

## SWING-HOVERING COMBINED WITH LONG TONGUE IN HAWKMOTHS, AN ANTIPREDATOR ADAPTATION DURING FLOWER VISITS

Lutz T. Wasserthal

Institute of Zoology I, University of Erlangen, Staudtstraße 5, 8520 Erlangen, Germany

**Abstract.** European and Madagassic hawkmoths have been observed during hovering at flowers in the field and flight cages. Six of seven species of the Acherontiinae genera *Agrius*, *Coelonia*, *Xanthopan* and *Panogena* perform conspicuous lateral swinging movements when hovering at diverse flowers with extended tongue like the pendulum of a metronome. The swing-hovering hawkmoths are skilled visitors also of non-sphingophilous flowers, even of small upright flowers of inflorescences. Most swing-hovering individuals were less successful or often fully uninterested in exploiting medium-sized angraecoid orchid flowers with long spurs. It is suggested that swing-hovering has evolved in connection with the long tongue, both characters serving for reducing the danger of being captured by predators during flower visits. Swing-hovering shortens the stay time on the spot, thus allowing the moth a full depletion of the nectarium during a single visit. Swing-hovering could be induced in primarily non-swinging individuals of *Agrius*, *Coelonia* and *Xanthopan* by startling stimuli. It is hypothesized that extreme tongue length has evolved before the flowers with deep nectaria became adapted to long-tongued hawkmoths. The Madagassic species *Panogena lingens*, which is known to visit and pollinate angraecoid orchids, never exhibits swing-hovering. This species can possibly afford to exhibit hovering on the spot for up to 20 s during exploitation of the long-spurred orchids owing to its extremely noiseless flight, which probably reduces the danger of being detected by acoustically oriented predators.

**Key words:** *Sphingidae*, *Xanthopan*, *Orchids*, *Angraecum*, *insect flight*, *flower visits*, *coevolution*, *predator avoidance*, *insect behaviour*, *Madagascar*.

### INTRODUCTION

The existence of long proboscis in Sphingidae has been interpreted as an adaptation of the moths to exploit deep tubular flowers. Already Darwin (1862) suggested that the length of the tongues of pollinating insects could increase as a result of a general size increase or because it increased their nectar foraging efficiency. On the basis of the famous Madagassic Star Orchid *Angraecum sesquipedale*, which has nectar-containing spurs of 35 cm in length, he postulated a hitherto unknown hawkmoth as pollinator. A promising potential candidate hawkmoth has been discovered (Rothschild & Jordan 1903) and was called *Xanthopan morgani praedicta*, an endemic subspecies in Madagascar. The pollination efficiency of this species in long-spurred *Angraecum* orchids has not yet been proven. The same is due to a second extremely long-tongued species *Coelonia solani*, which is an endemic species in Madagascar and some adjacent islands. A reliable pollinator of medium-sized Madagassic long-spurred orchids is *Panogena lingens* (Nilsson *et al.* 1985). Individuals of this rather small species carrying pollinaria of different orchids at different sites of the proboscis have been caught in central Madagascar, whereas the extremely long tongues of *Xanthopan* and *Coelonia solani* were void of pollinaria (Nilsson *et al.*

1987). In another study, the frontal scales of this species and of *Agrius convolvuli* have been found on the stigmas of *Aerangis ellisii* (Nilsson & Rabakonandrianina 1988), thus indicating the visits of two species.

Own observations of *Agrius convolvuli* moths in a flight room showed that certain individuals were not capable of exploiting flowers with deep nectar tubes at all. From these observations the supposition arose that a long proboscis might have evolved under a different functional context than exploitation of deep flower tubes, and a series of observations on the flower-visiting behaviour of hawkmoths in the field and the flight room was started in Europe and continued in Madagascar in the hope to meet rather ancestral conditions of moth-plant and moth-predator interrelations in a widely endemic and archaic ecosystem.

### MATERIALS, STUDY SITES AND METHODS

Hovering behaviour of hawkmoths was observed during flower visits using night vision goggles supported by infrared-diode illumination in full darkness. The investigation was focussed on the long-tongued Acherontiinae (Fig. 3), but at least few specimens of 26 (= almost all) European Sphingidae listed by Rougeot & Viette (1983) ex-

cept the genera *Dolbina* and *Sphingonaepiopsis* and 31 Madagassic species have been seen hovering. Watching in the field at flowering shrubs or trees was sporadically successful, but the determination of species of the hawkmoths was possible only exceptionally. Most systematical observations were therefore done in flight cages of 2 m side length, installed in a climatized room at Bochum (1980, 1982), a greenhouse in Düsseldorf (1984) and Erlangen (1987, 1988, 1992). The flight cages were exposed to the natural light conditions except from the Bochum climatized room, where dimmed lamps were used for simulation of dawn and dusk.

*Agrius convolvuli* were also observed in the open field near les Stes. Maries de la mer/Bouches du Rhône and near Gap en Provence/Southern France, at Purbach Leitha-Mountains/Eastern Austria and in Loutra Elefteron/Northern Greece. Larvae of *Agrius convolvuli* from Southern France, Gran Canaria and Germany and larvae of Madagassic *Panogena lingens* have been raised in the laboratory at 13 : 11 light-dark conditions and their offspring observed in the cages in Germany. The Madagassic hawkmoths species, including *A. convolvuli* have been observed at Périnet/East-Madagascar between 20 October to 18 December 1989 (= site 1), in the Ambohitantely-Forest near Manankazo/Central-Madagascar from 21 October to 17 November 1991 (= site 2) and in Kirindy Forest near Beroboka/West-Madagascar from 22 November to 9 December 1991 (= site 3). At least 3 of the 7 long-tongued species were available in all sites throughout the whole time.

The Madagassic species caught at light traps were directly transferred into the flight cages. Offspring of *Panogena lingens* from Manankazo has been additionally observed in a greenhouse at Erlangen (see above). Only few (2–6) moths (rarely up to 12 individually distinguishable moths) were simultaneously admitted to one observation cage, while the rest was kept in a second flight cage of the same type and size. During several nights both cages served as observation cages and two smaller cylindrical cages of 0.80 m in diameter and 1 m in height served for storage of further moths. The cage with 8 m<sup>3</sup> has been developed and improved on the basis of coarse patterned and loosely woven tissue since 1972. It was optimal for behavioural studies and mating even of problematic species. The moths have been nourished by a 10–20 % honey (sugar)-water solution, offered in artificial

flowers. They consisted of 10 ml glasses, covered with a white plastic disc of *Saponaria*-like shape with a central hole of 3–5 mm diameter. This type of resource was rapidly accepted by all hawkmoths species and exploited excessively. Those few individuals which were unable to feed on the artificial flowers were not used for observation.

Routinely all hawkmoths have been observed when hovering at the artificial flowers during at least half a dozen to about a dozen visits, each lasting some seconds to some minutes. In the observation cage, the hawkmoths were confronted with small numbers of different flowers, which have been observed to be visited in the field or which were assumed to be natural nectar sources, alternatively with the artificial flowers. The number of observed visits at each natural blossom was depending on their abundancy. While common plants as *Saponaria*, *Lantana*, *Mussaenda* and *Nicotiana* could be exchanged after three to half a dozen visits, the angraecoid orchids were used up to about a dozen visits during the first evening of anthesis and again during the following mornings and evenings until the flower began to change colour or to wither. The plant species are listed in connection with the observed species in the results. All Madagassic plants were taken from the natural surroundings of the hawkmoths habitat at the three sites.

For documentation in Germany a 16 mm movie camera (Arriflex SR) and strobelight (Drelloscope) and at Madagascar a Hi-8 Video-camera (Canovision EX with night-vision-adapter and infrared diode illumination) were used. The still pictures were taken with Nikon F3 and F4 cameras, 105 mm Micro-Nikkor or 300 mm Nikkor and infrared-light-trap and electronic flashes (National or Nikon).

The wing beat noise produced during hovering was recorded with the HIFI Stereomicrophone on the Canovision EX 1-recorder. This was installed 20 cm below the presumed hovering site of the moth and could be adjusted to different positions of the moths according to their different tongue lengths.

## RESULTS

Different types of hovering flight in *Agrius convolvuli*.

*Agrius convolvuli* of different populations and regions have been found to exhibit preferences for specific types of flowers combined with dif-

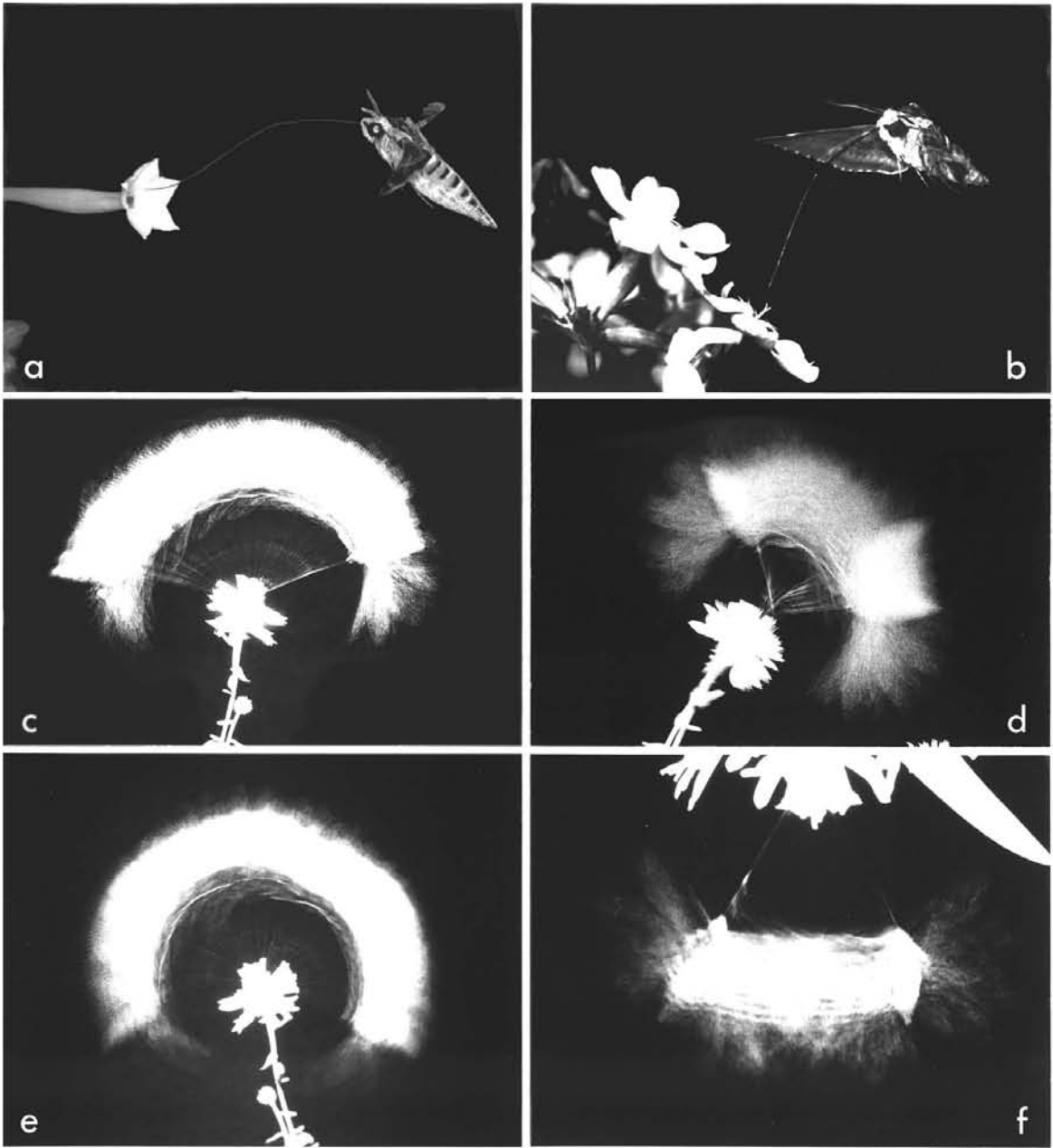


FIG. 1. *Agrius convolvuli* during hovering on the spot (a, b) and swing-hovering (c–f).

- a) A moth from Gran Canaria explores with the tip of its tongue during several seconds the disc of a *Nicotiana* flower without succeeding to insert it in the tube.  
 b) Same moth inserting its tongue from above into the upright flowers of *Saponaria*.  
 c–f) Photographs with strobelight (300 Hz) for documentation of complete phases of swing-hovering.  
 c–e) View from below at *Centaurea*.  
 c) 0.5 s exposure time covers a typical left-right swing.  
 d) 1 s exposure time with two overlapping swings and changing tip position of the tongue.  
 e) 1 s exposure of two phases forming together an angle of 225°.  
 f) View from above at *Pancratium*. The swinging angle is limited by the flower morphology.

ferent hovering behaviour. The European and Gran Canarian hawkmoths have been observed during their visits of artificial flowers and the following plants: *Centaurea scabiosa* L./Aster-

ceae, *Datura candida* Saff., *Nicotiana sylvestris* Spegazz. and *Comes/Solanaceae*, *Pancratium maritimum* L./Amaryllidaceae, *Phlox* spec./Polemoniaceae, *Saponaria officinalis* L./Caryophyllaceae,

*Scabiosa columbaria* L./Dipsacaceae. About 25 % of the offspring of parents from Southern France (N = 25), 70 % of the offspring of parents from Gran Canaria (N = 20) and more than 90 % of the Madagassic individuals (N = 28) were restlessly swinging from one side to the other and back again with a frequency of 1–2 Hz semicircular along the radius of the extended proboscis, the tip of which remained in the centre of the nectarium of the flower (Fig. 1c) or was skipping from flower to flower of one inflorescence (Fig. 1d). The longitudinal body axis moved within a sector with an angle between about 25 and 145° like the pendulum of a metronome. The resulting swinging amplitude was widest during visits of upright flowers like *Saponaria officinalis* and inflorescences of *Centaurea scabiosa* and *Scabiosa columbaria*. During visits of these inflorescences the angles of several consecutive swings could form almost a circle (Fig. 1e). In tubular flowers like *Pancratium maritimum* the swinging angle was limited by the free space offered by the morphology and proportions of the flower (Fig. 1f). The individuals with “swing-hovering” flight, but also those with normal hovering behaviour from Gran Canaria, had problems in penetrating with their tongues into deep flower tubes from *Nicotiana sylvestris* when the tube axis was horizontal or slightly bent downwards. These hawkmoths showed not even the “intention” to insert the tip of their tongue into the tube of the flower (Fig. 1a). Instead, they tried to search for nectar at the flower disc, mostly from above. This method allowed successful depletion of *Saponaria* flowers (Fig. 1b). They were also unable to force themselves into the hanging trumpet-shaped blossoms of *Datura candida* as did the French *A. convolvuli* and as has been described in *A. convolvuli* from the Adriatic coast by Kugler (1971). The swing-hovering French specimens exploited the tubular flowers of *Pancratium maritimum* (Fig. 1f). A series of individuals observed or caught in Germany, Austria and Greece and their offspring (N = 28) visited flowers with long tubes of *Nicotiana* and showed only a stable hovering flight in front of the visited flowers. 67 % of moths (N = 21) from caterpillars, found in Southern Germany in autumn 1991, showed swing-hovering. The specimens collected in Périnet and Manankazo/Madagascar were also capable to combine the swing-hovering flight with exploitation of the tubular flowers of three *Mussaenda*-species/

Rubiaceae. The swing-hovering flight started generally, when the tip of the tongue was in contact with the presumed or real nectarium of the flower and was performed in a rather stereotypic way. The swing-hovering is clearly discernable from normal hovering on the spot on the basis of a sudden and rhythmically repeated side-wise movement. There exists no behavioural continuum with hovering on the spot.

Is swing-hovering performed by Madagassic long-tongued hawkmoths?

Five of the six observed Madagassic species belonging to the genera *Coelonia*, *Xanthopan* and *Panogena* exhibited the swing-hovering flight with exception of *Panogena lingens* (Fig. 3). However, in almost all species there were individuals which did not show the swinging flight and the percentage of non-swinging among swing-hovering individuals seems to be different in the populations examined. Swing-hovering long-tongued (about 10 cm) hawkmoths (*Agrius* or *Coelonia mauritii*) and extremely long-tongued (about 20 cm) hawkmoths (*Xanthopan* or *Coelonia solani*, Fig. 2) have been seen at *Lantana camara* shrubs and small *Mussaenda* trees among other non-swinging smaller hawkmoths (site 1). At a white small-flowered *Clerodendron* liana (site 2) from a short distance one *Xanthopan*, two *Coelonia mauritii* among a number of non-swinging *Panogena lingens* and smaller Sphingids have been identified. As an undisturbed observation and identification of the hawkmoths in the wild was only sporadically successful, hovering behaviour of all long-tongued Acherontiinae species has been systematically observed in the flight cages, offering the artificial flowers, tubular flowers, long-spurred orchids, upright brush-shaped flowers and small-flowered inflorescences: *Panogena lingens* Butl., *Xanthopan morgani praedicta* R. & J., Madagassic *Agrius convolvuli* L. and *Coelonia mauritii* Butl. have been confronted with the following flowers: *Lantana camara* L./Verbenaceae (Fig. 2b) (at Périnet = site 1), *Mussaenda* spec./Rubiaceae (Fig. 2a) (site 1, and at Manankazo = site 2), *Pandaca* spec./Apocynaceae (site 2), long-spurred angraecoid orchids: *Aerangis monantha* Schltr. (site 2), *Angraecum arachnites* Schltr. (site 2), *A. compactum* Schltr. (site 2), *A. viguieri* Schltr. (site 1), *A. rutenbergianum* Kranzl. (Fig. 2c, site 1), *A. linearifolium* Garay. (site 1), *Jumellea c. f. similis* Schltr. (site 2), *Jumellea teretifolia* Schltr.

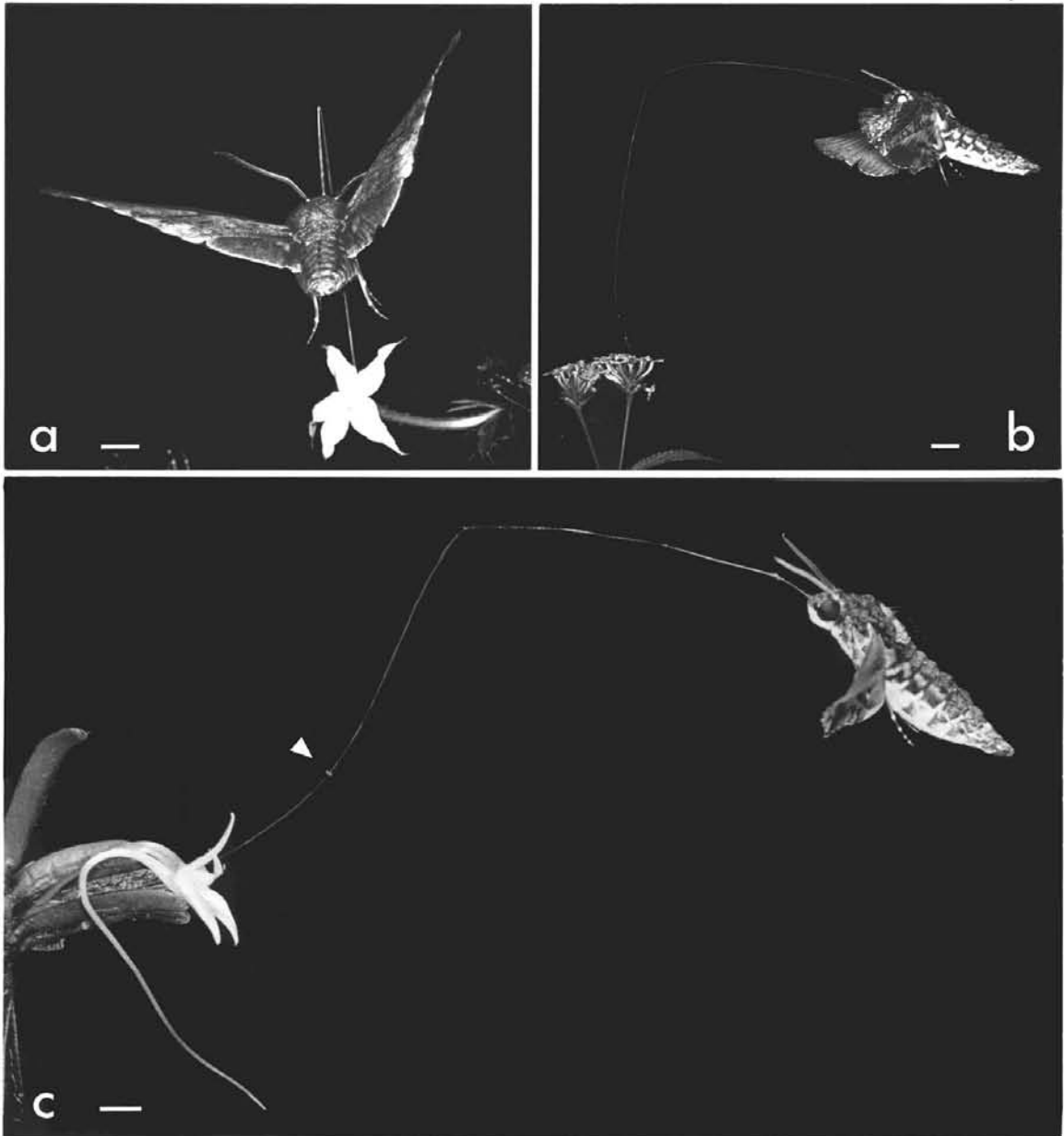


FIG. 2. Swing-hovering in the two extremely long-tongued hawkmoths at Madagascar (Périnet).  
 a) *Xanthopan morgani praedicta* in lateral turning manoeuvre with tip of the tongue fully inserted in the tube of the sphingophilous *Mussaenda*.  
 b) *Coelonia solani* swinging around the vertical part of the kneed tongue at *Lantana*.  
 c) *Coelonia solani* at the moment of tongue retraction from the medium-sized orchid *Angraecum rutenbergianum*. One pollinarium attached at the distal part of the tongue (arrow). With insertion of only the distal third of the tongue into the spur, swing-hovering during flower visit continued. The tongue-retraction lasted several seconds. Scale bar = 1 cm.

(site 2). *Panogena jasmini* Boisd. and *Coelonia solani* Boisd. have been additionally and *Coelonia brevis* R. & J. have exclusively been confronted (at Beroboka = site 3) with *Delonix boiviniana* (Baill.)/Caesalpiniaceae, *Euclinia suavissima* (Homoll ex Cavaco)/Rubiaceae, *Leuco-*

*salpa perrieri* Bonati/Scrophulariaceae and *Sobenikoffia robusta* Schltr./Orchidaceae.

The swinging flight was initiated generally after contact with the nectar region or the tube/spur cavity of the flower and was continued even if the proboscis was inserted about half of

its length. The swinging radius (length from abdominal tip to axis of rotation) was reduced by the amount of the inserted part of the proboscis with the consequence that the swinging amplitude (angle between lateral turning points) was smaller and the swinging frequency somewhat higher. The swinging frequency varied between about 1–2 Hz as in *Agrius convolvuli*. The swinging amplitude varied between 70° and 140°. It was highest during visits of inflorescences of *Lantana camara* and *Delonix boiviniana*, where the single swinging phases could make up a complete circle. During the swinging flight, the proboscis tip could “skip” between neighbouring flowers within the inflorescence of *Lantana*. If the plant structures allowed, the long tongued hawkmoths preferred a sucking position from above with the proboscis being bent almost vertically after half of its length (Fig. 2b). In this position, the moths could swing without being hindered by floral structures. This unhampered flight was performed during visits of more or less upright flowers or inflorescences with the small flowers or the artificial flowers, when being arranged upright. Since the nectar content of the fresh flowers was consumed within one second or maximally after 12 seconds, only one or few

swinging movements could be observed during each visit. If the nectar volume was high as in the artificial flowers, filled with up to 12 ml of honey-solution, the *Coelonia* and *Xanthopan* specimens exhibited permanent swinging throughout 1–2 minutes!

In *Panogena lingens* (N = 33) swing-hovering could never be observed. This species is distinguished by an extremely silent flight, which is still less audible for the human ear than the flight noise of *Coelonia* and *Xanthopan*. The flight sound is perfectly blimped, probably owing to the rough surface by the many vertically orientated wing scales.

In the Périnet population of *Panogena jasmini* the swing-hovering was performed by a high percentage of individuals (8 of 10), while only single specimens of Ambohitantely- (1 of 5) and Kirindy-Forest (1 of 9) exhibited this behaviour. The flight sound in *P. jasmini* is almost as low as in *P. lingens*. The flight noise has been recorded under comparable situations and the data will be precisely analysed and published elsewhere. In the flight cages *P. jasmini* lived only maximally one week, in contrast to *P. lingens*, which were able to survive 2 to 4 weeks under the same conditions. All other long-tongued Acherontiinae were likewise longliving species.

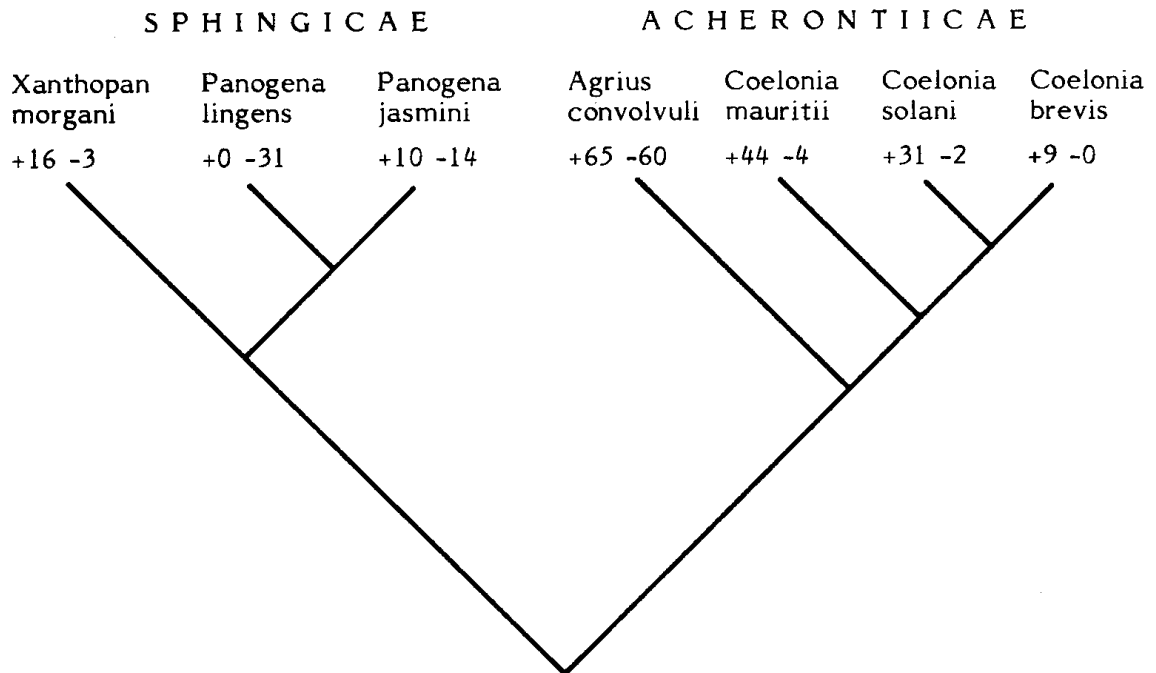


FIG. 3. Cladogram of the Madagassic long-tongued hawkmoths of the two related groups of Acherontiinae (according to Rothschild & Jordan 1903; the normal-tongued *Lomocyma oegrapha*, the short-tongued *Acherontia atropos* and the weak-tongued Sphingulicae are not considered).

Numbers indicate individuals with swing-hovering (+) and hovering on the spot (-).

Can swing-hovering be induced in primarily non-swinging individuals by artificial stimuli?

Swing-hovering has been induced in several cases in primarily non-swinging hawkmoth individuals within four species. After three days of captivity a *Xanthopan* male was photographed by a series of four flashlights during the long-lasting (= 7 s) tongue-retraction process at the end of a visit of a virgin *Angraecum compactum*. Exactly from this moment on and during all following flower visits observed, this male showed swing-hovering. Swing-hovering was neither induced by flashlight alone (during earlier visits of *Mussaenda* flowers) nor by the two preceding visits of other virgin flowers of *Angraecum compactum*. It must be concluded, that the combined stress of being jammed by the orchid's spur and of being dazzled by the flashlight induced the swing-hovering. This induction was persistent throughout two days (the rest of the observation time available). In two primarily non-swing-hovering *Coelonia mauritii*, one *Coelonia solani* and two *Agrius* swing-hovering was immediately induced by hand flapping from behind of the hovering moths. This sudden and vehement movement was applied in a manner to simulate the wing beat of a hunting bird or bat. In these individuals the swing-hovering was maintained stereotypically throughout the following days of observation time. Swing-hovering could not be induced in *Panogena lingens*. In swing-hovering *Agrius* and *Coelonia mauritii* the swinging intensity (frequency and amplitude) could be enhanced by hand flapping.

Are Madgassic swing-hovering hawkmoths able to exploit long-spurred angraecoid orchids?

The flowers of *Mussaenda*, *Delonix*, *Euclinia* and *Lantana* were rapidly detected and exploited by all observed long-tongued hawkmoths and seemed to be unproblematic for swing-hovering hawkmoths. However, the diverse swing-hovering hawkmoth species and even individuals reacted in a different way when being confronted with the angraecoid orchids with spur lengths of 8 to 17 cm.

All *Xanthopan morgani* at Périnet were fully uninterested in the large *Angraecum viguieri* and the medium-sized *Jumellea c. f. similis*. Only *Angraecum rutenbergianum* and *A. linearifolium* were visited a few times but they were not ex-

ploited, perhaps because the spur lumen was too narrow and especially in *A. linearifolium* because the flexible suspension by the slender pedicle of the blossom offered no sufficient resistance necessary for the insertion of the tongue into the spur. At Manankazo three *Angraecum compactum* flowers were exploited by a primarily non-swing-hovering *Xanthopan* which forced its tongue slowly into the spur of this relatively large and stiff *Angraecum* blossom and removed the pollinia two times at the basal third of the proboscis. The visits of each virgin blossom of *Angraecum compactum* lasted 14, 15 and 17 seconds. For tongue retraction half of the time was used. *Angraecum compactum* was the only long-spurred orchid, which seemed to be attractive for *Xanthopan*, while the smaller flowers of *Aerangis monantha*, *Angraecum arachnites* and *Jumellea teretifolia* were ignored by this species. After induction of swing-hovering in the above mentioned *Xanthopan* individual, it was unable to insert fully its proboscis into the flowers of *A. compactum* and no further pollinaria were removed.

*Coelonia solani* from Périnet exploited *Angraecum viguieri*, *A. linearifolium* and *Jumellea c. f. similis* without transporting the pollinaria. Only the pollinaria of *Angraecum rutenbergianum* at Périnet were removed two times after 18 visits of 5 different flowers. They were attached 3.5 and 5 cm behind the tip of the tongue (Fig. 2c). The visits of the virgin flowers took 8 to 12 seconds, also half of the time was spent for tongue retraction. At Manankazo *C. solani* visited the flowers of *Aerangis monantha* and *Angraecum compactum* without removal of the pollinaria. *Angraecum arachnites* and *Jumellea teretifolia* have been ignored. At Kirindy forest *C. solani* was the only species with a sufficiently long tongue to exploit the maximally 10 cm long tube-shaped flowers of *Leucosalpa perrieri*/Scrophulariaceae. *C. solani* seemed to be a more skilful visitor of the medium-sized orchids than *Xanthopan*.

*Coelonia mauritii* at Périnet ignored all exposed orchids. Two of three individuals from Manankazo repeatedly visited *Angraecum arachnites* without removing the pollinaria, but ignored the other orchid species from this site (s. above).

*Coelonia brevis* occurred only in Kirindy forest. The only long-spurred flowering orchid, found in December, was *Sobennikoffia robusta*.

Although *Coelonia brevis*, *C. solani* and *Panogena jasmimi* "explored" the blossoms, no single individual was capable of introducing the tongue into the upwards bent spur.

The swing-hovering at most medium-sized angraecoid orchids species rendered insertion of the tongue into the narrow spurlumen difficult, because the flowers bent aside if the tongue pressure was not applied medially towards the spur cavity.

## DISCUSSION

Is swing-hovering archaic or a secondary adaptation?

Although swing-hovering flight is very conspicuous, it has not been described in the literature as yet. It has been found in 6 species of 4 Acherontiinae genera: *Agrius* and *Coelonia* from the tribe Acherontiinae and *Xanthopan* and *Panogena* from the tribe Sphingicae. Rothschild & Jordan (1903) classify them as basic members in the taxon Acherontiinae. The extremely long tongues are limited to large hawkmoths and are postulated to be existent already in the ancestors of Acherontiinae (Rothschild & Jordan 1903). The swing-hovering flight is possibly a behavioural correlate of the long tongue. This hovering behaviour could only be observed in the six species mentioned in Fig. 3, but not in the many other sphingid moths, observed during flower visits. The latter comprise almost all European hawkmoths and the majority of the Madagassic fauna. Under the assumption that the swinging flight has not evolved parallelly in the four genera, the one species *Panogena lingens* and some individuals or populations of *Agrius convolvuli* and *Panogena jasmimi* must have lost this behaviour secondarily. If swing-hovering is an ancestral character in Acherontiinae, its occurrence should be expected worldwide in the related genera of this subfamily with extremely long-tongued species as *Megacorma*, *Meganoton* of the Palaeotropics and *Amphimoea*, *Cocytius*, *Neococytius* and *Manduca* of the Neotropics. The question, whether the long tongue and swing-hovering are plesiomorphic in Acherontiinae and represent relict characters or whether they are synapomorphic in Acherontiinae plus Sphingicae, must be left open, until a phylogenetic system of the hawkmoths will be established under consideration of a critical analysis of all characters.

What is the functional significance of swing-hovering?

The swing-hovering flight must be energetically very expensive, since the force for repeated lateral swing, stop and counter swing demands additional energy. The moths should maintain such an energy-consuming behaviour only if some selective factor is very effective at present. In addition, the swinging flight during visits of narrow-tubed or long-spurred flowers makes the tongue insertion difficult and is certainly not helpful for better exploitation of these flowers.

With regard to the sudden and unexpected positional changes during flower visits I assume, that this behaviour has evolved as a response against predators, hunting systematically at flowering shrubs or trees, where visits of moths are predictable, especially in exposed mass-blooming trees or shrubs like *Delonix*, *Mussaenda* or *Lantana*. Another example of such attractive trees may be the Baobabs *Adansonia/Bombacaceae*. Some of these Baobabs are visited and pollinated by some of the concerned sphingid moths (Baum 1991): The Australian *A. gregorii* is visited by *A. convolvuli*. From the Madagassic *Adansonia rubrostipa* the highest visitation rates of 18 visits per flower per hour by *Coelonia solani* are reported (Baum 1991). Especially *Coelonia solani* has a very conspicuous swing-hovering due to its extremely long tongue. Baum, who observed these hawkmoths in the Baobab trees at Kirindy forest, described no swing-hovering, but mentioned a rapid up and down movement during flower visit. Possibly it was difficult to recognize the real direction of the rapid body movements of the moths, since the observer — sitting in the tree — was forced to look at the flower from a fixed position and probably from oblique angles from below at the flower-visiting moths. Since in some non-swing-hovering individuals of *Agrius*, *Xanthopan*, *Coelonia mauritii* and *C. solani* swing-hovering was inducible by frightening stimuli (flashlight during tongue retraction or more frequently hand flapping) as a persistent change of hovering, it seems convincing that predator avoidance is the principal function of swing-hovering. It allows to deplete flowers thoroughly under permanent positional change.

The effect of rapid local changes during hovering reminds of the well-known juggling zig-zag-flight of Pierid butterflies during "normal straight" flight, and of up and down flight



of *Morpho* butterflies during escape from their avian predators with a deceptive and frustrating effect on hunting birds (Young 1971). The males of *Hepialus hecta*/Hepialidae exhibit a swinging flight within a constant small area in the late afternoon for volatilizing their pheromones (Bourgogne 1951). The swinging frequency and amplitude is comparable with that of the Spingidae and may convergently have evolved for predator avoidance during stationary flight which here primarily serves for alluring mates.

There are only few data about predators ambushing at flowering plants after sunset. This may have its cause in the difficulties of observation in the dark rather than in a small number of really existent crepuscular predators. Delf & Harris (1964) reported that mantids captured flower visiting *Agrius convolvuli* in Nigeria. In the perch-hunting *Hipposideros commersoni*, the largest African and Madagassic bat, prey was intercepted during free flight or was snatched from flower bearing terminal twigs of outer branches of *Acacia elatior* in Kenia (Vaughan 1977). At *Saponaria* a female spider *Pisaura mirabilis*/Pisauridae has been perching during several consecutive nights besides moth-frequented blossoms with extended forelegs, capturing noctuids (e.g., *Plusia gamma*) by a jump (Wasserthal 1991, unpublished observation). The spectrum of the natural potential of crepuscular predators is certainly very large and deserves much patience to be studied.

Behavioural limitations and flexibility of hawkmoths in utilisation of sphingophilous angraecoid orchids.

There is the curious situation of a rich flora of medium-sized angraecoid orchids with spur-lengths up to 15 cm in the primary forest of Ambohitantely, all of which are normally pollinated by one hawkmoth *Panogena lingens* (Nilsson *et al.* 1987), which is the only non-swing-hovering species of the long-tongued Acherontiinae. All the swing-hovering species, except *Coelonia brevis*, occur also in this forest. Their unimportant role in orchid pollination in this forest (Nilsson *et al.* 1987) and possibly also in the forest of Périnet may have some relation with swing-hovering. This behaviour conflicts basically with the exploitation of deep narrow tubular nectaries. As shown in this paper, the penetration of the tongue into the spur lumen is dif-

ficult and the performance of swing-hovering with the fully inserted proboscis is possible only if the blossoms are elastically suspended as in *A. linearifolium*. Visitation of the large *Angraecum* species as *A. sesquipedale* with a spur length of 20 cm or more and of *A. compactum* with a spur length of maximally 17 cm (Nilsson *et al.* 1987) with unflexible pedicles, is only possible if the normally swing-hovering extremely-long-tongued species (*Xanthopan* and *Coelonia solani*) omit the swing-hovering. The one *Xanthopan* from Ambohitantely, which exhibited no swing-hovering during the first three days of observation in captivity, was capable in exploiting and transporting pollinaria of two blossoms of *Angraecum compactum*.

After stress-induced swing-hovering, this individual was no more capable to introduce its tongue deeply into the spur and was unable to retract the pollinaria. This example shows, that individual moths might adapt their hovering behaviour either to more efficient — but time-consuming and probably risky — visits of flowers with deep nectaria or to more hectic and less embarrassed stay at flowers with easier accessible nectaria — if the selective pressure of specific predators is high. The change from normal hovering to swing-hovering was, however, in all examples where it could experimentally be induced, irreversible throughout the next days. The swing-hovering thus cannot simply be switched on and off. This suggests that in regions with high level of predation upon hawkmoths, the fertilization of certain extremely long-spurred orchids may be difficult. In regions with low specific predation pressure on large hawkmoths during flower visits, swing-hovering may be abandoned and long-spurred orchids may profit from the presence of non-swing-hovering hawkmoths other than *P. lingens*. This non-swing-hovering species is — despite its ability to deplete and pollinate the many orchids — an unspecialized forager, which in the wild exploited various types of flowers as *Adansonia* (Baum 1991), *Lantana*, *Clerodendron* and *Mussaenda*. In contrast to the other long-tongued moths, this species has a practically noiseless flight, which probably reduces the danger of being detected by acoustically oriented predators and therewith allows to deplete flowers which demand a long stay with a jammed proboscis.

Did a long proboscis primarily evolve for exploitation of deep nectaria or to facilitate escape of predator attacks during flower visits?

The idea of an evolutionary race between tongue length and spur length of Darwin (1862) is generally accepted and has recently partly been confirmed. An experimental analysis of the interdependence between spur length in European *Platanthera* orchids and tongue length of pollinating hawkmoths showed that flower fitness (fruiting success) increased with spur length, in accordance with Darwin's hypothesis of plant-hawkmoth-coevolution (Nilsson 1988): "... Such pollinators favour the evolution of longer floral tubes which in turn favours the evolution of still longer tongues in a reciprocal and escalating process." There is, however, evidence only for the adaptation of the long spurs of the flowers to the long tongues of the hawkmoths. No one could as yet offer hard data for the "reciprocal" process, that tongue-length follows the spur-length in evolution. The mere fact that there are always some plants the floral structures of which match the actual sphingid tongues in Madagascar and elsewhere, is only confirming that the plants have generally utilized the long-tongued species for specific pollination. The idea of concurrent speciation of modern orchids and hawkmoths has not always been supported: van der Pijl & Dodson (1966), who attributed this idea to Wallace, suggested that long-tongued insects may have developed the tongue length in response to the deep nectar tubes of other older plant families, e.g., early Apocynaceae, Zingiberaceae or Maranthaceae. "It would seem that the orchids have been quite facile at adapting to advantageous characteristics already present in existing pollinators."

The reciprocal selective pressure of long-spurred or -tubed flowers towards longer tongues in hawkmoths can be effective only if during most of the activity period of the adults, extremely long-tubed flowers are available and if they are more attractive and copious than the alternative not-long-tubed flowers. In the three regions selected for the observation of the long-tongued hawkmoths in Madagascar, there have been only few plant species with extremely long-tubed (more than 15 cm) flowers at all and furthermore these have been scarce. Moreover, the long-spurred angraecoid orchids at Ambohitantely (with

average lengths of 12.7 cm to 14.5 cm, Nilsson *et al.* 1987) are not even visited by the extremely long-tongued hawkmoths *Xanthopan* with 19.6 cm and *Coelonia solani* with 18.1 cm mean tongue-length (Nilsson *et al.* 1987). According to the own observations in the flight cages *Angraecum compactum* with its more rugged flowers with up to 17 cm spur length has been very attractive for *Xanthopan* and at Périnet some medium-sized angraecoid orchids and the larger *Angraecum viguieri* (none exceeding 15 cm spur length) have been exploited by *Coelonia solani* several times. Since these plant species were sparse at both sites and the visitation probability in the open field is smaller than in the cage, they certainly should have little importance for the nutrition of these large hawkmoths. At Périnet only *Crinum firmifolium*/Amaryllidaceae possibly depends on these extremely long-tongued hawkmoths. The role of this flower for the nutrition of *Xanthopan* and *Coelonia solani* deserves to be studied. At Beroboka at the beginning of the rainy season, *Leucosalpia perrieri*/Scrophulariaceae with a maximum tube-length of 10 cm was the sole candidate which was pollinated by *Coelonia solani* in the flight cage. But this flower is not long enough and too sparse to fulfil the postulate of selecting for extremely long tongues. Not only "normal"-tongued hawkmoths are not focussed on sphingophilous flowers as is known especially from diurnal or common and widely distributed species as *Macroglossum stellatarum*, *Hyles lineata* and *Agrius convolvuli* (Pinhey 1960, Kugler 1970) or has recently been described for hawkmoths of Costa Rica (Haber & Frankie 1989), but also the extremely long-tongued species are skillful visitors of minute flowers of endemic *Clerodendron* or introduced *Lantana* — not only in the flight cage but also in the wild. These generalist feeding habits are correlated with the paucity of extremely long-tubed flowers in the Madagassic flora. From the present situation, it is difficult to see a selective pressure from the plants for the evolution of an extremely long tongue. On the other side, the hectic swing-hovering and its inducibility by "hand flapping" suggest that the long tongue may have evolved to allow the depletion of most types of flowers without the — supposedly dangerous — necessity to stay very close and on a spot near the nectar source.

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