

The gynostegium of *Hoya spartioides* (Apocynaceae – Asclepiadoideae): A striking case of incongruence between molecular and phenotypic evolution

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Abstract

In molecular phylogenies *Hoya spartioides*, formerly regarded as the only species in a separate genus *Absolmsia*, is nested in the genus *Hoya*. It appears as sister to *H. curtisii* within a larger clade including *H. lacunosa*, *H. imbricata*, and *H. caudata*. In contrast to this close molecular relationship the floral morphology of *H. spartioides* differs considerably not only from that of its sister, *H. curtisii*, but from all other species of *Hoya* investigated so far. Of special interest are the differences in functional morphology of the pollinating apparatus, which in spite of its high degree of synorganization has undergone considerable evolutionary change in *H. spartioides*. Some of the new traits are even unique within the subfamily Asclepiadoideae as a whole. The large phenotypic distance between *H. spartioides* and *H. curtisii* is not reflected in corresponding differences in the tested marker genes, which raises the question of how the flower of *H. spartioides* has evolved.

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Introduction

Until recently, *Hoya spartioides* was treated as the only species in the genus *Absolmsia* Kuntze. Schumann (1895, p. 245, 249) placed *Absolmsia* within the tribe Asclepiadeae, mainly because of the annular corona of the gynostegium. Subsequently, several systematists pointed to similarities of the flower morphology with that of *Hoya* (Schlechter 1916; Omlor 1998). Based on similarities in the corona, pollinia, and seeds, Kloppenburg (2001) has subsumed *Absolmsia* under *Hoya*. The complex corona morphology in *Hoya* and possibly other Marsdenieae, recently clarified by the present authors (Kunze and Wanntorp 2008), supports Kloppenburg's

proposal. The “annular corona” noticed by Schumann results from the fusion of the anther skirt, not from an annular meristematic growth zone around the filament tube (C(is) in the nomenclature proposed by Liede and Kunze 1993), which is the origin of annular coronas in other Asclepiadeae. Thus, the annular structure in *H. spartioides* is not homologous with the annular corona (C(is)) found in other asclepiad genera and cannot be considered as indicative of a closer relationship.

Phylogenetic analyses based on the chloroplast *trnL* region and the *rbcL-atpB* spacer as well as on the nuclear ribosomal DNA ITS region (Wanntorp et al. 2006a, b) also clearly support a position of *Absolmsia* in *Hoya*, as part of a well-supported clade including *H. caudata*, *H. curtisii*, *H. imbricata*, and *H. lacunosa* (Wanntorp et al. 2006a, p. 593). The position of *H. spartioides* within the total sampling of *Hoya* species

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is shown in Fig. 1. In this tree, *H. spartioides* is sister to *H. curtisii*, although this sister-group relationship is to be regarded as a preliminary result due to limited taxon sampling. The inclusion of additional species in the molecular analysis will most likely detect species that are closer to *H. spartioides* than *H. curtisii* (Wanntorp and Forster 2007). The latter authors have noted that the two species differ substantially in flower morphology,

H. curtisii having a corolla with completely reflexed lobes and a corona lying on an annulus (Ca; Liede and Kunze 1993), whereas *H. spartioides* has a campanulate corolla and no annulus (Wanntorp and Forster 2007). Combinations of these character states only point to minor differences also found in other species of *Hoya*. None of the morphological analyses published so far has noticed the fundamental evolutionary changes in the construction of the pollinating apparatus in *H. spartioides*, which is unique in *Hoya* and even in the subfamily Asclepiadoideae.

The present paper analyses the flower morphology of the two sister species, *H. curtisii* and *H. spartioides*. *Hoya lacunosa* is also examined since it is part of the next-higher clade including the above two species (Fig. 1). Evaluation of the gynostegial structure takes into account the “inseparable relationship between form and function” (Kaplan 2001). Without considering the function of the individual structures, their specific shapes and positions remain unclear. The gynostegium of the Asclepiadoideae represents a highly synorganized complex structure (Kunze 1981; Endress 1990, 1996, p. 302–319; Soltis et al. 2005, p. 269, 270). Synorganization is defined as “the intimate structural connection of two or several neighbouring structural elements to form a functional system or apparatus” (Endress 1990, p. 155). A central aim of the present investigation is to evaluate the amount of evolutionary change separating the synorganized gynostegium of *H. spartioides* from those of other *Hoya* species.

Incongruence between the amounts of molecular and phenotypic evolution is encountered frequently. Kadereit (1994) described several cases of dramatic morphological divergence unaccompanied by differences of equivalent magnitude in phylogenetic marker molecules. In the examples described by him, the divergent morphological characters fall into “a very limited number of categories” (Kadereit 1994, p. 371). Regarding the flower, Kadereit mentions shape, structure and colour of petals, as well as number and shape of stamens. The present study is the first one comparing differences in the synorganization of complex structures to molecular divergence.

Material and methods

Microtome sections were made either applying 2-hydroxyethyl methacrylate embedding (Igersheim and Cichocki 1996), in which cases sections were cut at 10 mm and stained with toluidine blue and ruthenium red, or using paraffin embedding and staining with hematoxylin and safranin. Micrographs were made on an Olympus SZX-16 stereomicroscope with digital camera equipment. Flowers observed with a dissecting microscope were stained with sudan black and photographed immersed in 70% ethanol. Artificial insertion of

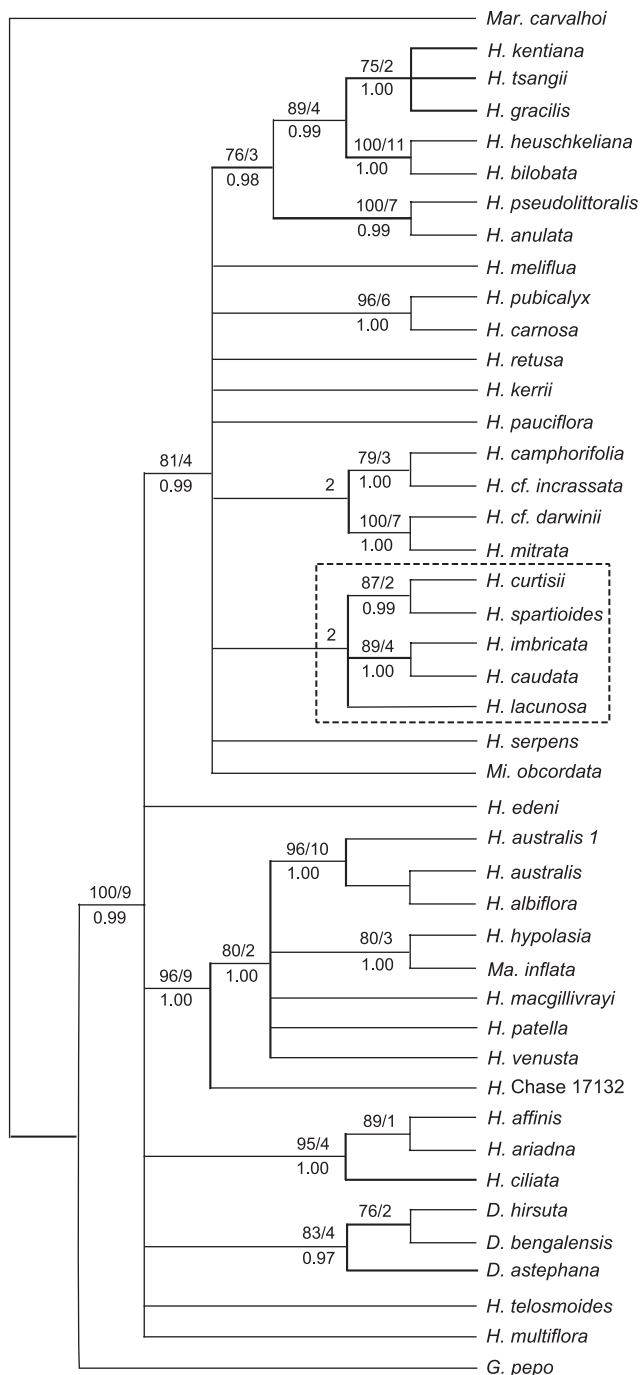


Fig. 1. Phylogeny of *Hoya*. Strict consensus of 64 most parsimonious trees obtained from combined ITS, *atpB-rbcL*, and *trnL* data. Redrawn from Wanntorp et al. (2006b).

a pollinium into the guide rail of *H. spartioides* was performed on alcohol-preserved flowers, using fine tweezers to extract the pollinarium and draw it upward along the guide rail.

Species examined

Hoya curtisii King & Gamble, Wanntorp L. 597, ex hort.

Hoya lacunosa Blume, HK 117, ex hort.

Hoya spartioides (Benth.) Kloppenb., Wanntorp L. 592, Sipitang, Borneo.

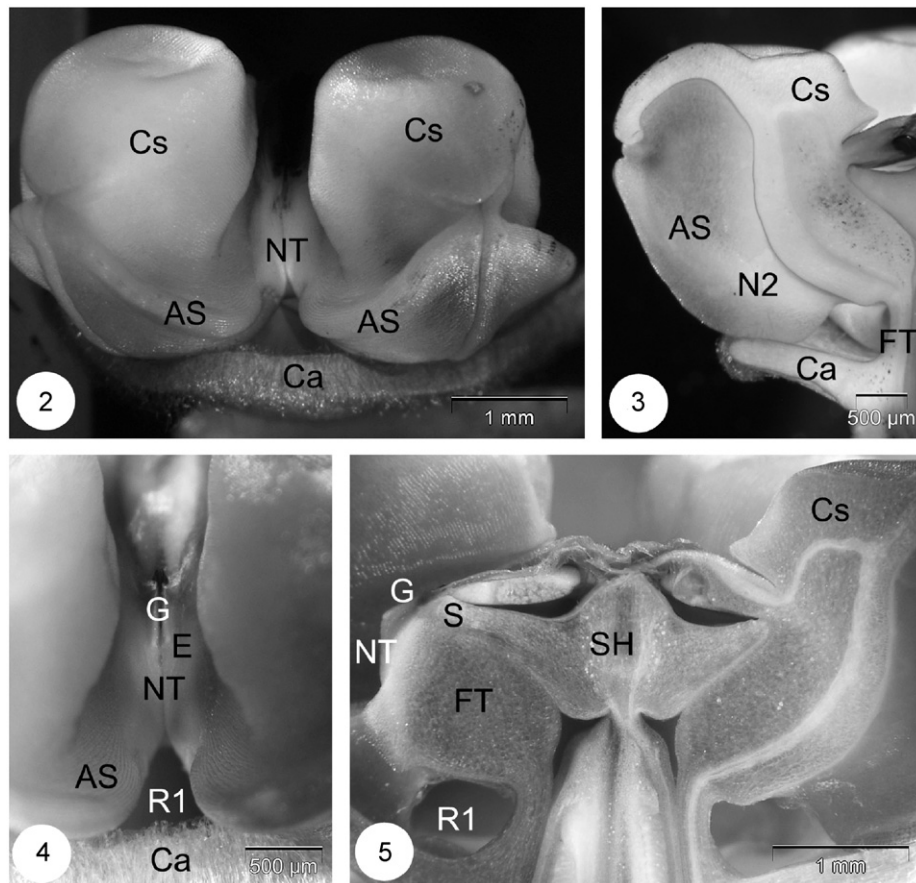
Results

Description of flower morphology

Hoya curtisii

In the mature flower the petals are recurved almost 180° and fused for only a short distance at their bases.

From this annular zone arises the filament tube, which bears a large, spreading annulus (Ca) with outer margins covered by outwardly curved hairs (Fig. 2). Although situated at the base of the filament tube, this annulus is homologous to the Ca in other species of *Hoya*. Radial shifts of coronal elements are encountered frequently in Asclepiadoideae (Kunze 2005). Moreover, the longitudinal section (Fig. 9) shows that in spite of its position the annulus is primarily formed of corolline tissue. The most conspicuous elements of the flower are the five knobs of the staminal corona (Cs; nomenclature see Liede and Kunze 1993), each of which is fused with the two lateral lobes of the anther skirt. An anther skirt is formed by the basal lobes of a ventrifixed anther (Kunze and Wanntorp 2008). These two lobes join below the Cs but do not fuse. The secondary nectary (N2 in Figs. 3 and 10) is at the base of the Cs, enclosed in a large hollow space formed by the revolute anther skirt lobes. This space is closed basally by the annulus. From this nectary the nectar can flow to both sides, where it collects at the base of the nectar tube (R1 in Figs. 4 and 5).



Figs. 2–5. Floral morphology of *Hoya curtisii*. (2) Outside view of pollinating apparatus. (3) Median longitudinal section of stamen showing secondary nectary inside anther skirt. (4) Arrangement of guide rail, nectar tube, reward, and annular corona. (5) Longitudinal section of gynostegium. AS = anther skirt; Ca = annular corona; Cs = staminal corona; E = entrance of guide rail; FT = filament tube; G = guide rail; iR = inner rail; N2 = secondary nectary; NT = nectar tube; R1 = location of reward; S = stigma; SH = stigma head.

Here it can be exploited by the pollinator, the proboscis of which may become wedged in the guide rail during retraction. Due to the basal elongation of the nectar tube, the opening for capturing the proboscis as well as for the insertion of the pollinial crest is situated half way up the slit formed by the two adjacent anther margins (E in Fig. 4). To establish adequate terminology, we use “guide rail proper” for the complete part (G in Fig. 4) and “nectar tube” (NT) for the basal elongation below the entrance (Kunze and Wanntorp 2008). Lateral ridges along the anther skirt may serve as additional guiding structures in the process of pollination.

The longitudinal sections (Figs. 5 and 8) show that the nectar tube and the guide rail proper meet at an angle of about 80°. Both are subtended by the greatly enlarged upper part of the filament tube. The guide rail proper is below the corpusculum and abaxial to the stigmatic area (S). Only the narrow pellucid margin (or crest) of the pollinium is inserted into the narrow guide rail (Fig. 6). Except for a small area directly below the style head (SH in Fig. 5) the filament tube tightly adjoins the gynoecium.

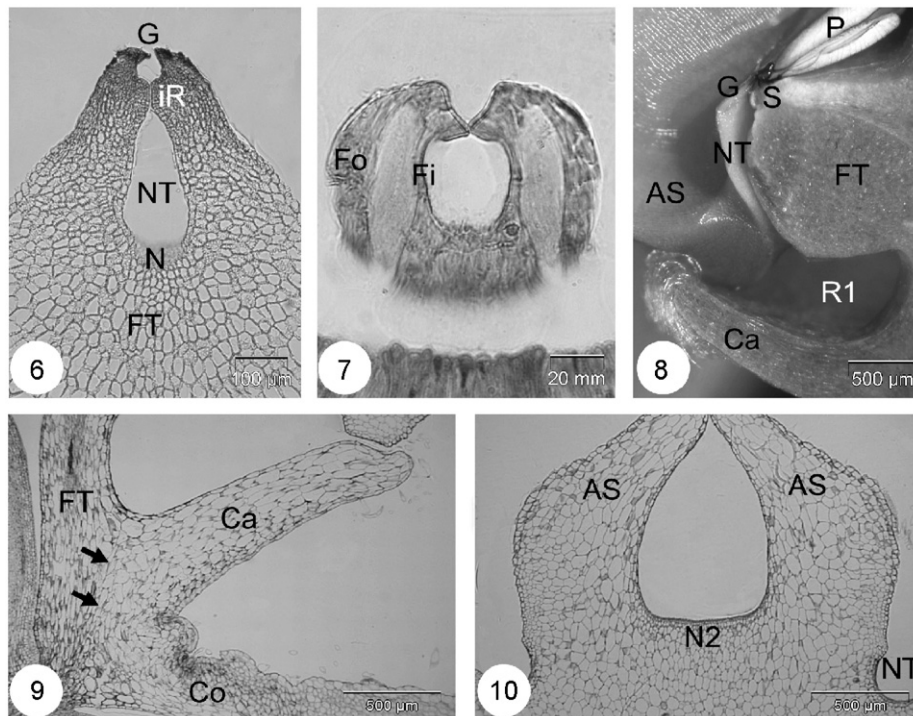
The cross section (Fig. 6) shows a guide rail structure typical of most Marsdenieae and Asclepiadoideae (Kunze 1996). Here outer and inner rails are visible, the outer ones serving to guide the proboscis and

pollinial crest, the inner ridges separating the nectar tube from the outer rails. The primary nectary (N) is located on this part of the nectar tube inside the guide rail proper; its primary function is the nourishment of the germinating pollen tubes (Galil and Zeroni 1965; Kevan et al. 1989). Morphologically, the base of this nectar tube is formed by the filament.

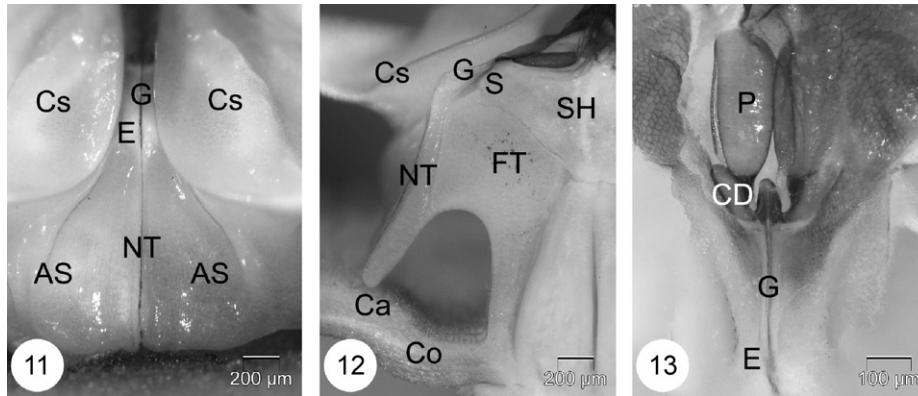
The corpusculum of *H. curtisii* (Fig. 7) has a broad floor and outer flanks that are well separated from the inner flanks, thus enclosing an inner space filled with translucent and softer substance.

Hoya lacunosa

Although the gynostegium of this species differs considerably from that of *H. curtisii* in appearance, its basic construction (“bauplan”) is much the same. The most conspicuous difference lies in the large anther skirt that surrounds the gynostegium below the staminal corona (Figs. 11 and 12). As in *H. curtisii* there is a secondary nectary enclosed by the lobes of the anther skirt below the staminal corona. An inconspicuous annulus is positioned on the corolla underneath the anther skirt (Ca in Fig. 12). Again the guide rail is divided into an upper guide rail proper and a basal nectar tube, which meet at an angle of about 80°. The distal part of the filament tube is enlarged as in *H. curtisii* (compare Figs. 8 and 12). The stigma is



Figs. 6–10. Floral morphology of *Hoya curtisii*. (6) Cross section of guide rail proper. (7) Cross section of corpusculum. (8) Longitudinal section of pollinating apparatus. (9) Longitudinal section of annular corona; arrows point to borderline between tissues of corolla and filament tube. (10) Cross section showing secondary nectary. AS = anther skirt; Ca = annular corona; Co = corolla; Fi, Fo = inner and outer flank of the corpusculum; FT = filament tube; G = guide rail; iR = inner rail; N = nectary; N2 = secondary nectary; NT = nectar tube; P = pollinium; R1 = location of reward; S = stigma.



Figs. 11–13. Floral morphology of *Hoya lacunosa*. (11) Arrangement of guide rail and nectar tube. (12) Longitudinal section of gynostegium. (13) Left anther margin removed to show positions of guide rail and pollinium. AS = anther skirt; Ca = annular corona; Cs = staminal corona; CD = caudicle; Co = corolla; E = entrance of guide rail; FT = filament tube; G = guide rail; NT = nectar tube; P = pollinium; S = stigma; SH = stigma head.

located below the corpusculum inside the guide rail proper (stigmatic chamber), thus cannot be seen from outside (Fig. 13). The small entrance of the narrow guide rail proper corresponds to the crest of the pollinium. The voluminous lateral processes to which the caudicles are attached (CD in Fig. 13) may be additional guiding structures that help insert the pollinal crest (see also Wanntorp and Forster 2007). In cross sections the corpusculum shows the same separation of outer and inner flanks as in *H. curtisii*.

Hoya spartioides

The gynostegium is dominated by the combined staminal corona and anther skirt, which form a regular pentagon resembling a starfish (Fig. 14). The lobes of the anther skirt are fused in the interstaminal sector, thus forming a closed margin resting on top of the corolla tube (Fig. 15). This margin is closely adpressed to the corolla tube, leaving no open access to the space between the corolla tube and the filament tube. The nectar tube ends in the middle of the anther skirt, without producing nectar (NT in Figs. 29 and 30). Nor is nectar produced below the staminal corona (in a secondary nectary as in *H. curtisii*). Instead, this area is covered with hairs (Fig. 16). The filament tube and the corolla tube are strongly pubescent, the space between them is filled with curly hairs. Due to the closure between anther skirt and corolla tube the pollinator cannot access this space as in the other species (Figs. 15 and 17).

In the interstaminal sections the filament tube ends directly at the lower end of the anther skirt and leaves a large hollow space around the stigma head. It contacts the styles only by an inward protrusion (Pr in Fig. 17), which might add to the stability of the gynostegium. Noteworthy is a weak annulus around the outside of the filament tube (Ca in Fig. 17). According to its position this annulus is homologous (homotopous) with the

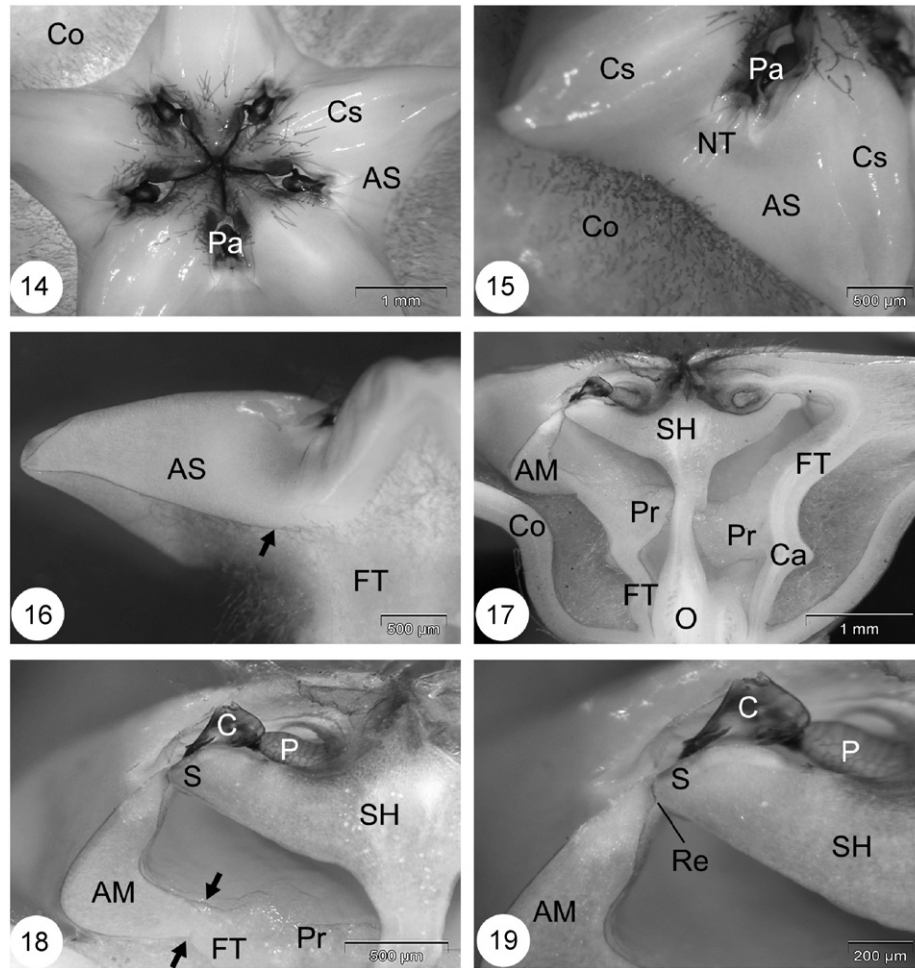
annulus (Ca) in *H. curtisii*, but it does not enclose a space below the anther skirt as in the latter species and does not seem to have any function.

Since the apical thickening of the filament tube is completely lacking, only the anther margins take part in the formation of the guide rail proper and the nectar tube (Figs. 16 and 17). Hence, both structures lack a floor and are reduced to just the lateral rails (see also cross sections in Figs. 27 and 28). Only a very small area of the anther margins is connected to the stigma head (retinaculum; Kunze 1996).

The pollinating apparatus (Figs. 20 and 21) differs considerably from that found in other species of *Hoya*. The two rails of the guide rail proper are very short, with a wide slit between them. This slit corresponds in size to the broad, shoe-like crest of the pollinium (Fig. 22), which fits exactly into the slit. Drawn upward with the caudicle first, the crest is captured with its smaller end and then becomes firmly locked into the guide rail. An artificially inserted pollinium is shown in Fig. 24. Since the two rails do not join, the stigma is openly exposed directly above the nectar tube (S in Fig. 21). Distal to the guide rail, the anther margins become hyaline.

Basally, the slit of the corpusculum widens considerably, the basal processes are bent outward and are attached to the anther margins by means of an adhesive (Fig. 20). Below these processes we found an arched, crusty substance separate from the corpusculum (R2 in Figs. 20 and 21). This is a secretion of the same glandular field on the style head, which produces the corpusculum (Figs. 23 and 27). Considering the functional cooperation of the parts of the pollinating apparatus, this crusty exudate is interpreted as some kind of reward or at least attractant for the pollinator. The following observations support this interpretation:

- (1) The usual nectar-producing and nectar-offering structures are reduced to non-functioning remnants.



Figs. 14–19. *Hoya spartioides*. (14) Gynostegium seen from above. (15) Closely adjoining corolla and anther skirt. (16) Corolla removed to show interstaminal fusion of anther skirt (arrow). (17) Longitudinal section of flower. (18 and 19) Longitudinal sections of pollinating apparatus; arrows point to margin between anther skirt and filament tube. AM = anther margin; AS = anther skirt; C = corpusculum; Ca = annular corona; Co = corolla; Cs = staminal corona; FT = filament tube; NT = nectar tube; O = ovary; P = pollinium; Pa = pollinarium; Pr = protrusion; Re = retinaculum; S = stigma; SH = stigma head.

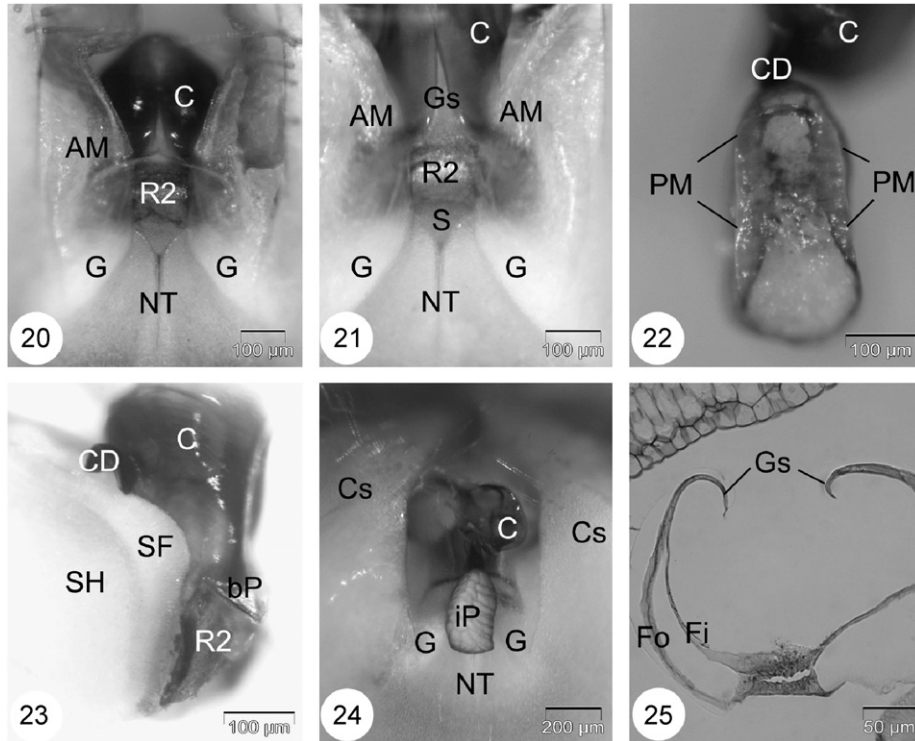
- (2) The slit of the guide rail is too broad to be able to catch the proboscis or any other part of the insect pollinator.
- (3) The crust is positioned directly at the base of the corpusculum.
- (4) The slit of the corpusculum is shaped so as to catch the proboscis of the pollinator, and thus has taken over this function from the guide rail proper.

From the scarce alcohol-preserved material available (in 70% ethanol) we could not obtain more information about the crusty exudate. Since it is preserved in alcohol, it cannot be liquid nectar. Most probably it is of a similar substance as the corpusculum itself, which consists of a mixture of hydrophilic and lipophilic components (Schnepf et al. 1979; Schick 1982). We hypothesize that this shiny crust serves as an attractant and possibly as a reward for the pollinator. Preliminarily

we use the term ‘reward’ (R2) for this crust, in contrast to the usual nectary in other species of *Hoya* (R1).

Although the corpusculum deviates from that in *H. curtisii* and *H. lacunosa* in its overall shape and in having very thin walls, two conspicuous features are shared: a short but distinct floor and rather large open spaces between the outer and the inner flanks (Fig. 25). At least in younger stages this intermediate space is filled with thin translucent material as in *H. curtisii* (Fig. 7).

Figs. 26–30 illustrate the unusual structure of the pollinating apparatus in cross sections. Fig. 27 shows the crust (R2) together with one of the two basal guiding processes of the corpusculum (bP). In Fig. 28, the anther margins are thickened, corresponding to the function of a guide rail. Basipetally the anther margins are divided into two ridges (Fig. 28, left anther), the upper one representing the guide rail, the lower ridge continuing



Figs. 20–25. Pollination apparatus of *Hoya spartioides*. (20 and 21) Positions of corpusculum, secondary reward, stigma, guide rail, and nectar tube. (22) Underside of pollinium. (23) Positions of corpusculum and secondary reward. (24) Artificially inserted pollinium. (25) Cross section of corpusculum. AM = anther margin; bP = basal process; C = corpusculum; CD = caudicle; Cs = staminal corona; Fi, Fo = inner and outer flank; G = guide rail; Gs = secondary guide rail; iP = inserted pollinium; NT = nectar tube; PM = pellucid margin; R2 = secondary reward; S = stigma; SF = secretory field; SH = stigma head.

downward to form the nectar tube (arrow). Between the two margins the stigmatic area is openly exposed. In the upper part the nectar tube consists only of the two adjacent anther margins, without an inner floor (Fig. 29). Since the inward closure normally afforded by the filament tube is lacking, the nectar tube actually represents only a cleft. Fig. 29 corresponds to the cross section of the guide rail of *H. curtisii* in Fig. 6. Comparison of the two figures demonstrates the considerable difference in guide rail structure between the two species. Farther down the two anther margins are fused, leaving only two small ridges together with sclerenchymatic tissue as remnants of the nectar tube (Fig. 30).

Evaluation of character states in *Hoya spartioides*

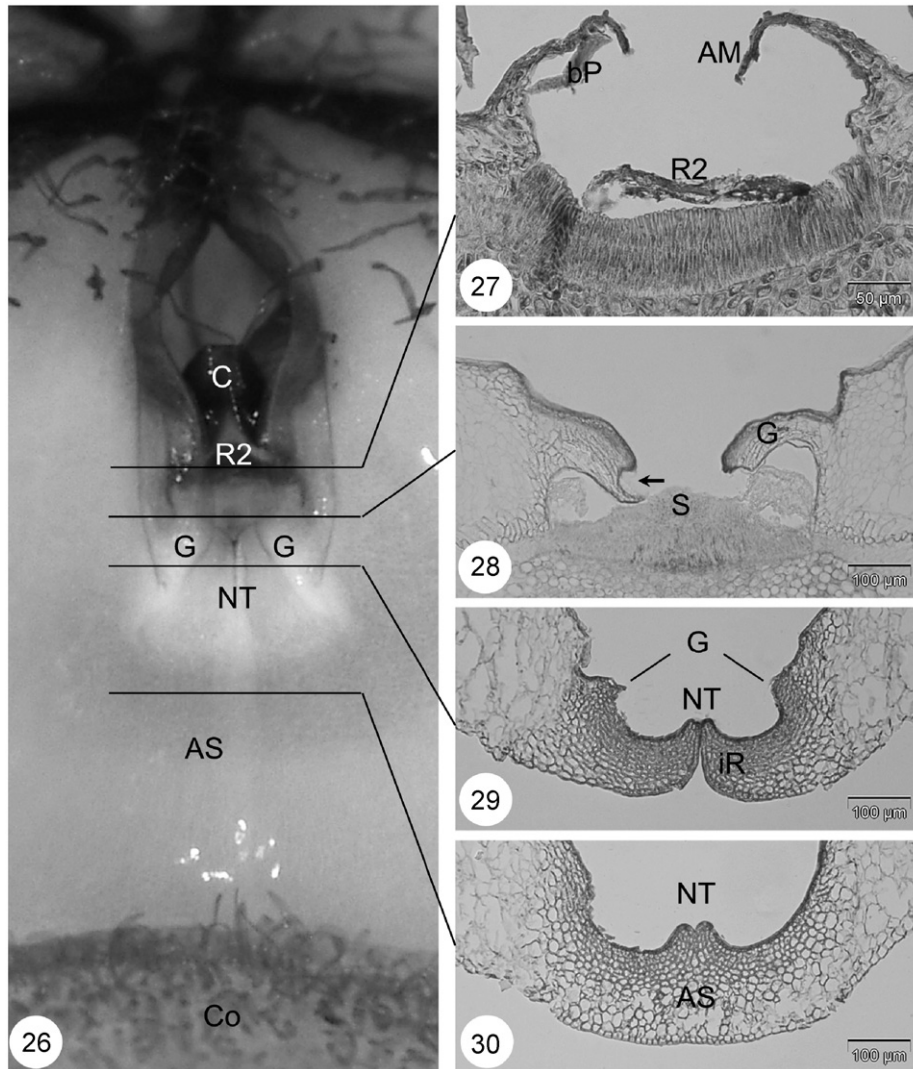
The results show that *H. curtisii* resembles *H. lacunosa* in all relevant basic traits. These traits are also shared with other species of *Hoya* investigated so far (Kunze 1990; Forster and Liddle 1991; Forster 1992; Omlor 1996; Wanntorp and Forster 2007; Kunze and Wanntorp 2008; Wanntorp and Kunze in press). Thus, the polarity of the transition is evident: the floral traits of *H. spartioides* described in the present paper are

derived. A schematic representation of the spatial arrangement of the pollinating apparatus comprising the filament tube, the anther margins, the stigma head, and the pollinarium is given in Figs. 31–34.

Hoya spartioides is a most remarkable exception in several respects. First of all, the offering of a nectar reward at or near the base of the guide rail has been replaced by a new attractant positioned above the guide rail (R2 in Fig. 32). Structures that are present in other species of *Hoya* – nectar tube, secondary nectary, nectar cup – are either lacking or reduced to functionless remnants. The guide rail is also largely reduced and serves only to receive the broad crest of the pollinium. The second function, guiding the proboscis of the pollinator towards the corpusculum, has been transferred to the slit of the corpusculum itself.

Fig. 34 shows the strong reduction of the filament tube, which leaves free space between it and the gynoecium. Thus, the anthers are fused with the stigma head only at very small areas (retinaculum). Counteracting this loss of stability is the basal fusion of the anther skirt.

Since comparison with other species of *Hoya* shows that all of these character states in *H. spartioides* are best interpreted as derived, the situation in *H. curtisii*



Figs. 26–30. *Hoya spartioides*, pollinating apparatus in cross sections; arrow points to splitting of anther margin into outer guide rail and inner nectar tube. AM = anther margin; AS = anther skirt; bP = basal process of corpusculum; C = corpusculum; Co = corolla; G = guide rail; iR = inner rail; NT = nectar tube; R2 = secondary reward; S = stigma.

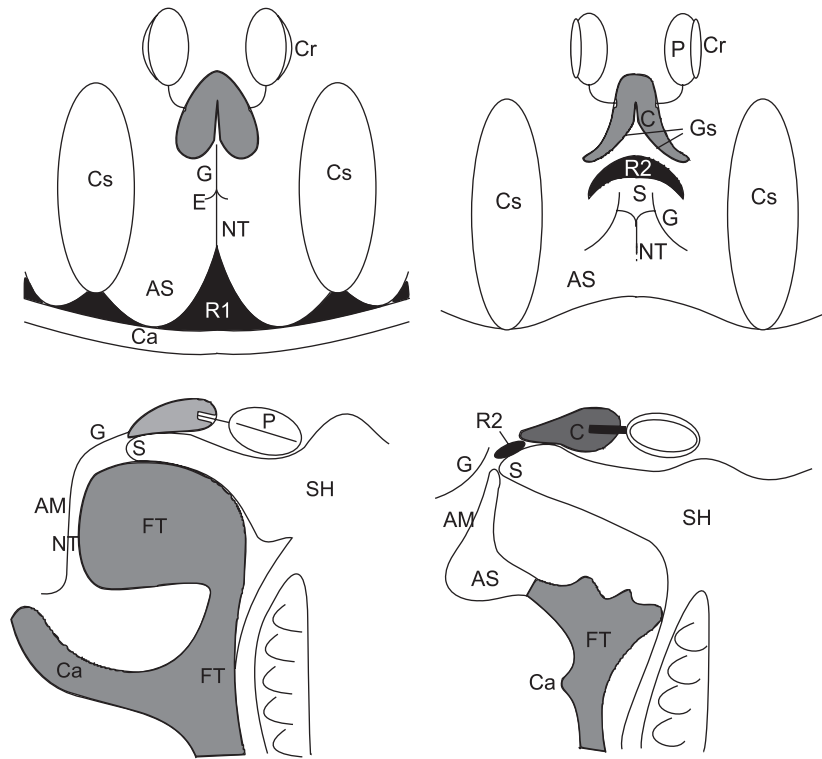
represents the features of the common ancestor of the sister species pair *H. curtisii* and *H. spartioides*. Consequently, the main evolutionary processes that have led to the morphology of the pollinating apparatus in *H. spartioides* are the following (see also Fig. 35):

- (1) *Reduction*: filament tube, annulus, nectar tube, secondary nectary, stigmatic chamber.
- (2) *Change in structure*: guide rail, crest of pollinium, corpusculum.
- (3) *New elements*: interstaminal fusion of basal lobes of anther skirt, crusty secretion as attractant or reward.

The functions of the reduced parts (item 1) have been taken over by the modified structures listed in items 2 and 3.

Although we have no standard measure of phenotypic divergence (Kellogg 2002), in an individual case at least

some estimates can be made by comparison to evolutionary changes within higher taxa (genera, tribes, subfamilies). To our knowledge, the structure of the pollinating apparatus, with nectar offered as a reward at or near the base of the guide rail, is universal within the subfamily Asclepiadoideae (Kunze 1991). Even in cases with secondary nectaries as in *Hoya* or in Gonolobinae (Kunze 1999), or in flowers with capillary flux of nectar into the hoods of the corona (Asclepiadinae; Kevan et al. 1989; Kunze 1997), the principal function always is to direct the proboscis or the foot of the pollinator to the basal opening of the guide rail. In all these cases the guide rail has a double guiding function: for the pollinator and for the inserted pollinium. *Hoya spartioides* has departed from this general principle by shifting the reward above the guide rail and by loss of the pollinator-guiding function of the anther margins. This implies



Figs. 31–34. Schematic representation of evolutionary changes in functional synorganization of *Hoya spartioides*. AM = anther margin; AS = anther skirt; C = corpusculum; Ca = annular corona; Cr = crest of pollinium; Cs = staminal corona; E = entrance of guide rail; FT = filament tube; G, Gs = primary and secondary guide rail; NT = nectar tube; P = pollinium; R1 and R2 = primary and secondary reward; S = stigma; SH = stigma head.

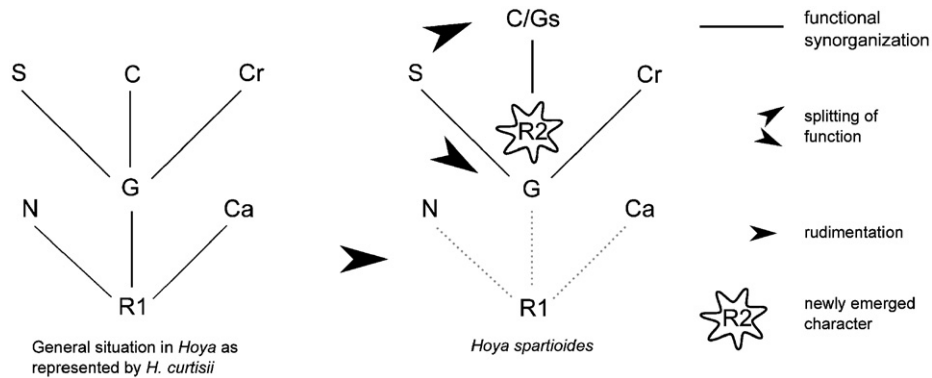


Fig. 35. Main evolutionary changes in functional synorganization of pollinating apparatus of *Hoya spartioides*. C = corpusculum; Ca = annulus; Cr = crest of pollinium; G = guide rail; Gs = secondary guide rail; N = nectary; R1 and R2 = primary and secondary reward; S = stigma.

structural changes not only of the guide rail in connection with the pollinal crest, but also of the corpusculum.

These evolutionary changes in the gynostegium in *H. spartioides* have affected an old and apparently conservative cooperation of structures in the subfamily. Even such structures seem to retain a high degree of evolutionary plasticity.

Although the reduction of the filament tube appears as a mere change in proportions, there are considerable structural and functional consequences. The guide rail loses its nectariferous inner tube, and the stability of the gynostegium is reduced. By contrast, in other species of *Hoya* the upper section of the filament tube is enlarged and stable and firmly fused with the stigma head (Wanntorp and Forster 2007; Kunze and Wanntorp

2008). Hence, the filigree structure of the filament tube in *H. spartioides* deviates significantly from the type usually found in the genus. The loss of the inner nectar tube raises the question whether there is any other source of the germination fluid usually provided by it, or whether this fluid is lacking altogether.

In *Hoya*, the revolute margins of the corona formed by the anther skirt usually contain secondary nectaries on their inside. This together with nectar cups at the base of the guide rails is considered as an autapomorphy of the genus *Hoya* (Kunze and Wanntorp 2008). *Hoya spartioides* has completely lost this reward system by reduction of the nectar tube, closing the access to the nectar cups between the filament tube and the corolla tube, and by loss of the secondary nectaries. These changes point to a considerable phenotypic distance between the two sister species, *H. spartioides* and *H. curtisii*, that far transcends the differences between other species of *Hoya* analysed so far.

Discussion

Comparative analysis of floral morphology in the sister species pair *H. curtisii* and *H. spartioides* shows a significant difference between the phenotypic and the genotypic level. The evolutionary changes that have led to the gynostegium of *H. spartioides* are not accompanied by comparable changes in the marker genes.

Similar cases have been reported in other Asclepiadoideae. In their analysis of the genera *Fockea* and *Cibirhiza*, which comprise the tribe Fockeeae, Verhoveven et al. (2003) found that, although the morphological and molecular evidence clearly supports recognition of the tribe Fockeeae (Kunze et al. 1994), the two genera have significantly different types of pollinia, a structure that elsewhere in the family is used to distinguish subfamilies. Even more noticeable is the same phenomenon in some New World groups of Asclepiadoideae. Discussing the very diverse Metastelmatinae, Oxypetalinae, and Gonolobinae, Rapini et al. (2003, p. 45) remark that “this huge morphological diversity, however, is not reflected in molecular diversity of *trnL-F*, contrasting with the morphologically less diverse American *Cynanchum* clade, which is characterised by a much greater level of molecular change.” *Hoya spartioides* shows a far reaching reconstruction of not only coherent but functionally cooperating and interdependent structures of high complexity within the genus. In the following discussion we briefly analyse current hypotheses to explain the underlying evolutionary processes.

The classical gradualistic approach proposed by Darwin (1859) and elaborated in the modern synthesis requires numerous small steps, each with small, but decisive advantages to the bearer. The gradualistic model is the basis of the modern theory of evolution

to this day (Futuyma 2005). Following this approach, we should expect some intermediate phenotypes between the two sister species *H. curtisii* and *H. spartioides*. Wanntorp et al. (2006a) mentioned the rather limited sampling of their molecular analysis, which leaves open the possibility of finding species with a closer morphological and molecular relationship to *H. spartioides* than *H. curtisii*. Because of its functional synorganization the evolution of the pollinating apparatus in *H. spartioides* must have involved processes of internal adaptation. What has occurred is not evolution of a complex morphology from a simple one by successive addition of new elements, but a change of a pre-existing complex structure into a different one of similar complexity. We can only hypothesize some intermediate forms that may have been evolutionary steps towards *H. spartioides*. We will now consider the potential adaptive value of these modifications to the flower of *H. spartioides*.

The species has been described as a sparsely branched, non-twining epiphyte with small fleshy (succulent) leaves that are shed in the adult stage (Omlor 1998, p. 149; Albers and Meve 2002). Photosynthesis is then taken over by the long peduncles of the inflorescence. Although *H. spartioides* is an inhabitant of the tropical rain forest in Borneo, the xeromorphic character suggests adaptation of the plant to dry microclimatic conditions in the tree crowns. The floral traits described in the present paper could well be related to this. The complete suppression of the nectar and its replacement by a more or less solid, non-liquid attractant can be interpreted as a measure to conserve water. The closed access to the nectar cup between the corolla and the filament tube points in the same direction. The reduction of the filament tube at least saves energy and material, and may be a response to the limited supply of resources in the canopy habitat. Thus, the complex alterations of the floral construction can provisionally be related to adaptation to dry climatic conditions. Considering the gradualistic approach, this implies that the first step could have been the reduction of the openly exposed nectar and its replacement by some exudates below the corpusculum. The basal processes of the corpusculum are usually formed to receive the upward moving proboscis of the pollinator; therefore some elongation and outward bending of these processes would suffice to adjust to the new function of serving as a secondary guide rail, etc. While this rather speculative scenario necessitates a more detailed investigation of floral morphology in the genus *Hoya* with the aim of finding intermediate phenotypes, two main problems still remain: (1) the high degree of synorganization, and (2) the fact that these gradual changes, if they required many mutations at many loci, would contrast with the small degree of genetic divergence between the two species.

In contrast to the gradualistic approach, which relies on a particulate view of the organism, the functional and structural repatterning of the pollinating apparatus in *H. spartioides* rather points to the possibility of a macromutational genesis of the novel features. Information on the development of phenotypic integration and the genesis of novelties by discontinuous evolutionary change is accumulating rapidly (Schlichting and Pigliucci 1998). Instead of assuming the accumulation of small mutational changes, this theory concentrates on the role of epigenetics in the formation of evolutionary novelty. Epigenesis is here understood as the sum of the processes that determine the transformation of a zygote into an adult phenotype (Müller and Newman 2003). Also, correlated shifts in multiple quantitative traits that are traceable to regulatory changes have often been observed (West-Eberhard 2003). In his overview of cases of incongruence between phenotypic and molecular evolution, Kadereit (1994) argued that in some instances mutations of major morphogenetic genes may play a role. This would lead to significant morphological changes in one short step, without giving marker genes enough time to diversify accordingly. Moreover, the complex synorganization of the floral traits in *H. spartioides* suggests a high degree of internal regulation and epigenetic adjustments. The evolution of the pollinating apparatus means that one change required changes to other functionally cooperating parts. The widening of the guide rail is understandable only with the simultaneous evolution of a broader pollinial crest, otherwise the transferred pollinium would not stick to the guide rail, and pollination would fail. With the widening, the guide rail loses its capacity of guiding the pollinator, which in turn would require a new guiding system. In addition, the previously hidden stigma becomes openly exposed, which raises the question of where the liquid for germination of the pollen tubes comes from. Hence, the central question resulting from the present investigation is how synorganized, cooperating structures can evolve into a new synorganization of similar elaboration in a few steps. Evolutionary changes in the epigenesis of the involved traits, including a repatterning of the existing genetic architecture (Schlichting and Pigliucci 1998), seem to offer the most plausible explanation.

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