

Morphological Adaptations for Bird Pollination in *Nicolaia elatior** (Jack) Horan (Zingiberaceae)

REGINE CLASSEN

Institute of Botany, Department of Plant Morphology
R.W.T.H. Aachen, West Germany

Abstract

A report is given in detail on the behaviour of *Anthreptes malacensis* when visiting the inflorescence of *Nicolaia elatior*, with special reference to the Singapore Botanic Gardens. It is shown how in *Nicolaia* ornithophily became a realistic alternative to psychophily by the formation of a dense inflorescence unit, the main steps of which being the aggregation of flowers and the expansion of (sterile) bracts.

Nicolaia elatior is often cultivated in tropical gardens. Its popularity is attributed to the spice which the flower buds provide and the ornamental value of the intensively red and glossy blossom† (plate 1) attracting nectar-searching animals, especially birds. Knuth (1904, 183) had observed sunbirds on the flowering heads of *Nicolaia elatior*, but he took them for 'more harmful than useful' visitors. His

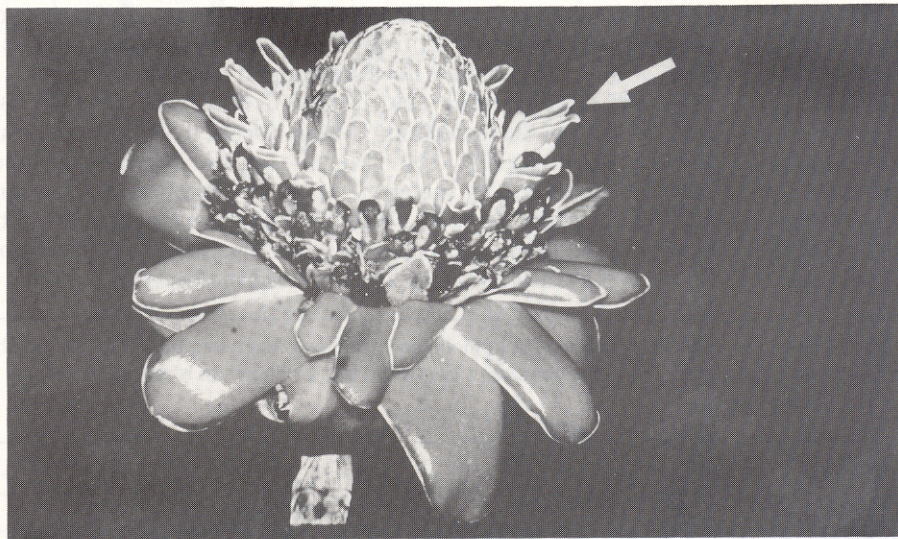


Plate 1. The flower head of *Nicolaia elatior* surrounded by showy, extrafloral bracts.

Within the inflorescence, the open flowers form a whorl and present their yellow signals (arrow); below, ripening fruits; above, flowers still in bud.

* More familiar synonyms are *Elettaria speciosa* Bl. and *Phaeomeria magnifica* (Roscoe) Schum. For a more complete list see Valetton (1921: 138), Burt and Smith (1972: 210-211), and Weber (1980: 152). Presently, *Etlingera elatior* (Jack) R.M. Smith is the correct name. This new combination (Smith, 1986) has reduced *Nicolaia elatior* to a synonym.

† The term 'blossom' is used in the sense of Faegri & v.d. Pijl (1979: 21), that is as an ecological term. In the morphological point of view, a blossom may be an inflorescence (pseudanthium), a flower (euanthium) or a part of a flower (meranthium).

opinion was that the birds visited the blossoms only for catching insects there, and if they happened to insert their bill into the blossoms it was only incidental and pollination was not effected. My observations at the Botanic Gardens in Singapore strongly supports the view that *Anthreptes malacensis* is a pollinator.

Nicolaia elatior (Jack) Horan is a perennial herb which grows naturally in primary and secondary forests in SE. Asia. Frondose leaves on the vegetative stems measure several meters long and loosely shade over the reproductive, shaft-like stems, which are 1-2 m long. On these are exposed a terminal flower head. Apart from the large showy leaves which are integrated into the habit of the blossom these reproductive stems bear only small bracts.

The inflorescence looks like a simple cephalium with about 300 flowers spirally set on an undetermined apex. But recently, Weber (1980: 158) and Kunze (1985: 127) have shown that this flower head is a simple, highly reduced polytelic thyrus.

The base of the flower mass is surrounded by large showy bracts, which form a pseudocorolla of 20-cm diameter (pl. 1) and are the most conspicuous element of the blossom. Except for a narrow pale margin, both sides are intensively carmine and show a fine brightness which is caused by the waxy surface. The proximal leaves are sterile and follow on abruptly the inconspicuous bracts of the shaft while the distal, flower-subtending bracts gradually reduce in size. Before flowering, the showy leaves completely envelop the flower buds; then, during anthesis they stick out horizontally and finally, in the postfloral phase, they hang down retrorsely. Anthesis of a head is 3 weeks. Every day, the flowers of a whorl would open simultaneously and fade a few hours later. Thus the flowering zone shifts upwards along the inflorescence axis which elongates from 5 to 15 cm. While the flowers at the top are still in bud, young fruits would have developed at the base.

The flower is sessile and zygomorphic (pl. 1, figs. 1 & 2). Its characteristic boat-shape is brought about by the labellum* which forms a staminodial tube together with the fertile stamen (fig. 2). The style is — in the typically zingiberaceous manner — fixed in its position by the anther (fig. 4). Pollen-sacs and stigma are oriented towards the labellum (fig. 3). By the unique arrangement of the labellum, anther and stigma, pollination occurs whenever a sucking organ is dipped into the tube (fig. 5) — as Knuth (1904) has already described in some detail.

* Weber (1980) interprets the labellum as a homologon to the two inner staminodes of the zingiberaceous flower. Kunze (pers. comm.) however is convinced that the labellum is represented by all the five staminodes together.

Facing Page

Fig. 1 Habit of a flower of *Nicolaia elatior*.

pr, prophyll; *ca*, calyx; *co*, corolla lobe; *lab*, labellum.

Fig. 2. Diagram of a flower of *Nicolaia elatior* (empirical, see note 3 on p. 41).

sb, subtending bract; *ax*, axillary bud; *sta*, fertile stamen; *ep*, epigynous gland; *gyn*, gynoecium; *solid*: staminode tube.

Fig. 3. Optical longitudinal section showing the position of the anther-stigma-complex in relation to the labellum.

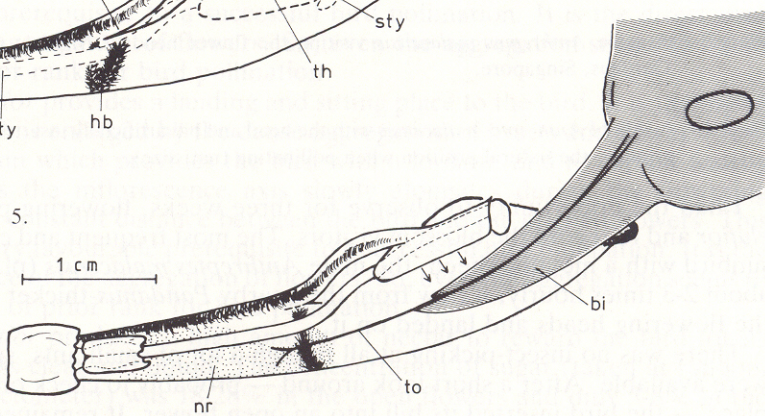
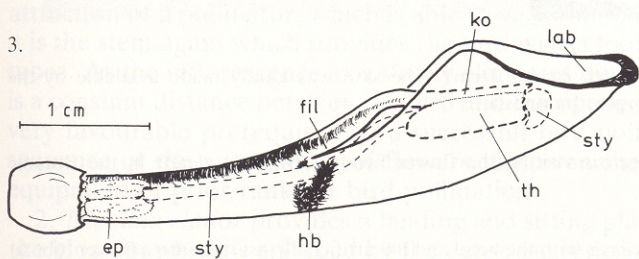
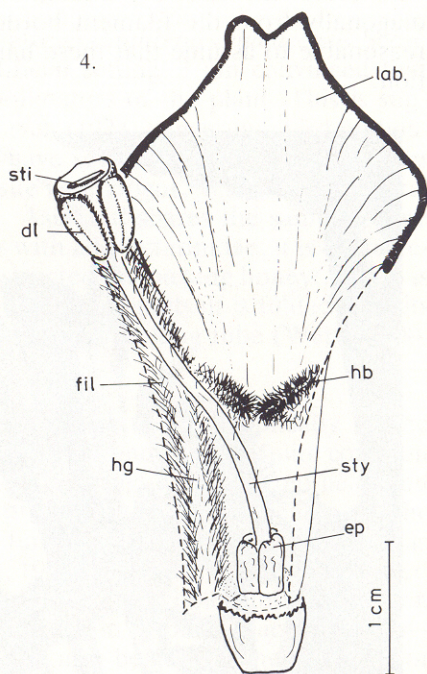
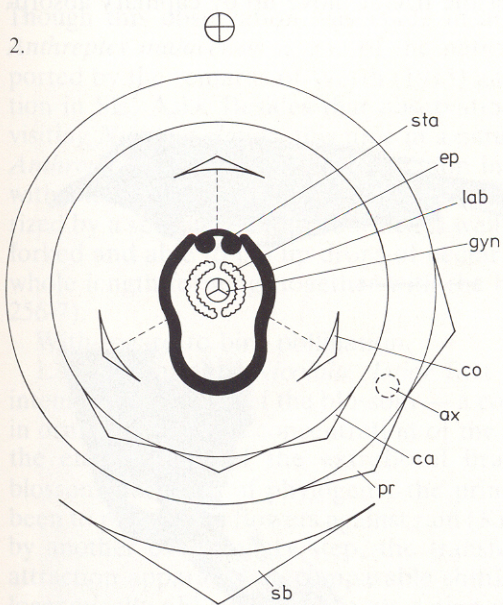
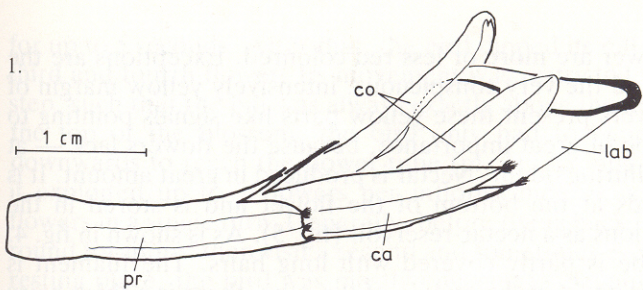
sty, style; *th*, theca; *ko*, connective; *fil*, filament; *hb*, hairy belt.

Fig. 4. A flower of *Nicolaia elatior*, longitudinally opened.

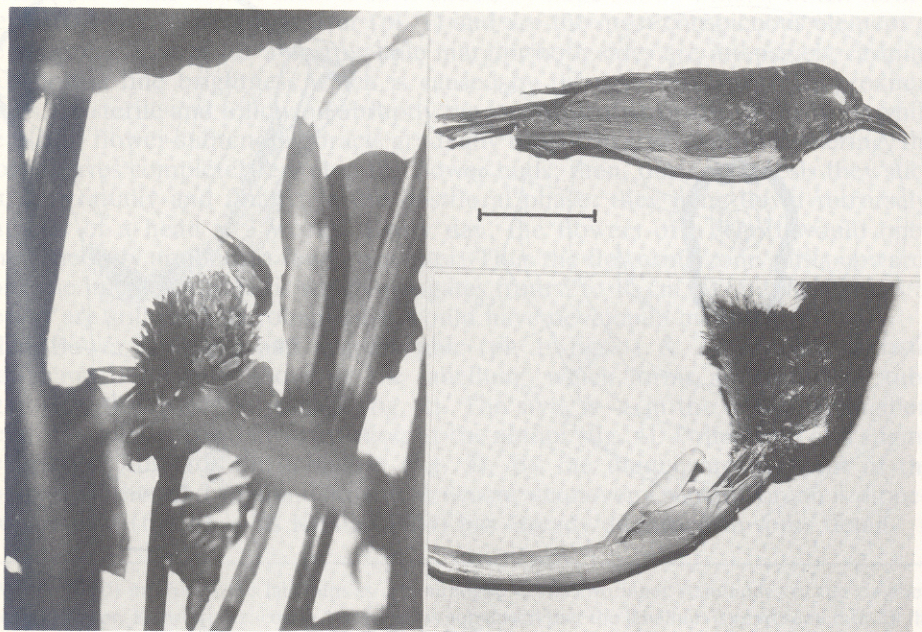
sti, stigma; *dl*, dehiscence line of pollen sac; *hg*, hairy groove of the filament.

Fig. 5. Flower of *Nicolaia elatior* as pollination apparatus.

to, tongue; *bi*, bill; → pollen transference; *nr*, nectar reservoir.



Nearly all parts of the flower are more or less red coloured. Exceptions are the pale, hardly visible anther and the very conspicuous, intensively yellow margin of the labellum. The open flowers present these yellow parts like signals pointing to the nectar-store. This may be of great importance, because the flowers lack — at least not detectable — any alluring odour. Nectar is produced in great amount. It is secreted by epigynous glands at the bottom of the flower and is stored in the staminode tube, which functions as a nectar-reservoir (fig. 5). As is shown in fig. 4, the inner surface of the tube is partly covered with long hairs. The filament is densely hirsute and, approximately in the middle of the tube, there is a thick hairy belt. Here, the hairs are arranged around two cuticular protuberances running diagonally from the filament border to the median of the labellum. It is quite reasonable to assume that these hairs let the nectar move up by capillary absorption.



Upper right

Plate 2. A male *Anthreptes malacensis* (scale: 2 cm). The skin was kindly made available by the Zoological Museum in Bogor, Indonesia.

Left

Plate 3. A male *Anthreptes malacensis* visiting the flower head of *Nicolaia elatior* in the Botanic Gardens, Singapore.

Lower right

Plate 4. A skin of *Anthreptes malacensis* with the head and bill artificially inserted into a flower tube to simulate the natural position when pollinating (nat. size).

I had the opportunity to observe for three weeks, flowering plants of *Nicolaia elatior* and to record the blossom visitors. The most frequent and conspicuous was a sunbird with a metallic sheen, the male *Anthreptes malacensis* (pl. 3). At intervals, about 2-3 times hourly, it flew from the nearby *Pandanus*-thicket directly to one of the flowering heads and landed on it.

There was no insect-picking at all though a lot of small ants, spiders and others were available. After a short look around — probably to check on the safety of the place — the bird inserted its bill into an open flower. It remained in that position

for up to 5 seconds. After that, the bird dipped its bill systematically into a second, third and fourth flower. Its movement was restricted to a mere turnabout, step by step, such that the bill was always exactly above the next open flower. Standing on the top of the blossom, the bird only had to bend the front part of its body downwards to reach the flower tube (pl. 3). As long as the bird was undisturbed, it exploited up to 7 flowers per inflorescence, thus, less than half of the open flowers in a single turn. Generally, before flying back into the thicket, it would look round for more, then visit a second and sometimes even a third inflorescence. In its resting place, the bird was mostly engaged in cleaning its bill and its plumage. It rested for 10 minutes or as much as an hour before it returned to visit the blossoms in the described manner.

Obviously, the blossoms of *Nicolaia elatior* attract *Anthreptes malacensis* Scop. Though this observation was made in an artificial setting, I am convinced that *Anthreptes malacensis* is one of the natural pollinators of the plant. This is supported by the remarks of Werth (1915) and Porsch (1924) concerning bird pollination in SE. Asia. Besides that observation, I have seen another male *Anthreptes* visiting *Nicolaia elatior*, this time in a natural site near Bogor, W. Java. In general *Anthreptes malacensis* is very common in SE. Asia and shares the same biotope with *Nicolaia elatior* (King *et al.* 1984: 413). As with all Nectarinidae, it is characterized by a specialized tongue which is well constructed for sucking honey: the tip is forked and able to lap up drops of nectar while the tongue itself is folded over its whole length forming, together with the bill, a perfect sucking tube (Werth 1900: 256-7).

With regard to bird pollination,

1. it is clear that *Nicolaia elatior* first of all attracts the bird optically by the intensive red colour of the blossom — a colour which is known to be quite common in ornithophily. The concentration of the flowers to a highly compacted head and the enlargement of the extrafloral bracts promote the attractiveness of the blossom. In terms of phylogeny, the primary function of the bracts probably has been to protect the flowers against rain (Knuth, 1904: 182) which was then followed by another evolutionary step, the transformation of the whole blossom into an attraction apparatus. A comparable shifting of function of plain bracts from phylogenetically old structures to attraction units can also be seen in the blossoms of some Verbenaceae (Classen 1986).

Presumably the display of the blossom plays an important role in the efficient attraction of a pollinator, which is able to vagabondize distantly. In *Nicolaia elatior* it is the stem again which provides the bird with a lookout to exploit nearby flower tubes. As the inflorescence axis slowly elongates during the flowering period, there is a constant distance between the bird and the opened flowers. This is, of course, a very favourable prerequisite to a successful bird pollination. It is the direct consequence of the aggregation of flowers. So, even the aggregation seems to be an equipment of prior rank for bird pollination.

2. *Nicolaia elatior* provides a landing and sitting place to the bird. It is the top of the blossom which is enlarged by the dense aggregation of bracts and flowers. And it is the stem again which provides the bird with a lookout and to exploit nearby flower tubes. As the inflorescence axis slowly elongates during the flowering period, there is a constant distance between the bird and the opened flowers. This is, of course, a very favourable prerequisite to a successful bird pollination. It is the direct consequence of the aggregation of flowers. So, even the aggregation seems to be an equipment of prior rank for bird pollination.

3. *Nicolaia elatior* produces a high amount of nectar to reward the bird for its visit. The nectar is clear and liquid. The concentration of sugar (taken at random with a field refractometer) was 18-28% in the open flowers and only 5-8% in the

nectar of just fading flowers, which are not visited any more by the bird. The presentation of the contrasting yellow signal helps the bird to find the entrance to the nectar store. Pollination should take place as soon as the bird has dipped its bill into the flower tube: At first, the pollen brought along from another flower is wiped off on the stigma and then the pollen of the flower actually under visitation is deposited on the underbill (fig. 5). As the pollination mechanism is very much the same for all kinds of pollinators, Knuth's description (1904: 182) concerning pollination by butterflies is acceptable for bird pollination too. The small membranous lip below the stigma assures that the pollen will not touch the stigma when the bill is retracted.

According to Knuth (1904: 183) the flowers are said to be damaged by the hard and curved bill. This was the main reason that he did not consider that bird pollination takes place in *Nicolaia elatior* — an objection which has already been rejected by Werth (1915: 370). I did not notice any flower being damaged by the bird — all staminodial tubes remained completely intact. Obviously, the flower is very well adjusted to the bill, the staminodial tube and the bill showing a high similarity in curvature (fig. 5, pl. 4). As the labellum is hardened on its abaxial side and equipped with a slippery inner surface, its construction is just a slide and would function as a leading groove for the bill. The ovary is protected by its hypogyny and by the length of the flower tube (up to 5 cm). As the nectar is capable of rising within the tube, it is by no means necessary that the bill (or tongue or proboscis of any visitor) is as long as the tube. So, even bees and butterflies with quite short sucking organs can become successful pollinators (see Knuth 1904: 182).

4. *Nicolaia elatior* flowers continuously. There are always several inflorescences of different ages on any one plant and each of them has a flowering period of about 3 weeks. Thus the plant probably can make nectar available to its visitors throughout the year.

Without doubt, the blossom of *Nicolaia elatior* is adapted to bird pollination. But, it is not exclusively an ornithophilous blossom, it is visited as well by diverse butterflies especially *Lycaenidae* and *Danaiidae*. The insects sit down on one of the outer bracts and insert their sucking organ bowl-like from below into the flower tube. Though the sucking behaviour is quite different, the success of pollination is unquestionable. In general, 'the differences between the psychophiles and ornithophiles are rather indistinct' (Faegri & v.d. Pijl 1979: 126) and so it is idle to separate them artificially.

In terms of phylogeny we can draw a consistent line: recalling the specific parameters which promote bird pollination it is clear that in the case of *Nicolaia elatior* the transition of the zingiberaceous inflorescence into an inflorescence-blossom (pseudanthium) has been the most important step. While psychophily — based on the flower structure — is also possible without any special aggregation and modification of the inflorescence, the development towards ornithophily only depends on the special inflorescence-construction, especially on flower aggregation, bract integration and display by a shaft-like stem.

So, the flowering head of *Nicolaia elatior* shows an example for the evolution of an inflorescence-blossom, one that opens new pollination chances for a certain species. This may also help to understand how the succession of well operating pollinators happened in the evolutionary process.

Acknowledgements

I am very grateful to Dr. Chang Kiaw Lan, Curator of the Herbarium at the Singapore Botanic Gardens, for the working facilities at the Garden, and to Dr. Sao Kyu Win, Singapore Polytechnic, for her hospitality during my stay in Singapore. I also like to thank the Deutsche Forschungsgemeinschaft, which has given financial support (Cl 81/2-1).

Literature cited

- Burt, B.L. & R.M. Smith (1972). Key species in the taxonomic history of Zingiberaceae. *Not. Roy. Bot. Gard. Edinb.* 31: 177-227.
- Classen, R. (1986). Organisation und Funktion der blumenbildenden Hochblatt-hüllen bei Symphoremnoideae (Verbeaceae). *Beitr. Biol. Pfl.* 60: 383-402
- Faegri, K. & L. v.d. Pijl (1979). The principles of pollination ecology. Edition 3, Pergamon Press, Oxford.
- King, B. Woodcock, M. & E.C. Dickinson (1984). *A Field Guide to the Birds of South East Asia*. Collins, London.
- Knuth, P. (1904). *Handbuch der Blütenbiologie* III./1. — Leipzig.
- Kunze, H. (1985). Die Infloreszenzen der Marantaceen und ihr Zusammenhang mit dem Typus der Zingiberales-Infloreszenz. *Beitr. Biol. Pfl.* 60: 93-140.
- Porsch, O. (1924). Vogelblumenstudien I. *J. wiss. Bot.* 63.
- Smith, R. (1986). New combination in *Etlingera* Giseke (Zingiberaceae). *Notes Roy. Bot. Gard. Edinburgh* 43: 243-254.
- Valeton, Th. (1921). *Nicolaia* Horan. Description of new and interesting species. *Bull. Jard. Bot. Buitenzorg ser. 3*, 3: 128-140.
- Weber, A. (1980). Die Homologie des Perigons der Zingiberaceen. Ein Beitrag zur Morphologie und Phylogenie des Monokotylen-Perigons. *Pl. Syst. Evol.* 133: 149-179.
- Werth, E. (1900). Blütenbiologische Fragmente aus Ostafrika. *Abh. Bot. Ver. Prov. Brandenburg* 42 (13): 222-260.
- . (1915). Kurzer Überblick über die Gesamtfrage der Ornithophilie. *Bot. Jahrb.* 53.