on the type specimen, Santa Ana, Monte Verde. The latter locality is about 20 km E of Monte Toro. In the distribution map (Fig. 11D), the locality given on the type sheet was used.

Within *Gonolobinae*, the erect, solid, and ligulate structure of the connective appendages of *Tylodontia urceolata* is exceptional. Grisebach (1866: 173) noticed the stipitate gynostegium; however, neither Grisebach (1866) nor Schlechter (1899) noted the prominent interstaminal corona closely attached to the base of the stipe. This character would have excluded this taxon from *Astephanus*. Schlechter (1899: 240), however, noted the overall similarity of the corolla with *T. cubensis*.

Additional specimen investigated — CUBA: Prov. Guantánamo: Santa Ana, Alto Iberia, c. 600 m, dwarf rainforest on plateau, 7 Mar 2002, R. D. Mangelsdorff RMC 233 (FR) and in Bot. Gard. Frankfurt am Main, 2 Dec 2005 (fl.) (FR [in alcohol]).

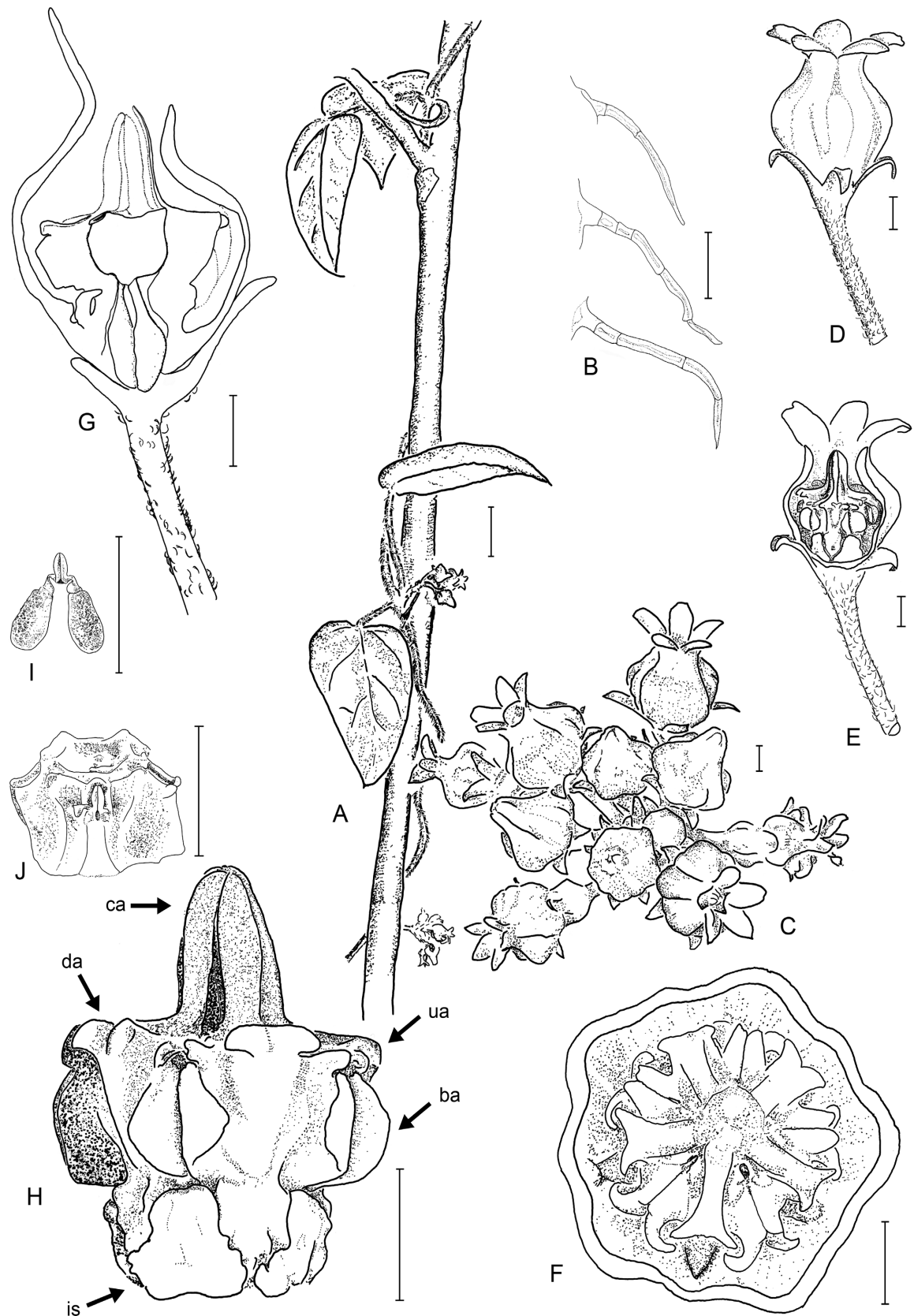


Fig. 10. *Tylodontia urceolata* – A: flowering stem; B: trichomes on shoot; C: inflorescence; D: flower, side view; E: flower, side view, front of corolla removed; F: base of corolla with gynostegium, top view, corolline corona, basal anther wings, dorsal anther appendages, connective appendages; G: longitudinal section of flower; H: gynostegium side view, ca: connective appendages, da: dorsal anther appendages, ba: basal anther wing part, ua: upper anther wing part, is: interstaminal corona; I: pollinarium; J: style-head. – Scale bars: A = 1 cm; C–H, J = 1 mm; B, I = 0.1 mm. – Origin: A–J: RMC 233. – Drawn by R. D. Mangelsdorff.

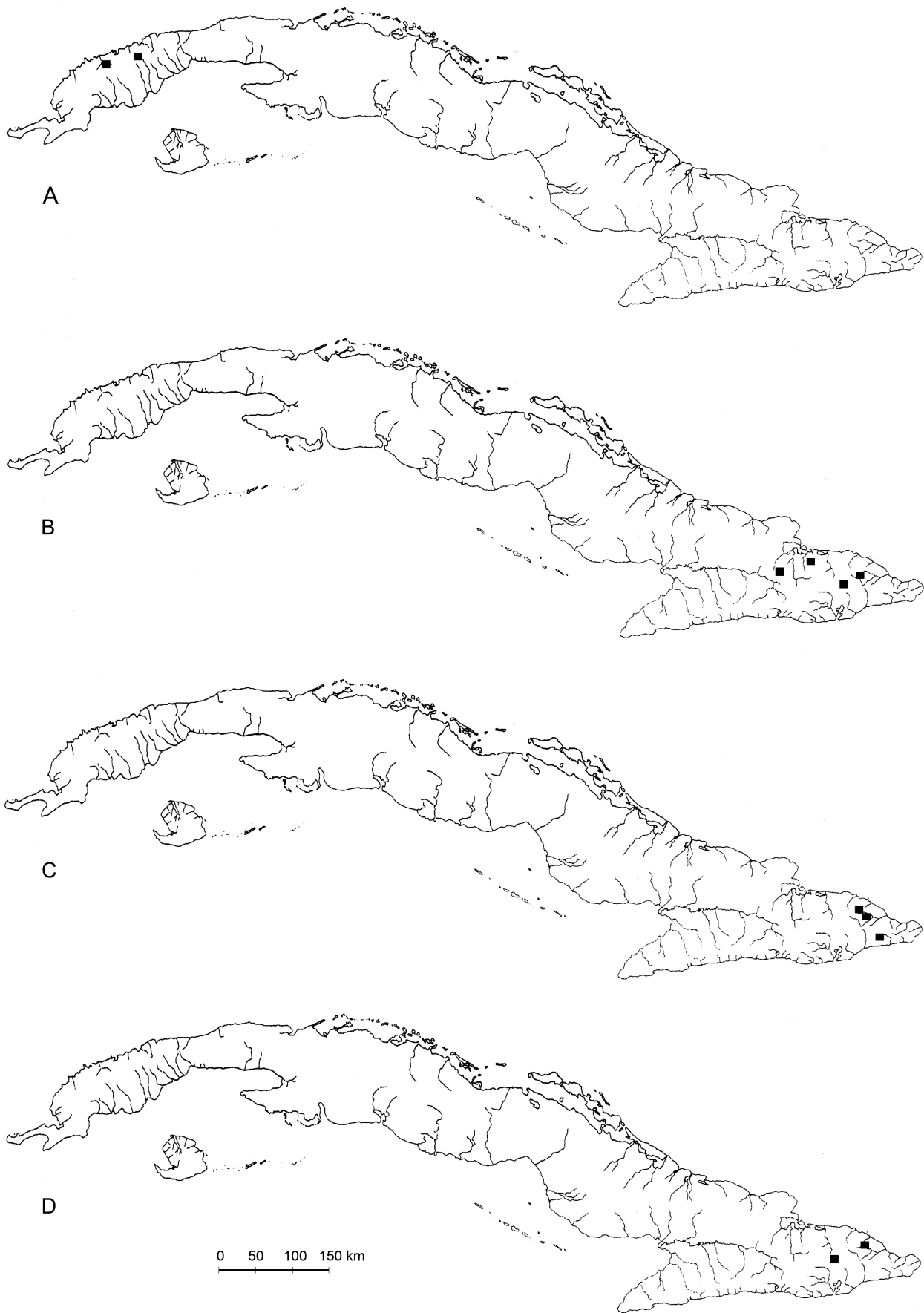


Fig. 11. Distribution of the species of *Tylodontia* – A: *T. cubensis*; B: *T. fuscula*; C: *T. stipitata*; D: *T. urceolata*.

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Appendix. Species, vouchers, origin and GenBank accession numbers.

Species	Voucher	Country of origin	<i>trnT-L</i> spacer	<i>trnL</i> intron	<i>trnL-F</i> spacer	<i>rps16</i> intron	<i>LEAFY</i>
<i>Pentacyphinae</i> (outgroup)							
<i>Pentacyphus andinus</i> (Ball.) Liede	<i>Liede & Meve 3451</i> (UBT)	Peru	AJ492149	AJ492150	AJ492151	AJ699335	–
<i>Pentacyphus lehmannii</i> (Schltr.) Liede	<i>Liede 3333</i> (cult. Bayreuth)	Ecuador	AJ290890	AJ290889	AJ290888	AJ704928	–
<i>Diplolepiniae</i>							
<i>Diplolepis boerhaviifolia</i> (Hook. & Arn.) Liede & Rapini	<i>Liede & Conrad 3062</i> (MSUN, ULM)	Chile	AJ428606	AJ428607	AJ428608	AJ699331	–
<i>Diplolepis diemii</i> (T. Mey.) Hechem & C. Ezcurra	<i>Naumann 1347</i> (MB)	Argentina	AJ699301	AJ699304	AJ699302	AJ699303	–
<i>Diplolepis geminiflora</i> (Decne.) Liede & Rapini	<i>Heyne 103</i> (MSUN)	Chile	AJ410181	AJ410182	AJ410183	AJ699332	–
<i>Diplolepis hieronymi</i> (Lorentz) Liede & Rapini	<i>Liede & Conrad 3052</i> (MSUN, ULM)	Argentina	AJ410211	AJ410212	AJ410213	AJ699333	–
<i>Diplolepis menziesii</i> Schult.	<i>Liede & Conrad 3060</i> (K, MSUN, ULM)	Chile	AJ699274	AJ699273	AJ699275	AJ699276	–
<i>Diplolepis nummulariifolia</i> (Hook. & Arn.) Liede & Rapini	<i>Liede & Conrad 3050</i> (MO, MSUN, ULM)	Argentina	AJ290853	AJ290852	AJ290851	AJ699334	–
<i>Metastelmatinae</i>							
<i>Barjonia chlorifolia</i> Decne.	<i>Rapini 485</i> (SPF)	Brazil	–	AY163667	AY163667	AJ704463	–
<i>Barjonia chlorifolia</i>	<i>Rapini 1395</i> (SPF)	Brazil	JN701896	–	–	–	–
<i>Blepharodon glaucescens</i> (Decne.) Fontella	<i>Ollerton 187</i> (UBT)	Guyana	AJ699290	AJ699289	AJ699291	AJ699292	–
<i>Blepharodon grandiflorum</i> Benth.	<i>Liede & Meve 3318</i> (UBT)	Venezuela	AJ290836	AJ290837	AJ290838	AJ699337	–
<i>Blepharodon lineare</i> (Decne.) Decne.	<i>Forzza 2027</i> (SPF)	Argentina	AJ704465	AY163668	AY163668	AJ704466	–
<i>Blepharodon mucronatum</i> Decne.	<i>Liede 3243</i> (UBT)	Belize	AJ290841	AJ290840	AJ290839	AJ699338	–
<i>Blepharodon pictum</i> (Vahl) W. D. Stevens	<i>Rapini 938</i> (SPF)	Brazil	AJ704468	AY163669	AY163669	AJ704467	–
<i>Ditassa anderssonii</i> Morillo	<i>Matezki SM 141</i> (UBT)	Ecuador	HE611702	HE611761	HE611800	HE611839	–
<i>Ditassa banksii</i> R. Br. ex Schult.	<i>Konno 754</i> (SPF)	Brazil	AJ704474	AY163674	AY163674	AJ704473	–
<i>Ditassa burchellii</i> Hook. & Arn.	<i>Krapovickas 41170</i> (NY)	Argentina	AJ699294	AJ699296	AJ699295	AJ699293	–
<i>Ditassa endoleuca</i> Schltr.	<i>Liede & Meve 3564</i> (UBT)	Ecuador	HE611703	HE611762	HE611801	HE611840	–
<i>Ditassa hispida</i> (Vell.) Fontella	<i>Konno 779</i> (SPF)	Brazil	AJ704479	AJ704478	AJ704480	AJ704477	–
<i>Ditassa mucronata</i> Mart. & Zucc.	<i>Arbo & al. 3885</i> (NY)	Brazil	AJ704270	AJ704259	AJ704278	AJ704279	–
<i>Ditassa obcordata</i> Mart.	<i>Cervi 4073</i> (NY)	Brazil	AJ428750	AJ428751	AJ428752	AJ699340	–
<i>Ditassa retusa</i> Mart.	<i>Coradin & al. 6075</i> (NY)	Brazil	AJ704281	AJ704283	AJ704282	AJ704280	–
<i>Ditassa tomentosa</i> (Decne.) Fontella	<i>Konno 780</i> (SPF)	Brazil	AJ704485	AJ704484	AJ704486	AJ704483	–
<i>Hemipogon acerosus</i> Decne.	<i>Wood & Goyder 15689</i> (K)	Bolivia	AJ704289	AJ704291	AJ704290	AJ704288	–
<i>Hemipogon andinus</i> Rusby	<i>Wood & Wasshausen 16626</i> (K)	Bolivia	AJ704293	AJ704292	AJ704294	AJ704295	–
<i>Hemipogon sprucei</i> E. Fourn.	<i>Wood & Goyder 15719</i> (K)	Bolivia	AJ704297	AJ704299	AJ704298	AJ704296	–
<i>Metastelma linearifolium</i> A. Rich.	<i>Urquiola & al. 561</i> (FR)	Cuba	AJ428807	AJ428808	AJ428809	AJ699341	–
<i>Metastelma</i> aff. <i>parviflorum</i> R. Br.	<i>Liede & Meve 3328</i> (UBT)	Venezuela	AJ428777	AJ428778	AJ428779	AJ699342	–
<i>Metastelma schaffneri</i> A. Gray	<i>Liede & Conrad 2962</i> (UBT)	Mexico	AJ410214	AJ410215	AJ410216	AJ699343	–
<i>Minaria acerosa</i> (Mart.) T. U. P. Konno & Rapini	<i>Ribas & Santos 889</i> (NY)	Brazil	AJ699286	AJ699288	AJ699287	AJ699285	–
<i>Minaria decussata</i> (Mart.) T. U. P. Konno & Rapini	<i>Arbo & al. 4039</i> (NY)	Brazil	AJ704218	AJ704220	AJ704219	AJ704217	–
<i>Minaria grazielae</i> (Fontella & Marquete) T. U. P. Konno & Rapini	<i>Omlor 147</i> (MJG)	Brazil	AJ410202	AJ410203	AJ410204	AJ699339	–

Species	Voucher	Country of origin	<i>trnT-L</i> spacer	<i>trnL</i> intron	<i>trnL-F</i> spacer	<i>rps16</i> intron	LEAFY
<i>Minaria magisteriana</i> (Rapini) T. U. P. Konno & Rapini	Rapini 597 (SPF)	Brazil	AJ704481	AY163681	AY163681	AJ704482	–
<i>Nautonia nummularia</i> Decne.	Liede & Conrad 3031 (ULM)	Argentina	AJ410226	AJ410227	AJ410228	AJ699344	–
<i>Nephradenia acerosa</i> Decne.	Philcox 3303 (K)	Brazil	AJ704497	AY163704	AY163705	AJ704496	–
<i>Nephradenia asparagoides</i> (Decne.) E. Fourn.	Irwin 13012 (K)	Brazil	AJ704498	AY163706	AY163707	AJ704499	–
<i>Peplonia asteria</i> (Vell.) Fontella & E. A. Schwarz	Fontella sub Konno 773 (SPF)	Brazil	AJ704301	AJ704300	AJ704302	AJ704303	–
<i>Peplonia organensis</i> (E. Fourn.) Fontella & Rapini	Konno 854 (SPF)	Brazil	AJ704487	AY163688	AY163688	AJ704488	–
<i>Petalostelma sarcostemma</i> (Lillo) Liede & Meve	Liede & Conrad 3090 (MSUN, ULM)	Argentina	AJ428786	AJ428787	AJ428788	AJ699345	–
Orthosiinae							
<i>Jobinia chlorantha</i> (K. Schum.) Malme	Wolff 110 (UBT)	Ecuador	HE611704	HE611751	HE611751	HE611842	–
<i>Jobinia formosa</i> (N. E. Br.) Liede & Meve	Liede & Conrad 3061 (MSUN)	Chile	AJ428639	AJ428640	AJ428641	AJ699346	–
<i>Jobinia umbellata</i> (Rusby) Liede & Meve	Goyder sub Wood 15798 (K, UBT)	Bolivia	AJ704317	AJ704316	AJ704318	AJ704319	–
<i>Monsanima morrenioides</i> (Goyder) Liede & Meve	Omlor 160 (MJG)	Brazil	AJ428684	AJ428685	AJ428686	AJ699348	–
<i>Orthosia ellemannii</i> (Morillo) Liede & Meve	Liede & Meve 3457 (UBT)	Ecuador	AJ428780	AJ428781	AJ428782	AJ699350	–
<i>Orthosia kunthii</i> Decne.	Valdés & al. 1961 (NY)	Mexico	HE611720	HE611774	HE611813	HE611857	–
<i>Orthosia scoparia</i> (Nutt.) Liede & Meve	Axelrod 8409 (NY)	Puerto Rico	HE611726	HE611780	HE611819	HE611862	–
<i>Scyphostelma beckii</i> (Morillo) Liede & Meve	Liede & Conrad 3141 (MSUN, ULM)	Bolivia	AJ704305	AJ704307	AJ704306	AJ704304	–
<i>Scyphostelma ecuadorensis</i> (Schltr.) Liede & Meve	Harling & Ståhl 26512 (S)	Ecuador	HE611741	HE611791	HE611830	HE611874	–
<i>Scyphostelma harlingii</i> (Morillo) Liede & Meve	Liede & Meve 3460 (UBT)	Ecuador	AJ704309	AJ704308	AJ704310	AJ704311	–
Oxypetalinae							
<i>Araujia angustifolia</i> Steud.	Liede & Conrad 3012 (UBT)	Argentina	AJ699290	AJ699289	AJ699291	AJ704333	–
<i>Araujia plumosa</i> Schltr.	Liede & Conrad 3070 (MSUN, ULM)	Argentina	AJ704335	AJ704337	AJ704336	AJ704334	–
<i>Araujia sericifera</i> Brot.	Liede & Conrad 3007 (ULM)	Argentina	AJ428792	AJ428793	AJ428794	AJ699352	–
<i>Funastrum angustifolium</i> (Pers.) Liede & Meve	Liede & Conrad 3401 (UBT)	U.S.A.	AJ428759	AJ428760	AJ428761	AJ699353	–
<i>Funastrum arenarium</i> (Decne. ex Benth.) Liede	Liede & Conrad 2952 (GA, ULM)	Mexico	AJ290859	AJ290858	AJ290857	AJ699354	–
<i>Funastrum clausum</i> (Jacq.) Schult.	Liede & Conrad 2599 (MO, MSUN)	Mexico	AJ290860	AJ290861	AJ290862	AJ699355	–
<i>Funastrum odoratum</i> Schltr.	Liede & Conrad 2560 (MO, MSUN)	Mexico	AJ290871	AJ290870	AJ290869	AJ699356	–
<i>Morrenia odorata</i> (Hook. & Arn.) Lindl.	Liede & Conrad 3009 (MO, MSUN, ULM)	Argentina	AJ704343	AJ704345	AJ704344	AJ704342	–
<i>Oxypetalum balansae</i> Malme	Liede & Conrad 3015 (ULM)	Argentina	AJ704347	AJ704346	AJ704348	AJ704349	–
<i>Oxypetalum banksii</i> Schult.	Rapini 911 (SPF)	Brazil	AJ704503	AY163710	AY163710	AJ704502	–
<i>Oxypetalum brachystemma</i> Malme	Liede & Conrad 3069 (MSUN, ULM)	Argentina	AJ704351	AJ704353	AJ704352	AJ704350	–
<i>Oxypetalum capitatum</i> Mart	Mello-Silva 1923 (SPF)	Argentina	AJ704504	AY163711	AY163711	AJ704505	–
<i>Oxypetalum coccineum</i> Griseb.	Galetto 562 (CORD)	Argentina	AJ704328	AJ704329	AJ704326	AJ704327	–
<i>Oxypetalum coeruleum</i> (D. Don ex Sweet) Decne.	Liede & Conrad s.n. (ULM)	Argentina	AJ704355	AJ704354	AJ704356	AJ704357	–
<i>Oxypetalum dactylostelma</i> Goyder.	Wood 15195 (K, UBT)	Bolivia	AJ704339	AJ704338	AJ704340	AJ704341	–
<i>Oxypetalum lanatum</i> Decne.	Rapini 929 (SPF)	Brazil	AJ704509	AJ704507	AJ704508	AJ704506	–
<i>Oxypetalum minarum</i> E. Fourn.	Rapini 908 (SPF)	Brazil	AJ704510	AY163713	AY163713	AJ704511	–

Species	Voucher	Country of origin	<i>trnT-L</i> spacer	<i>trnL</i> intron	<i>trnL-F</i> spacer	<i>rps16</i> intron	LEAFY
<i>Oxypetalum pannosum</i> Decne.	Rapini 935 (SPF)	Brazil	AJ704515	AJ704513	AJ704514	AJ704512	–
<i>Oxypetalum pentasetum</i> (Rusby) Goyder & Rapini	Liede & Conrad 3128 (ULM)	Bolivia	AJ704253	AJ704252	AJ704254	AJ704255	–
<i>Oxypetalum solanoides</i> Hook. & Arn.	Liede & Conrad 3004 (MO, MSUN, ULM)	Argentina	AJ704359	AJ704361	AJ704360	AJ704358	–
<i>Oxypetalum sublanatum</i> Malme	Rapini 937 (SPF)	Brazil	AJ704516	AY163715	AY163715	AJ704517	–
<i>Oxypetalum sylvestre</i> (Hook. & Arn.) Goyder & Rapini	Liede & Conrad 3024 (K, MO, MSUN, ULM)	Argentina	AJ410244	AJ410245	AJ410246	AJ699363	–
<i>Oxypetalum warmingii</i> (E. Fourn.) Fontella & Marquete	Rapini 906 (SPF)	Brazil	AJ704521	AJ704519	AJ704520	AJ704518	–
<i>Oxypetalum wightianum</i> Hook. & Arn.	Rapini 705 (SPF)	Brazil	AJ704522	AJ704524	AJ704523	AJ704525	–
<i>Philibertia boliviana</i> (Baill.) Goyder	Wood & al. 15286 (K)	Bolivia	AJ704231	AJ704233	AJ704232	AJ704230	–
<i>Philibertia candolleana</i> (Hook. & Arn.) Goyder	Liede & Conrad 3055 (ULM)	Argentina	AJ410175	AJ410176	AJ410177	AJ699357	–
<i>Philibertia discolor</i> (Schltr.) Goyder	Mello-Silva 1887 (SPF)	Argentina	AJ704527	AY163700	AY163700	AJ704526	–
<i>Philibertia fontellae</i> Goyder	Wood & Goyder 15543 (K, UBT)	Bolivia	AJ492152	AJ492153	AJ492154	AJ699358	–
<i>Philibertia gilliesii</i> Hook. & Arn.	Liede & Conrad 3054 (MO, MSUN, ULM)	Argentina	AJ290896	AJ290895	AJ290894	AJ699359	–
<i>Philibertia globiflora</i> Goyder	Wood 15803 (K, UBT)	Bolivia	AJ704235	AJ704234	AJ704236	AJ704238	–
<i>Philibertia latiflora</i> (Griseb.) Goyder	Liede & Conrad 3091 (MSUN, ULM)	Argentina	AJ704240	AJ704242	AJ704241	AJ704239	–
<i>Philibertia lysimachioides</i> (Wedd.) T. Mey.	Liede & Conrad 3139 (MSUN, ULM)	Bolivia	AJ290902	AJ290901	AJ290900	AJ699360	–
<i>Philibertia multiflora</i> (T. Mey.) Goyder	Wood & Serrano 14466 (K, UBT)	Bolivia	AJ704244	AJ704243	AJ704245	AJ704246	–
<i>Philibertia parviflora</i> (Malme) Goyder	Liede & Conrad 3113 (UBT)	Argentina	AJ410223	AJ410224	AJ410225	AJ699361	–
<i>Philibertia peduncularis</i> (Benth.) Goyder	Wood & Goyder 15444 (K, UBT)	Bolivia	AJ704249	AJ704251	AJ704250	AJ704247	–
<i>Philibertia picta</i> Schltr.	Liede & Conrad 3104 (K, MO, MSUN, ULM)	Argentina	AJ290903	AJ290904	AJ290905	AJ699362	–
<i>Tweedia brunonis</i> Hook. & Arn.	Liede & Conrad 3058 (UBT)	Argentina	AJ704257	AJ704260	AJ704258	AJ704256	–
Tassadiinae							
<i>Tassadia berteriana</i> (Spreng.) W. D. Stevens	Nee 36277 (NY)	Bolivia	AJ428789	AJ428790	AJ428791	AJ699336	–
<i>Tassadia guianensis</i> Decne.	Wolff 528 (UBT)	Ecuador	AJ699278	AJ699280	AJ699279	AJ699277	–
<i>Tassadia obovata</i> Decne.	Matezki 332 (UBT)	Ecuador	AJ699282	AJ699281	AJ699283	AJ699284	–
Gonolobinae (study group)							
<i>Anemotrochus eggersii</i> (Schltr.) Mangelsdorff & al.	Liede & Meve 3592 (UBT)	Cuba	HF547076	HF547131	HF547131	HF547185	LN901538
<i>Anemotrochus eggersii</i>	Neil 270 (FTG)	Caicos Islands	HF547077	HF547132	HF547132	HF547186	LN901539
<i>Anemotrochus eggersii</i>	RMC 387 (FR)	Cuba	HF547078	HF547133	HF547133	HF547187	LN901540
<i>Anemotrochus viridivenius</i> (Alain) Mangelsdorff & al.	Veloz & al. 836 (JBSD)	Dominican Republic	–	–	EU031637	EU038890	EU038969
<i>Anemotrochus viridivenius</i>	Clase & al. 5609 (JBSD)	Dominican Republic	LN901501	LN901496	LN901496	LN901514	LN901527
<i>Anemotrochus yamanigüeyensis</i> Mangelsdorff & al.	Mangelsdorff RMC 222a (FR)	Cuba	LN901511	LN901555	LN901548	LN901524	LN901535
<i>Anemotrochus yamanigüeyensis</i>	Mangelsdorff RMC 222b (FR)	Cuba	LN901512	LN901556	LN901549	LN901525	LN901536
<i>Anemotrochus yamanigüeyensis</i>	Mangelsdorff RMC 357 (FR)	Cuba	LN901513	LN929898	LN929899	LN901526	LN901537
<i>Chloropetalum denticulatum</i> (Vahl) Morillo	Hammel 9304 (DUKE)	Costa Rica	–	–	EU031614	EU038867	EU038933
<i>Fischeria panamensis</i> Spellman	Folsom 9364 (DUKE)	Costa Rica	–	–	EU031577	EU038832	EU038896
<i>Fischeria scandens</i> DC.	Krings 1407 (NCSC)	Jamaica	–	–	EU031578	EU038833	EU038897

Species	Voucher	Country of origin	<i>trnT-L</i> spacer	<i>trnL</i> intron	<i>trnL-F</i> spacer	<i>rps16</i> intron	<i>LEAFY</i>
<i>Gonolobus albomarginatus</i> (Pittier) Woodson	Taylor & Skotak 4455 (DUKE)	Costa Rica	–	–	EU031579	EU038834	EU038898
<i>Gonolobus arizonicus</i> (A. Gray) Woodson	van Devender 2004-893 (ARIZ)	Mexico	–	–	EU031580	EU038835	EU038899
<i>Gonolobus barbatus</i> Kunth	Conrad 9325 (UBT)	Mexico	AJ704262	AJ704261	AJ704263	AJ704264	–
<i>Gonolobus barbatus</i>	Taylor 2227 (DUKE)		–	–	–	–	EU038900
<i>Gonolobus bibarbatulus</i> W. D. Stevens	Cowan 5620 (TEX)	Mexico	–	–	EU031581	EU038836	EU038901
<i>Gonolobus breedlovei</i> L. O. Williams	King 2778 (TEX)	Mexico	–	–	EU031582	EU038837	EU038902
<i>Gonolobus chloranthus</i> Schltdl.	Cowan 5513 (TEX)	Mexico	–	–	EU031583	EU038838	EU038903
<i>Gonolobus fraternus</i> Schltdl.	Fishbein 5164 (ARIZ)	Mexico	–	–	EU031585	EU038840	EU038904
<i>Gonolobus gonoloboides</i> (Greenm.) Woodson	Reina 2003-884 (ARIZ)	Mexico	–	–	EU031587	EU038842	EU038905
<i>Gonolobus grandiflorus</i> (Cav.) Schult.	Fishbein 5114 (ARIZ)	Mexico	–	–	EU031588	EU038843	EU038906
<i>Gonolobus iyanolensis</i> Krings	Krings SLI (NCSC)	Saint Lucia	–	–	EU031589	EU038844	EU038907
<i>Gonolobus jaliscensis</i> B. L. Rob. & Greenm.	Fishbein 5121 (ARIZ)	Mexico	–	–	EU031590	EU038845	EU038908
<i>Gonolobus jamaicensis</i> Rendle	Krings 1393 (NCSC)	Jamaica	–	–	EU031591	EU038846	EU038909
<i>Gonolobus niger</i> (Cav.) Schult.	Mayfield & al. 860 (TEX)	Mexico	–	–	EU031592	EU038847	EU038910
<i>Gonolobus ophioglossa</i> Woodson	Mangelsdorff RMP 1296 (FR)	Panama	LN901502	LN901497	LN901497	LN901515	–
<i>Gonolobus pectinatus</i> Brandegee	Prinzle & Lozada 202 (TEX)	Mexico	–	–	EU031593	EU038848	EU038911
<i>Gonolobus stapelioides</i> Desv. ex Ham.	Krings 1395 (NCSC)	Jamaica	–	–	EU031595	EU038850	EU038912-15*
<i>Gonolobus stenosepalus</i> (Donn. Sm.) Woodson	Taylor 2536 (DUKE)	Mexico	–	–	EU031596	EU038851	EU038916
<i>Gonolobus stephanotrichus</i> Griseb	Krings & al. s.n. (NCSC)	Cuba	–	–	EU031597	EU038852	EU038917
<i>Gonolobus suberosus</i> (L.) R. Br.	ex Wyatt s.n. (GA)	U.S.A.	AJ704275	AJ704277	AJ704276	AJ704274	–
<i>Gonolobus suberosus</i>	Krings FL9 (NCSC)	U.S.A.	–	–	–	–	EU038918
<i>Gonolobus uniflorus</i> Kunth	van Devender 2003-1323 (ARIZ)	Mexico	–	–	EU031601	EU038855	EU038919
<i>Gonolobus waitukubuliensis</i> Krings	Krings 1386 (NCSC)	Dominica	–	–	EU031602	EU038856	EU038920
<i>Gonolobus youroumaynensis</i> Krings	Krings 1374 (NCSC)	Saint Vincent	–	–	EU031603	EU038857	EU038921
<i>Ibatia rubra</i> (H. Karst.) Morillo	Proosdij & al. 667 (NY)	Aruba	–	–	EU031632	EU038885	EU038954
<i>Macrocephala diademata</i> (Ker Gawl.) W. D. Stevens	Heyne s.n. (UBT)	Guatemala	AJ704266	AJ704268	AJ704267	AJ704265	LN901541
<i>Matelea bicolor</i> (Britton & P. Wilson) Woodson	Krings 1410 (NCSC)	Cuba	–	–	EU031606	EU038860	EU038925-27*
<i>Matelea bicolor</i>	Liede & Meve 3583 (UBT)	Cuba	LN901503	LN901498	LN901498	LN901516	LN901528
<i>Matelea cordata</i> (Brandegee) Woodson	Tenorio 11556 (TEX)	Mexico	–	–	EU031608	EU038862	EU038928
<i>Matelea cordifolia</i> (A. Gray) Woodson	Stevens 1517 (MSC)	Mexico	–	–	EU031609	EU038863	EU038929
<i>Matelea correllii</i> Spellman	Correll 48157 (DUKE)	Bahamas	–	–	EU031610	EU038864	EU038930
<i>Matelea cyclophylla</i> (Standl.) Woodson	Barad s.n. (UBT)	Mexico	AJ704271	AJ704269	AJ704272	AJ704273	–
<i>Matelea cyclophylla</i>	Stevens & al. 2299 (MSC)	Mexico	–	–	–	–	EU038931
<i>Matelea decaisnei</i> Woodson	Tucker 2766 (DUKE)	Mexico	–	–	EU031612	EU038866	EU038932
<i>Matelea dictyantha</i> Woodson	Stevens & al. 2311 (MSC)	Mexico	–	–	EU031614	EU038868	EU038934
<i>Matelea ekmanii</i> (Urb.) Woodson	Krings 1411 (NCSC)	Cuba	–	–	EU031615	EU038869	EU038935-39*
<i>Matelea gonoloboides</i> (B. L. Rob. & Greenm.) Woodson	Stevens 1349 (MSC)	Mexico	–	–	EU031616	EU038870	EU038940
<i>Matelea hemsleyana</i> Woodson	Stevens 1399 (MSC)	Mexico	–	–	EU031617	EU038871	EU038941

Species	Voucher	Country of origin	<i>trnT-L</i> spacer	<i>trnL</i> intron	<i>trnL-F</i> spacer	<i>rps16</i> intron	<i>LEAFY</i>
<i>Matelea inconspicua</i> (Brandege) Woodson	Panero 5804 (TEX)	Mexico	–	–	EU031618	EU038872	EU038942
<i>Matelea lanata</i> (Zucc.) Woodson	Hinton & al. 23755 (TEX)	Mexico	–	–	EU031619	EU038873	EU038943
<i>Matelea nipensis</i> (Urb.) Woodson	Krings 1412 (NCSC)	Cuba	–	–	EU031622	EU038876	EU038944
<i>Matelea nipensis</i>	Mangelsdorff RMC 318 (FR)	Cuba	LN901504	LN901550	LN901543	LN901517	LN901529
<i>Matelea oblongata</i> (Griseb.) Woodson	Krings 1413 (NCSC)	Cuba	–	–	EU031623	EU038877	EU038946-48*
<i>Matelea phainops</i> Krings	Liogier 16617 (NY)	Dominican Republic	–	–	EU031626	EU038879	EU038949
<i>Matelea prosthecidiscus</i> Woodson	Stevens & Fairhurst 1811 (DUKE)	Mexico	–	–	EU031627	EU038880	EU038950
<i>Matelea pubiflora</i> (Decne.) Woodson	Orzell & Bridges 20226 (USCH)	U.S.A.	–	–	EU031628	EU038881	EU038951
<i>Matelea quirosii</i> (Standl.) Woodson	Steinmann 1084 (NY)	Mexico	–	–	EU031630	EU038883	EU038952
<i>Matelea reticulata</i> (Engelm. ex A. Gray) Woodson	Krings L3 (NCSC)	U.S.A.	–	–	EU031631	EU038884	EU038953
<i>Matelea sintenisii</i> (Schltr.) Woodson	Krings 1405 (NCSC)	Puerto Rico	–	–	EU031633	EU038886	EU038955-58*
<i>Matelea tamnifolia</i> (Griseb.) Woodson	Krings 1414 (NCSC)	Cuba	–	–	EU031634	EU038887	EU038959-65*
<i>Matelea tamnifolia</i>	Mangelsdorff RMC 125 (FR)	Cuba	LN901505	LN901499	LN901499	LN901518	LN901530
<i>Matelea trachyantha</i> (Greenm.) W. D. Stevens	Stevens & al. 2300 (DUKE)	Mexico	–	–	EU031635	EU038888	EU038966
<i>Matelea variifolia</i> (Schltr.) Woodson	Krings 1397 (NCSC)	Puerto Rico	–	–	EU031636	EU038889	EU038968-69*
<i>Schubertia grandiflora</i> Mart. & Zucc.	Liede & Conrad 3033 (MSUN, UBT, ULM)	Argentina	AJ428825	AJ428826	AJ428827	AJ699364	LN901542
<i>Tylodontia</i> cf. <i>cubensis</i> Griseb.	Liede & Meve 3593 (UBT)	Cuba	LN901506	LN901500	LN901500	LN901519	–
<i>Tylodontia fuscula</i> (C. Wright) Mangelsdorff & al.	Mangelsdorff RMC 327 (FR)	Cuba	LN901507	LN901551	LN901544	LN901520	LN901531
<i>Tylodontia stipitata</i> Mangelsdorff & al.	Mangelsdorff RMC 332 (FR)	Cuba	LN901509	LN901553	LN901546	LN901522	LN901533
<i>Tylodontia stipitata</i>	Mangelsdorff RMC 333 (FR)	Cuba	LN901510	LN901554	LN901547	LN901523	LN901534
<i>Tylodontia urceolata</i> (Griseb.) Mangelsdorff & al.	Mangelsdorff RMC 233 (FR)	Cuba	LN901508	LN901552	LN901545	LN901521	LN901532

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