

## CORONA STRUCTURE IN *CYNANCHUM*: LINKING MORPHOLOGY TO FUNCTION

Jeff Ollerton<sup>1</sup> & Sigrid Liede<sup>2</sup>

<sup>1</sup>School of Environmental Science, University College Northampton, Park Campus, Northampton, NN2 7AL, UK

<sup>2</sup>Dept. of Plant Systematics, University of Bayreuth, 95440 Bayreuth, Germany

*Key words:* Apocynaceae, Asclepiadaceae, *Cynanchum*, Gabon, mutualism, pollination, reproductive ecology.

The complex floral morphologies found in the Asclepiadoideae (Apocynaceae *sensu* Endress & Bruyns 2000) have intrigued and perplexed botanists for two centuries. Recent work has given us a good idea of broad-based concepts of structure, anatomy, and homology (e.g., Kunze 1990, 1995, 1997; Civeyrel 1994; Verhoeven & Venter 1994; Klackenberg 1995, 1996; Liede 1996a). However, little of this work has been placed in a functional context, except as laboratory-based hypotheses as to the function of specific tissues and organs (though see Kunze 1998, 1999). Valuable though such speculations are, they require confirmation from field data. On the other hand, pollination ecologists have usually dealt with taxa whose morphologies are comparatively well known and which exist as large populations in developed countries (e.g., the well studied genus *Asclepias*; see review by Wyatt & Broyles 1994), or have recorded limited data on the links between form and function (though see Vogel 1961, Kunze 1991). For the vast majority of the “asclepiads” we have no idea of the exact role (if any) in pollination of particular combinations of flower morphology, color, patterning, scent, etc.

A characteristic floral structure of the Asclepiadoideae is the possession of a corona of staminal or corolline origin (for typology, see Liede & Kunze 1993). In *Asclepias*, and some other genera, the corona lobes function as nectar receptacles which effec-

tively serve to position an insect into the appropriate orientation for removal and/or insertion of pollinia. In other genera the function of the corona is not so clear, though it may act to mechanically guide an insect's body parts to the guide rails. In some taxa with reduced or absent coronas (for example *Microlooma*, *Astephanus*) this function is transferred to the corolla or trichomes originating on the inner corolla surface. Observations of pollinator behavior in relation to corona morphology are urgently required in order to gain a fuller understanding of corona function.

*Cynanchum* is a large genus of some 400 described species with a tropical and subtropical distribution in Africa, Madagascar, Australia, North and South America, and parts of Asia (Liede 1997). It is characterized by a staminal corona originating from a ring-shaped meristem (Kunze 1991) that can be extremely variable in shape and relationship to the gynostegium, especially in Madagascar, which is a center of diversity for the genus. Pollination observations in *Cynanchum* are scarce; only eight species have ever been observed for pollinators (Ollerton & Liede 1997; see ASCLEPOL, our on-line database of pollinators of the “Asclepiadaceae”, at: <http://www.uni-bayreuth.de/departments/planta2/research/floral.htm>).

During fieldwork in Gabon in 1997, the opportunity arose for one of us (JO) to observe pollinators visiting *Cynanchum adalinae* subsp. *adalinae* (K. Schum.) K. Schum. and to make observations on the relationship between corona structure and function in this tropical African taxon. In addition, the second author (SL) has collected data on variation in fruit

\* e-mail: jeff.ollerton@northampton.ac.uk

set on herbarium specimens while working on *Cynanchum* for various African floras and the Flora of Madagascar. These data are here used to test the hypothesis that differential levels of fruit set are associated with particular coronal morphologies. Specifically, we hypothesize that those species with “closed” coronas (see Methods) may be pollen limited because successful pollination is restricted to a narrower spectrum of flower visitors that possess long tongues.

## METHODS

A small population of *Cynanchum adaliniae* subsp. *adaliniae* was studied between 18 and 20 January 1997 in a clearing within old secondary rainforest on the forestry concession of the Compagnie Equatoriale des Bois, Bambié, Gabon (00° 44' 07" S, 12° 58' 19" E). The main woody vegetation within the clearing were the species *Ricinodendron heudelotti* (Euphorbiaceae) and *Trema occidentalis* (Ulmaceae). Also present were a range of other vines and scramblers, including *Dalechampia ipomoeifolia* (Euphorbiaceae) and *Periploca nigrescens* (Apocynaceae: Periplocoideae). The underlying soil was an orange-brown clay.

Observations were made of floral morphology, scent production, and pollinator activity. Voucher specimens were collected of the plant (Ollerton 73, duplicates at the herbaria of Libreville, Kew, and Bayreuth) and the insects (samples at Oxford University Museums).

A total of 1367 herbarium specimens of African *Cynanchum* and 922 specimens of Madagascan *Cynanchum* were scored for fruits. This is only a crude measure of the probability of species setting fruit because fruiting specimens are more rarely collected than flowering ones, and species in which not all flowers are shed when the fruits appear have a higher chance of being collected than those where fruits develop only after all flowers have fallen. However, the latter species are evenly spread across the different categories of flower morphology (see below) and so there ought to be no systematic bias in the analysis.

The flowers of these African and Madagascan species were grouped into three categories: “open” flowers in which neither the corona nor corolla obstruct access to the guide rails (Fig. 1a), “half-closed” flowers, in which the access to the guide rails is partly obstructed (Fig. 1b), and “closed” flowers, in which either the corona (Fig. 1c) or corolla (Fig. 1d) completely hide the gynostegium. The genera *Pentar-*

*rhinum* E. Meyer, *Folotsia* Jum. & H. Perrier, and *Karimbolea* Desc., which ought to be included in *Cynanchum* (Liede & Täuber 2002), are included in this study.

## RESULTS AND DISCUSSION

*Cynanchum adaliniae* subsp. *adaliniae* is a thin-stemmed herbaceous scrambler (within *Ricinodendron* scrub at the Bambié field site) with white latex. Flowers are small (up to 10 mm in diameter) with very pale yellow petals and a distinctive, tall white corona (Fig. 1e). The flowers emitted a sickly sweet odor during the day, which faded in the evening. Duration of anthesis is unknown.

The flowers were regularly visited by a number of small and medium-sized bees, which purposefully foraged between flowers on the same plant. Clearly this species produces nectar in sufficient quantities to hold the attention of the bees, though it was not possible to measure the quantity or sugar content of the nectar with the equipment then available. The bees ranged in size between 5mm and 9mm and were identified as male *Thricostoma* sp. (solitary or primitively social members of the family Halictidae) and female *Allodape* sp. (semi-social members of the family Anthophoridae). Both species had pollinaria attached to their mouth parts, with up to four corpuscula in the case of one individual.

As the bees landed on each flower, they grasped the cone-shaped corona with their legs and inserted their tongues into the opening at the top of the corona. This was too narrow for the bee's head or thorax to enter and therefore access to the nectar was restricted to those insects with tongues long enough to reach to the bottom of the corona. Any insect so doing would also pick up and/or deposit pollinia.

There are limited data on the pollinators of other species of *Cynanchum* (Ollerton & Liede 1997). All confirmed pollinators have so far been identified as belonging to the “wasp” families Vespidae, Scoliididae, and Ichneumonidae, though honeybees have also been implicated in areas outside of their natural range (Kugler 1973, Sundell 1981, Volovnik 1982, Liede 1994, C. Heyne, Münster, unpubl.). This is therefore the first published data on what appears to be specialized bee pollination in the genus.

The majority of African *Cynanchum* possess coronas which partially or completely cover the gynostegium (illustrations in Liede 1993, 1996b, 1996c;

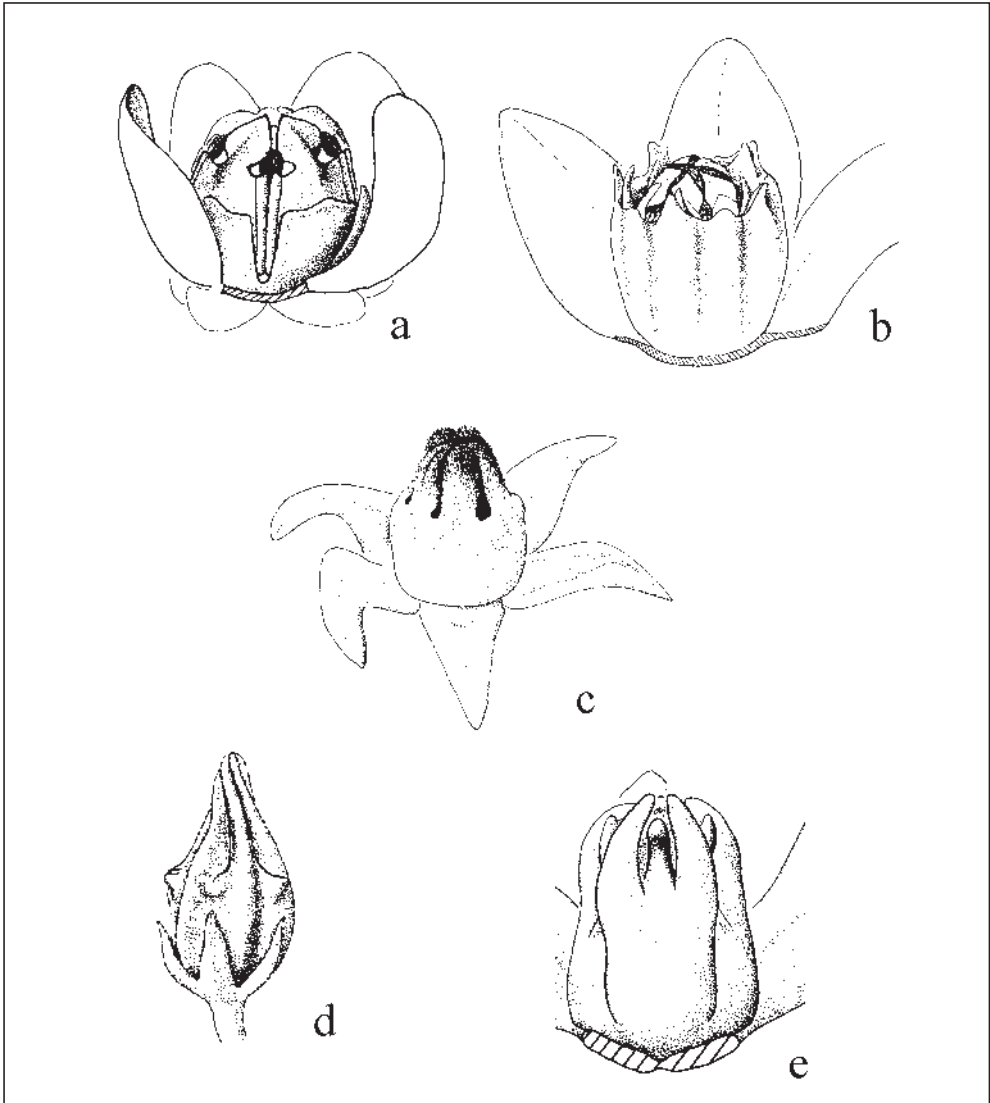


FIG. 1. Examples of corona structure in the genus *Cynanchum*. (a.) *C. graminiforme* as an example of an "open" *Cynanchum* flower. Staminal and interstaminal corona parts are basally fused, the interstaminal parts do not form a lobe. (b.) *C. baroni* as an example of a "half-closed" *Cynanchum* flower. Staminal and interstaminal corona parts are fused for most of the entire corona length; the interstaminal parts form a lobe smaller than the staminal ones which bear a ligule at the adaxial side. (c.) *C. decaryi* as an example of a "closed" *Cynanchum* flower, in which closure is effected by the corona. Staminal and interstaminal corona parts are fused for about 3/4 of total corona length; the prominent folds are effected by the interstaminal corona parts. The gynostegium is only accessible between the folds, directly in front of the guide rails. (d.) *C. junciforme* as an example of a "closed" *Cynanchum* flower, in which closure is effected by the corolla. The corona is rather small and does not obstruct the gynostegium, which is accessible only through the bulges at the top of the tube. (e.) Flower of *C. adalinae* ssp. *adalinae*, representing a "closed" flower. Staminal and interstaminal corona parts are fused completely and the gynostegium is accessible only through the hole at the top of the corona.

Liede & Meve 1996; Meve & Tessier 1996). As well as *C. adalinae*, species with notably enclosing coronas include *C. clavidens* subsp. *clavidens*, *C. galgalense*, *C. gerrardi*, *C. longipes*, and *C. rungueense*. Further afield, at least two Malesian species possess similar coronas, *C. corymbosum* and *C. tuberculatum* (Liede 1999). Clearly, such coronas may function as excluders for illegitimate flower visitors in many *Cynanchum* species.

Data on fruit set observed in herbarium specimens are presented in Table 1. Of the 33 species in Africa, 7 have open flowers, 22 have half-closed flowers, and 4 have closed flowers. Overall fruit set is rather low, at 16.4% of all specimens scored. There is no statistically significant association between corona type and fruit set (G test of association;  $G = 0.81$ ,  $df = 2$ ,  $P > 0.05$ ). Madagascar, with 73 species an area of extreme diversity for the genus, has 20 species with open flowers, 36 with half-closed flowers, and 17 with closed flowers. Overall fruit set is once again low (14.7%) and there is no statistically significant association between corona type and probability of fruit set (G test of association;  $G = 2.95$ ,  $df = 2$ ,  $P > 0.05$ ). Likelihood of fruit set in both the African and Madagascan specimens appears not to be a function of corona morphology, and is probably much more determined by the ecological context in which the plant was growing rather than by morphological adaptations. A closed corona may limit pollination to long-tongued insects such as some bees, but those bees may be more likely to visit such flowers because they are not competing with other, generalist insects which visit open flowers.

Not all flower visitors act as pollinators and the lack of fit between floral morphology and visitor size, shape and/or behavior can incur a cost for a plant whose nectar is "robbed" in the absence of pollina-

tion. Strategies to exclude illegitimate pollinators have evolved many times in a wide range of plant families (Proctor *et al.* 1996). Of these, the commonest strategy has been the evolution of narrow, tubular corollas which limit flower visitors to those whose mouth parts are long enough to reach the nectar secreted at the base of the tube. This strategy is commonly encountered in those subfamilies originally contained within the Apocynaceae *sens. strict.*, but is rare in the Asclepiadoideae (e.g., *Stephanotis*, *Schubertia*, *Stapeliopsis*, plus the special case of *Ceropegia*). The occurrence of closed corollas in some species of *Cynanchum* (e.g., *C. junci-forme*) suggests that there are no developmental constraints on the evolution of closed flower types within the genus. However, it has evolved rarely, compared with the evolution of flowers with closed coronas. The evolution of closed coronas may be driven by the utility of using an already wholly or partially fused structure which can potentially enfold the reproductive structures while allowing the petals to continue to function as attractive devices. One disadvantage to narrow corolla tubes is that it reduces the surface area of the front of the flower on view to foraging animals and therefore may reduce the visitation rates to those flowers; see Dafni *et al.* (1997) for a review of experimental studies in this area. To offset this reduction in frontal surface area, many species with tubular corollas splay out the opening of the fused tube (in the Apocynaceae, e.g., *Vinca* spp.). This provides a larger surface area to attract foraging insects while at the same time restricting visitors to those animals that can access the nectar and contact anthers and stigma. The evidence presented here for *Cynanchum adalinae* suggests that a rather different strategy has evolved that may be unique within the family. This taxon also restricts visits by insects to those bees whose tongues are long enough to reach the nectar inside the flower.

TABLE 1: The numbers of fruiting and non-fruiting herbarium specimens of African and Madagascan *Cynanchum* in relation to flower morphology.

|              | African <i>Cynanchum</i> |             |        | Madagascan <i>Cynanchum</i> |             |        |
|--------------|--------------------------|-------------|--------|-----------------------------|-------------|--------|
|              | open                     | half-closed | closed | open                        | half-closed | closed |
| non-fruiting | 278                      | 885         | 182    | 152                         | 388         | 292    |
| fruiting     | 50                       | 144         | 26     | 29                          | 58          | 35     |

However, it achieves this not by use of a narrow, fused corolla tube but by a narrow, partially fused corona tube. This allows the petals to retain their main function of visitor attraction. To our knowledge it is rare to encounter plant families which have evolved a system for pollinator exclusion of illegitimate flower visitors which is not based on modifications of the corolla. The evolution of closed coronas in *Cynanchum* equates with a switch from pollinia placement on legs and mouthparts (e.g., in open-flowered *Sarcostemma*) to pollinia placement only on mouthparts. This in turn may indicate a change in pollinator type, though as yet we have too few data on the pollinators of *Cynanchum* to test this idea. Mapping corona type onto a molecular phylogeny of the Madagascan species of *Cynanchum* shows that corona morphology is an evolutionary labile trait, with multiple origins of open, half-closed, and closed corona types (Liede & Täuber 2002). Further fieldwork to identify the pollinators of *Cynanchum* species is needed in order to establish any links between particular morphologies and specific pollinators.

#### ACKNOWLEDGMENTS

JO would like to thank Scott Armbruster for facilitating the trip to Gabon and to Scott and Liv Antonsen for companionship during the trip. Thanks also to Chris Wilks for arranging accommodation and to the Compagnie Equatoriale des Bois for permission to undertake fieldwork. The following are acknowledged for their artistic skills: Jim Conrad (Figs. 1a and e, by permission of the editors of *Adansonia* and the *Annals of the Missouri Botanical Garden*) and Graziela Hintze (Figs 1b, c, and d). The original text of this paper was improved by the comments of two anonymous reviewers, and of the editor, Karl-L. Schuchmann. Finally, thanks to Chris O'Toole (Oxford University Museum of Natural History) for identifying the bees.

#### REFERENCES

- Civeyrel, L. 1994. Variation et évolution des types polliniques de genre *Secamone* (Asclepiadaceae, Secamonoideae). *C. R. Acad. Sci. Paris, Sciences de la vie* 317: 1159–1165.
- Dafni, A., Lehrer, M., & P.G. Kevan. 1997. Spatial flower parameters and insect spatial vision. *Biol. Revs.* 72: 239–282.
- Endress, M.E., & P.V. Bruyns. 2000. A revised classification of the Apocynaceae s.l. *Bot. Rev.* 66: 1–56.
- Klackenberg, J. 1995. Taxonomy and phylogeny of the SE Asian genus *Genianthus* (Asclepiadaceae). *Bot. Jahrb. Syst.* 117: 401–467.
- Klackenberg, J. 1996. Revision of the Malagasy genus *Pervillea* (Asclepiadaceae) and its phylogenetic relationship to *Calyptanthura*. *Nord. J. of Bot.* 16: 165–184.
- Kugler, H. 1973. Zur Bestäubung von *Cynanchum acutum* L. durch Faltenwespen (Vespidae). Pp. 61–68 in Brantjes, N.B.M., & H.F. Linsgens (eds.). *Pollination and dispersal symposium*, Pp. 61–68. Univ. Nijmegen, Fakulteit der Wiskunde.
- Kunze, H. 1990. Morphology and evolution of the corona in Asclepiadaceae and related families. *Trop. Subtrop. Pfl. Welt* 76: 1–48.
- Kunze, H. 1991. Structure and function in asclepiad pollination. *Pl. Syst. Evol.* 176: 227–253.
- Kunze, H. 1995. Floral morphology of some Gonolobaceae (Asclepiadaceae). *Bot. Jahrb. Syst.* 117: 211–238.
- Kunze, H. 1997. Corona and nectar system in Asclepiadiaceae (Asclepiadaceae). *Flora* 192: 175–183.
- Kunze, H. 1998. Floral structure and pollination biology in *Matelea lanata* (Asclepiadaceae). *Asklepios* 75: 23–27.
- Kunze, H. 1999. Pollination ecology in two species of *Gonolobus* (Asclepiadaceae). *Flora* 194: 309–316.
- Liede, S. 1993. A taxonomic revision of the genus *Cynanchum* L. (Asclepiadaceae) in southern Africa. *Bot. Jahrb. Syst.* 114: 503–550.
- Liede, S. 1994. Some observations on pollination in Mexican Asclepiadaceae. *Madroño* 41: 266–276.
- Liede, S. 1996a. Anther differentiation in the Asclepiadaceae-Asclepiadeae: form and function. Pp. 221–235 in D'Arcy, W.G., & R.C. Keating (eds.). *The anther: form, function, and phylogeny*. Cambridge.
- Liede, S. 1996b. A revision of *Cynanchum* (Asclepiadaceae) in Africa. *Ann. Mo. Bot. Gard.* 83: 283–345.
- Liede, S. 1996c. The Cynanchinae (Asclepiadaceae) in Madagascar: more new leafy and leafless species and subspecies. *Adansonia* 18: 103–135.
- Liede, S. 1997. American *Cynanchum* (Asclepiadaceae) – a preliminary infrageneric classification. *Novon* 7: 172–181.
- Liede, S. 1999. The genera *Cynanchum* and *Vinctoxicum* (Apocynaceae-Asclepiadoideae) in Malesia. *Blumea* 44: 471–495.
- Liede, S., & H. Kunze 1993. A descriptive system for corona analysis in Asclepiadaceae and Periplocaceae. *Pl. Syst. Evol.* 185: 275–284.
- Liede, S., & U. Meve. 1996. Two new species and one new combination in leafless Malagasy *Cynanchum* (Asclepiadaceae). *Novon* 6: 59–63.

- Liede, S., & A. Täuber. 2002. Circumscription of the genus *Cynanchum* (Apocynaceae-Asclepiadoideae). *Syst. Bot.* 27: 789–800.
- Meve, U., & M. Teissier. 1996. A new species of leafless *Cynanchum* (Asclepiadaceae) from Madagascar. *Bradleya* 14: 10–13.
- Ollerton, J., & S. Liede. 1997. The evolution of pollination systems in the Asclepiadaceae: a survey and preliminary analysis. *Biol. J. Linn. Soc.* 62: 593–610.
- Proctor, M., Yeo, P., & A. Lack. 1996. *The natural history of pollination*. London.
- Sundell, E. 1981. The New World species of *Cynanchum* subgenus *Mellichampia* (Asclepiadaceae). *Evol. Mon.* 5: 1–62.
- Verhoeven, R.L., & H.J.T. Venter. 1994. Pollen morphology of the Periplocaceae from Madagascar. *Grana* 33: 295–308.
- Vogel, S. 1961. Die Bestäubung der Kesselfallen-Blüten von *Ceropegia*. *Beitr. Biol. der Pflanz.* 36: 159–237.
- Volovnik, S. 1982. On biocoenotic relations between *Cynanchum acutum* and some insects. *Zhurn. Obsh. Biol.* 43: 729–731.
- Wyatt, R., & S.B. Broyles. 1994. Ecology and evolution of reproduction in milkweeds. *Ann. Rev. Ecol. Syst.* 25: 423–441.

*Accepted 24 May 2002.*