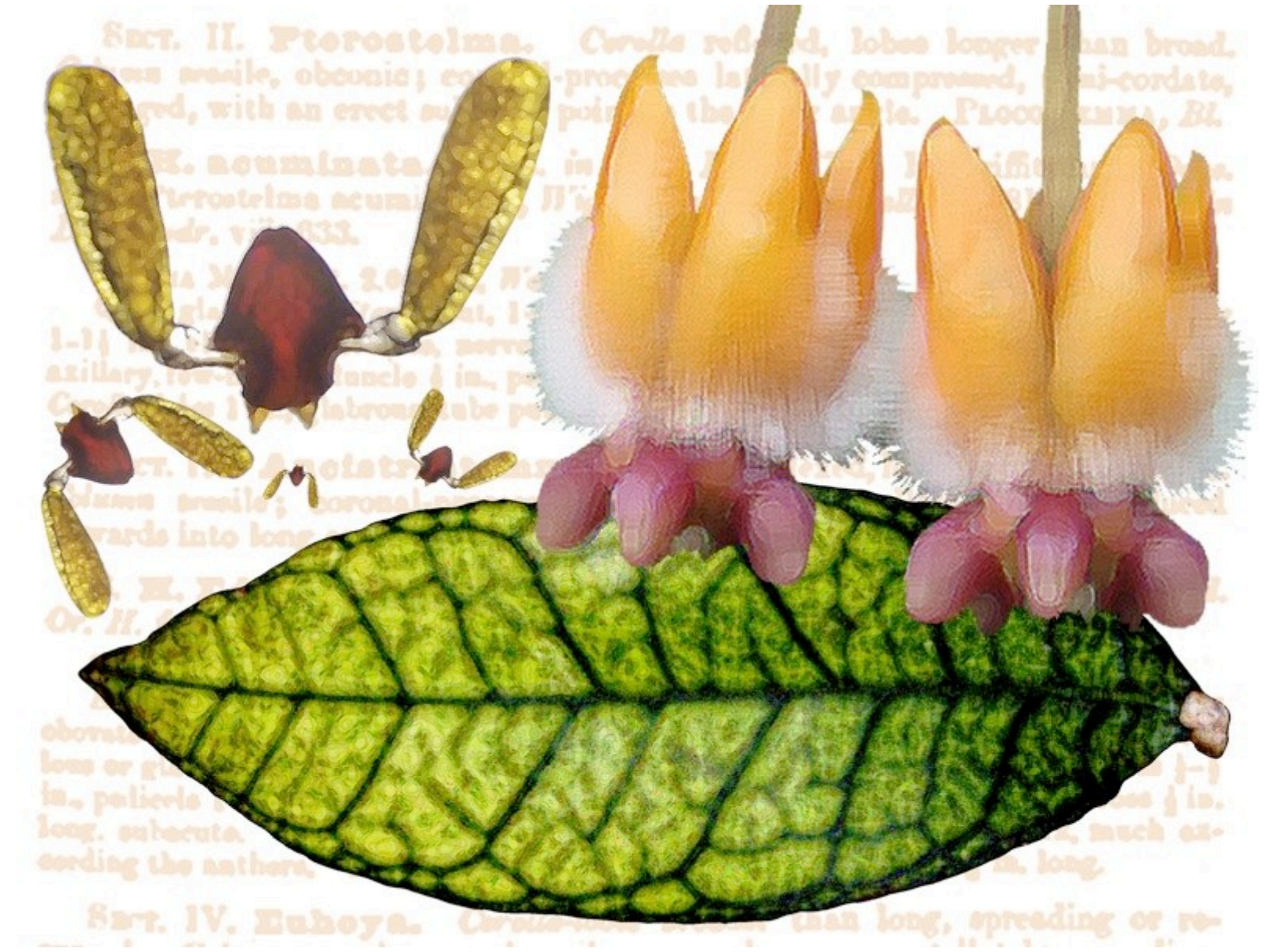
Stemma



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On the cover: *H. praetorii* (photo by Eddie Huey & Epiforums.com), pollinarium of *H. griffithii* (microphotograph by Torill Nyhuus), leaf of *H.* sp. aff. finlaysonii & Photoshop by MR.

Editor's Note

This issue features a long-planned interview with Sylvine Bruneau, one of the finest photographers working with *Hoya* today. We are proud to have a series of photographs from Sylvine presented in the **Photography** section starting on page 4. Sylvine's photos are a constant source of inspiration to us at the ***Stemma*** offices. The interview was conducted by Gerbrand Caspers, who, along with his son Christiaan, translated the text into English.

This issue features the first in a series of three articles examining the sectional divisions of *Hoya*. Thanks to their technical (and often contrary) descriptions and tongue-twisting Latin names, the sections are a mystery to most collectors

Infrageneric division within *Hoya* (classification within the genus, but above the species level) received some attention in the mid-19th to early 20th centuries- the last important attempt to refine the sections during this period came from the German botanist R. Schlechter in 1914.

More recent attempts have been made to organize, re-describe and expand the sections by Dale Kloppenburg (1993) and Christine Burton (1995/96).

In the series of articles starting in this issue of ***Stemma***, I will attempt to show some of the relevant sectional divisions published or proposed in the past, and will propose a few new sections to delineate groups of species which have not been officially recognized before, or which have been grouped into sections with a physically dissimilar type species.

The **Back Page** *Hoya* for this issue is *Hoya* sp. square, a new and very interesting species recently introduced into cultivation by plant collectors in Thailand.

photo by Sylvine Bruneau

Photography

Sylvine Bruneau

interview by Gerbrand Caspers

Please tell us your name and where you live.

My name is Sylvine Bruneau, I am 42. I live near Paris, but in a few weeks we will move to le Finistère (in the far west of France).

What do you do for a living?

I am an accountant.

Do you have professional training in photography?

No. I cannot explain how I make a photo. I do not have a proper grounding in photography; maybe one day I will take a course with an amateur photographer's club.

What was your first interest: photography or Hoyas?

My passion for photography started quite early. At 20, I loved making family portraits; at 30, it was outdoor photography; and now, at 40, I only do macro photography with Hoyas!

I encountered my first Hoya in a garden center years ago: I was attracted by its fragrance- it was a *Hoya bella*. I really got my collection going with cuts acquired from Paul Shirley (http://www.paulshirleysucculents.nl), in the late '90s. Then, in 2005, I discovered Christina Karlsson's website (http://www.myhoyas.com), as well as the site of Djamel (http://dwaittaleb.free.fr) and Céline's forum (http://hoyas.monforum.fr).

What do you think makes a good Hoya photograph?

What makes me fall in love with a particular Hoya are photos of the flowers. A good photograph really does justice to the Hoya, and makes it more attractive.

I can't get enough of the photos of Eva-Karin Wiberg (http://web.telia.com/~u24312304/fotoalbum.htm), Torill Nyhuus (http://www.swedishhoyasociety. com) and Christina Karlsson.

A good photo, of a Hoya or of any other subject, should communicate an emotion (www.pbase.com/gilazouri/root). Hoyas can take you anywhere from childhood, with the softness of the furry flowers of *Hoya fraterna*, to meditative contemplation with the purity of a *H. bella* flower. But since emotions are quite personal, it is very difficult to make THE photo that will enchant everybody. I am always surprised when I see that visitors of my website are enthusiastic about photos that I find merely satisfactory, while photos that for me represent moments of joy are completely ignored.

A beautiful photo combines good (preferably natural) lighting, balanced whites ensuring maximal colour fidelity, a judicious exposure, a tripod to prevent undesirable haziness – and the Hoya's beauty does the rest!

What kind of camera and lens do you use?

I have had a Nikon D70S with a 60 mm macro lens since 2006.

What are your favourite Hoyas? Why?

I love any Hoya in flower. Every encounter is a moment of wonder, and the photo allows me to see more detail.

Every flowering of *H. praetorii* is for me a moment full of emotion – and it flowers profusely. But I also love *H. l. ssp. bella*, *H. cystiantha (Cystidianthus laurifolius)*, *H. obscura*, *H. retusa*, *H.* sp. CMF-8 and *H. cagayensis*, for their fragrance; *H. parviflora* and *H. elliptica* for the beautiful design of their flowers; and I love all Hoyas that have not yet flowered!

Tell us about your website.

My original plan for the website was to create a convenient space where I could stock all my photos, the correct names of the Hoya species, the many hyperlinks to images of every Hoya species (there is still a lot to be done!), the internet addresses of my suppliers and of my favorite websites.

Since a website proved to be more practical than a notebook, I took the plunge and 'le portail des hoyas' (http://sylvinebr.free.fr/) was born! I always go there when I need the correct spelling of a specific Hoya or when I want to look at an image of it.

With Dominique Cassagne (co-founder) and Sylvain Aubert (chronicler), we have launched a new project: Wikihoya (www.wikihoya.org), a french-language site to promote the cultivation of Hoyas. The site is comprised of articles, and every article can be commented upon by internet users, just like any other Wiki site. Right now, we focus on cultivation advice, one file for every Hoya species. For the future, we want to develop a space for the identification of Hoyas: as yet, no french-language resource on that subject exists. Research on Hoya identification progresses steadily, but the results are only accessible to anglophone readers. We will also give exposure to the collectors and their set-up.

Apart from the ones already mentioned, I find the following websites particularly helpful:

www.hoyor.net
www.simones-hoyas.de
www.thailandhoyaclub.com/webboard
http://hoyas.ca/

How many Hoya collectors are there in France? Is there a collectors' association?

I don't know the exact number, but I do know that it is on the increase. French websites and forums are very active. Meetings, exchanges and shows are arranged every year. Last October in the Serres d'Auteuil, during the year's concluding convention of the AFAHo, we had three distinguished guests: Torill Nyhuus and Stephan and Ylva Kallander. Torill gave a lecture about her many travels.

It is impossible to mention all the active or passive collectors in France, but here are some weblinks:

http://perso.orange.fr/mes.hoyas/
http://hoya.over-blog.com/
http://www.orchideefantome.com/forum/hoyas-f47.html
www.flickr.com/groups/hoyasmonforumfr

After its dissolution in January 2008 and a four-month break, the AFAHo (Association Francophone des Amateurs de Hoya) has just been re-launched with a new office staffed by four enthusiasts. The journal ***Asclep-Hoya*** is also back on track: issue number 3 will be out in August/September 2008. From September onwards the office can be contacted for information and subscription: please contact Alexandre GAVRUS (kl55555@club-internet.fr) – k as in kilogramme, l as in litre – or to Vanessa Gonnot (vgonnot@gmail.com).

HOYA ELLIPTICA

HOYA NUMMULARIOIDES

HOYA VANUATUENSIS IML 0071

HOYA CORIACEA

HOYA BUOTII

HOYA FRATERNA

A look at Hoya Sections

part 1

by Mark Randal

A "section" is a taxonomic rank specified by the International Code of Botanical Nomenclature (ICBN), the system which sets the rules for naming and classifying the plant kingdom. The rank "section" fits into the system of classification like so (here using *Hoya bilobata* to demonstrate some of the rank names):

Family	*Apocynaceae*
Subfamily	*Asclepiadoideae*
Tribe	*Marsdenieae*
Genus	*Hoya* R. Br.
Section	*Acanthostemma* (Blume) D. Kloppenburg
Species	*Hoya bilobata* Schltr.

The ICBN does not give much detail on what level of similarity should determine sectional groupings, specifying only that this level of division lies between the genus and species levels. Most sectional divisions contain species which have visually recognizable similarities in their morphological characteristics.

Many of the *Hoya* sections have been created by an author moving a group of plants formerly considered to be separate genus into the genus *Hoya*. In these cases the species moved in this fashion become *Hoya*, and the old genus name is retained as a section name, describing a group of similar species within the genus (for instance, the genus *Otostemma* Blume, created in 1848, was moved into the genus *Hoya* by F. A. W. Miquel in 1856 . The name of the type species for that genus, *Otostemma lacunosum* Blume, then became *Hoya lacunosa* Blume, and was placed into section *Otostemma* as its type species).

Other sections have been established to house groups of species already within the genus *Hoya* (Blume created section *Physostemma* in 1848 to house *Hoya coriacea* Blume).

The purpose of this study is to discuss the morphological and molecular characteristics that have been used to group together species, to present the history of *Hoya* sectional classification to date, and to propose a list of sections which seem to be relevant for classification purposes today (though the presented list requires additional study and molecular testing to confirm monophylly).

Several new species complexes are proposed in this study to contain groups of species which have not formerly been recognized as sections, or which have been placed into sections whose type species is blatantly dissimilar from the subject.

The complexes presented (or proposed) in detail in this series are not meant to be valid taxonomic publications, and cannot be considered as such according to ICBN Article 29.1.

The section list is a work in progress, so feedback of any sort is welcome. Please send comments or critiques to the author at: markroy68@yahoo.com

The value of the sections to collectors

Infrageneric classification is of scientific interest to those exploring the evolutionary history of various plant groups, but it can also be a useful tool for collectors and horticulturalists for a number of reasons.

The sections, as they ideally represent groups of similar species that differ significantly from other groups of species, are useful in exploring the diversity within the genus *Hoya*, and also may provide some insight into cultivation preferences for individual species.

Here are a few examples of some established or proposed sections, and some of the cultivation factors that may be inferred from a species' placement in that group:

Species grouped into section *Eriostemma* are large-scale terrestrial lianas, which require high heat, humidity and vigorous air movement to perform their best. They are very different from species grouped with *Hoya lanceolata*, which are dainty epiphytic danglers, generally from cooler climates. Section *Acanthostemma* species are mostly vigorous, smaller stature plants which bloom early and generously in cultivation, whereas species in section *Hoya* can become quite large, and some species tend to not bloom until the plants have become fairly mature.

All of these qualities (and many more which pertain to specific sections) should be of some interest to collectors. While not all species grouped with each section conform exactly to all of their section mate's characteristics and needs, there is a tendency for them to do so, so that knowing something about a species' close relatives may yield clues as to how to care for it.

Above left: *Hoya* 'Optimistic', a section *Eriostemma* hybrid.

Above right: *Hoya praetorii*, a section *Plocostemma* species (photo courtesy of Eddie Huey and Epiforums.com).

Lower left: *Hoya carnosa*, the type species for section *Hoya*.

Lower right: *Hoya erythrostemma*, a species placed in section *Pachystelma*. (photo courtesy of Bob Ely).

Physical and molecular factors in species grouping

All forms of botanical classification are based on comparison. Plants or groups of plants are observed and their characteristics, either anatomical or, in the case of molecular testing, sequences of molecules in the chloroplast or nuclear DNA, are compared with each other. Plants which share many features in common are thought to be more closely related than plants with more dissimilar characteristics. In the genus *Hoya*, species were first grouped together based on details of the corolla and corona (Miquel, 1856; Schlechter, 1914). Later efforts recognized the pollinarium as a useful classification tool (Rintz, 1978; Kloppenburg, 1993; Wanntorp, 2007). In the last several decades molecular testing has been developed and applied to *Hoya* and related genera (Sennblad and Bremer, 1996; Wanntorp et al., 2006a & 2006b).

These characteristics, all used together in a consistent manner, should allow a phylogeny (an evolutionary history) for the genus *Hoya* to be established. Work in the field of molecular testing is ongoing (see the series of articles authored by Wanntorp et al. cited on pg. 21), and should alter the traditional and proposed sectional scheme in many ways. However, many of the basic units of species placed as sections by past and present authors should remain recognizable, as they are based on the same morphological features (corona lobe structure, corolla orientation, pollinarium structure) that are used to define some key sections that have been corroborated by early molecular testing results- studies by Wanntorp et al. (2006a, 2006b) present evidence to support three traditional sections- *Eriostemma*, *Acanthostemma*, and *Angusticarinatae*.

Vegetative form and structure

Probably the earliest distinctions humankind made about the plant kingdom were based on overall plant form- “bush”, “tree”, “vine” (The *Rigveda*, ancient). As humankind became more sophisticated in his classification schemes, other details of plant morphology became more important. Specific types of leaves, bark, branching habit and flower shape and structure became important diagnostic tools.

leaves of (left) *Hoya obovata* and (right) *Hoya meredithii*.

Eventually it was realized that basic flower structure was more constant in related plants than were details of vegetative parts (Linnaeus, 1753). Even before the advent of genetic testing most of the great families of the plant kingdom had been recognized based primarily on floral characteristics (J. Lindley, 1846). Given the tendency of related species to have a greater diversity in vegetative parts rather than in basic flower structure (C. A. Stace, 1991), plant form and leaf shape and venation are sometimes dismissed in favor of purely floral characteristics for classification purposes (Burton 1995/96).

As taxonomic rankings become smaller (from family to genus to section to species) the plants in each group tend to display more and more similar morphological characteristics. This is not always the case, as there is sometimes great diversity even at the species level For instance, *Hoya australis* R. Br. ex J. Traill has subspecies that range in form from lush rainforest vines to stocky, succulent bushes. However, most taxa at rankings slightly above the species level display a high degree of physical likeness, so that vegetative features can be used as a guide in classification (in a supporting role) though they are not sufficient alone to create sectional groupings.

Showing some of the diversity in leaf form and size in the genus *Hoya* are (1) *H*. sp. aff. latifolia, (2) *H. magnifica*, (3) *H*. sp. aff. finlaysonii, (4) *H. lanceolata*, (5) *H. waymaniae*, (6) *H. kanyakumariana*, (7) *H. dickasoniana*, (8) *H*. sp. aff. compacta, (9) *H. pubicalyx*, (10) *H. linearis* and (11) *H*. 'Iris Marie'.

Floral features

The various reproductive parts of *Hoya* are all considered to have some merit in determining species and sectional placement, although some features are given more importance than others.

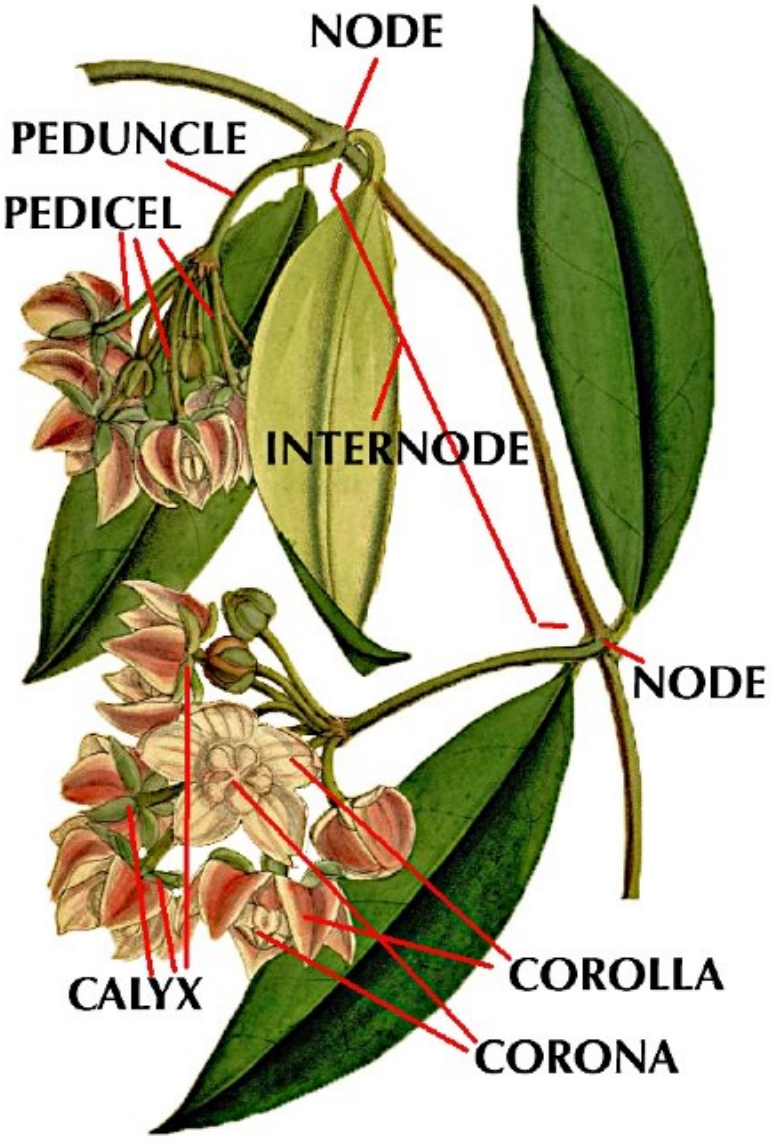
The parts of *Hoya* flowers, as they occur from the plants' stem outwards, are:

Peduncle (including the **Rachis)**
Pedicel
Calyx
Corolla
Corona
Pollinarium

In the genus *Hoya* flowers are borne on persistent (or occasionally temporary) modified fertile branches called **peduncles**. The peduncles, usually resembling smooth green or woody stalks in most *Hoya* species, are borne at the leaf nodes from between the leaf bases. In species with persistent peduncles the end of the peduncle is a lengthening, rough tissued area called the **rachis**. Peduncles vary in life span (temporary versus persistent), length, diameter, color and orientation (some tending to grow straight down, others tending to grow horizontally or upright).

Flowers are borne from the tip of the peduncle on temporary stems called **pedicels**, in clusters usually referred to as **umbels,** although the term **raceme** is more correct for most *Hoya* species. The growth point of the persistent peduncle grows in a minutely spiral fashion, so that the oldest flowers will be at the edge of the raceme, and the youngest at the raceme's center. Those species which have temporary peduncles form true umbels, in which the flowers emerge from the same point and mature at roughly the same pace.

Pedicels are usually grouped in one of two ways: 1- all of the same length (resulting in a spherical or convex raceme) or 2- arranged with the pedicels in gradually decreasing lengths (from oldest at the rim to youngest at the raceme's center), so that the raceme is flat or slightly concave. Pedicels also vary in length, color, diameter and degree of pubescence (hairiness).

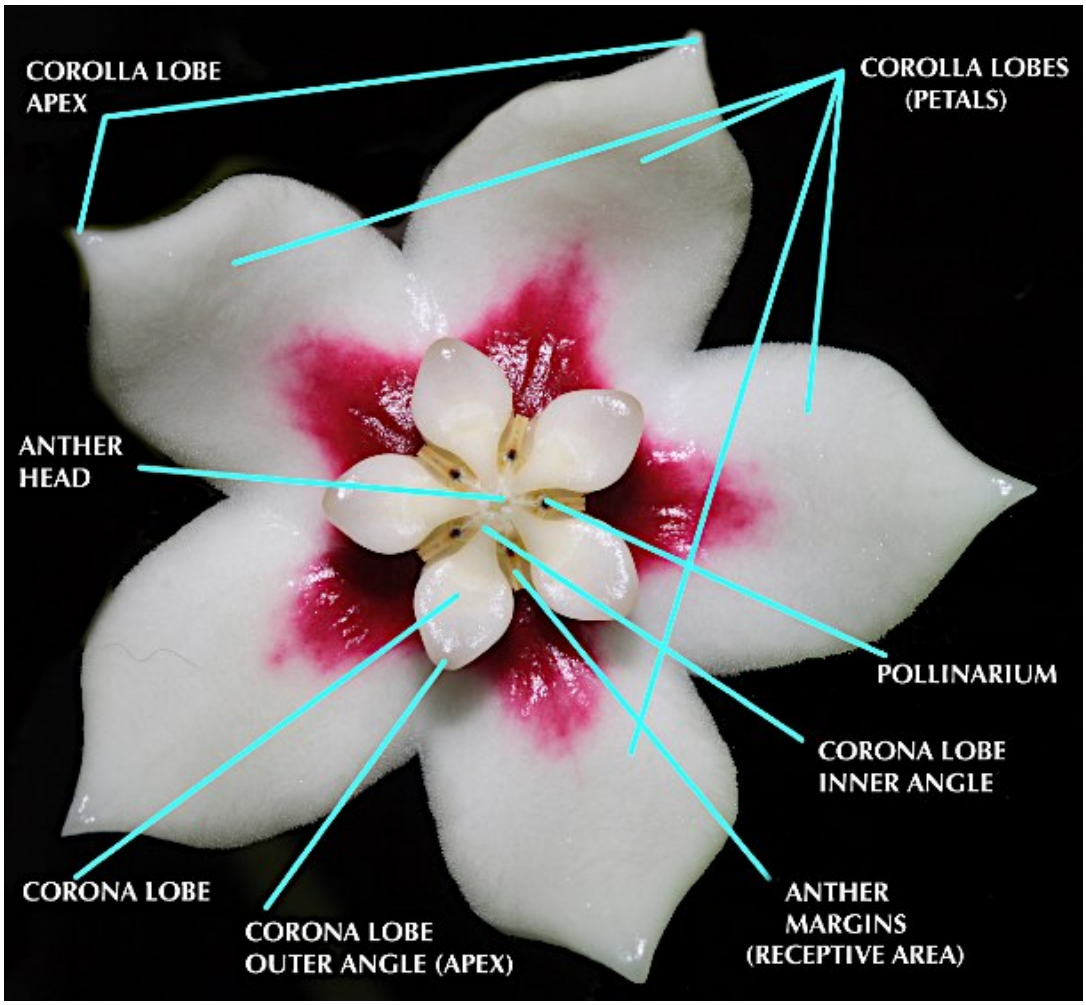


Background image above of *Hoya griffithii* from Curtis' Botanical Magazine plate 6877

The shape of the raceme has been used in some classification attempts in the genus. R. Rintz (1978) divided the species he was working with into three groups- 1) with geotropic (facing the ground) & concave racemes, 2) with geotropic & convex racemes and 3) with negatively geotropic (facing upwards) & convex racemes. The first group corresponded to species in the sections *Otostemma*, *Acanthostemma* and *Peltostemma*. This does appear to be a useful classification tool- these three groups along with those species similar to *Hoya diptera* Seem. and *Hoya lanceolata* Wall ex D. Don all have roughly geotropic, concave racemes or umbels, as well as other characteristics which suggest that they are related groups of species (see sections 1-5). All other sections or complexes have convex racemes, although the degree of geotropism in most sections seems to be somewhat variable.

The next three floral structures are comprised of whorls of five highly modified leaves.

The **calyx** is the most leaf-like of these three structures. It is comprised of five tiny leaves which surround and protect each developing flower bud. When flowers are mature, the calyx is usually visible at the juncture with the pedicel of the outside of the corolla. The five individual leaves of the calyx are called **sepals**. Sepals vary in shape, size, color, and degree of overlap with one another. The calyx has been used in a supporting role in some classification schemes within this genus (Kloppenurg, 1993; Burton, 1995/96).



The next whorl of five modified leaves is the **corolla**, the usually conspicuous portion of the flower. The five individual leaves of the corolla are commonly called **petals**. The petals vary in size, degree of fusion with adjacent petals, shape, color, orientation and degree of pubescence. The corolla has been used commonly for classification within this genus, especially in earlier attempts (Miquel,1856; Hooker, 1885). There is a great degree of variation of the corolla, even sometimes in closely related species (see section 3).

The third structure composed of modified leaves is the **corona**. In most flowers there are two individual whorls of leaves here- the **stamens** (comprised of the **filaments** and the pollen producing **anthers**) and the **pistils** (comprised of the **ovary**, **style** and the pollen-receptive **stigma**).

In the *Hoya* flower these two whorls have become partially fused into a structure called the **gynostegium**, which comprises the central portion of the corona and encases the ovaries. The lower portion of this structure, especially when it is elongated, is referred to as the **column**. The column, when elongated, may stand high above the corolla surface (as in *Hoya multiflora* Blume) or may be imbedded in the corolla tissue, so that the corona appears sessile to the corolla surface (as in *Hoya coronaria* Blume).

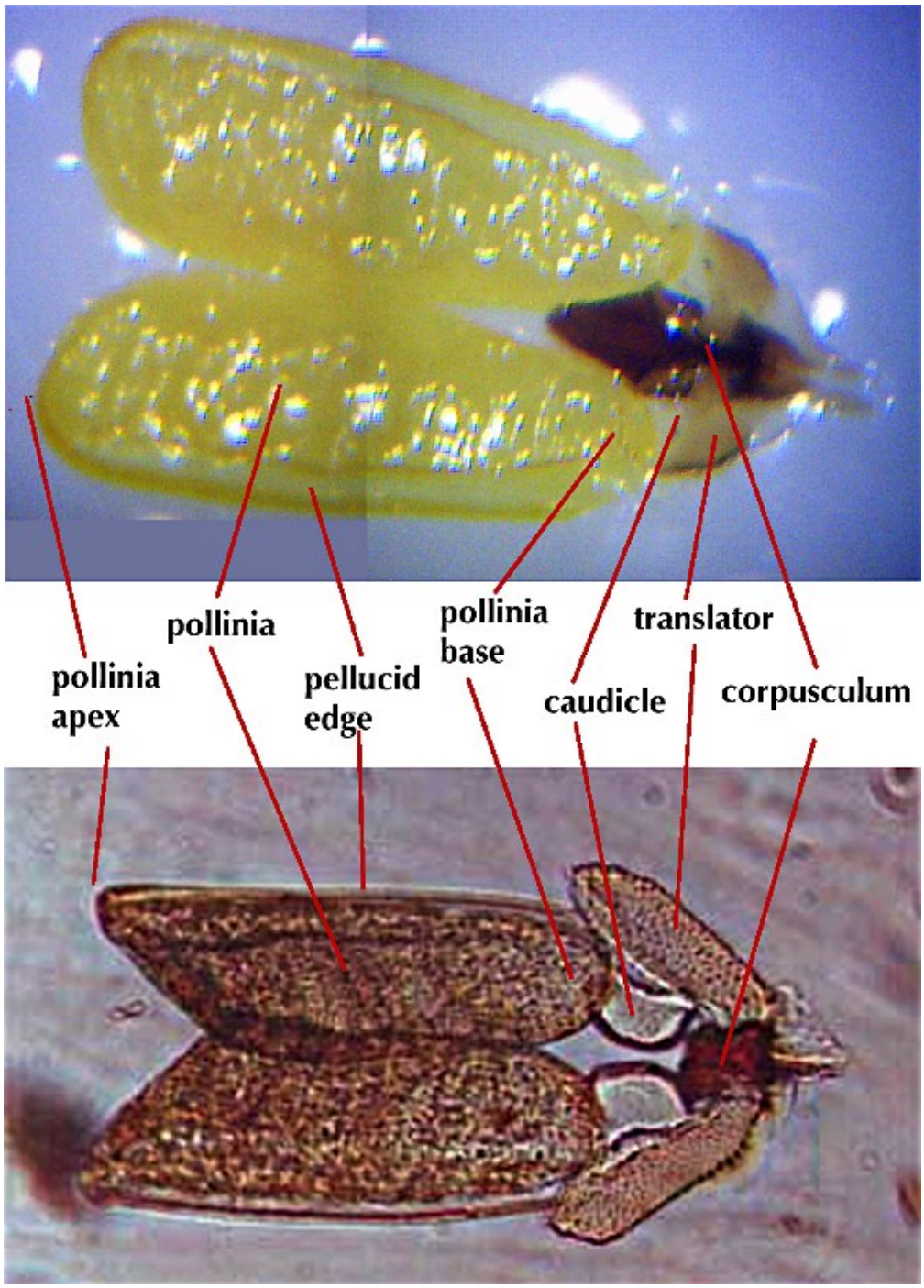
Around the gynostegium are five **corona lobes** or **scales**. The corona lobes appear to be solid structures, but are in fact comprised of relatively thin tissue which forms the top of the coronal scale and then (in the great majority of species) wraps down and under, forming a hollow scale with a **furrow** along the bottom where the two edges of tissue meet. Between the coronal scales, on the surface of the gynostegium, are five vertical slits called **anther margins, anther wings** or **guide rails**, into which the pollinia must be wedged to achieve fertilization (pollination in *Hoya* is not well-documented, but this process is well-documented for many closely related genera (primarily *Stapelia* (Barad, 1990)) which share the same basic flower structure. The inner end of each guide rail gives access to the pollen receptive **stigma**.

Each of the features of the gynostegium vary from species to species, but by far the most variable aspect of the corona are the corona lobes, which vary in shape, size relative to the corolla, ratio of height to width, height relative to the anther head, and color. The corona varies minutely between closely related species, and dramatically throughout the genus. It is the single feature which has been used most commonly for classification purposes in this genus (Hooker, 1885; Schlechter, 1914; Kloppenburg, 1993; Burton, 1995/96).

At the very center of the corona is a (usually) conical structure comprised of five triangular anther appendages (membranaceous outgrowths from the inner portion of the corona lobes), which will for this study be called the **anther head**, which forms a covering for the **style head**, which rests atop the gynostegium. The anther head seems to vary somewhat in degree of flatness, but has not been used extensively for classification purposes.

Laying near the inner end of the guide rails of mature flowers are the five **pollinaria**. The pollinaria (plural; singular **pollinarium**) consist of two waxy bundles of pollen called **pollinia** (plural; singular **pollinium**) which are joined by means of connective substances called **caudicles** and **translators** to a central structure called a **corpusculum** (some researchers prefer the term **retinaculum**, but a survey of recent articles (***Asklepios*** 98-100) shows a near universal use of the term **corpusculum** (singular; plural **corpuscula**) for this structure in *Hoya* and other *Asclepiadoideae*).

The pollinia are usually oblong, but range in shape from almost round to linear to rectangular, with rounded or truncate, often inwardly angled apexes. The outward margin of the pollinia are keeled and usually somewhat transparent. This area, called the **pellucid edge**, is free of individual pollen grains. When fertilization occurs the pollen grains in the pollinia grow tubes through (or around) this region to make contact with the stigma. One section, *Eriostemma*, lacks a pellucid edge on its pollinia. This will be discussed in part three of this article.



Above: pollinaria of (top) *H. cinnamomifolia* and (bottom) an unidentified section *Acanthostemma* species (DK).

The corpuscula vary in length, width, shape, and size relative to the pollinia. There are two separate parts of the connecting structures between the corpusculum and the pollinia. The **caudicles** are usually transparent, mostly comma-shaped objects which join within the corpusculum's side at their narrow end and hold the pollinia base at their wide end. Emerging from just below the base of the caudicles are the **translators**, which usually show in microphotographs as a darker, amber colored substance. The translators are "v" shaped in cross-section and wrap around the base of the caudicles, which are of a softer, less rigid material (Kloppenburg, 1996). The translators usually extend outwards to the base of the pollinia. In some species the translators are very broad, exceeding the width of the pollinia. These enlarged translators are usually referred to as **wings**, or as "**winged translators**" and vary in width, outline and orientation.

Below: microphotographs of pollinaria of (l-r):, *H. heuschkeliana, H. elliptica* and *H. finlaysonii*, all by DK.

Hybridization

Hoya species do not seem to hybridize readily, and to date all recorded *Hoya* hybrids have been between morphologically similar species. Examining the cross fertility in these species may provide some corroboration of infra-generic groupings.

Some recorded hybridizations include:

Hoya meredithii x Hoya incrassata (Hoya 'Goldeneye'), both from the *Hoya pottsii* complex.
Hoya macgillivrayi x Hoya archboldiana (H. 'Kaimuki') both from the *H. macgillivrayi* complex.
Hoya lacunosa x Hoya obscura (Hoya 'Sunrise') both from section *Otostemma*.
Hoya australis x Hoya subcalva (Hoya 'Pinkie') both from section *Pterostelma*.
Hoya pachyclada x Hoya pottsii (Hoya 'Christine'), both from the *Hoya pottsii complex.*
Hoya odorata x Hoya schneei (Hoya 'Iris Marie'), both may be from section *Pterostelma*.
Hoya 'MM' x *Hoya ciliata* (*Hoya* 'Optimistic') both from section *Eriostemma*.

Molecular Testing

Until recently, all classification schemes for living organisms have been based on the comparison of morphological features. The advent of molecular testing has made it possible to compare portions of the molecular structure of organism's DNA, RNA and proteins, and in so doing to infer relationships of tested species or groups to one another.

A recent series of papers authored primarily by Livia Wanntorp (Wanntorp et al., 2006a & 2006b) have reported and discussed attempts to map the genetic relatedness of species within the genus *Hoya* by focusing on molecular testing. 39 *Hoya* species, along with some species from the related genera *Dischidia* R. Br., *Marsdenia R. Br.* and *Gunnessia* P. I. Forster were tested and placed in a phylogeny .

The results of this molecular approach seem to confirm some pre-existing groupings in *Hoya* classification- the species tested that have been traditionally placed in the sections *Acanthostemma*, its subsection *Angusticarinatae*, and section *Eriostemma* showed results which suggest a close genetic relationship of the tested species traditionally placed within each group.

A group of Australian and New Guinean species are also suggested as being closely related in these studies- *Hoya australis* and *Hoya albiflora* Zipp. ex Blume, associated with section *Pterostelma,* grouped with *Hoya macgillivrayi* F. M. Bailey, *Hoya venusta* Schltr. and *Hoya patella* Schltr. These latter three species have been grouped previously with *Hoya campanulata* Blume (in section *Physostelma* by Schlechter (1914) and Kloppenburg (1993), or in section *Cystidianthus* by Burton (1995/96)). Also grouping with the above species were *Hoya hypolasia* Schltr., previously placed in section *Plocostemma* (by Schlechter, 1914) and *Hoya inflata* (P.I.Forst., D. Liddle & I.M.Liddle) L.Wanntorp & P.I.Forst., previously determined as belonging to the genus *Madangia* by Forster & Liddle (1997). These seven species have been suggested as having similar pollinarium structure, which would support a close genetic relation among them (Wanntorp, 2007).

These studies do not resolve many infrageneric relationships (Wanntorp, 2007), suggesting that the range and quantity of species selected for testing may not have been adequate to confirm or redefine many traditional groupings.

Some results of these studies do not support the close relationship of species which share many similar morphological characters (*H. lacunosa* Blume does not place near the *Acanthostemma* species in this study, *Hoya carnosa* and *Hoya serpens* Hook. f. do not place closely together), indicating that further study or testing is needed to resolve these apparent discrepancies.

History of sectional division

The first tentative steps towards organizing the Genus *Hoya* into sectional divisions began with Robert Wight's ***Contributions to the Botany of India*** in 1834, where two divisions of the genus were suggested. The subject has advanced over the years with the addition of former genera added to the genus *Hoya* as sections as well as with the original description of taxa as sections.

By the time of J. D. Hooker's 1885 work ***The Flora of British India 4***, followed closely by works by Schumann (1895) and Schlechter (1914/16) which recognized the same basic framework, approximately eight sections were recognized for the genus.

Later authors (R. Rintz, 1978; K. D. Hill, 1988) discussed the sections in general terms, but no comprehensive study was attempted until the publication of ***Hoya Sections*** by Dale Kloppenburg in 1993, which recognized 16 sections, followed closely by a proposed revision of the sections presented by C. M. Burton in ***The Hoyan*** (1995/96), which recognized 19 sections.

Current molecular studies led by Livia Wanntorp (2006a, 2006b, 2007) are attempting to verify whether *Hoya* sections are monopyhletic. This approach may dramatically alter the sectional divisions.

Here is a timeline of some of the important publications dealing with infra-generic classification in the genus *Hoya*. This is not an exhaustive list of every work mentioning the subject, these are the more relevant publications which introduce new sections (or future sections) or attempt revision.

1834. Wight, R. *Contributions to the Botany of India*: 35--40

Two vague subgeneric divisions are described, 1- *Hoya verae*, 2- unnamed, containing *H. viridiflora* R. Br.

Described as separate genera are *Pterostelma* and *Physostelma*.

1838. Don, G. *A General History of the Dichlamydeous Plants: comprising complete descriptions of the different orders.* (or *A General System of Gardening and Botany*) 4: 125--128

Often cited as an important work, the portion involving *Hoya* is mostly only an English translation of Wight's Latin descriptions from ***Contributions to the Botany of India 4.***

1836-1840. Endlicher, S. *Genera Plantarum secundum ordines naturales disposita*: 595--596

Two subgeneric divisions are listed, 1- *Hoya verae,* 2- *Wattahaka* (based on *Asclepias volubilis L. f.*, now considered to be *Dregea volubilis (L. f.)* Benth. ex Hook. f.).

1838. Decaisne, A. *Annales les Science Naturalles; Botanique* 9 (2): 271

Centrostemma is described as a genus.

1838. Bennet, J.J. *Plantae Javanicae Rariores, descriptae iconibusque illustratae* 1: 90

Cyrtoceras is described as a genus.

1843. Hasskarl, J. K. In: Hoev. & De Vriese's *Tijdschrift voor Natuurlijke Geschiedenis en Physiologie* 10: 125

Cystidianthus is described as a genus.

1844. Decaisne, A. In: De Candolle's *Prodromus Systematis Naturalis Regni Vegetabilis* 8: 633--640

Three subgeneric divisions are listed, 1- *Hoya verae*, 2- unnamed (containing *Hoya fusca* Wall. and *Hoya laurifolia* Decne.), 3- *Wattahaka (*containing *Hoya viridiflora* R. Br. and *H. lacuna* Buch.-Ham.).

1849. Blume, C. L. *Rumphia* 4: 29--33

Two sectional divisions are listed, 1- *Hoya verae*, 2- *Physostemma* (not to be confused with *Physostelma* (then a genus)), containing *Hoya coriacea* Blume, is described. *Acanthostemma*, *Otostemma*, and *Cathetostemma* are described as separate genera.

1849. Blume, C. L. *Museum Botanicum Lugduno-Batavum* 3: 43--46 & 4: 57--60

Plocostemma is described as a genus.

1856. Miquel, F. A. W. *Flora van Nederlandsch Indie* 2: 513--527

Six sections of the genus *Hoya* are accepted: 1- *Euhoya* (a new name for *Hoya verae*), 2-*Physostemma*, 3- *Sperlingia* (re-ranked here, with *Acanthostemma* as a synonym), 4- *Otostemma* (re-ranked here), 5- *Cathetostemma* and 6- *Plocostemma (re-ranked here)*.

1876. Bentham, G. & Hooker. J. D. *Genera Plantarum* 2: 776--777

Cyrtoceras (with *Centrostemma* as a synonym) and *Pterostelma* are absorbed into the genus *Hoya*, but not discussed substantively as subgeneric divisions.

1885. Hooker, J. D. *The Flora of British India* 4: 52--63

4 sections are listed: *Cyrtoceras* (re-ranked here, misspelled as "*Crytoceras*", with *Centrostemma* as a synonym), *Pterostelma* (re-ranked here), *Ancistrostemma* (described here) and *Euhoya*.

1895. Schumann, K. In: A. Engler's *Die Naturlichen Pflanzenfamilien* 4: 289--290

Often cited as an important work, this merely repeats the sectional scheme as seen by J. D. Hooker.

1907. King, G. "Flora of the Malayan Peninsula". Journal of the Royal Asiatic Society, Bengal Branch 74 (2): 559--563

Section *Kloiphora* is described.

1914. Schlechter, R. "Die Asclepiadaceen von Deutsch-Neu-Guinea". *Botanische jahrbucher fur Systematik, Pflanzengeschichte und Pflanzengeographie* 50 (sup.): 81--164

Seven subgeneric divisions are listed, 1- *Otostemma*, 2- *Eu-Hoya*, 3- *Plocostemma*, 4- *Pterostelma*, 5- *Oresostemma* (described), 6-*Physostelma*, and 7- *Eriostemma* (described).

1916. Schlechter, R. "Neue Asclepiadaceen von Sumatra und Celebes". *Beihefte zum Botanischen Centralblatt* 34: 1--18

Section *Peltostemma* is described.

1974. Tsiang & Li, P. T. *Acta Phytotaxonomica Sinica* 12: 126

Section *Antiostelma* is described.

1993. Kloppenburg, D. *Hoya Sections*

16 subgeneric divisions are listed, 1- *Peltostemma*, 2-*Otostemma*, 3- *Kloiphora*, 4- *Skenostemma (*described*)*, 5- *Sperlingia* (later corrected to *Acanthostemma*), 6- *Eriostemma*, 7- *Cathetostemma*, 8- *Centrostemma* (with *Cyrtoceras* as a synonym), 9- *Rudimentalia (*described*)*, 10- *Ancistrostemma*, 11- *Pterostelma*, 12- *Physostelma*, 13- *Oreostemma*, 14- *Plocostemma*, 15-*Amblyostemma (*described*)*, and 16- *Hoya*.

1995/96. Burton, C. M. "A tentative alternative arrangement of Hoya sections". *The Hoyan. 17 (2 part 2):10--12. 17 (3 part 2): 14--18. 18 (1 part 2):3--5. 19 (2 part 2):9--11.*

19 subgeneric divisions are listed, 1- *Otostemma*, 2- *Acanthostemma*, 3- *Peltostemma*, 4- *Pseudohoya (*described, a synonym of D. Kloppenburg's subsection to *Acanthostemma, Angusticarinatae)*, 5- *Hoya* (with subsection *Accersuccus (*described*)* and subsection *Lactisuccus (*described*)*), 6- *Physostemma*, 7- *Plocostemma*, 8-*Oreostemma*, 9-*Psuedopterostelma* (described, based on *Pterostelma*), 10- *Angustialatus* (described), 11- *Latiretinacula (*described*)*,12- *Amblyostemma*, 13- *Cystidianthus*, 14-*Physostelma*, 15- *Pachystelma* (described), 16- *Cyrtoceras*, 17- *Cathetostemma*, 18- *Ecarinatus (*described*)*, 19- *Eriostemma*.

2006a. Wanntorp, L. et al. "Wax plants disentangled: A phylogeny of *Hoya* (*Marsdenieae, Apocynaceae*) inferred from nuclear and chloroplast DNA sequences". *Molec. Phylog. Evol.* 39: 722--733

2006b. Wanntorp, L. et al. "Towards a Monophyletic *Hoya* (*Marsdenieae, Apocynaceae*): Inferences from the Chloroplast *trnL* Region and the *rbcL-atpB* spacer". *Syst. Bot.* 31(3): 586--596

2007. Wanntorp, L. "Pollinaria of *Hoya* (*Marsdenieae, Apocynaceae*) — shedding light on molecular phylogenetics". *Taxon* 56(2): 465--478

The last three papers present molecular evidence from nuclear and chloroplast DNA sequence testing and morphological evidence from a pollinaria study to try to resolve infrageneric organization for the genus *Hoya*. Traditional classification schemes are discussed in relation to these findings, although more recent efforts (Kloppenburg,1993; Burton,1995/96) are given less emphasis. A preliminary phylogeny for *Hoya* is presented.

Relevant *Hoya* sections today

The primary problem in discussing traditional sectional divisions within *Hoya* is the lack of consistent morphological characters which clearly distinguish one group of species from another. This situation was summed up by D. Kleijn and R. Van Donkelaar (2001) in this way: "...subdivision of the genus into well-defined sections (e.g. see attempts by Burton, 1985 and Kloppenburg, 1994) are still unsatisfactory (Ormlorr, 1997); only the sections *Eriostemma* Schltr. and *Acanthostemma* (Blume) Koord. are relatively unambiguous."

It does seem that the genus *Hoya* displays a great deal of variation in most of the morphological characteristics of most of its taxa, and that plants that are united by many close physical characteristics and accepted as closely related may display dramatic physical differences in one or more of their key features. *Hoya lanceolata* Wall ex D. Don and its subspecies *bella* (Hook.) D. H. Kent, morphologically similar plants, have differing corona lobe shape, one of the key features used to group or separate *Hoya* species. *Hoya erythrostemma* Kerr and *Hoya elliptica* *Hook. f.*, which resemble each other greatly in floral structure, have pollinaria that differ markedly in appearance.

The species of the genus *Hoya* display such variation that it seems the best course towards reviewing traditional classification schemes is to re-evaluate the sections based on a wide range of physical structures. A greater emphasis should be placed on relatively stable traits such as pollinarium and corona structure, but with all traits given consideration. Past revisional attempts have focused mostly on one or two morphological characteristics- earlier classifications focused on corona and corolla structure (Hooker, 1885; Schlechter, 1914), while at least one modern attempt (Burton, 1995/96) has looked at classifying the genus based almost solely on corona structure. The pollinarium, one of the most morphologically consistent features found in species which appear to be closely related, has been looked at extensively in relation to classification attempts only by Kloppenburg and Wanntorp, and to date have not been examined for a truly representative cross section of the genus and used as a prime feature in combination with other anatomical characteristics for classification purposes.

Right: a comparison photo of *H. calycina* (with large, divided semicampanulate white corolla) and *H.* sp. DS-70 (with small, revolute pink corolla).

A comparison of the flowers of *H. cinnamomifolia* (a member of the *Hoya pottsii* complex), left, and *Hoya carnosa* (the type of section *Hoya*), right.

Another issue in classifying *Hoya* is the use of *Hoya carnosa*, the type species of the genus, as a base of comparison for all other species and sections. From a phylogenetic approach, that is, an approach that seeks to classify *Hoya* species in a way that may reflect actual genetic relationships, it makes more sense to use *Hoya pottsii* Traill and its close relatives as a basis of comparison. The species close to *Hoya pottsii* display clear and consistent morphological differences from *Hoya carnosa* and its close relatives (see the entries for section *Hoya* (pg. 50) and the *H. pottsii* complex (pg. 41). The *H. pottsii* group inhabits a much greater range than the *H. carnosa* group (the *H. pottsii* complex seems to have at least 45 members across almost the entire range of the genus, while section *Hoya* is represented by only five or six unambiguous species so far, mostly from southern China (*H. carnosa)* through Thailand (*H. monnetae* T. Green) and the Philippines (*H. pubicalyx* Merr.). It seems a logical assumption that the more ubiquitous *H. pottsii* group is more likely to have genetic links or intergrades with other species groups than the *carnosa* complex. Therefore, *Hoya pottsii* is used as a basis of comparison with the other species and groups considered in this study.

For this author's evaluation of the sections, factors of classification were considered in the following order of importance (from most important to least):

1- pollinarium structure
2- corona structure
3- raceme (or umbel) orientation and form
4- molecular data (from the 2006 Wanntorp studies)
5- corolla structure
6- plant form
7- leaf shape/size/venation
8- geographical distribution

When the mass of *Hoya* species are viewed in this light, approximately twenty-six distinct groups of species with coherent distinguishing features seem to emerge. These groups, as seen by this author, are represented by the following pre-existing or proposed groups:

1- section ***Otostemma*** (Blume) Miq.- type: *H. lacunosa* Blume

2- section ***Acanthostemma*** (Blume) D.Kloppenburg- type: *H. rumphii* Blume

3- section ***Peltostemma*** Schltr.- type: *H. imbricata* Decne.

4- the ***Hoya lanceolata*** Wall. ex D. Don complex (proposed)

5- section ***Angusticarinatae*** D. Kloppenburg (proposed re-ranking)- type: *H. diptera* *Seem.*

6- the ***Hoya cumingiana*** Decne. complex (proposed)

7- the ***Hoya pottsii*** Traill complex (proposed)

8- the ***Hoya blashernaezii*** D. Kloppenburg complex (proposed)

9- section ***Amblyostemma*** D. Kloppenburg- type: *H. meliflua* (Blanco) Merr.

10- the ***Hoya longifolia*** Wall. complex (proposed)

11- section ***Hoya-*** *type: H. carnosa* R. Br.

12- the ***Hoya polyneura*** Hook. f. complex (proposed)

13- section ***Angustialatus*** C. M. Burton (proposed)- type: *H. flavescens* Schltr.

14- the ***Hoya patella*** Schltr. complex (proposed)

15- the ***Hoya macgillivrayi*** F. M. Bailey complex (proposed)

16- section ***Pterostelma*** (WIght) Hooker f.- type: *H. acuminata* Benth. ex Hook. f.

17- section ***Physostemma*** Blume- type: *H. coriacea* Blume

18- section ***Plocostemma*** (Blume) Miq.- type: *H. lasiantha* Korth. ex Blume

19- section ***Pachystelma*** C. M. Burton- (proposed) type: *H. mindorensis* Schltr.

20- section ***Oreostemma*** Schltr.- type: *H. oreostemma* Schltr.

21- section ***Latiretinacula*** C. M. Burton (proposed)- type: *H. griffithii* Hook. f.

22- section ***Cystidianthus*** (Hassk.) King & Gamble(?)- type: *H. campanulata* Blume

23- section ***Kloiphora*** King & Gamble- type: *H. curtisii* King & Gamble

24- section ***Centrostemma*** (Decne.) Hook. f.(?)- type: *H. multiflora* Blume

25- section ***Antiostelma*** Tsiang & P. T. Li- type: *H. manipurensis* Deb

26- section ***Eriostemma*** Schltr.- type: *H. coronaria* Blume

While all of these groups have distinct traits which delimitate them, only sections *Kloiphora*, *Antiostelma*, *Eriostemma* and *Centrostemma* seem to have breaks in continuity between themselves and other *Hoya* sections: there appear to be no known species which are intermediate between these four sections and any other. The other sections listed above seem, in many instances, to intergrade somewhat into each other, suggesting evolutionary links between the various groups.

For instance, species closely related to *Hoya coriacea*, placed in section *Physostemma*, seem to show traits of both section *Pterostelma* and section *Plocostemma* species.

Species placed in section *Physostemma* may constitute a genetic link between sections *Pterostelma* and *Plocostemma*: *Hoya buotii* (second from left) has the raised, rounded outer corona lobes and divided semi-campanulate corollas of the *Pterostelma* section species, like *Hoya graveolens (left)*. *Hoya fraterna* (second from right) has upright corona lobe apexes and reflexed, pubescent corolla lobes, as are found in *Hoya lasiantha* (right), placed in section *Plocostemma*.)

One of the difficulties in evaluating the relevance of the individual sections is the ambiguous nature of the rank "section". There are no clearly defined rules setting the exact level of physical similarity or difference which should define each group. Early placement of other genera into the genus *Hoya* as sections argues for a fairly broad level of inclusion for the sections (the species contained in a group different enough from the type of the genus, *Hoya carnosa*, to be considered a different genus should be very distinct). Other publications separate groups with relatively small differences from other recognized sections (section *Peltostemma* species are distinct from section *Acanthostemma* species only in the lack of coronal bi-lobes and the presence of elongated anther appendages in *Peltostemma* species- section *Angustialatus* is distinct from section *Hoya* species only in subtle details of the corona and pollinarium and in the milky versus clear sap).

Over time the general trend seems to have been towards defining sections more narrowly, based on finer detail, thus the sections and complexes chosen for inclusion here are also rather narrowly defined. The species placed in groups here have been segregated from one another by at least one clear, consistent physical characteristic of the pollinarium or corona, with consideration also given to corolla orientation and division, raceme or umbel configuration, overall plant habit and leaf structure, molecular data and geographic occurrence.

About the suggested section/complex entries:

Photo credits are as stated. Where no photographer is cited the photo is by Mark Randal.
The following abbreviations are used for frequent contributors:
DK= Dale Kloppenburg, **TN**= Torill Nyhuus, **SS**= Surisa Somadee, **BE**= Bob Ely, **CN**= Carol Noel.

Some approximate size parameters for floral/ vegetative descriptions in the next section:

Leaves: **small-** (less than 4 cm long and 2.5cm wide, **medium-** (between 4 and 10cm long, between 2.5 and 7 cm wide, **large**- between 10 and 20cm long long, between 7 and 10cm wide, **giant-** over 20cm long and over 10cm wide

Flowers (measured in diameter when pressed flat): **small-** (less than 1cm, **medium-** between 1 and 2cm, **large**-between 2 and 3cm, **giant**- over 3cm.

In part one of this article, the first eleven sections of this suggested list of relevant sections will be examined. The entries here are of three types: 1) traditionally published sections, like *Otostemma* and *Pterostelma*, 2) sections proposed, but not published, by C. M. Burton (1995/96) like section *Angustialatus* and section *latiretinacula*, and 3) groups of species which have not been previously recognized as constituting a distinct section, which are presented here as species complexes based on a "type", like the *Hoya pottsii* complex and the *Hoya cumingiana* complex. A "species complex" as presented here is roughly of the same taxonomic rank as a section, but has not been officially named or published.

The species listed in each entry as also belonging to that section or complex are suggested as closely conforming to the parameters of that entry. Not all unambiguous species have been placed into groups for this study- a few do not fit clearly into the classification scheme presented here. Some of these species will be discussed in part three of this article.

Some of the species names used in this article are in dispute. An effort was made to select the name that seems to be the most widely recognized for that species, but the name selected for use here should not be construed as being an endorsement by the author for that specific determination. A complete checklist of correct species names for the genus is outside the scope of this article.

A few species listed here do not have valid determinations- like *Hoya* sp. DS-70 and *Hoya* sp. 93039 from Rundum. The undetermined species included here are fairly wide-spread in cultivation.

There are many more species names published for the genus than are listed here- the species selected for classification in this study are readily available in cultivation and, while they may have disputed names, the species themselves in most cases are easy to identify as biological entities.

No effort has been made to classify species that are not in cultivation. The availability of fresh floral material for photographing and study is essential to accurate determination and classification. The use of species identified only by dried herbarium sheets has led to trouble in many instances, especially when used as a type species (as are *H. acuminata* Benth. ex Hook. f., the type species for section *Pterostelma*, and *H. rumphii* Blume, the type species for section *Acanthostemma*).

The first eleven sections/complexes presented here seem to represent a rage of variation between two of the major groups of species in the genus- the small, revolute flowered species typified by sections *Otostemma* and *Acanthostemma* and the larger flowered species with roughly horizontal corona lobes typified by the *Hoya pottsii* complex and section *Hoya*.

Distributions for the section/complexes are approximate, based on historic and modern collections. The actual distribution for most groups may be somewhat larger.

1-Section *Otostemma* (Blume) Miquel

Etymology: "oto"="**ear**", Gr. + "stemma" (or "stelma")="**crown**", Gr.

Type species: *Hoya lacunosa* Blume

Overall form: mostly small to medium-leaved, pendant or weakly climbing epiphytic vines. Flowers are ball-shaped, small, fuzzy, usually in shades of white to pale pink, rarely orange (*H. endauensis*), usually intensely fragrant (the scent of *H. lacunosa* is often compared to that of carnations), and borne in flat or slightly concave clusters.

Distribution: Malaysia, Thailand, Burma, and the western portion of Indonesia.

Publication: ***Rumphia 4*, 1849 (as a genus)*, Flora van Nederlandsch Indie 2*, 1856 (as a section).**

Original description: (as a genus) (translated from Latin by DK) "Calyx five-parted. Corolla five-parted, lobes revolute. Corona of 5 segments adnate to the elevated gynostegium; corona segments boat shaped, fleshy, spreading widely, above concave, with the interior angle prolonged into a tooth overtopping the anthers, and beneath with two-toothed, acute appendix bent downward. With the anthers incumbent on the stigma, with the apex simple, acute. Pollinia attached at the bases, close together, linearly compressed. Stigma scarcely apiculate. Follicles smooth. Many seeds, with a hairy tufted umbilicum. Herbs of the Indian Archipelago, rooting in trees; leaves opposite or rarely whorled, fleshy, glabrous, umbels with moderately long peduncles; with small white flowers."

Revised descriptions: Miquel,1856 (translated from Latin by MR) "Flowers small, white; corolla revolute; leaves of staminal corona boat-shaped, beneath with two-teeth lying backwards. Anther apex acute."

Schlechter, 1913 (translated from German by DK & Dieter Paul) "*Otostemma* is a small section, the species not always easy to separate, whose type is *H. lacunosa* Blume. The gynostegium is very characteristic, because it always forms a wide cone, continual with the coronal scales, while the scale clearly extends upwards in two rounded off ears. The flowers are always fairly small, the calyx is tiny." - (Schlechter was here apparently also describing section *Acanthostemma* species, which he included in this section in his 1913 work.)

Kloppenburg, 1994 "...I add that the most prominent character of this section is the pentamerous skirt which hangs from the base of the outer corona scale lobes and lack of sulcation below."

Salient features-

Pollinarium: pollinia are oblong, roughly twice as long as wide, with truncated, inwardly angled apexes. Caudicles are large, almost the same size as the corpusculum. Translators are broad, with the outer margin following the line of the caudicles, and usually exceed the outer margin of the pollinia.

Corona: conical, with the inner angles raised above the outer angles. The coronal tissue, after forming the corona lobe top, does not travel down perpendicular to the corona surface and roll under to form a hollow lobe, as in members of all other *Hoya* sections. Instead, the tissue projects to form the corona lobe upper surface and then cuts back in towards the gynostegium. The lower corona lobes are modified into a five parted coronal skirt, which hides the raised column that forms the base of the gynostegium. The furrows which normally occur on the lower surface of the coronal lobe are present as divisions in the coronal skirt.

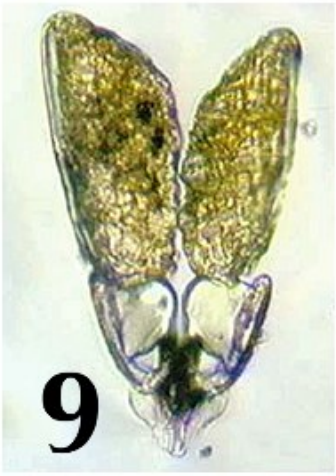
Corolla: revolute, densely pubescent.

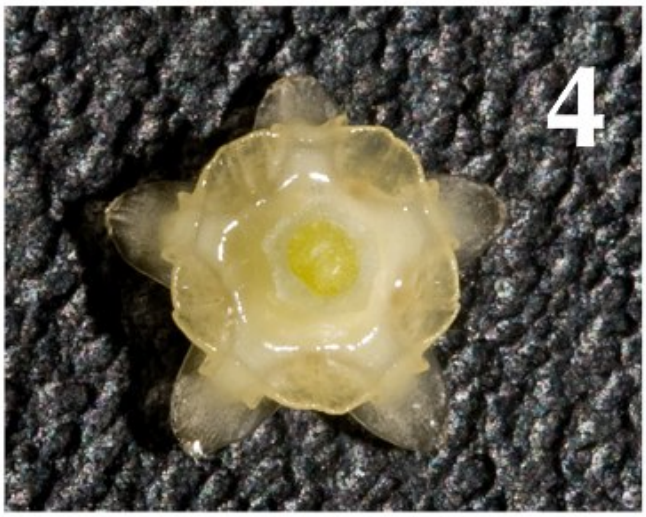
Raceme: flat or concave.

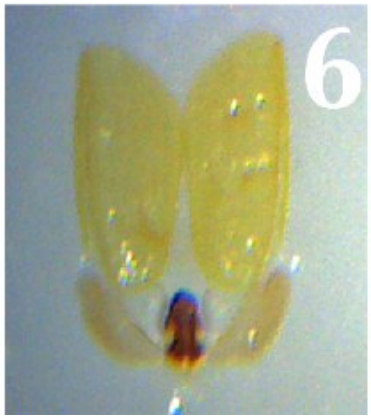
Species thought to belong to this section/complex:

H. lacunosa Blume (**type**)	***H. endauensis*** Kiew	***H. nabawanensis*** D. Klopp. & Wiberg
H. obscura Elmer ex C. M. Burton	***H. pusilla*** R. E. Rintz	***H. sipitangensis*** D. Klopp. & Wiberg
H. walliniana D. Klopp. & Nyhuus		

Taxonomic considerations: Section *Otostemma* is one of the few sections with no overt taxonomic problems. The descriptions are quite clear, the type species in unambiguous and common in cultivation. The "two-toothed, acute appendix" in the original description seems to refer to the coronal skirt (see image 5).







Section *Otostemma*. (1) *Hoya* 'Sunrise' (courtesy of Christina Karlsson). (2) *Hoya lacunosa*. (3) *Hoya wallin-iana*. (4) bottom of corolla of *H. lacunosa* showing coronal skirt. (5) side view of *Hoya lacunosa*. Pollinaria of (6) *H. lacunosa* and (7) *H. sipitangensis* (DK). (8) A mature plant of *Hoya lacunosa* (photo courtesy of Doug Chamberlain). (9) Pollinarium of *Hoya walleniana* (DK).

2-Section Acanthostemma (Blume) Kloppenburg

Etymology: "acantho"="**thorny**", Gr. + "stemma"="**crown**", Gr.

Type species: *Hoya rumphii* Blume

Overall form: mostly small or medium-leaved pendant or weakly climbing epiphytic vines. Flowers are small, ball-shaped and range in color from deep purple-red (*H*oya sp. 93039 from Rundum) to white *(Hoya gigantangensis*) to yellow (*Hoya puber*). The flowers, which occur in flat or slightly concave clusters, are fragrant, usually smelling of butter or caramel.

Distribution: The Philippines, Thailand, Malaysia, Indonesia, Melanesia, and tropical Australia.

Publication: ***Rumphia 4***, 1849, as a genus; ***Hoya Sections,*** 1993, as a section.

Original description: (as a genus) (translated from Latin by DK) "Calyx five-parted. Corolla rotate, five-parted. Corona of five segments, adnate to the short gynostegium, segments sagittate, fleshy, erect, with the inner angle produced into a tooth, incumbent on the anther. With the anther terminal membranaceous, incumbent upon the stigma. Pollinia affixed at the base erect somewhat divergent, oblong with compressed narrow sides. Stigma apiculate. Follicles smooth. Many seeds with a hairy tufted umbilicus. Herb, falsely parasitic, rooting climber, widely dispersed in insular Asian tropics and New Guinea; foliage fleshy opposite or verticillate; umbels or racemes shaped like umbels often many flowered; with flowers small, dark or dilute purple."

Revised descriptions: Miquel, 1856 (as section *Sperlingia*) (translated from Latin by MR) "Flowers small, corolla laciniate, revolute; leaves of staminal corona sagitate (underneath?)."

Kloppenburg, 2001 (***Hoya Sections (revised)***) "This section has small pubescent ball shaped flowers with (revolute corolla) flowers looking much like those of the Section *Otostemma*. Most have geotropic umbels which are concave or flat. The calyx is small, the gynostegium short adnate. The apex of the corolla lobes are bare and hidden in the revolute fold, difficult to discern in herbarium material. The corona is upright to very upright, with a tooth-like inner apex and blunt outer apex, the lateral sides of the scales are shelved and extended beyond and often above the outer apex as two ligule-like structures, the lower part of the scale is sulcate recurved to form a groove. The pollinia have curved translator arms supporting clear caudicles (described as winged). The pollinia are affixed at the base and have a pellucid outer border but not all the way to the caudicles. The styler head (stigma) is apiculate."

Burton, 1995/96 "Corolla five parted, flat or revolute; corona lobes upright, or nearly so (inner apex higher than outer apex), slender, exterior angle emarginate (actually having the two sides elongated); translators of pollinia winged."

Salient features-

Pollinarium: pollinia are oblong, roughly twice as long as wide, with truncated, inwardly angled apexes, as in section *Otostemma* species. Caudicles are large, almost the same size as the corpusculum. Translators are broad, often rounded, with the translator outer margin often exceeding the outer margin of the pollinia. Very similar to the pollinaria of section *Otostemma* species, though the translators of section *Acanthostemma* species often have more of a rounded outer margin.

Corona: conical, with the inner angles raised above the outer angles. The margins of the coronal tissue along the furrow are folded inward and extend past the upper corona apex, appearing from above as two thorn-like projections in most species placed here.

Corolla: usually densely pubescent and revolute, rarely rotate (as in *Hoya davidcummingii*) or urceolate (as in *Hoya heushkeliana*).

Raceme: flat or concave.

Species thought to belong to this section/complex:

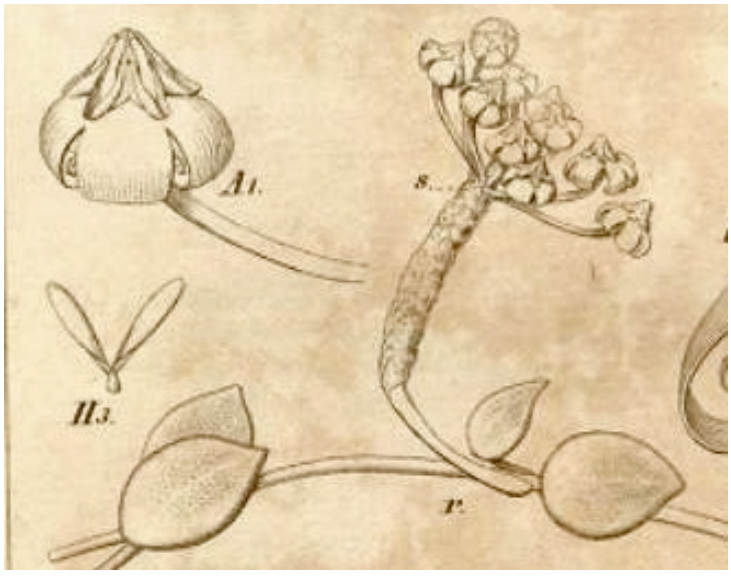
H. rumphii Blume (**type)**	***H. bilobata*** Schltr.	***H. brevialata*** Kleijn & Van Donkelaar
H. burtoniae D. Kloppenburg	***H. davidcummingii*** D. Kloppenburg	***H. gigantangensis*** D. Kloppenburg
H. halophila Schltr.	***H. heuschkeliana*** D. Kloppenburg	***H. incurvula*** Schltr**.**
H. inconspicua Hemsley	***H. kentiana*** C. M. Burton	***H. kloppenburgii*** T. Green
H. leytensis Elmer ex. Burton	***H. litoralis*** Schltr.	***H. loherii*** D. Kloppenburg
H. lucyae D. Kloppenburg & Siar	***H. memoria*** D. Kloppenburg	***H. micrantha*** Hooker f.
H.myrmecopa Kleijn & Van Donkelaar	***H. pallilimba*** Kleijn & Van Donkelaar	***H. panchoi*** D. Kloppenburg
H. parviflora Wight	***H. parvifolia*** Schltr.	***H. puber*** Blume (syn. *H. picta* Miq.)
H. sigillatis T. Green	***H.* sp. DS-128**	***H.* sp. DS-70**
***H.* sp. 93039 from Rundum**	***H. tsangii*** C. M. Burton	***H. wayetii*** D. Kloppenburg

Taxonomic considerations: The type species, *Hoya rumphii*, is of ambiguous status. For discussion of this see Kloppenburg, 1994, ***Hoya Section Acanthostemma* .**

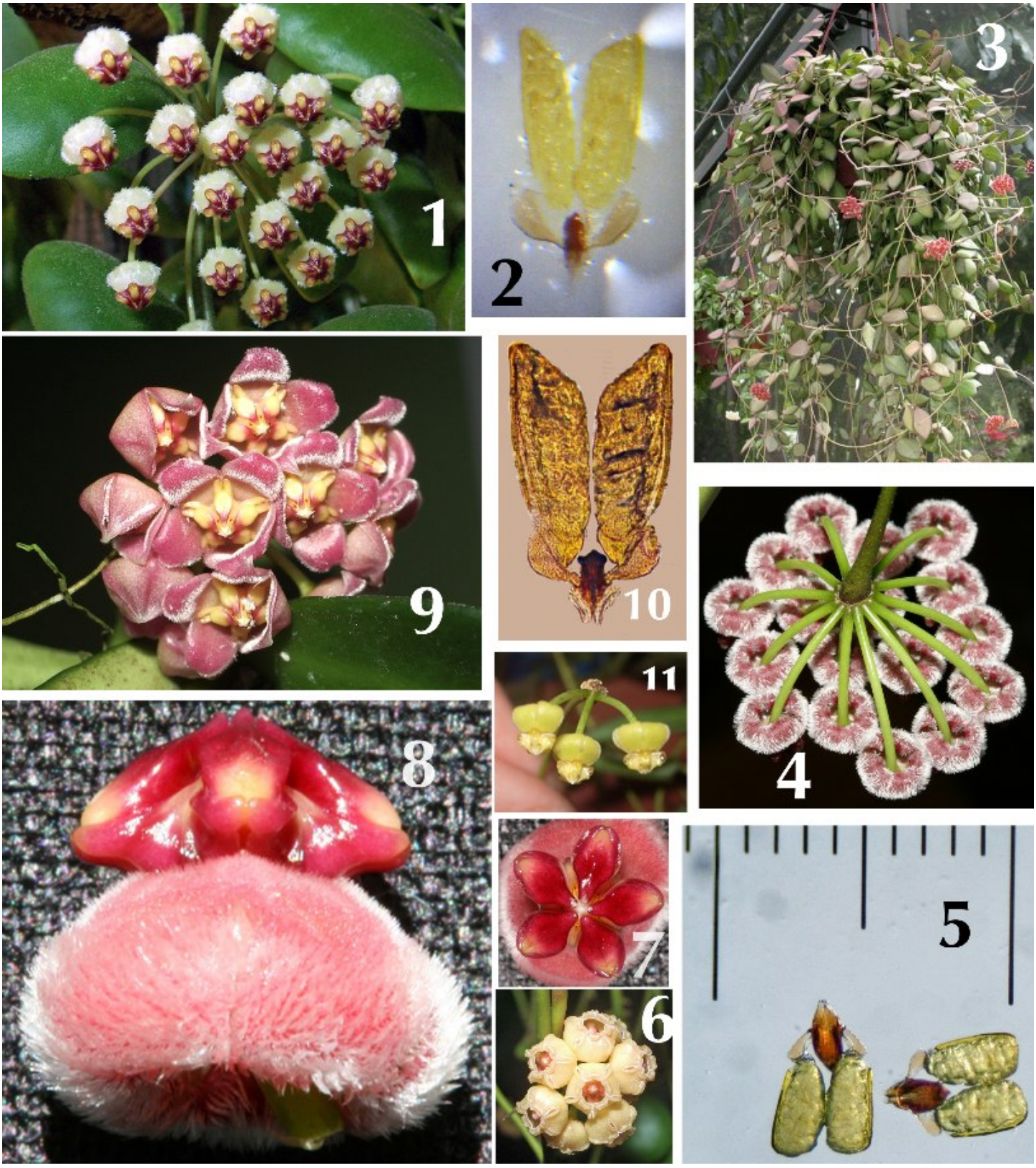
The original description does not clearly mention the most distinctive feature of the group of species placed here, the bilobed coronal extensions, but the accompanying illustration (for *A. pictum*) from ***Rumphia 4*** shows these structures clearly (see below).

Acanthostemma is well defined, and, with around 30 species placed here, represents the second largest group of morphologically similar species after the *Hoya pottsii* complex, which contains at least 45 known species.

Livia Wanntorp's recent series of papers (2006a, 2006b) considering the results of preliminary molecular testing on the genus suggests that *Acanthostemma* and *Otostemma* species are not closely related, and shows *Otostemma* species clustering together with *Peltostemma* species. The morphological evidence does not seem to support this finding, as Wanntorp notes in a study of *Hoya* pollinarium (Wanntorp, 2007). The grouping of *Otostemma* and *Peltostemma* species seems to suggest a faulty finding here, as *Peltostemma* species seem to be more similar to *Acanthostemma* species than *Otostemma* species, differing only in the lack of coronal bi-lobes and the extended anther appendages in *Peltostemma*.



left: illustration of *Acanthostemma pictum* Blume (now considered to be *Hoya puber* Blume) from *Museum Botanicum Lugduno-Batavum*, 1849.



Section *Acanthostemma*. (1) *Hoya brevialata* (photo courtesy of Brenda Medel). (2) pollinarium of *Hoya wayetii*. (3) *Hoya* sp. DS-70 (photo courtesy of Linda Vosbury). (4) *Hoya wayetii*. (5) pollinaria of *Hoya heuschkeliana* (TN). (6) Flowers of *Hoya heuschkeliana*. *Hoya wayetii* flower, top (7) and side (8) views. (9) *Hoya davidcummingii*. (10) Pollinarium of *Hoya brevialata* (DK). (11) *H. puber*.

3-Section *Peltostemma* Schlechter

Etymology: "pelt"="**shield**", L. + "stemma"="**crown**", Gr.

Type species: *Hoya imbricata* Decne.

Overall form: Epiphytic vines with medium-sized, hard leaves. *Hoya imbricata* has both leaves from each node fused together (or one leaf of the pair aborts) and the rim pressed tightly against the trunk of its host tree. The space beneath the leaf is filled with roots, which are protected from direct sun and dry air, and inhabited by potentially symbiotic ants. *Hoya caudata* and *Hoya flagellata* are more typical vines. Flowers are small, ball-shaped or flat, sometimes fragrant, yellow or white, held in flat or slightly concave clusters.

Distribution: The Philippines, Thailand, Malaysia, Indonesia.

Publication: ***Beihefte zum Botanischen Centralblatt***, 1916

Original description: (translated from German by DK and Dieter Paul) "*Hoya maxima* (Karst.) Warburg together with *Hoya imbricata* Decaisne from the Philippines constitute the section, which I here name *Peltostemma*, because of the shield- forming leaves, as well as in the habit (of growth), but also the structure of the blooms which are remarkably characteristic. The apparently dovetailed (imbricate) regular, almost circular, close- fitting leaves, which are fastened to the substrate, are pretty little things and stand upon a pedestal, complete growing leaf pairs, that in their arrangement are closely fitted in such manner, botanically speaking that resemble the *Conchophyllum* and for sure the *Dischidia* species of the Section *Collyris*. In the blooms the Section *Peltostemma* is distinguished through the inclined corona scales and the long extended anther appendages. In addition the stigma head is hollow on the point and slow to open in comparison to the rest of the sections. Type species (designated here) *Hoya maxima* (Karst) Warburg."

Revised descriptions: Kloppenburg, 1993 " This section was established to cover a small group of hoyas in which one leaf of a pair aborts or otherwise fails to develop. The leaves are circular convex on top with the concave surface covering the stem and appressed to the substrate (usually tree trunks). Many rootlets develop from under these leaves attaching to the substrate, and often the spaces are occupied by small ants. The corona scales are very upright with long emerging anther appendages extending from the flower center, rising above the scale's inner lobe. The anther wings are prominent. The pollinia are rather long and narrow, and the translators broad and scapulate with the caudicles long and narrow as is also the retinaculum."

Burton, 1995/96 "Corollas rotate-recurved or revolute; corona lobes more or less upright, with inner apexes higher than outer apexes and having extremely long caudate anther appendages, channeled beneath and in some species having double appearing anther wings; translators of the pollinia winged. In some, but not all, species of the section, there is but a single leaf per node, the result, it is speculated, of one leaf of a pair having aborted in its embryonic stage, however, Schlechter stated that there were two leaves per node that had become fused. A close examination of *H. imbricata* leaves, seems to confirm Schlechter's claim."

Salient features-

Pollinarium: pollinia are oblong, slightly more than twice as long as wide, with truncated, inwardly angled apexes, as in section *Otostemma* and section *Acanthostemma* species. Caudicles are relatively large, being slightly smaller than the corpusculum. Translators are broad, with the translator outer margin exceeding the outer margin of the pollinia. Difficult to distinguish from the pollinaria of section *Acanthostemma* species

Corona: conical, with the inner angles raised above the outer angles. The anther appendages of the species here are elongated, and stand high above the corona lobe inner angles.

Corolla: Densely pubescent, revolute (*H. imbricata*), rotate (*H. caudata*) or divided semi-campanulate (*H. flagellata*).

Raceme: flat or concave.

Species thought to belong to this section/complex:

Hoya imbricata Decne. **(type)**	***Hoya caudata*** Hook f.	***Hoya flagellata*** Kerr

Taxonomic considerations: the name *Peltostemma* refers to the "peltate" leaves, in which the petiole appears to connect to the leaf in the laminas interior, not at the apparent leaf margin, although the margin is actually conniving and does meet the petiole base. The use of the peltate leaves as a distinguishing character is of little use here- the species included share coronal features which clearly unite them, but do not share this specific vegetative morphology.

The type species cited by Schlechter, *Hoya maxima* (Karst.) Warburg, was placed as a synonym to *Hoya imbricata* by D. Kleijn and R. Van Donkelaar (2001).

This section appears to be very closely related to section *Otostemma* and section *Acanthostemma*- their conical coronas, mostly pubescent, revolute corollas and broad translators argue that they share a close evolutionary descent.

(see also "Taxonomic considerations" under section *Acanthostemma*, pg. 30.)

The underside of a leaf of *Hoya imbricata*, filled with roots and ants. Photo courtesy of Merlin Sy.

Section *Peltostemma*. (1) *Hoya imbricata*. (2) *Hoya caudata* (photo courtesy of Eva-Karin Wiberg. (3) Pollinarium of *Hoya imbricata* (DK). (4) Side view of flower of *Hoya caudata* (BE). (5) *Hoya flagellata* (BE). (6) Buds of *Hoya flagellata* (BE). (7) *Hoya imbricata* (SS).

4- The *Hoya lanceolata* complex

Overall form: Epiphytic danglers which do not seem to climb by twining or by adventitious roots. Leaves are small, narrow, hairy, and closely set along the stems. Flowers are small, flat, white with translucent purple or yellow coronas, and borne on temporary peduncles, in flat or slightly concave clusters, usually only at the ends of the stems. All are fragrant, with a variety of sweet, candy-like scents. The species included here all prefer or tolerate cooler conditions than the bulk of *Hoya* species.

Distribution: eastern India, Nepal, Bangladesh, Bhutan, Burma, northern Thailand.

Publication: not published in this form, considered by Kloppenburg (1993) and Burton (1995/96) as belonging to section *Acanthostemma* subsection *Angusticarinatae* or its synonym, section *Pseudohoya*, respectively (see next entry for section *Angusticarinatae*).

Salient features-

Pollinarium: pollinia are oblong, almost 3 times as long as wide. Translators are broad. The outer edge of the translator is sharply defined, unlike the translators in those species in section *Angusticarinatae* (proposed re-ranking).

Corona: corona lobes are roughly flat, raised slightly at the interior angle. The coronas of *Hoya linearis* and *Hoya lanceolata* resemble those of the species placed in section *Angusticarinatae* (which have longer, more narrow corona lobes than the more rounded corona lobes of the other species placed here.).

Corolla: glabrous or nearly so, rotate or slightly reflexed (*Hoya linearis*, *Hoya chinghungensis*).

Umbel: flat or concave. This complex, along with section *Eriostemma*, are the only two species groups with true umbels. All other sections have flowers borne in racemes.

Species thought to belong to this section/complex:

H. lanceolata Wall. ex. D. Don **(type)**	***H. l.* ssp. *bella*** (Hook.) D. H. Kent	***H. chinghungensis*** (Tsiang &P. T. Li) et al.
H. dickasoniana P. T. Li	***H. engleriana*** Hosseus	***H. linearis*** Wall.

Taxonomic considerations: The most striking differences between these species and those placed in section *Angusticarinatae* (proposed) are the pendant, non-twining habit of all the species included here and the life span of the peduncles- the species in the *H. lanceolata* complex grow peduncles and set flower then shed the peduncle, while section *Angusticarinatae* species have persistent peduncles. The leaves, internodes and peduncles of the *Angusticarinatae* species are generally much larger/longer than those of the species included here with *H. lanceolata*, making those species allied to *Hoya diptera* much larger in scale than those similar to *H. lanceolata*. The pollinaria of species grouped here with *H. lanceolata* have broad translators with sharply defined edges- the species placed in *Angusticarinatae* have broad, rough textured translators with diffuse edges.

The *Hoya lanceolata* complex. (1) *Hoya lanceolata* ssp. *bella* (photo courtesy of Montserrat Pous). (2) *Hoya linearis* (photo courtesy of Sylvine Bruneau. (3) *Hoya lanceolata* ssp. *bella* (top) and *Hoya lanceolata* (bottom) (TN). (4) *H*oya *chinghungensis* (photo courtsey of Eva-Karin Wiberg). (5) *H. linearis* (photo courtesy of Sylvine Bruneau). (6) Pollinarium of *Hoya dickasoniana* (the clear caudicles are difficult to see here). (7) *Hoya engleriana* (photo courtesy of Eva-Karin Wiberg). (8) Side view of *Hoya dickasoniana*.

5- Section *Angusticarinatae* D. Kloppenburg (proposed re-ranking)

Etymology: "angusti"="**narrow**", L. + "carinatas"="**keeled**", L.

Type species: *Hoya diptera* Seem**.**

Overall form: These species are twining epiphytic vines with medium sized leaves. The stems are wiry, the leaves are fairly hard and non-succulent. The flowers, which are borne in flat or slightly concave clusters, are medium sized, flat, white, pink or yellow, and fragrant.

Distribution: Melanesia, Australia.

Publication: (as subsection to *Acanthostemma*) cf. Repert. Pl. Succ. (I.O.S.), 44: 10 (1993 publ. 1994).

Original description: (translated from Latin by MR) "Sides of corona leaves with rounded narrow (lobes?)" and, in English "Type species is *Hoya diptera* Seemann."

Revised descriptions: Burton (1995/96) (as section *Psuedohoya*) "Corolla lobes rotate, margins and apexes revolute; corona lobes more or less flat, channeled beneath; translators of the pollinia winged. Most *Hoyas* in this section appear exactly as those of the *Hoya* section, except for the winged translators. Also, they generally have much smaller sepals."

Salient features-

Pollinarium: pollinia are oblong, roughly twice as long as wide, with truncated, inwardly angled apexes, as in section *Otostemma* and section *Acanthostemma* species. Caudicles are relatively large, approximately half the size of the corpusculum. Translators are broad, the outer margin seems to be poorly defined.

Corona: lobes upper surfaces approach horizontal, slightly raised at the inner angle in some species. The lobes are more narrow than in most *Hoya pottsii* complex species.

Corolla: slightly pubescent, rotate.

Raceme: flat or slightly concave.

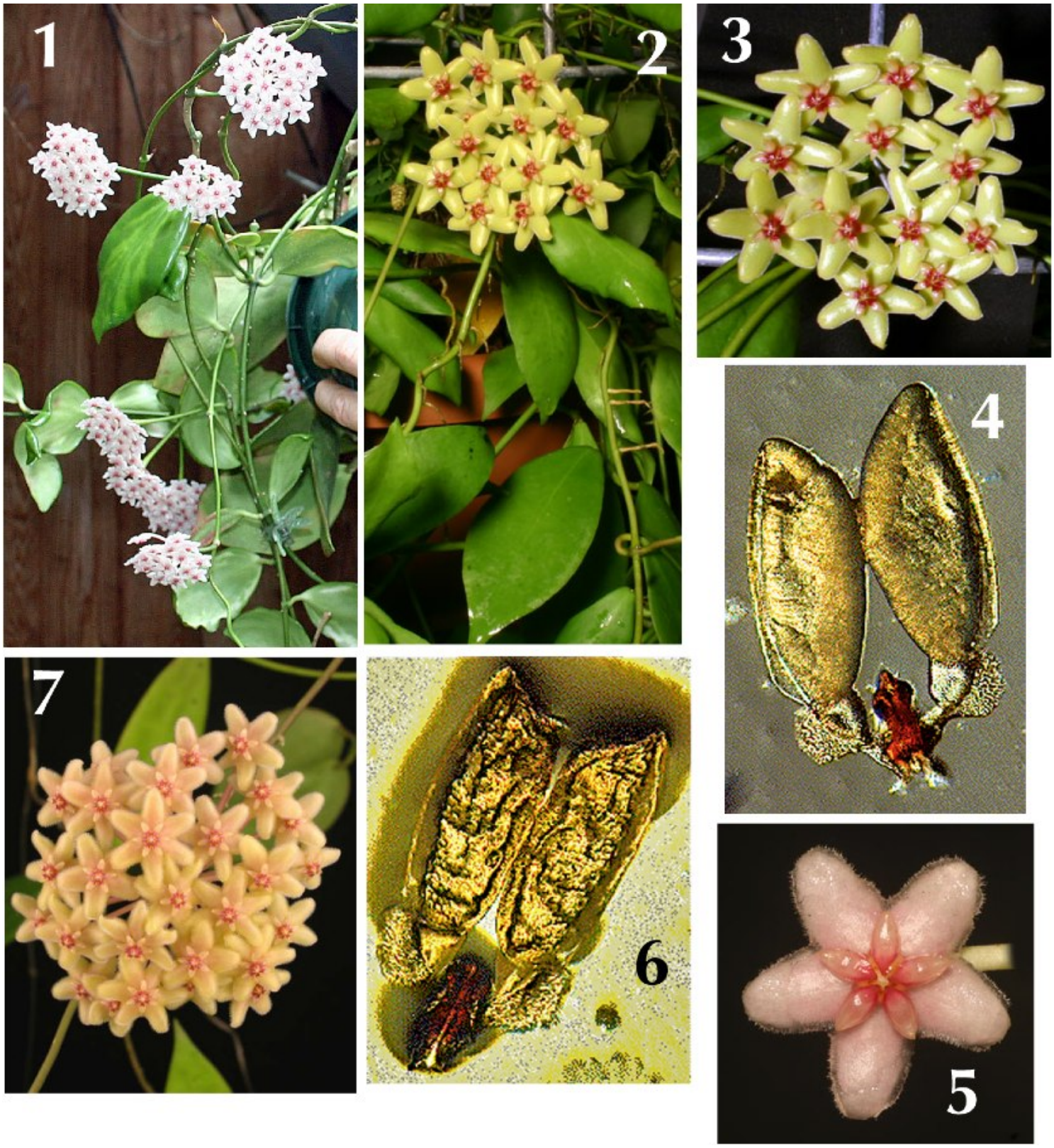
Species thought to belong to this section/complex:

H. diptera Seem. **(type)**	***H. anulata*** Schltr.	***H. eitapensis*** Schltr.
H. flavida P.I. Forster & D. Liddle	***H. vanuatensis*** T. Green	***H. kastbergii*** D. Kloppenburg

Taxonomic considerations: Kloppenburg described these plants as being intermediate between sections *Acanthostemma* and *Hoya*. They do seem to be, having the broad translators and flat or convex racemes of section *Acanthostemma* species, and the horizontal coronas and rotate corollas of section *Hoya* species. This intermediate status seems to be true of several sections or complexes (section *Angusticarinatae*, the *H. lanceolata* complex and the *H. cumingiana* complex), all of which have some features of *Acanthostemma* species and some features of species grouped in section Hoya or with the Hoya pottsii complex, and so it is here proposed that Kloppenburg's subsection be re-ranked as a section, to highlight this group (and the others mentioned) as truly intermediate groups between section *Acanthostemma* and the *Hoya pottsii* complex.

Kloppenburg's original grouping of species in this subsection included those species closely related to *Hoya lanceolata*, which are similar to *H. diptera* and its allies, but have some distinctions and are separated geographically from each other. *Hoya lanceolata* and its allies are therefore proposed here as a separate sectional group (pg. 35).

Burton's section *Pseudohoya* should be considered a synonym to Kloppenburg's subsection *Angusticarinatae*, as it contains the same species and type as subsection *Angusticarinatae*.



Section *Angusticarinatae* (proposed re-ranking). (1) *Hoya anulata* (CN). (2) *Hoya diptera* (CN). (3) *Hoya diptera* (BE). (4) Pollinarium of *Hoya anulata* (DK). (5) Close-up of *Hoya anulata* (BE). (6) Pollinarium of *Hoya diptera* (DK). (7) *Hoya flavida* (Photo courtesy of David Liddle).

6- the *Hoya cumingiana* complex

Overall form: this trio of species has a sprawling, scrambling habit. Leaves are small and relatively thin, on wiry, mostly non-twining stems. In bright light and dry conditions *H. cumingiana* and *H. densifolia* may develop more succulent leaves and more upright, compact branches. Flowers are yellow or white, with reflexed corollas, borne in slightly concave clusters, and highly fragrant. Their fragrance is often compared to that of coconut.

Distribution: The Philippines, Malaysia, Java.

Publication: unpublished in this form.

Salient features-

Pollinarium: similar to the pollinaria of *Hoya pottsii* complex species, with oblong pollinia with inwardly angled apexes. The pollinia are distinctly shaped, being noticeably narrower at the base than at the slightly out-turned apex. Caudicles are very small relative to the Corpusculum, also as in *Hoya pottsii* complex species. Translators are narrow.

Corona: raised at the inner angle, the outer lobe is roughly horizontal. Similar to the coronas of the *H. lanceolata* complex species.

Corolla: reflexed, glabrous.

Raceme: convex.

Species thought to belong to this section/complex:

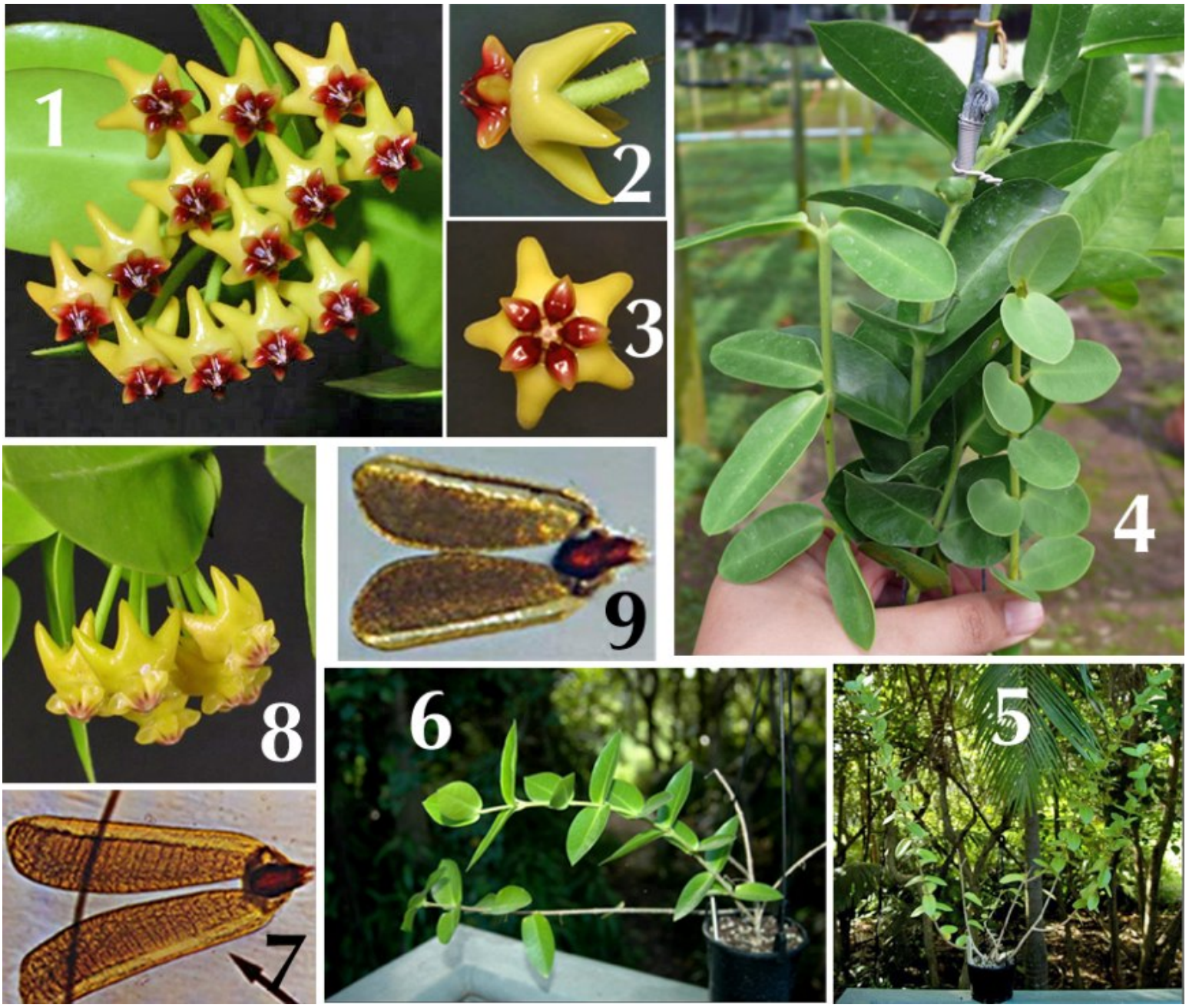
H. cumingiana Decne. (type)	***H. densifolia*** Turcz.	***H. golamcoana*** D. Kloppenburg

Taxonomic considerations: The three species listed above are sometimes considered as a single species or two species, and the names "*cumingiana*" and "*densifolia*" are thought to be reversed from their proper place by some authorities (C. M. Burton, ***P.S. The Hoyan*** V.7, #1, 2008).

This group (or variable single species) does not fit closely with any other established section or proposed group. The closest fit seems to be with the *Hoya pottsii* complex based on the similar pollinarium shape.

The coronas have a basic resemblance to those of the species of some groups intermediate between sections *Otostemma* and *the Hoya pottsii* complex, especially those of some species in the *Hoya lanceolata* complex (*H. l.* ssp. *bella*, *H. engleriana*), being slightly raised at the inner angle and roughly horizontal at the outer angle.

This complex is here tentatively placed between section *Otostemma* and the *Hoya pottsii* complex pending further study.



The *Hoya cumingiana* complex. (1)- *H. cumingiana* (BE). (2 & 3) close-ups of *H. cumingiana* (BE). (4)- foliage comparison of- left: *H. golamcoana*, middle: *H. densifolia*, right: *H. cumingiana* (SS). (5)- growth habit of *H. densifolia* (photo courtesy of David Liddle). (6)- growth habit of *H. cumingiana* (photo courtesy of David Liddle). (7) pollinarium of *H. cumingiana* (DK). (8) Hoya densifolia (photo courtesy of David Liddle). (9) pollinarium of *H. densifolia* (DK).

7- The *Hoya pottsii* complex

Overall form: mostly epiphytic twining plants with glabrous leaves. Leaf size ranges from small to very large (*H. latifolia*, *H. glabra*), flower sizes ranges from small (*H. camphorifolia*) to large (*H. rigida*), but are usually medium-sized and fragrant, with a wide range of scents. Flowers are usually white or pastel, rarely bright pink or reddish (*H. camphorifolia*, *H. aldrichii*,) with usually reflexed or rarely slightly cupped corollas *(H. macrophylla, H. clandestina*). A few species from seasonally dry areas of Thailand have developed thick, succulent leaves and stems and a shrubby habit (*H. pachyclada*, *H. subquintuplinervis*).
Distribution: The whole range of the genus, except for Japan and possibly southern India (*H. ovalifolia* may belong to this section).
Publication: unpublished in this form, the species included here were considered to specifically belong to section *Hoya* at least since the work of Schlechter (1914). These species were defined as belonging to section *Hoya* subsection *Lactisuccus* by Burton (1995/96).
Original description: (as section Hoya) (translated from Latin by G. Don) **"**Twining, scandent or decumbent shrubs, usually radicant. Leaves fleshy. Leaflets of the corona furrowed beneath."
Revised descriptions: Decaisne, 1844 (translated from Latin by MR)- **"**...leaflets of staminal corona horizontal...".
Hooker, 1885 (as "Euhhoya") "Corolla lobes broader than long, spreading or recurved. Column sessile or subsessile; coronal-processes stellately spreading, inner angle acute or produced into an erect or recurved simple spine."
Schlechter, 1914 (as "Euhoya")(translated from German by DK & Dieter Paul) "The corolla is radial or usually slightly bent backwards. The corona scales are situated more or less horizontal to the anthers, they are flat above or slightly shell-shaped, concave, on the top outer end rounded off sharply and on the undersides rounded with a long furrow. The blooms are mostly midsize and the calyx is small. Type of the section is *H. carnosa* R. Brown."
Hill, 1988 (as "Hoya") "Peduncles ageotropic. Pedicels equal. Corolla reflexed. Coronal scales narrowly to broadly trapezoidal, flat above with a slight median ridge, inner and outer angles acute. Caudicles unwinged...".
Kloppenburg, 1994 "...Corona furrowed below (sulcate or channeled)... staminal corona approximating horizontal... corona scales flat above or slightly cupped... corona scales, outer end acute... calyx small...".
Burton (1995/96) (as section *Hoya* subsection *Lactisuccus*) "Foliage fleshy; sap milky; corolla lobes flat or reflexed; corona lobes more or less flat on top but often elevated at the outer tips; translators appear to arise out of a vase-like appendage to the retinaculum; retinaculum winged."

Salient features-

Pollinarium: pollinia oblong, approximately 3 times as long as wide, with obtuse, slightly inwardly angled apexes. The caudicles are very small relative to the pollinia and corpusculum size (compared to most *Hoya* sections not closely related to the *Hoya pottsi* complex) and are often almost completely obscured by the darker colored translators, so that the caudicles are difficult to see in microphotographs. Corpuscula are often slightly broader than those in section *Hoya* species.

Corona: the corona lobes are usually diamond-shaped, acute at either end, similar in shape to those of section *Hoya* species from above, but in profile the lobe tops of *H. pottsii* complex species are usually very flat, and have sharp edges to the upper surface's margin. Some species (*H. acuta*, *H. bhutanica*) have slightly raised outer corona lobe angles.

Corolla: usually glabrous, usually sharply reflexed, rarely rotate or slightly cupped (*H. macrophylla*, *H. clandestina*).

Raceme: convex to globular.

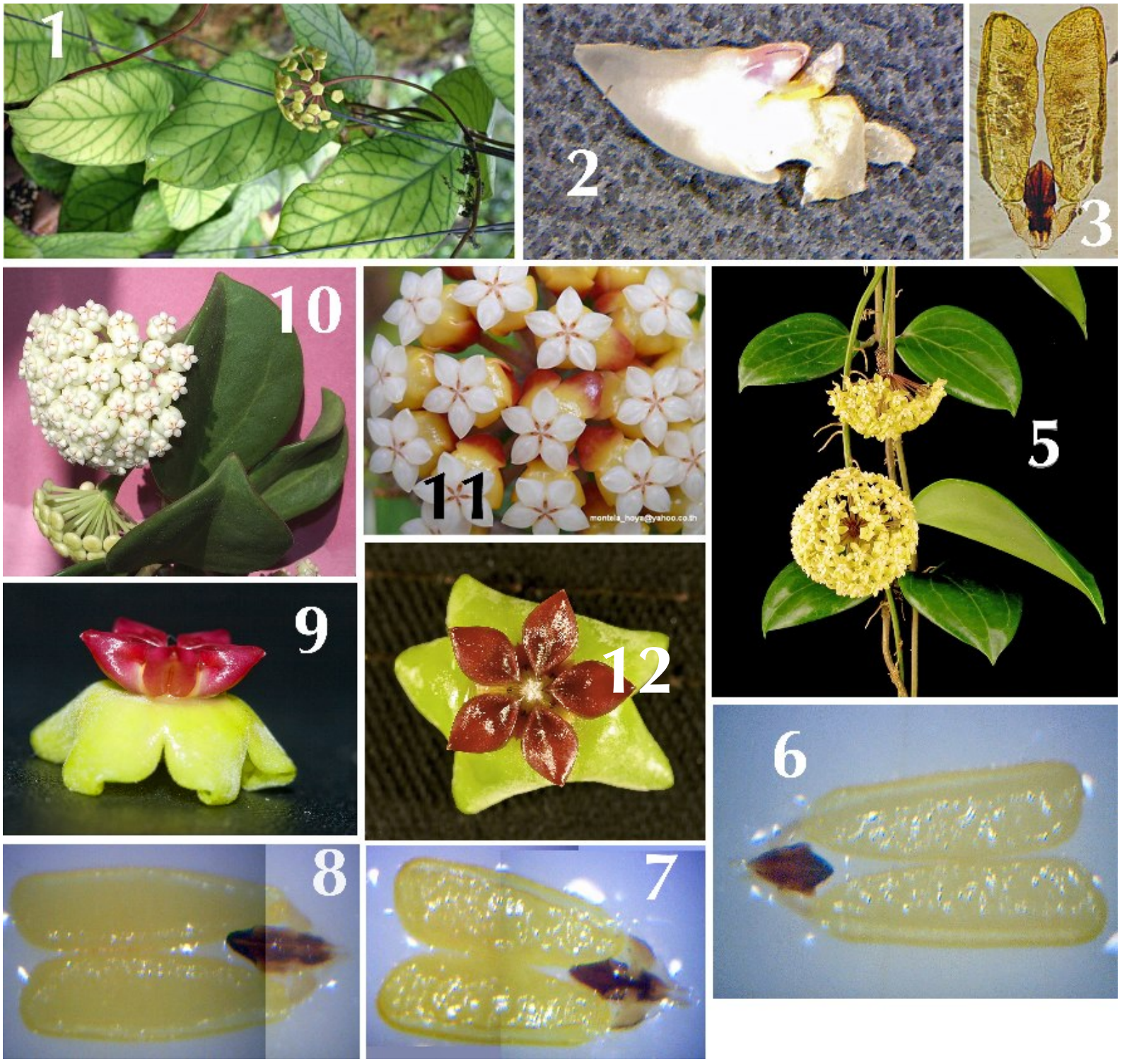
Species thought to belong to this section/complex:

H. pottsii Traill **(type)**	***H. acuta*** Haw.	***H. aldrichii*** Hemsley
H. amoena Bakh f.	***H. arnottiana*** Wight	***H. bhutanica*** Grierson & D.G.Long
H. benguetensis Schltr.	***H. bordenii*** Schltr.	***H. callistophylla*** T. Green
H. camphorifolia Warburg	***H. cardiophylla*** Merr.	***H. chunii*** P. T. Li
H. cinnamomifolia Hook.	***H. citrina*** Ridley	***H. clandestina*** Blume
H. clemensiorum T. Green	***H. cominsii*** Helmsley	***H. deykeae*** T. Green
H. dolichosparte Schltr.	***H. erythrina*** R.E. Rintz	***H. finlaysonii*** Wight
H. fuscomarginata N. E. Brown	***H. glabra*** Schltr.	***H. hellwigiana*** Warburg
H. incrassata Warburg	***H. juanngoiana*** D. Kloppenburg	***H. latifolia*** G. Don
H. limoniaca S. Moore	***H. macrophylla*** Blume	***H. meredithii*** T. Green
H. merrillii Schltr.	***H. neo-caledonica*** Schltr.	***H. neo-ebudica*** Guillaumin
H. nicholsoniae F. Muell.	***H. ovalifolia*** Wight & Arn.	***H. pachyclada*** Kerr
H. pentaphlebia Merr.	***H. polystachya*** Blume	***H. purpureofusca*** Hooker
H. rigida Kerr	***H. samoensis*** Seem.	***H.* sp. CMF-8**
***H.* sp. aff. parasitica**	***H. subquintuplinervis*** Miq.	***H. tjadasmalangensis*** Bakh. f.
H. tomataensis T. Green & Klopp.	***H. verticillata*** (Vahl) G. Don	***H. vitellina*** Blume
H. vitellinoides Bakh. f.		

Taxonomic considerations: The species in this group seem to be part of a coherent group of morphologically similar species which differ significantly from the type species of section *Hoya* (*H. carnosa)*, and so are recommended here to be considered a separate section (see the entry for section *Hoya* on page 50 for more details).

The *H. pottsii* complex seems to be the largest group of morphologically similar species in the genus *Hoya*, with at least 45 species belonging here, and has the widest distribution, occurring in nearly the entire range of the genus (see ***Stemma*** V.2, #1: p. 27).

There are several groups of species placed here that could be described as sub-groups of the *H. pottsii* complex. Those species similar to *Hoya macrophylla* (*H. polystachya*, *H. clandestina*, *H. tjadasmalangensis*) have divided semi-campanulate corollas and often have branched peduncles. Those species similar to *Hoya finlaysonii* (*H. callistophylla*, *H. dekeae*, *H. meredithii*) often have distinctly two-toned flowers and leaves with dark, ornate venation. Not enough study has been done for these two potential sub-groups at this time, so they are placed here with *Hoya pottsii*.



The *Hoya pottsii* complex. (1) *Hoya meredithii* (BE). (2) Side view of a corona segment of *Hoya* sp. aff. parasitica from Laos. (3) Pollinarium of *H*oya *purpureofusca* (DK). (5) *Hoya merrillii* (photo courtesy of David Liddle). Pollinaria of (6) *H*. sp. aff. parasitica from Laos, (7) *Hoya cinnamomifolia* (plant material contributed by Julia Scheeres), and (8) *Hoya subquintuplinervis*. (9) *Hoya cinnamomifolia*. (10) *Hoya pachyclada*. (11) *H*. sp. finlaysonii nova (SS). (12) *Hoya cinnamomifolia*.

8- The *Hoya blashernaezii* Complex

Overall form: these species are epiphytic vines with medium to large, tri-nerved leaves similar to the leaves of some *Hoya pottsii* relatives (like *H. bordenii)*. Flowers are small, borne in slightly convex clusters, with cup-shaped or reflexed corollas, brightly colored (pink, yellow or orange) and have little fragrance.

Distribution: The Philippines.

Publication: not published in this form.

Salient features-

Pollinarium: pollinia approximately twice as long as wide, translators slightly broader than is usual in *Hoya pottsii* complex species, but not as wide as the translators of section *Otostemma* or *Acanthostemma* species. Caudicles are relatively small, less than 1/3 the size of the corpusculum.

Corona: inner angle below the anther appendages, inner portions of upper lobe surfaces are set much farther away from the anther head than those of any other section. Outer angle narrow, acute, raised to exceed the height of the anther head.

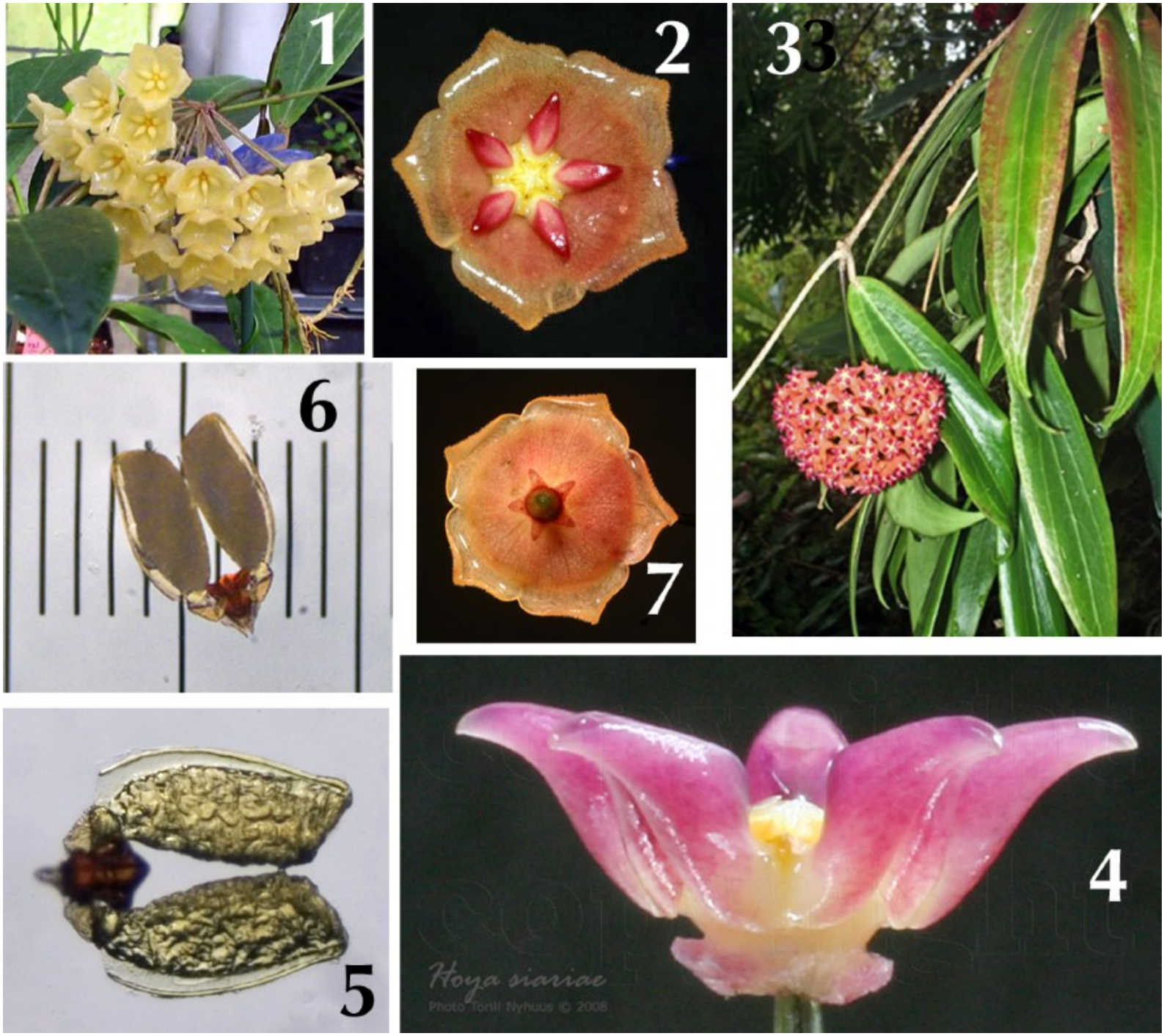
Corolla: glabrous, semi-campanulate (*H. blashernaezii, H. siariae*) or reflexed (*H.* sp. IML 0831).

Raceme: convex.

Species thought to belong to this section/complex:

H. blashernaezii D. Klopp. **(type)**	***H. siariae*** D. Kloppenburg	***H.* sp. IML 0831**

Taxonomic considerations: Possibly this group should be considered as a sub-complex to the *H. pottsii* complex. A few Philippine members of the *H. pottsii* complex seem to share similar characteristics with the three species considered here- *Hoya benguetensis* and *Hoya bordenii* have very similar leaves (oblong lanceolate, acute, trinerved) and *Hoya bordenii* in particular has corona features that suggest the more widely set, narrow corona lobes of the *H. blashernaezii complex*. *Hoya* sp. IML0831, with its reflexed orange corollas, has many similar characteristics to *Hoya bordenii*.



The *Hoya siariae* complex. (1) *Hoya blashernaezii* (BE). (2) *Hoya siariae* (BE). (3) *Hoya* sp. IML 0831. (4) Corona of *Hoya siariae* (TN). Pollinarium of (5) *Hoya siariae* (TN) and (6) *Hoya blashernaezii (TN)*. (7) Back of corolla of *Hoya siariae (BE)*.

9- Section *Amblyostemma* D. Kloppenburg

Etymology: "amblys"="**blunt**", Gr. + "stemma"="**crown**", Gr.

Type species: *Hoya meliflua* (Blanco) Merr**.**

Overall form: these species have very thick, succulent leaves and stems. Those of *H. kerrii* are especially hard and thick- this species verges on being a true succulent. All species included here are extremely vigorous twining epiphytic vines, and all produce large amounts of sticky amber or brown nectar when in bloom. Flowers are small to medium sized, flat or reflexed, hairy, cream or pastel orange or pink, and stained darker orange or brown by the colored nectar the flowers produce. Some species are mildly fragrant.

Distribution: The Philippines, Thailand, Malaysia, Indonesia.

Publication: ***Hoya Sections,* 1993**

Original description: (translated from Latin by MR) "Leaves thick-fleshy, glabrous on both sides, margins reflexed. Peduncles short. Petioles short. Corolla with lobe margins revolute, outside glabrous, inside papillose. Corona lobes thick-fleshy, underside caniculate, top concave-excised with a small swelling in the cavity, lower surface sulcate. Stigma apiculate. Flowers large".

Revised descriptions: none

Salient features-

Pollinarium: very similar to the pollinarium of *Hoya pottsii* complex species, with no special features to distinguish them from the *pottsii* group.

Corona: very similar to the coronas of those species placed here in the *H. longifolia* complex. The corona lobes have cuspidate inner angles and rounded outer angles, the inner angles are slightly raised but the outer angles are usually not raised significantly, unlike those species in the *H. longifolia* complex.

Corolla: pubescent, rotate or reflexed.

Raceme: Convex.

Species thought to belong to this section/complex:

H. meliflua (Blanco) Merr. **(type)**	***H. diversifolia*** Blume	***H. excavata*** Teijsm. & Binn.
H. kerrii Craib		

Taxonomic considerations: The species grouped here are quite similar to section *Hoya* species. The pollinaria of these two groups do not seem to differ significantly, but the distinctive aspect of the succulent leaves and stems of this group, coupled with the differently shaped corona lobes and the copious, colored nectar, argue for recognition of this complex as a section.

Section *Amblyostemma*. (1) *Hoya kerii*. (2) *Hoya kerii*. (3) *Hoya excavata* (SS). (4) *Hoya meliflua* (SS). (5) Corona of *Hoya kerrii*. Pollinaria of (6) *Hoya meliflua* (DK) and (7) *Hoya kerrii*. (8) Side view of corona lobe of *Hoya diversifolia* (DK). (9) Photo progression of nectar dripping from *Hoya diversifolia* (photo courtesy of Christina Karlsson.

10- The *Hoya longifolia* complex

Overall form: The species included here are twining epiphytic vines with leaves that are more narrow than those of most section *Hoya* species, to which these species are very similar. The flower clusters are usually small and contain fewer flowers than do most section *Hoya* species' racemes. Flowers are medium sized, usually white to pale pink, flat or slightly cupped, hairy, and sweetly scented.

Distribution: eastern India, Nepal, Burma, Thailand.

Publication: unpublished in this form.

Salient features-

Pollinarium: appear to be extremely similar to those of the section *Hoya* species.

Corona: inner lobe angles are raised slightly and are cuspidate, the outer angle is raised above the anther head and is round. The overall shape of the corona lobe, as seen from above, is round with a circular depression in the center. The underside of the lobes are canaliculate. The shape of the corona is very similar to those of species in section *Amblyostemma*, and somewhat similar to those of species in section *Eriostemma*.

Corolla: pubescent, rotate or slightly cupped.

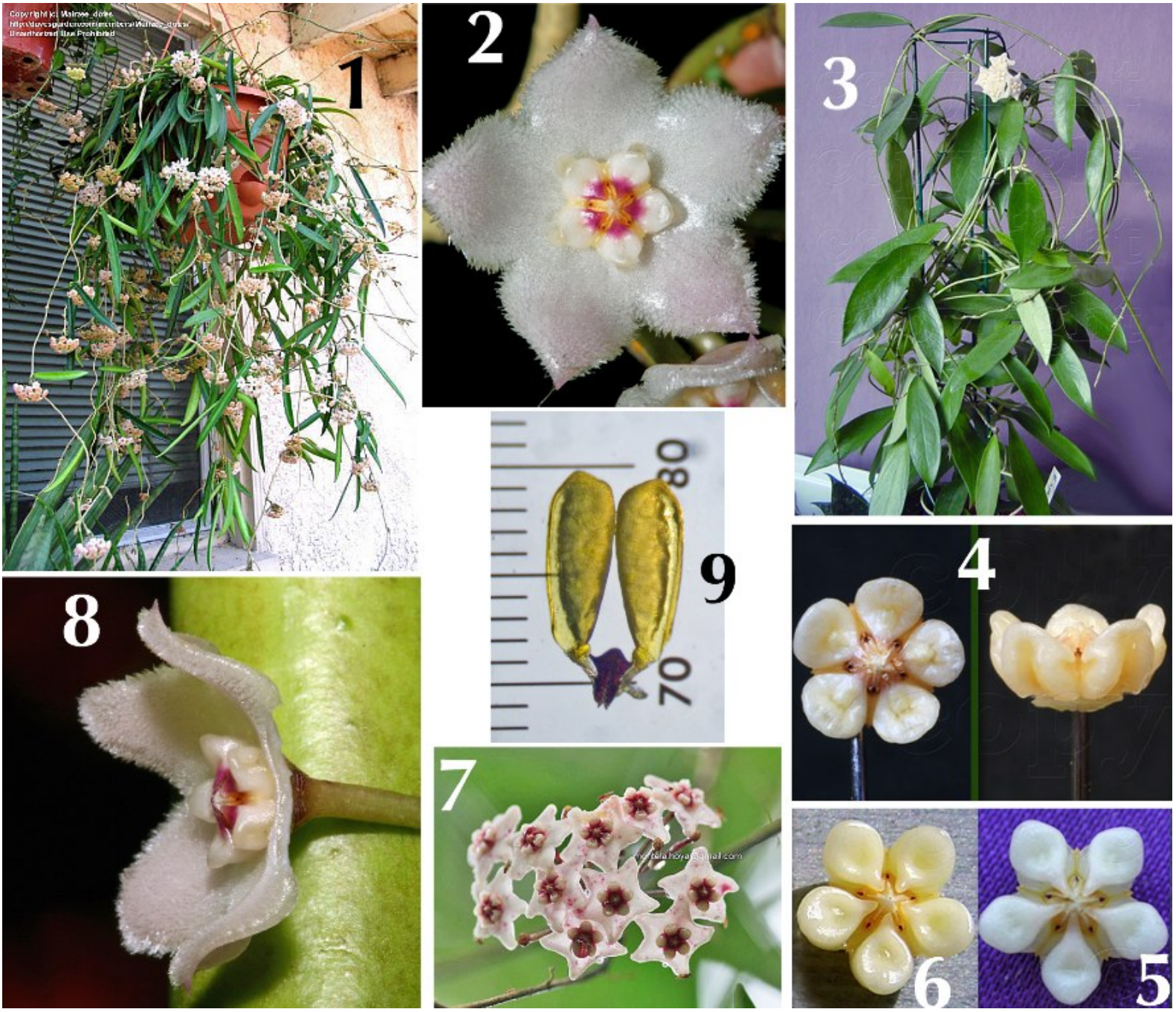
Raceme: convex.

Species thought to belong to this section/complex:

H. longifolia Wallich **(type)**	***H. siamica*** Craib	***H. stoneana*** D. Klopp. & Siar
H. shepherdii Short ex Hook.		

Taxonomic considerations: The pollinaria of all of these species have not been examined by this author, but those of *longifolia* and *shepherdii* appear to match quite well to the pollinarium of section *Hoya* species. It may be that these species should be included in section *Hoya*, but the particulars of the corona differ from section *Hoya* species, and the sap of the species included here is milky, not clear, so that some recognition of this group as a distinct taxon seems appropriate.

An apparent hybrid between *Hoya carnosa* and *Hoya shepherdii* (*Hoya* '*Minnibelle*') argues a close relationship between those two species.



The *Hoya longifolia* complex. (1) *Hoya shepherdii* (photo courtesy of Marcy Durst). (2) *Hoya shepherdii*. (3) *Hoya siamica* (TN). (4) Front and side view of corona of *Hoya longifolia* (TN). (5) corona of *Hoya siamica* (TN). (6) Corona of *Hoya stoneana* (photo courtesy of Tina Elfstrom). (7) *Hoya siamica* (SS). (8) *Hoya shepherdii*. (9) Pollinarium of *Hoya stoneana* (TN).

11-Section *Hoya* (autonym)

Etymology: "*Hoya*"="**in honor of Thomas Hoy**", Latinized. The section which includes the type species for the genus automatically bears the genus name as well.

Type species: *Hoya carnosa* R. Br.

Overall form: The species grouped here are mostly medium to large-leaved, vigorous epiphytic twiners with clear or amber sap (most *Hoya* species have a milky white sap). Flowers are medium sized, mostly pale pink or white, hairy, flat, borne in rounded clusters and have a sweet scent often compared to the smell of chocolate. *Hoya serpens*, included here, is on the borderline of this section, matching in the pollinarium and corolla details, but with different corona details, and having milky (rather than clear) sap. *H. serpens* has hybridized with *H. carnosa*, (*H.* 'Mathilde') suggesting a close genetic relationship between them.

Distribution: The southern island of Japan, southern China, Vietnam, Cambodia, the Philippines, Thailand.

Publication: ***Contributions to the Botany of India,* 1834** as "*Hoya verae*". This section name is automatically corrected to "*Hoya*" according to article 22.1 of the ICBN.

Original description: (translated from Latin by G. Don) **"**Twining, scandent or decumbent shrubs, usually radicant. Leaves fleshy. Leaflets of the corona furrowed beneath."

Revised descriptions: Decaisne, 1844 (translated from Latin by MR)- **"...**leaflets of staminal corona horizontal...".

Hooker, 1885 (as "Euhhoya") "Corolla lobes broader than long, spreading or recurved. Column sessile or subsessile; coronal-processes stellately spreading, inner angle acute or produced into an erect or recurved simple spine."

Schlechter, 1913 (as "Euhoya") (translated from German by DK & Dieter Paul) "The corolla is radial or usually slightly bent backwards. The corona scales are situated more or less horizontal to the anthers, they are flat above or slightly shell-shaped, concave, on the top outer end rounded off sharply and on the undersides rounded with a long furrow. The blooms are mostly midsize and the calyx is small. The type of the section is *H. carnosa* R. Brown."

Hill, 1988 (as "*Hoya*") "Peduncles ageotropic. Pedicels equal. Corolla reflexed. Coronal scales narrowly to broadly trapezoidal, flat above with a slight median ridge, inner and outer angles acute. Caudicles unwinged...".

Kloppenburg, 1994 "...Corona furrowed below (sulcate or channeled)... staminal corona approximating horizontal... corona scales flat above or slightly cupped... corona scales, outer end acute... calyx small...".

Burton (1995/96) (as section *Hoya* subsection *Acersuccus*) "Foliage fleshy with maple-syrup like sap: sepals large, hairy; corolla rotate, pilose or papillose, margins & apexes revolute; corona lobes rotate, usually narrow, pointed at both ends; pollinia outer margins keeled, with translators not winged, however there is a lot of extra material surrounding or adjacent the retinacula and translator, for which I do not have a name."

Salient features-

Pollinarium: difficult to discern from the pollinaria of *Hoya pottsii* complex species. Pollinia are oblong, approximately 3 times as long as wide, with obtuse, slightly inwardly angled apexes. The caudicles are very small relative to the pollinia and corpusculum size (compared to most other *Hoya* sections) and are often almost completely obscured by the darker colored translators, so that the caudicles are difficult

to see in microphotographs. The outline of the pollinaria of species grouped here tend to have a more streamlined look, with a smoother line formed by the junction of the corpusculum, translators and pollinia than in Hoya pottsii complex species. There is a slight tendency for the species grouped here to have more acutely angled outer pollina apexes than species grouped with *Hoya pottsii*, and the corpusculum tends to be thinner in section *Hoya* species.

Corona: approaching horizontal, slightly raised at the inner angle and slightly raised along the corona scale's median, acute at inner and outer angles.

Corolla: densely pubescent, rotate, with revolute margins.

Raceme: convex to globular.

Species thought to belong to this section/complex:

H. carnosa R. Brown **(type)**	***H. compacta*** C. M. Burton	***H. crassifolia*** (Jacq.) Haw.
H. dasyantha Tsiang	***H. fungii*** Merr.	***H. monetteae*** *T. Green*
H. pubicalyx Merr.	***H. salweenica*** Tsiang & P. T. Li	***H. serpens*** Hook. f.
***H.* sp. Kunming Kina**		

Taxonomic considerations:

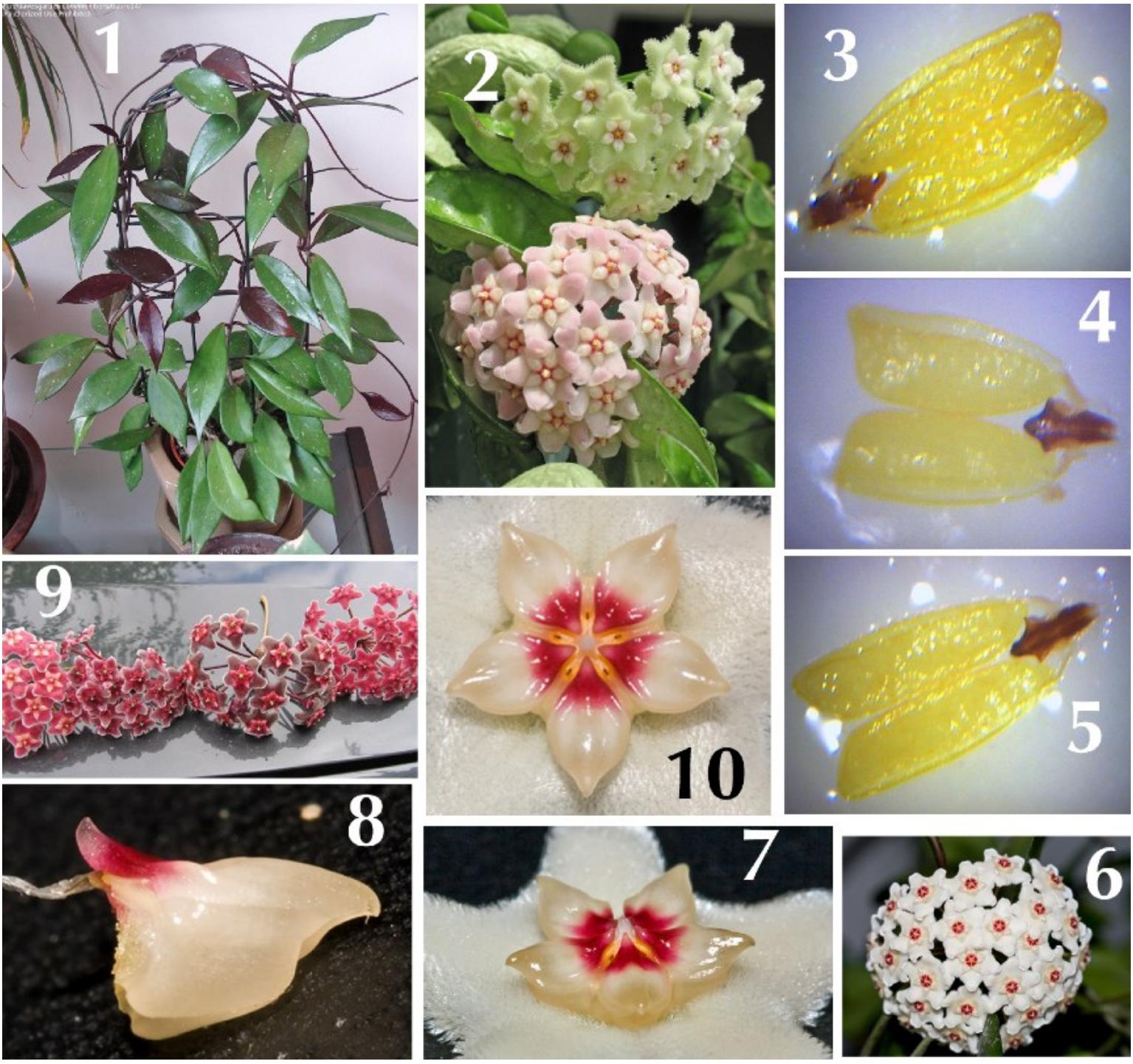
A prime problem with delimitating section *Hoya* species has been the tendency of various authors to place species which defy easy classification, but differ blatantly from the section type species, *H. carnosa*, into this section. K. D. Hill (1988) wrote, referring to the sections, that "As with many such systems, several groups with distinctive advanced or primitive characters are established, and a large, amorphous remainder (paraphyletic residue) is relegated to a category of convenience" (section *Hoya*).

Kloppenburg (2003) also noted that due to this section being used as a "dumping ground", additional sections were needed to add structure to this section by removing extraneous species.

C M. Burton (1995/96) recognized two groups of species which corresponded to the sectional description and related closely to *Hoya carnosa*, the type of the genus and the section. The first subsection, called by Burton "*Acersuccus*", was designed to hold *Hoya carnosa* and species which conformed closely to its characteristics. This group of species includes *H. fungii, H. compacta, and H. pubicalyx*.

The second subsection, called "*Lactisuccus*", was created to house *Hoya pottsii* (the type species) and species which conformed closely to its description. Those species differ from those placed in *Acersuccus* with *Hoya carnosa* in several important ways. 1) Those species similar to *Hoya carnosa* have raised inner corona angles and a slight hump in the corona lobe median, while those species similar to *H. pottsii* have very flat (in profile) tops to the corona lobes (occasionally the outer angle is raised slightly). 2) Those species similar to *Hoya carnosa* have rotate, densely pubescent corollas, while those species similar to *Hoya pottsii* have mostly glabrous, mostly reflexed corollas. 3) Those species similar to *Hoya carnosa* have pollinarium with a more smooth curve to the junction of the corpusculum, translators and pollinia, while those species similar to Hoya pottsii have pollinaria with a wider base, as the translators are held out slightly more laterally and the corpusculum is slightly wider than is section *Hoya* species.

Due to these broad differences, it is here recommended that the species grouped into subsection *Lactisuccus* by Burton be considered as a separate (but closely related) section, the *Hoya pottsii complex* (see page 41).



Section *Hoya*. (1) *Hoya pubicalyx* (photo courtesy of Gabi Rothman). (2) *Hoya serpens* (top) and *Hoya compacta* (bottom) (photo courtesy of Eddie Huey and Epiforums.com). Pollinaria of (3) *H*oya *carnosa*, (4) *H*oya 'Mathilde' and (5) *H*oya *compacta*. (6) *Hoya carnosa* raceme. (7) *Hoya carnosa* corona. (8) Side view of corona segment of *H. carnosa*. (9) A selection of *Hoya pubicalyx* cultivars (photo courtesy of Marcy Durst). (10) *H. carnosa* corona.

TO BE CONTINUED IN STEMMA V.2,#4

Department of Corrections

by Mark Randal

In ***Stemma*** Volume 1, #3 the photo of *Hoya* sp. 3 from Thailand on page 42 (reproduced below) was taken by Dr. Piyakaset Suksathan of the Queen Sirikit Botanic Garden (QBG), Mae Reim, Chiang Mai, not by Sutthisak Sangkhakorn, as was credited.

In ***Stemma*** Volume 1, #2, in the Back Page feature, *Hoya* sp. IML 0831 was cited as being closely related to *Hoya bordenii* and *Hoya benquetensis*. It was brought to my attention by Michele Rodda that the correct spelling of the last *Hoya* cited is "*Hoya benguetensis*", not *"Hoya benquetensis*".

Source Material

For "A Look at *Hoya* sections":

For most of the literature involving *Hoya* sections, the full citations appear on pp. 19 - 21.

Additional sources:

Anonymous. c. 1500 - 1000 BCE. The ***Rigveda***. (An ancient collection of Indian sanskrit hymns.)

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Burton, C. M. 1991-1993. "Hoya Sections". The ***Hoyan*** 12(3):67--69. 12(4): 95. 13 (1): 28--29. 14 (1): 10--11.

Forster P. I., Liddle, D. J. & Liddle, I. M. 1997. "*Madangia inflata* (*Asclepiadaceae*: *Marsdenieae*), a new genus and species from Papua New Guinea". ***Austrobaileya*** 5: 53--57.

Hill, K. D. 1986. "A revision of *Hoya* (*Asclepiadaceae*) in Australia". ***Telopea*** 3(1): 241--255

Kleijn, D. & Van Donkelaar, R. 2001. "Notes on the taxonomy and ecology of the genus *Hoya* (*Asclepiadaceae*) in central Sulawesi". ***Blumea*** 46: 457--483

Kloppenburg, D. 1994. ***Hoya section Acanthostemma.***

Kloppenburg, D. 1996. ***Hoya Pollinaria: a photographic study***.

Lindley, J. 1846. ***The vegetable kingdom; or, the structure, classification, and uses of plants, illustrated upon the natural system.*** London.

Linnaeus. 1753**.** ***Species Plantarum***.

Sennblad, B. and Bremer, B. 1996. "The familial and subfamilial relationships of *Apocynaceae* and *Asclepiadaceae* evaluated with *rbcL* data." ***Plant Systematics and Evolution*** 202: 153--175.

Stace, C. A. 1991. ***Plant Taxonomy and Biosystematics***, 2nd ed.

Glossary

Anther: a part of the male reproductive organs of higher plants which produces pollen.
Anther head: the union of the five anther appendages at the center of the corona, usually forming a cone.
Anther margins (or **anther wings**): the five slits between the corona lobes on the gynostegium, which give access to the pollen receptive stigma underneath.
Calyx: collectively, the five modified leaves (sepals) which surround and protect developing flower buds.
Canaliculate: with a longitudinal groove or channel.
Caudicle: the soft, flexible, usually transparent and comma shaped structure which connects a single pollinium to the corpusculum.
Corolla: collectively, the five modified leaves (petals) which are the (usually) showy portion of a flower.
Corona: the partially fused stamens and pistols which form the center of an Asclepiad flower, usually resembling a five-pointed star.
Corpusculum: the hard, central portion of a pollinarium, to which the pollinia are connected by means of the caudicles and translators.
Cuspidate: having a pointed apex formed by the meeting of two concave arcs.
Filament: a part of the male reproductive organs of higher plants, usually a stalk which supports the anther.
Gynostegium: a reproductive plant structure found in Asclepiadoideae, Orchidaceae, and Aristolochiaceae. A fusion or partial fusion of both male and female reproductive parts.
Morphological: relating to the physical form of an organism.
Monophyletic: Pertaining to a set of organisms consisting of all of the descendants of a common ancestor species.
Ovary: the swollen part of the female reproductive organs in higher plants that contain the ovules or immature seeds.

Pedicel: the stalk of an individual flower.

Peduncle: the stalk of a group of flowers. In *Hoya*, a usually persistent, rarely temporary structure.

Pellucid edge: the pollen-free, transparent outer margin of a *Hoya* pollinium.

Petal: one of the five highly modified leaves which together form the corolla.

Phylogenetic: In biology, phylogenetics (Greek: phyle = tribe, race and genetikos = relative to birth, from genesis = birth) is the study of evolutionary relatedness among various groups of organisms.

Pistil: the collective female reproductive organ found in higher plants, usually consisting of an ovary, style and pollen receptive stigma.

Pollinarium: a structure composed of two waxy bundles of pollen connected to each other via a corpusculum, caudicles and translators. This structure is found in the subfamily *Asclepiadoideae* (of family *Apocynaceae*) and in the family *Orchidaceae*.

Pollinium: a structure formed by a collection of pollen grains into a coherent mass.

Raceme: an indeterminate inflorescence with a simple, elongated axis and pedicellate flowers.

Rachis: the apex of a peduncle, which slowly elongates (in persistent peduncles). The rachis (in *Hoya*) usually has a rough texture resulting from the pedicel scars of old flowers.

Retinaculum: an alternate name for the corpusculum.

Sepal: one of the five highly modified leaves which form the calyx.

Species complex: a group of species which share similar anatomical features and are believed to be closely related.

Stamen: the collective male reproductive organ found in higher plants, usually composed of the filament and the pollen-producing anther.

Stigma: a part of the female organ of reproduction found in higher plants, receptive to pollen.

Style: a part of the female organ of reproduction found in higher plants, it usually connects the ovary and stigma.

Style head: a structure found in asclepiads, it sits atop the gynostegium just under the anther head. Often referred to erroneously in older literature as the stigma or stigma head.

Translator: the connective structure in a pollinarium which supports the softer, more flexible caudicle.

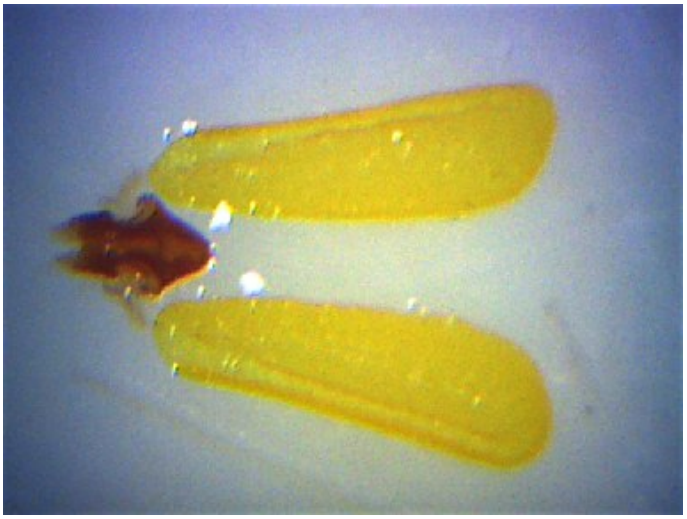
Umbel: A flat-topped or rounded determinate flower-cluster in which the individual flower stalks arise from the same point. Most Hoya have flower clusters that are more properly called a "raceme".

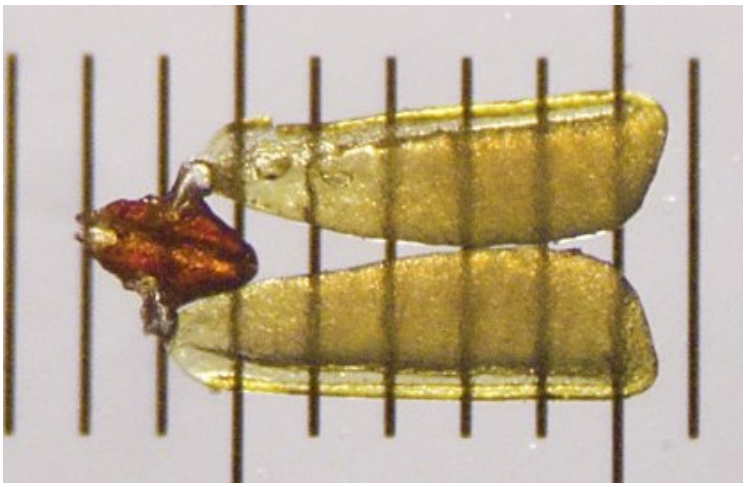
Back Page

Hoya sp. square

photos by Simone Merdon-Bennack, Surisa Somadee, Antone Jones, Torill Nyhuus & MR.

Country of Origin: Burma (Myanmar).
Related/Similar Species: Uncertain. The flowers of this plant closely resemble those of *Hoya* of the *Acanthostemma* or *Otostemma* sections, with their revolute, pubescent corollas and conical coronas, but the pollinaria (shown this page) lack the characteristic broad translators of those species, and more closely resemble the pollinaria of *Hoya cumingiana*.
Synonyms: often sold (incorrectly) as *Hoya lyi* H. Lev.
Flower Color: white.
Flower Size: c. 1.5cm in diameter when pressed flat.
Flower Form: revolute .
Scent: mild.
Leaf size: medium.
Collector: A local vendor in Kanchanaburi Province, Thailand, near the Thai border with Burma (Myanmar).
Water Requirements: average.
Light Requirements: filtered sun.





Pollinaria from *Hoya* sp. square.

Above: MR; left: Torill Nyhuus

Photo credits, clockwise from top left: Simone Merdon-Bennack; Surisa Somadee; Antone Jones; Surisa Somadee; Antone Jones.