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The Pollinators of the Malagasy Star Orchids *Angraecum sesquipedale*, *A. sororium* and *A. compactum* and the Evolution of Extremely Long Spurs by Pollinator Shift

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Abstract: The pollination process of the extremely long-spurred orchids *Angraecum sesquipedale* and *A. sororium* is described and documented here for the first time. The pollinaria and viscidia load was examined in moths captured in central and south Madagascar. Visits to orchids by hawkmoths were rarely observed in the field and were therefore systematically recorded in large flight tents using a night-vision video technique and flashlight photography. *Angraecum sesquipedale* in Fort Dauphin is pollinated by *Xanthopan morgani praedicta* and *A. sororium* on Mt. Angavokely by *Coelonia solani*. By combining a deep nectar spur of extraordinary length with a protruding labellum functioning as a landing platform, these orchids overcome the moth's stereotypic swing-hovering flight thus enabling full insertion of the long tongue. *Angraecum compactum* in Forêt d'Ambohitantely is pollinated by both the shorter and longer-tongued forms of *Panogena lingens* which never swing-hover but is also exploited by *X. morgani* and *C. solani* with wastage of pollinaria. The duration of tongue insertion, nectar exploitation and tongue withdrawal were analyzed: legitimate and illegitimate visitors differ in their time budget and approach to the flower. Nectar volume, nectar level and sugar concentration of *A. sesquipedale* and *A. sororium* were compared with the nectar requirements of the pollinating hawkmoths. The evolution of very long spurs in these orchids is likely to have involved a series of pollinator shifts. The orchids adapted to different hawkmoth species with increasingly long tongues which primarily evolved to avoid predator attacks during visits to less specialized flowers. This "pollinator shift" model modifies the classical "coevolutionary race" model. The relevance of the taxon *Angraecum bosseri* Senghas is questioned.

Key words: *Angraecum*, coevolution, hawkmoths, orchids, pollination, Sphingidae.

Introduction

Sphingophilous flowers typically have long tubes or spurs with deeply situated nectar accessible exclusively to hawkmoths. The most famous example of such a flower is *Angraecum sesquipedale*. Darwin (1862) and later Wallace (1891) hypothesized that this flower must have evolved its long spur as an adaptation to the long tongue of a hawkmoth and that the tongue must have increased its length in the course of an evolutionary race. This idea of coevolution between tongue length and spur length has recently been emphasized, and there is experimental evidence that spur elongation is advantageous for increasing the plants' fruiting success in the European *Platanthera* species (Nilsson, 1988). However, no foraging advantage has been demonstrated for the postulated reciprocal elongation of hawkmoth tongues.

A potential pollinator of *A. sesquipedale*, the Malagasy hawkmoth *Xanthopan morgani praedicta* with a tongue length of about 22 cm, was described by Rothschild and Jordan (1903). Since then this species has generally been assumed to be the pollinator of *A. sesquipedale* in spite of a lack of field confirmation (van der Pijl and Dodson, 1966). Published photographs of *X. morgani*, visiting *A. sesquipedale* (Senghas, 1973; Attenborough, 1995) are composed illustrations without claim to be authentic. Denso (1943), who spent five years in Madagascar in search of the pollinators of *A. sesquipedale*, did not observe any moths visiting the flowers. As he found only six individuals of *X. morgani praedicta* during these five years, most of them outside the flowering season of *A. sesquipedale*, he doubted the specific pollinator role of this hawkmoth. Previous to the present study, the pollinators of the other long-spurred star orchid *A. sororium* were also unknown, and the potential pollinator role of a second extremely long-tongued Malagasy hawkmoth, *Coelonia solani*, with a proboscis length of up to 20 cm, had not been considered.

Previous research on hawkmoth species with long or extremely long tongues visiting small flowers in the wild and in flight cages revealed a stereotypical swing-hovering flight partly combined with an incapability of exploiting long-tubed flowers (Wasserthal, 1993). This behaviour seemed to be inappropriate for the exploitation of extremely long-spurred orchids, because a stiff and narrow tube would impede the lateral movement with fully inserted tongue. This raised the question of, if and how complete tongue insertion is ensured during the swing-hovering flight. The present paper describes the pollination of *A. sesquipedale* and *A. sororium* focusing on hovering flight behaviour and its relation to flower morphology. For comparison with the extremely long-spurred *A. sesquipedale* and *A. sororium*, a third species, *A. compactum*, with a spur of intermediate length was studied. For evaluating the significance of these orchids as nectar sources, their nectar offer will be compared with the nectar demand and flight activity of the pollinating moths.

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Material and Methods

Study sites and time

The interaction between the flowers of three *Angraecum* species and the hawkmoths visiting them were observed in three different areas of Madagascar during their peak flowering periods:

Site A: *Angraecum compactum* in a relict forest on the central plateau "Forêt d'Ambohitantely" (altitude between 1,500 and 1,632 m), east of Manankazo from 05 to 16 November 1991. **Site B:** *Angraecum sesquipedale* on the rocky slopes of the coast north of Fort Dauphin in south-eastern Madagascar from August 09 to 31, 1992. **Site C:** *Angraecum sororium* on the granite inselberg "Mt. Angavokely" (altitude 1,790 m) near Carion, east of Antananarivo (Tana, Central Madagascar) from January 27 to February 15, 1996.

From 1992 until 1996, data on nectar consumption and flight activity patterns of captured and reared *P. lingens, C. solani* and *X. morgani* moths were collected in the greenhouse of the Zoological Institute in Erlangen.

Capturing and recording techniques

Three techniques were used to obtain information about pollinators: (1.) Observation in the field with night vision devices on exposed flowers. (2.) Capture of hawkmoths with a light trap within the range of the orchids and analysis of the attached pollinaria. A 250 W mercury-vapour lamp supplied by a 220 V generator and suspended on a 2.20 m high tripod illuminated a white reflector tissue of about 3 × 3 m. The captured moths were stored in a cylindrical cage of 80 × 60 cm (height × diameter) which was illuminated by the light trap, prior to being transferred into the flight tents. (3.) Observation in large flight tents of the behaviour of individual captured hawkmoths confronted with intact orchids which were brought into the tent. The tents were constructed of textile gauze, with a side length of 1.80 m at site A, B, and C, and additionally 3.60 m × 3.60 m × 2.50 m (height) at site B. They were installed in the field under natural climatic conditions. The hawkmoths were routinely nourished with a 12–17% honey-solution, available *ad libitum* from artificial flowers of *Saponaria* shape. *Angraecum* orchids and other flowering plants were only offered in the presence of the observer.

The moth visits to the flowers were protocolled with a Hi-8-video camcorder Canon EX 1 with Litton light-intensifier (20,000 ×) and an Ernitec 1.2/12.5–75 mm TV lens, using infrared diode illumination when light conditions were poor (Fig. **9**). Photographs were taken with a Nikon F4 and a 2.8/105 mm AF-Micro-Nikkor or 4/300 mm AF-Nikkor and Nikon speedlights SB 24 on Kodachrome 64 and 200 ASA film. The video sequences were analyzed with a Sony Hi-8 Recorder EV S1000 E and a Miro Motion NuBus-frame grabber card in a Macintosh Quadra 950.

Nectar content was measured by extracting it portionwise with a 1 ml syringe before successively cutting spurs in 30 mm long sections beginning from the spur mouth. In addition, fluid level was reconstructed in single specimens of mean size by injecting defined quantities of black-stained 15% sugar-solution from the spur end and observing the increasing position of the fluid-level under transmittent illumination. The sugar concentration was measured by a temperature-compensated pocket refractometer (ATAGO ATC-1, Karlsruhe).

P. lingens were reared from females captured at Forêt d'Ambohitantely in 1991 and at Tana in 1996. The parental generations of *C. solani* and of *Xanthopan morgani* were captured at Périnet in 1994.

Results

Angraecum sesquipedale

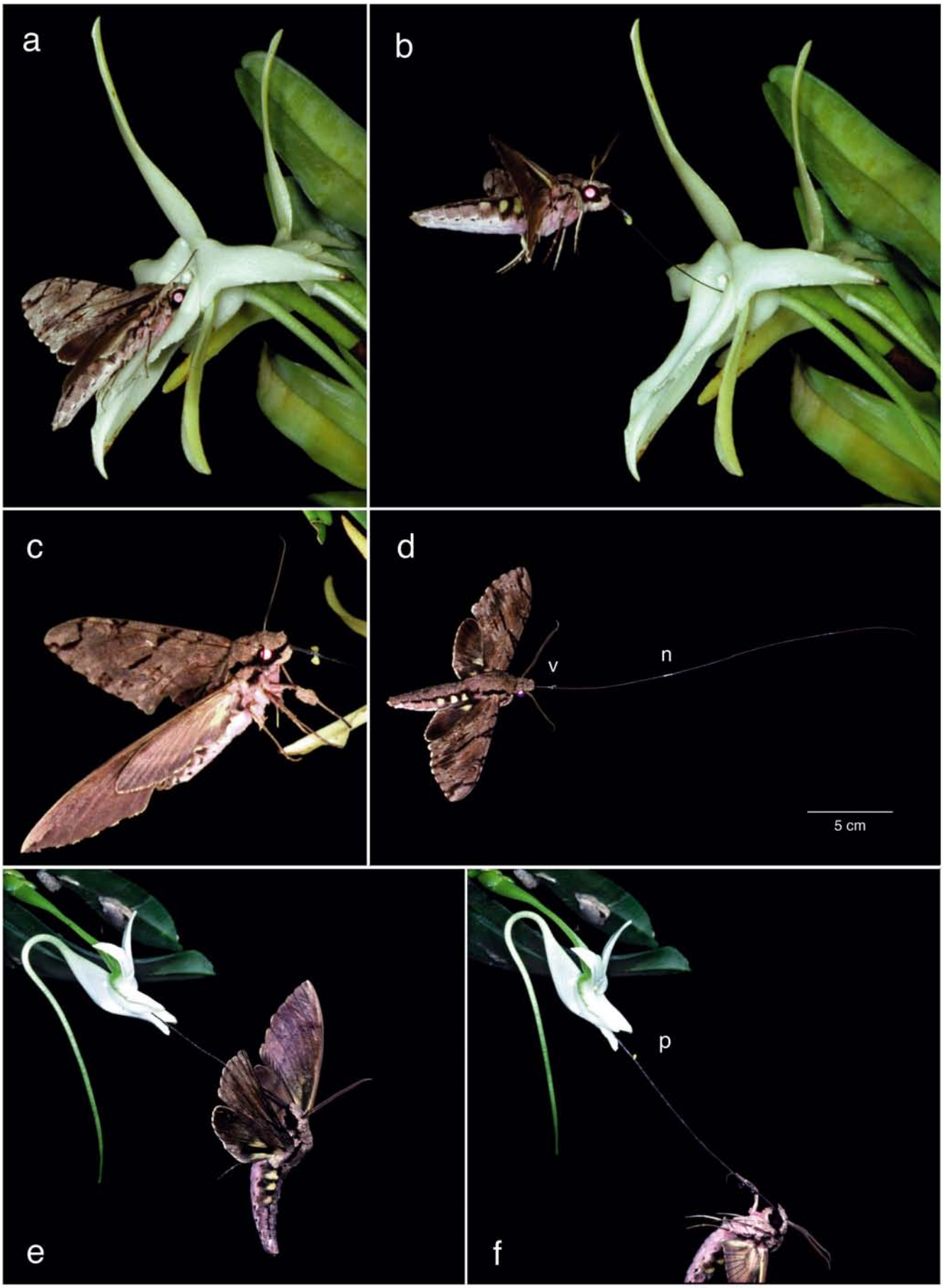
Angraecum sesquipedale is an epiphytic or epilithic species of eastern Madagascar, occurring near the coast, at lower altitudes on the eastern mountains below 100 m (Perrier de la Bathie, 1941) and up to 300 m according to our observations. The panicles of epilithic plants near Fort Dauphin consist of 1–5 flowers. Most of the *circa* 100 plants checked had 2–3 flowers. The operative tube length, i. e. the spur length between the rostellum at the spur entrance which prevents the moth's head from penetrating any deeper and the inner end of the spur lumen, was 33.3 cm ± 4.60 (N = 15), range 27–43 cm. In the field, the flowers display a characteristic age-dependent colour change, much more conspicuous than in the greenhouse plants of *A. sesquipedale*, and than observed in the other two species of *Angraecum*. The colour of the petals changes from light green to white, yellow and when wilting from orange to brown. The sepals remain greenish for longer, and darken earlier than the petals. The upper sepal especially contrasts with the brighter labellum by the anterograde orientation of this sepal shadowing itself and by the lip well exposed to the light from above. Therefore, mainly the triangular petal star is visible at longer distances. At the end of August most flowers were wilted and of about 200 flowers which were checked at five separate locations in the mountains and one in a primary lowland forest, only one recent fruit set could be found on a very exposed rocky summit. Ligneous seed capsules from previous seasons were not detected. In a hotel garden in the centre of Fort Dauphin another developing seed capsule was found among a dozen wilted flowers.

Hawkmoths captured in the vicinity of Angraecum sesquipedale

The low fruit set in relation to the high frequency of flowers indicated that there was no chance of observing a pollinator

Xanthopan morgani praedicta during insertion of its tongue from below into the spur of a virgin *Angraecum sesquipedale*. Full introduction of the tongue lasts about 1 s. Spur length was 33.2 cm, tongue length 22 cm.

Fig. 1 *Xanthopan morgani* visiting *Angraecum sesquipedale* with pollinaria transfer (a–d) and *Angraecum compactum* without pollinaria transfer (e, f). **a)** The male sits on the prominent labellum during exploitation. **b)** Upward flight during withdrawal with pollinaria extraction. Immediately after attachment the stalks of the pollinaria are parallel, close beside the tongue. **c)** Female with pollinaria exposed laterally for deposition. **d)** Male in free flight in the flight tent immediately after capture. A viscidium at the tongue base (v) and a glossy remnant at 7.9 cm distant from the base (n), probably nectar is shown. **e)** Moment of maximum tongue insertion at beginning of withdrawal. **f)** During mid-tongue withdrawal a set of pollinaria (p) is removed.



Figs. 1 a-f

on *A. sesquipedale* in the wild. Therefore moths were captured and confronted with virgin flowers under optimal conditions in a large flight tent. The light trap was set up at two localities facing slopes on which *A. sesquipedale* was growing: (1) on seven evenings on the bank of a series of flooded rice fields about 3 km north of Fort Dauphin and (2) on three evenings on a cleared slope facing a continuous residual forest about 8 km north of Fort Dauphin. In spite of the abundance of several endemic Sphingidae, neither *X. morgani praedicta* nor other long-tongued hawkmoths were attracted to site 2, whereas the only two *X. morgani* individuals captured were from site 1. Only the following, widely distributed migrating hawkmoth species were attracted to the latter site: *Agrius convolvuli* (1), *Acherontia atropos* (2), *Daphnis nerii* (1), and *Hippotion celerio* (2). The first *X. morgani*, a female, was captured with a mist net on August 22 at 19:00 h. The second individual, a male, was attracted to the light trap on August 27 at 20:30 h before a thunderstorm.

Visits to Angraecum sesquipedale *by* Agrius convolvuli *and* Xanthopan morgani

On the nights of August 25 and 26, two *A. sesquipedale* flowers were exposed in the large flight tent to one *A. convolvuli*, one *D. nerii* and five *Euchloron megaera*. Only *A. convolvuli* with a tongue length of 9.8 cm repeatedly visited all exposed *A. sesquipedale* blossoms, inserting its tongue as deeply as possible into the spur mouth. The visits lasted 1.7 to 2.3 s (n = 7). The moth did not remove the pollinaria. The other hawkmoths species did not visit the orchids although they exploited the artificial flowers as well as the flowers of *Catharanthus roseus* (Apocynaceae) and a *Clerodendron* species (Verbenaceae), introduced into the flight tents. These sources were also frequently visited by *A. convolvuli*.

From August 22 to 28 the virgin *X. morgani* female was uninterested in visiting flowers but primarily rested in an alluring position. After copulation with the captured male, it began searching for flowers. The female visited two *A. sesquipedale* flowers on August 29, while the male visited two on August 28 and three more on August 30. A photograph, taken of the flying male with extended proboscis prior to the first floral visits in the flight tent revealed the presence of a viscidium of *A. sesquipedale* on the proboscis, which must have been taken up in the wild prior to capture (Fig. **1d**).

Although both female and male exhibited swing-hovering later on during visits to *Clerodendron*, *Lantana* and artificial flowers, no such behaviour was performed during the rapid tongue insertion into the *A. sesquipedale* spur which lasted only about 1 s ± 0.16 (cover photograph). Both hawkmoths seized the protruding labellum of the flower and pressed their heads as closely as possible towards the rostellum and rested 6 s ± 0.84, shivering scarcely or not at all (Fig. **1a** and Fig. **11**). They approached the flower from below (cover photograph) and withdrew the tongue flying backward and upward (Fig. **1b**). This lasted for 0.9 s ± 0.45. In all cases, pollinaria were removed from the flowers and attached to the moths' tongues 4–9 mm distant from their base. Some seconds later, the pollinaria stalks bent aside at a right angle from their initial orientation parallel to the tongue axis (Fig. **1c**). During the following visits, the pollinia were deposited. When entering a new flower from below, the tongue with the pollinaria passed unhindered through the wide opening of the spur mouth. During withdrawal, the tongue was guided by the dorsal slit in the rostellum and the laterally exposed pollinia were transferred to the sticky surfaces of the stigma. The removal and the deposition of the pollinaria took place when the moth was in leg contact with the labellum. The last pair of nondeposited pollinaria at the tongue base of the female remained undamaged from August 29 to September 21, when the moth died in the Erlangen greenhouse.

Nectar content of Angraecum sesquipedale

The analyzed spurs contained quite different quantities of nectar. In 5 of 20 flowers no nectar could be extracted at all although they contained pollinaria and the spurs were undamaged. This aspect needed to be considered for the flowers seemed to be highly attractive as nutrition for *Oplurus quadrimaculatus* (Iguanidae) which appeared to show no preference in feeding on the spurs. Nectar thieves like small ants were not detected. The extracted nectar volume varied between 40 to 300 μl (N = 15) with a nectar level between 7 to 25 cm (height in the spur: Figs. **2, 3, 4**). The greatest volume was measured in flowers with the longest spurs (Fig. **2**). Mean nectar volume was 165 μl ± 89.91 and mean length of the nectar column was 16.9 cm ± 5.98 (Figs. **3, 4**). The continuous nectar column reached from the tip to the upper meniscus. The nectar levels of a 32.5 cm spur achieved by injecting the same volumes of liquid resulted in corresponding liquid levels. The sugar concentration was 16.5% ± 4 (range: 12 to 20%), and a dilution effect upon the nectar by fog or rain was not noticed.

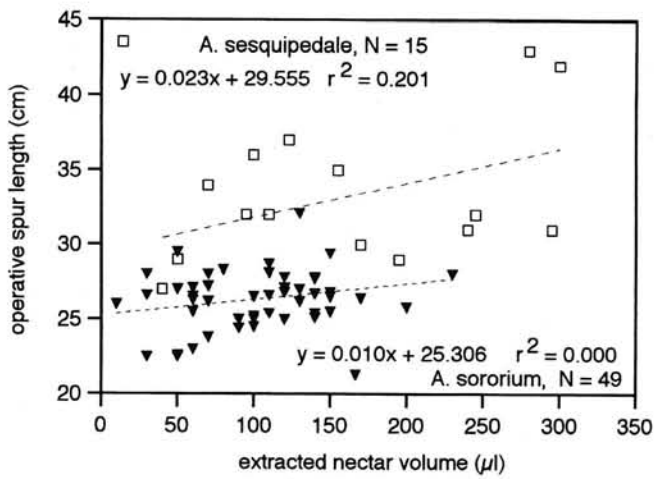


Fig. 2 Comparison of operative spur length and nectar volume in *Angraecum sesquipedale* and *Angraecum sororium*. In *A. sesquipedale* some of the longest spurs contained the highest nectar volumes whereas in *A. sororium* the nectar volume in unexploited flowers was not correlated with spur length.

Tongue length, body weight, nectar consumption and flight activity of Xanthopan morgani *at Fort Dauphin*

The *X. morgani* male (female) had a tongue length of 22 (21.4) cm and a wing length of 7.3 (8.2) cm (Tab. **2**). The male weight varied between 1.7 g and 2.9 g, depending mostly on nectar intake. The female reduced its net weight from 4.36 (Sept. 7) to 2.64 g (Sept. 10), after having laid the bulk (= 70) of 89 eggs and to 1.96 g one day before death (Sept. 24) (Tab. **3**). Each

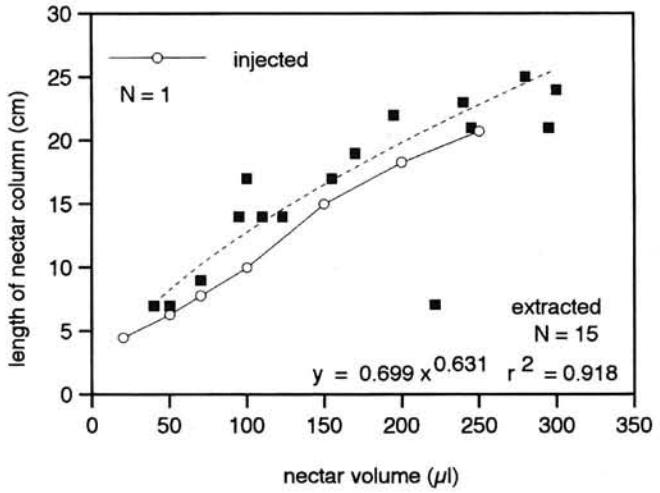


Fig. 3 Correlation of nectar volume and length of nectar column in *A. sesquipedale*. The values obtained by extraction and injection were identical.

X. morgani consumed between 0.4 g and 1.0 g during each night of the last two weeks (female) and four weeks (male) of their lives when they were nourished with artificial flowers *ad libitum*. As there was a lack of consumption data in the early life of the two captured adults, the mean consumption of 15% honey solution per night and individual was measured throughout the entire lifetime of the four reared *X. morgani*: they ingested 1.2 g when the artificial flowers were covered with a *Hymenocallis* corolla (Tab. **3**). The mean consumption values of the four reared individuals were higher than those of the wild individuals because nectar demand was increased in the first three weeks of adult life, whereas in the last week it was the same as in the individuals from Fort Dauphin. The flight activity of the captured male (female) from August 27 (28) to October 10 (25 September) began at about 18 : 10 h in Madagascar and lasted continuously for about 20 to 50 minutes. No second phase of flight activity before dawn was observed.

Spontaneous and induced swing-hovering in Xanthopan *from Fort Dauphin*

The female spontaneously performed swing-hovering, when visiting artificial flowers and verbenacean (*Clerodendron* and *Lantana*) inflorescences. The male did not show spontaneous swing-hovering. However, hand-flapping from behind during visits to artificial flowers caused an escape response, and subsequent slight swing-hovering. The moth reacted with pronounced swing-hovering after being frightened by a brief touching stimulus. It maintained this behaviour from September 09 to October 12.

Angraecum sororium

Angraecum sororium Schltr. is an epilithic orchid which is distributed on the rocky slopes of several mountains between 1600 and 2000 m in central, north and east Madagascar (Perrier de la Bathie, 1941). Because a high fruit set was always found during short visits in 1989, 1991 and 1992 in the population on Mt. Angavokely, there was a real chance of observing or capturing the pollinators with attached pollinaria. In 1996, about 30% of the flowers were in anthesis in the last week of January. In mid-February about 60% were at the end of anthesis, while about 20% were already developing fruit. The plants had one to five flowers, mostly two or three. The flower showed no obvious colour change: it was white as a late bud, was clear white at the beginning of anthesis and became dull ivory-white before wilting or after pollination. The sepals and petals are less elongate than in *A. sesquipedale*. The upper sepal is bent retrograde being illuminated by the skylight like the labellum and thus well visible from above. The starlike silhouette is more compact than in *A. sesquipedale* and, owing to its brillant white, visible over long distances. The operative tube length varies from 22 to 32.5 cm, with a mean length of 26.4 cm ± 1.97 (N = 90).

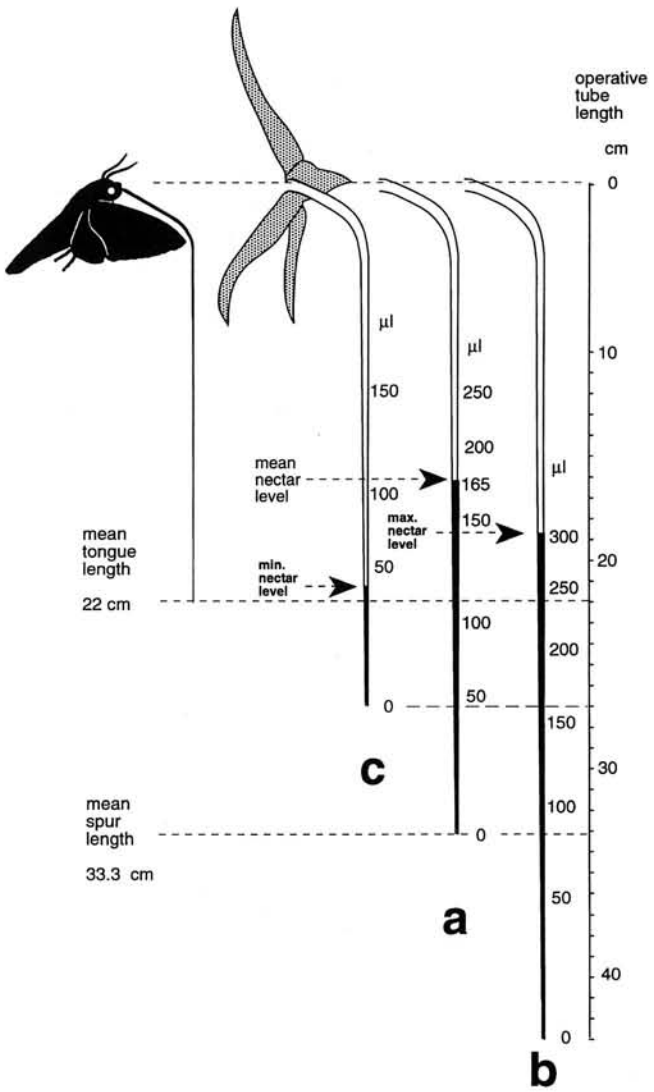


Fig. 4 Accessibility of nectar in the spur of *A. sesquipedale* to *X. morgani*. **a)** Moths with a mean tongue length of 22 cm can exploit a mean volume of about 50 µl out of a spur with a mean length of 33.3 cm and a mean nectar volume of 165 µl. **b)** A spur of 43 cm would offer nectar for the same moths only if it contained more than 165 µl. **c)** The shortest spurs of 27 cm length allow the exploitation of some of the smallest measured volumes.

Hawkmoths captured in the vicinity of Angraecum sororium

A light trap was set up on three evenings with calm weather (February 2, 8 and 11) on a rock directly facing a slope with *A. sororium*. Of the captured 11 species only *C. solani* (2 males) and *P. lingens* (10 males) had sufficiently long tongues to be capable of exploiting *A. sororium*. They were checked for attached pollinaria immediately after capture: one *P. lingens* had a set of pollinaria of *A. sororium* attached 5.8 cm from the base of the 11.7 cm long proboscis. The distal windings of the proboscis were glued together by the relatively large viscidium which made uncoiling impossible.

The first *C. solani* male, captured on February 8 at 19:40 h, had one set of *A. sororium* pollinaria on the tongue 10 mm distant from its base. The second one, captured on February 11 at 19:30 h, had two sets of pollinaria at 8.6 and 9 mm respectively, from the base.

Visits to Angraecum sororium *by* Coelonia solani *and* Panogena lingens

A single *C. solani* visit to *A. sororium* was observed in the field on February 15 at 19:20 h. During this short, about 1 s, visit the proboscis was inserted incompletely (about ¾ of its length) and no pollinaria were taken up.

The two captured *C. solani*, six *P. lingens* (5 males and 1 female), two *N. densoi* and two *N. comma* were confronted with potted plants of *A. sororium*. Only *C. solani* and *P. lingens* visited the orchid, while both *Nephele* species ignored it. The visits of *P. lingens* were always very short, less than 1 s, and during about 30 trials of *P. lingens* with nine different flowers, no pollinaria were removed.

With both *C. solani*, the pollinia collected in the wild were deposited on a stigma during one of the first visits to *A. sororium* in the tent (Fig. **5**), whereas new pollinaria were rarely taken up: Among 43 recorded visits to nine flowers between February 9 to 13, three new pollinaria became attached to the tongue (8 to 11 mm distant from the base). Pollinia deposition occurred in all cases in the course of the next dozen visits. This cross-transfer of pollinia resulted in the setting of two fruits. The first visits even to unexploited flowers were often shorter than 1 s, and due to swing-hovering, which was performed by both *C. solani* individuals, the tongue was incompletely inserted. In the course of one swinging movement, the moth inserted its tongue into the spur mouth. After a short stay of about 1 s, withdrawal was again accompanied by swinging movement. For full insertion of the proboscis into a virgin *A. sororium* flower (N = 7), the moths needed 1.1 s ± 0.21 (Fig. **11**). After seizing the labellum with the legs, the stay lasted 1.7 s ± 0.35 (Fig. **5c**). The moths needed only 0.6 s ± 0.19 for withdrawal (Fig. **5d, e** and **11**). The spur lumen is wide enough for two *C. solani* to insert their tongues simultaneously as was observed once in captivity.

Nectar content in Angraecum sororium

Owing to the abundance of several hundred plants on one slope, more spurs (total N = 90) were cut off and analyzed in this species than could be justified with *A. sesquipedale*. Spurs of flowers of different exposure, age and pollination status were distinguished (Tab. **1**). No correlation between the operative spur length and nectar volume could be detected (Fig. **2**). Flowers hidden by vegetation and therefore unexploitable for hawkmoths contained a mean liquid column of 13.4 cm with 107 μl nectar and a sugar concentration of 10.3% (Fig. **6**). The injected specified volumes of a stained 15% sugar solution were identical with the quantities obtained with subsequent extractions from the same spur. The lower values of the injected spur of 23 cm length (Fig. **7**) were due to variability in the spur diameter. The extraction and the injection technique reveal a geometric correlation between column length and nectar volume, dependent upon the increasing diameter of spur lumen. Flowers without pollinaria had a high fluid content (17.0 cm corresponding to 182 μl) but almost no sugar content (2.1%) (Tab. **1**, Fig. **8**). The fluid column was sometimes discontinuous. These flowers were exposed not only to moth visits but also to wind, fog and rain. On the other hand, the highest sugar concentrations (11–19%) were found in spurs of plants which were well exposed to the sun, but to a lesser extent to wind, and which were frequented by ants (Tab. **1**). In contrast, plants shaded by trees during the greater part of the day had lower mean nectar concentrations (6.4–11.2%).

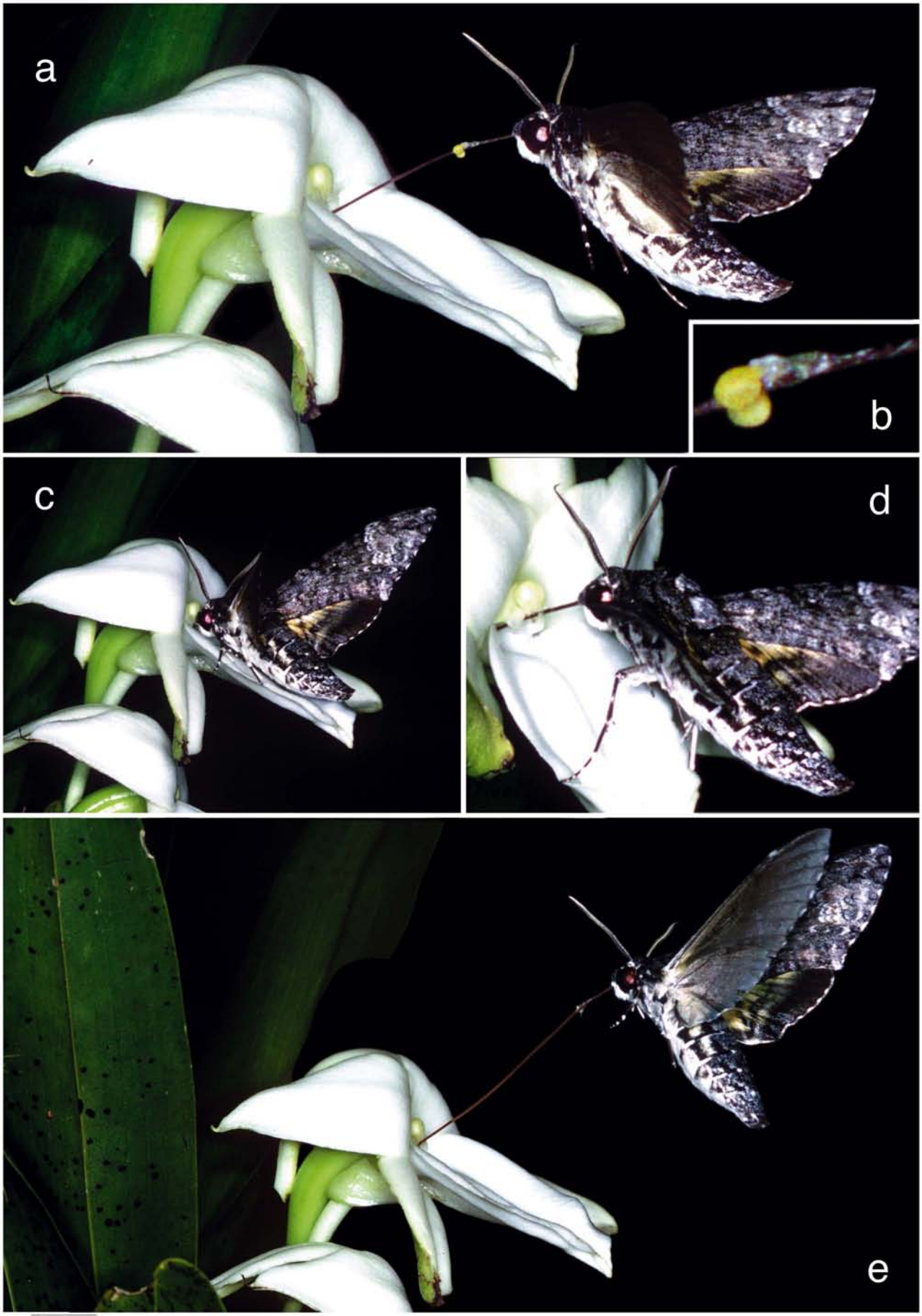
Tongue length, body weight, nectar consumption and flight activity of Coelonia solani *at Mt. Angavokely and Forêt d'Ambohitantely*

The two males had similar tongue (19.3 and 19.2 cm) and wing lengths (5.1 and 5.3 cm) (Tab. **2**). Regarding the ratio of tongue length to wing length, *C. solani* has the relatively longest proboscis of all Malagasy hawkmoths. Body weight was not measured at Mt. Angavokely, but net weight of males of about the same size from Forêt d'Ambohitantely after capture was 1.9 g, diminishing to 1.5 g before death (Tab. **3**).

In the flight tent, both males began flight activity between 18:45 and 19:05 h and the first activity phase, which was always used to imbibe the natural nectar offered from *A. sororium*, lasted about 20 minutes. A second activity phase was observed between 20:20 and 20:50 h and a third of about 2–20 minutes in the morning before sunrise.

The two *C. solani* males in the flight tent showed very similar flight activity patterns. The entire activity time of both moths was about 40 to 80 min per night (Tab. **3**). When the spurs of *A. sororium* were fully exploited after 2 to 3 visits, the flowers were exchanged for fresh ones. In the pause after the first or the second activity phase, a pipette filled with honey solution was connected to the spur after cutting its tip. The spur was repeatedly refilled such that the moths were forced to fully insert their tongues to gain access to the nectar. Nectar consumption of *C. solani* was measured in the Erlangen greenhouse by weighing artificial flowers filled with a 15% honey solution and covered with a *Hymenocallis* corolla (Tab. **3**). The mean volume ingested per moth per night was 3.23 g.

Fig. 5 Pollinaria transfer in *Angraecum sororium* by *Coelonia solani*. ▶ **a)** *C. solani* introducing its tongue into the spur. The pollinaria 10 mm distant from the tongue base came from a visit in the wild. **b)** Details of complete pollinaria with an older more basal viscidium. **c)** During nectar exploitation the moth rests on the protruding labellum forcing its head against the spur mouth. **d)** Deposition of pollinia at the beginning of tongue retraction through the slit of the rostellum. **e)** Withdrawal and upward flight without pollinaria.



Figs. 5 a-e

Table 1 Nectar content and sugar concentration extracted from the spurs of *A. sororium* with varying pollination status and from different sites.

	N	spur length (cm)	liquid column (cm)	liquid volume (μl)	sugar concentration (%)
unexploited, various sites	54	26.4 ± 2.0	13.4 ± 4.1	107 ± 60	10.3 ± 3.8
unexploited, sunny site, with ants	10	24.9 ± 2.1	10.1 ± 3.5	66 ± 35	14.7 ± 2.8
unexploited, shadowy site, wood	14	26.9 ± 1.8	15.2 ± 4.5	121 ± 57	8.1 ± 2.3
no pollinaria, sunny site	14	26.1 ± 2.4	17.0 ± 4.0	182 ± 81	2.1 ± 1.4

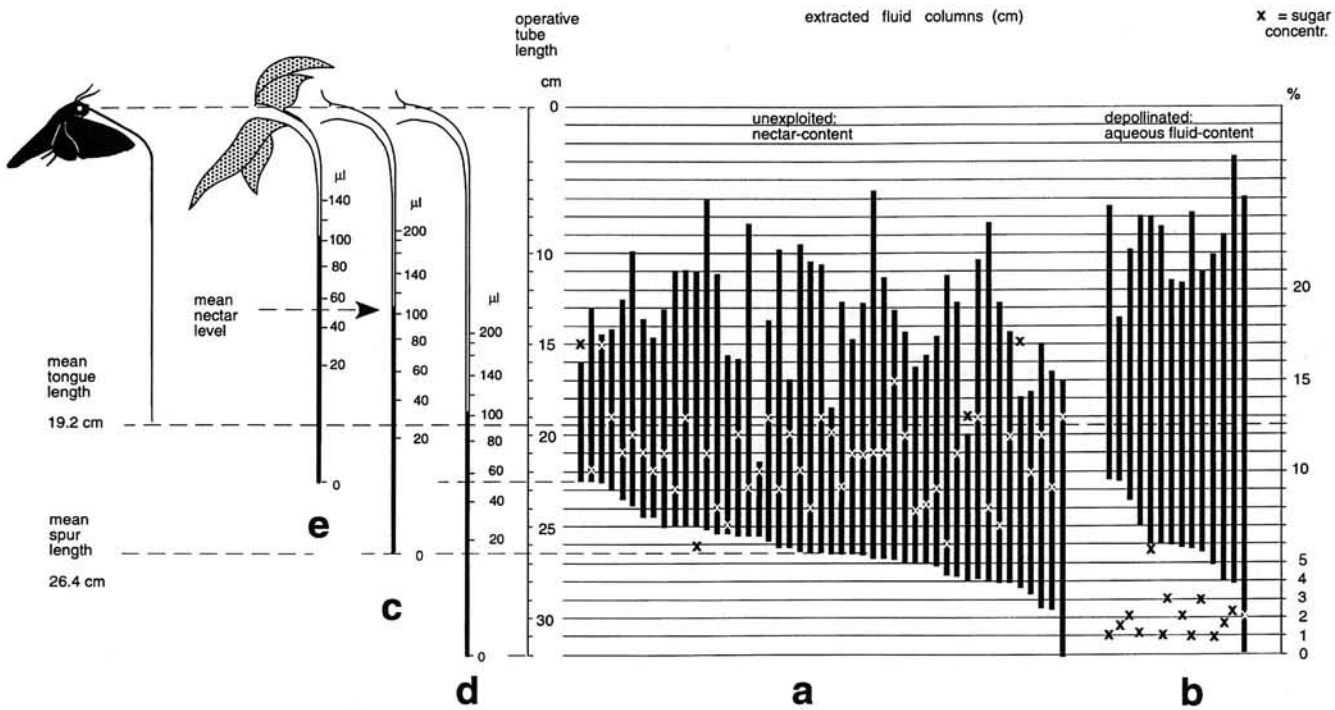


Fig. 6 Accessibility of nectar in the spur of *A. sororium* to *Coelonia solani*. **a)** Extracted fluid columns of unexploited flowers, arranged according to increasing spur length; **b)** same for depollinated flowers. White and black crosses indicate corresponding sugar concentration. **c)** Moths with a mean tongue length of 19.2 cm can exploit a mean volume of about 75 μl out of a spur with a mean length of 26.4 cm and a mean nectar volume of 107 μl. **d)** Most nectar in the longest spurs is unattainable by the moth tongue. **e)** The shorter spurs allow depletion of most of the mean nectar volume.

Angraecum compactum

Angreacum compactum Schltr. is an epiphytic species with a characteristically curved spur and dilated spur mouth (Figs. **1e, f**). It was described by Perrier de la Bathie (1941) to occur in the forests of the central plateau, of the northern and eastern mountains at altitudes from 700–2000 m. Nine plants in anthesis were found in the visual range below the canopy scattered in the forest of Ambohitantely between November 09 to 16, 1991. They had one to three flowers. The light greenish-white sepals and white petals exhibited no conspicuous colour change during anthesis. The sepals and lip are oriented anterograde, the upper two petals retrograde. This orchid has stouter flowers of a greater size than the other epiphytic angraecoid orchids of this forest, and was therefore a candidate to be visited also by larger hawkmoths. The operative tube length was 14 to 18 cm. Due to the small number of flowers available, the nectar content was not determined in this species, in order not to lose the option of later recording the duration of exploitation by the hawkmoth in the flight cage. The meniscus obtained by injecting stained sugar solution from the tip into a spur with an operative length of 14 cm was 7 cm with 10 μl and 11.5 cm with 20 μl.

Long-tongued hawkmoths captured in the vicinity of Angraecum compactum

From the hawkmoths captured on seven nights during the flowering period of *A. compactum*, only one male *X. morgani* carried one set of pollinaria 14 mm distant from the tongue base of its 18.7 cm long tongue. None of the other 20 hawkmoth species captured at the light trap during that time had *A. compactum* pollinaria, although 6 long-tongued (Acherontiinae) species were represented by a number of individuals: *X. morgani praedicta* (3), *Panogena jasmini* (8), *P. lingens* (45), *A. convolvuli* (2), *Coelonia mauritii* (19), *C. solani* (5).

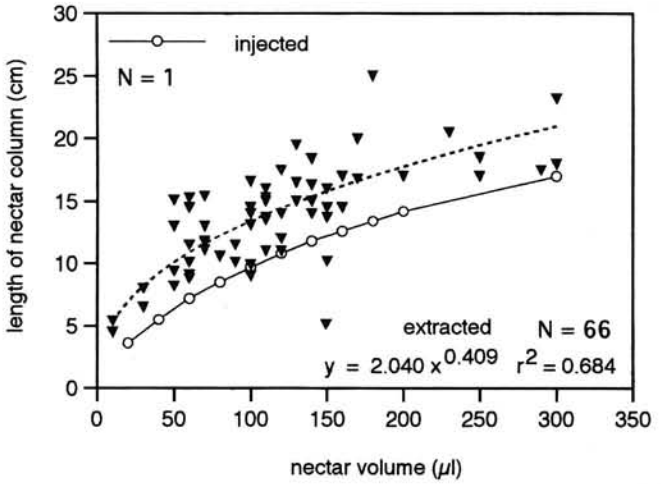


Fig. 7 Correlation of nectar volume and length of nectar column in *A. sororium*. The curve of the injected volumes of a single spur corresponds to the geometric regression curve of the extracted values of 66 spurs (dotted line).

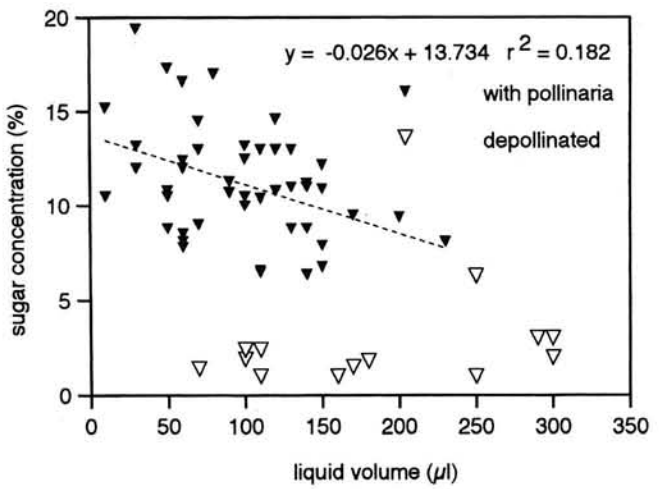


Fig. 8 The relationship between nectar volume and sugar concentration in *A. sororium*. In unexploited flowers a higher volume is correlated with lower nectar concentration. In depollinated flowers nectar concentration is always minimal and independent of the liquid volume.

Visits to A. compactum *by* P. lingens, X. morgani *and* C. solani

Only one hawkmoth visit was observed in the field. At early dusk (18:10 h) one male *P. lingens* visited one flower and extracted one set of pollinaria directly at the base of the tongue.

Nine *A. compactum* flowers were presented to a female and a male *X. morgani* in one of the two neighbouring flight tents. The female performed spontaneous swing-hovering and made only a few brief visits to *A. compactum*, inserting its tongue no deeper than about 6 cm into the spur and removing no pollinaria. The male, however, displayed no spontaneous swing-hovering and exploited three *A. compactum* flowers. (Figs. **1e, f, 9**). It inserted the distal 11 to 12 cm of its 18.7 cm long tongue while hovering from below and needed 6 to 7 s to slowly push its tongue into the spur (Figs. **9, 11**). This moth already carried one set of pollinaria from the wild 1.4 cm from the base of the tongue (Fig. **9**: arrow). These pollinaria were, however, out of reach of the *A. compactum* stigmas which had been presented. Instead of being transferred they were scraped off by the struggling legs during the third observed tongue withdrawal. On the other hand, the moth extracted the pollinaria of two flowers which adhered 7.3 and 6.5 cm, respectively, from the base of the tongue (Figs. **1f, 9**). These more distally attached pollinaria were lost during the following hours. During tongue withdrawal of the visit documented above, the moth was probably upset by being photographed four times with a flash. Thereafter it exhibited swing-hovering and was incapable of inserting its tongue into the spurs of further virgin flowers of *A. compactum*.

The six *A. compactum* flowers that were not exploited by *X. morgani* were exposed to six *P. lingens* in the neighbouring flight tent. All individuals were males, two of the short-tongued form (tongue length: 7.4 cm) and four of the long-tongued form (tongue length: 11.5 cm) (Tab. **2**). All six hawkmoths exploited *A. compactum* and each transported at least one pollinarium (Fig. **10c**). The duration of flower visits was recorded from all individuals. Short-tongued individuals needed about half the time required by the long-tongued individuals (Fig. **11**).

All the flowers were later exposed to one female and three males of *C. solani*. While three individuals exhibited swing-hovering and were unable to poke their tongues deeply into the spurs, one male without spontaneous swing-hovering made a few short visits. As these were preceeded by visits of *X. morgani* and *P. lingens*, pollinaria and nectar were no longer

Table 2 Length of proboscis, forewings and body and the ratio of proboscis length/wing length in the three pollinating hawkmoth species.

Species	origin	N	length of proboscis	length of forewing	length of body	ratio of proboscis length/ forewing length
C. solani	Angavokely	02	19.2 ± 0.07	5.2 ± 0.14	5.4 ± 0.14	3.7 ± 0.11
X. morgani	Fort Dauphin	02	21.7 ± 0.42	7.7 ± 0.63	6.5 ± 0.70	2.8 ± 0.28
P. lingens, short	Angavokely	05	7.8 ± 0.81	4.2 ± 0.12	4.5 ± 0.23	1.8 ± 0.15
P. lingens, short	Ambohitantely	29	7.4 ± 0.78	4.2 ± 0.24	4.2 ± 0.21	1.7 ± 0.13
P. lingens, long	Angavokely	05	11.1 ± 0.80	4.2 ± 0.23	4.5 ± 0.13	2.6 ± 0.19
P. lingens, long	Ambohitantely	69	11.5 ± 0.72	4.4 ± 0.16	4.5 ± 0.17	2.5 ± 0.14

Table 3 Body weight, duration of flight activity and consumption of "nectar" (= 15% honey solution) per night in the pollinating hawkmoth species. Ambient temperature during "nectar" consumption in the greenhouse: 20–23 °C; during flight activity in the field at dusk: 16–18 °C, at dawn: 12–16 °C.

	body weight (g)		flight activity (minutes)			"nectar" consumption		
	male /female	N male /fem.	dusk	dawn	N moths /nights	min. (max.) (g)	mean (g)	N moths /nights
X. morgani	1.9 ± 0.15 / 3.0 ± 0.31	16/3	20–50	0	2/28	0.26 (2.33)	1.20 ± 0.35	4/28
C. solani	1.7 ± 0.25 / 1.8 ± 0.15	13/4	40–60	2–20	2/ 5	1.69 (6.95)	3.23 ± 1.21	7/25
P. lingens	0.7 ± 0.19 / 0.9 ± 0.09	13/5	10–30	2– 8	6/ 5	0.01 (0.55)	0.24 ± 0.08	32/30

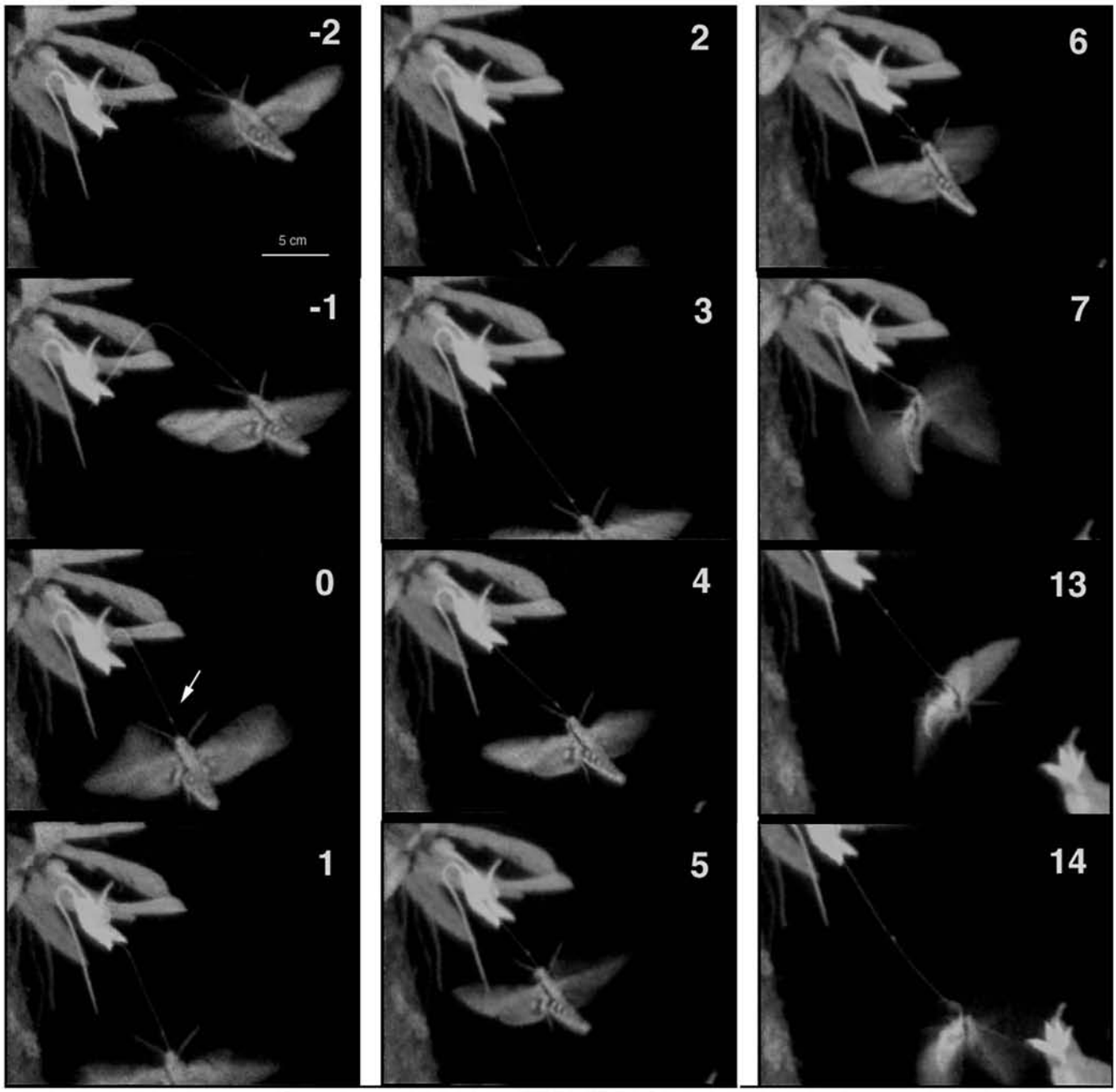


Fig. 9 *Angraecum. compactum* and a clumsy visit by *Xanthopan. morgani praedicta*. Frame sequence from a video with light intensifier under IR-diode illumination. The moth exhibited no spontaneous swing-hovering prior to this visit. After having targeted the spur mouth (–2, –1), the moth pushed its tongue slowly from below into the spur (0–6). A set of pollinaria near the tongue base (arrow) originated from a former visit in the wild. The moth reached maximum tongue insertion after 6 s. The withdrawal began at 7 s. As the tongue was longer than the spur, the pollinaria did not come close enough to be transferred to the stigma of this flower but were wasted by the struggling forelegs (7) whilst the moth hung from the flower during tongue retraction. The complete visit lasted 14 s and a new set of pollinaria was removed (visible at 7.3 cm distance from the tongue base).

available and these trials were not included in the time budget calculation (Fig. **11**). In the Erlangen greenhouse the pollinaria of one *A. compactum* exposed to three swing-hovering *C. solani* were wasted in the first night of confrontation.

Tongue length, body weight, nectar consumption and flight acitivity in P. lingens

The *P. lingens* individuals captured at Ambohitantely and Angavokely can be attributed to either the long-tongued or the short-tongued type (Tab. **2**). The offspring of two short-tongued females, one captured in 1991 at Ambohitantely, the other one captured at Tana in 1996, have developed long- and short-tongued forms in all generations reared up until the present. The tongue length of the original captured specimens were 11.5 cm in the long-tongued form and 7.4 cm in the short-tongued form. The resulting tongue length/wing length ratio in both populations is about 2.5 in the long-tongued form and 1.7 in the short-tongued form (Tab. **2**). *Panogena lingens* were never observed swing-hovering (N > 300). In the evening flight activity began some minutes earlier than that of the other observed Acherontiinae hawkmoths (*C. solani, C. mauritii, P. jasmini, X. morgani*). On a flowering well exposed *Mussaenda prostrata* (Rubiaceae) tree of about 10 m height, *P. lingens* were observed between 17:45 and 18:30 h (N = 6 nights with 222 visits), while in the darker observation tent, flight activity began earlier at 17:32 h and stopped at 18:13 h (N = 5 nights, ambient temperature: 16–18 °C). In the flight tent, the dusk activity of an individual lasted 10 to 30 minutes. At dawn, *P. lingens* started flight activity from 5:00 to 5:08 h, later than the other Acherontiinae observed (N = 6 nights, ambient temperature: 12–16 °C) and flew for only 2–8 minutes. The mean consumption of a 15% nectar solution offered *ad libitum* in artificial flowers, decorated with corollae of *Nicotiana, Stephanotis* or *Hymenocallis* varied between 0.056 and 0.55 g with a mean of 0.24 g per moth (Tab. **3**). In the greenhouse, *P. lingens* often imbided only 0.01 g or less and did not exploit flowers every night although they were vital for several weeks.

Discussion

The systematic position of the observed epilithic A. sesquipedale *from Fort Dauphin*

The epilithic population in Fort Dauphin was described as *A. sesquipedale* var. *angustifolium* (Bosser and Morat, 1972). Based on greenhouse plants from the same population, Senghas (1973) established the species *A. bosseri*. Around Fort Dauphin a single morph of *A. sesquipedale* was found, the floral traits of which differ considerably from the cultivated plants described by Senghas (1973). This suggests that the smaller, and apparently uniflorous "*A. bosseri*" is a depauperate form resulting from suboptimal greenhouse conditions. The chemical differences in scent composition between *A. sesquipedale* and "*A. bosseri*" (Kaiser, 1993) could be due to differences between the epilithic and the epiphytic forms of *A. sesquipedale*, or both forms could react in a different way to greenhouse conditions.

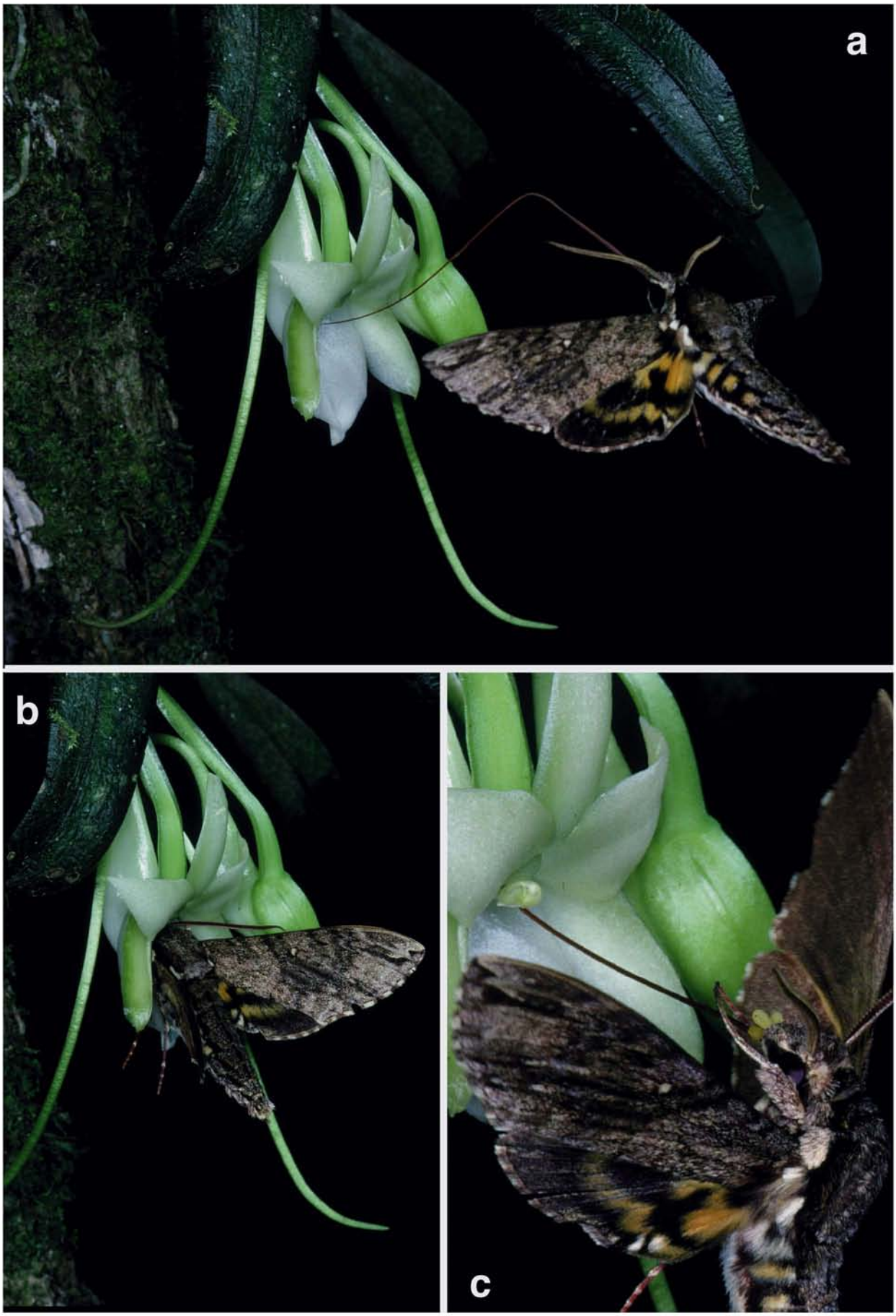
The pollinator roles of three different hawkmoth species on Angraecum *orchids*

The two Malagasy star orchids with the longest spurs are pollinated by the two unusual long-tongued hawkmoths: *A. sesquipedale*, the species from the coast and lower mountains is pollinated by *X. morgani praedicta. Angraecum sororium*, the species of the higher mountains, is pollinated by *C. solani*. That individuals of both hawkmoth species were captured with viscidia or pollinaria and that they were capable of removing and depositing pollinaria in the confrontation experiments confirms Darwin's (1862) assumption of the pollinator role of *long-tongued hawkmoths* in long-spurred orchids. Almost all observed visits to *A. sesquipedale* by *X. morgani* were accompanied by pollinaria removal or deposition. In contrast to this, visits by *C. solani* to *A. sororium*, were short and often performed without complete tongue insertion and without pollinaria transfer. The deposition of pollinaria by both captured *C. solani* and the subsequent fruit set in the experimental flowers of *A. sororium*, shows, however, that *C. solani* can effectively pollinate these flowers. The high percentage of seed capsules in the population of Mount Angavokely implies an efficient pollinator. Both *Angraecum* species were also exposed to intermediate long-tongued hawkmoth species, *A. sesquipedale* to *A. convolvuli* and *A. sororium* to *P. lingens*, which are both described as pollinators of smaller angraecoid orchids (Nilsson et al., 1985, 1987; Nilsson and Rabakonandrianina, 1988). The *A. convolvuli* captured at Fort Dauphin and *P. lingens* at Angavokely carried neither pollinaria or viscidia at the base of their tongue nor were they able to remove the pollinaria in the confrontation experiments despite frequent visits with complete tongue insertion. Unfortunately, we had no opportunity to test if *X. morgani* is capable of pollinating *A. sororium*. As *X. morgani* is occasionally found at Angavokely (Nilsson et al., 1988), this species might function as *A. sororium* pollinator too. No *C. solani* were observed at Fort Dauphin during our stay and none of the six *C. solani* reared from offspring of a female caught near Périnet confronted with two flowers of epiphytic *A. sesquipedale* in the Erlangen greenhouse, explored them. At late dusk the more yellowish, less contrasting flowers of *A. sesquipedale* compared to *A. sororium*, seemed to be invisible or unattractive to *C. solani*.

Angraecum compactum with spurs of 13 to 18 cm operative tube length is probably the largest of the intermediate-sized angraecoid orchids in the forest of Ambohitantely. The long-tongued form of *Panogena lingens* has already been shown to carry pollinaria of this orchid and of several other smaller angraecoid species (Nilsson et al., 1985, 1987). In our confrontation experiments also the short-tongued morph of *P. lingens* visited *A. compactum* and transported some pollinaria. While Nilsson and Rabakonandrianina (1988) found no indication of a bimodality in tongue length of this species of Mount Angavokely, our *P. lingens* captured at the same location belonged either to the short-tongued or to the long-tongued morph (Tab. **2**)

Adaptations of angraecoid orchids to hawkmoth morphology and behaviour

Both *A. sesquipedale* and *A. sororium* have adapted to the structure of the extremely long-tongued pollinators by their long and wide spurs and by the proportions of their sexual



Figs. 10 a-c

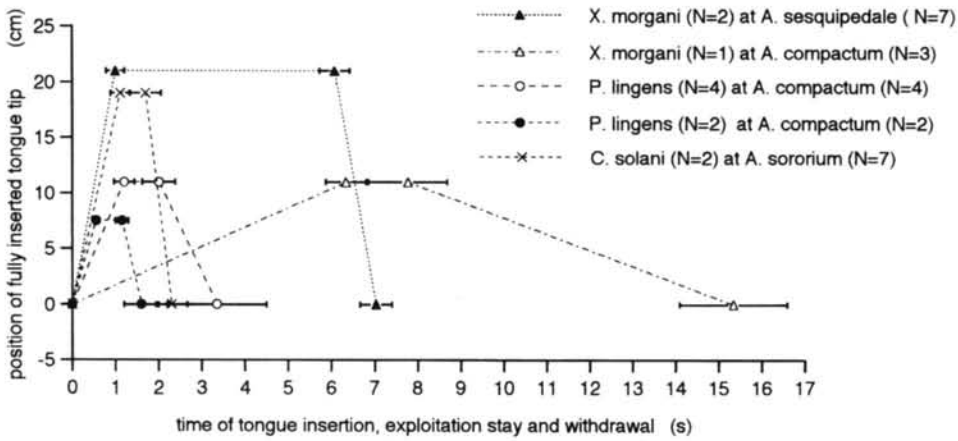


Fig. 11 Time budget of legitimate and illegitimate visitors of 3 *Angraecum* species. Duration of tongue insertion, stay with fully inserted tongue and withdrawal. The data are taken from video sequences. N = number of different moths and different virgin blossoms (= number of considered visits).

organs, in order to prevent pollinaria wastage by shorter-tongued species. These *Angraecum* species have also adapted to the swing-hovering behaviour which is generally performed spontaneously by both extremely long-tongued sphingid species (Wasserthal, 1993): by means of the resupinate protruding large labellum, which functions as a landing platform, the moths are forced to alight for full tongue insertion. They are thus freed from the dilemma of being unable to interrupt the stereotypical swing-hovering with fully inserted tongue. The wide spurs facilitate a quick insertion of the tongue. Thus a typical characteristic of sphingophilous flowers, namely that they allow the continuation of hovering flight, is absent in these flowers. They combine the attributes of a sphingophilous salver-shaped flower (Vogel, 1954) with that of a labellum flower, typical in flowers adapted to visits of Hymenoptera. Sitting moths reduce or even stop shivering and thus probably become less conspicuous for predators such as bats (Kober and Schnitzler, 1990) and heteropodid spiders (Wasserthal, 1994) attracted by flutter stimuli. *Angraecum sesquipedale* and *A. sororium* meet the postulate of Darwin (1862) and Nilsson (1988) that the orchid's spur has to be somewhat longer than the tongue of the hawkmoth for successful pollination. As the spurs exceed the hawkmoth's tongue by 7 to 21 cm (mean difference 11 cm) in *A. sesquipedale* and 3 to 13 cm (mean difference 7 cm) in *A. sororium*, they always withhold some nectar from the moths, thus forcing them to press their heads against the column of the flower to obtain as much nectar as possible.

Although *A. compactum* is pollinated by *P. lingens* which does not exhibit swing-hovering, it also prevents normal hovering by its resupinate flower with a protruding lip. Its shorter lip, however, cannot be used as a resting platform. The moth is forced to push its anterior body into the funnel-like lip and to continue shivering during exploitation, with wings and antennae held in a retrograde position. The long-tongued form of *P. lingens* needs up to 3 s for tongue retraction while the short-tongued form needs less than one second. This behavioural difference may confirm the assumption that the curved spur produces some friction on the inserted and retracted tongue (Nilsson et al., 1987). Increased resistance at the beginning of tongue retraction may stimulate the moth to enhance wing beat activity and lift production, therewith pressing the tongue base forcibly against the orchids sexual organs. Friction by spur curvature is more effective if the tongue is long enough to be inserted deep into the spur. This may explain why pollinaria of the smaller angraecoid orchids with curved spurs such as *A. arachnites* are more rarely found in the short-tongued *P. lingens* morph (Nilsson et al., 1985; Walther, 1995).

◀ **Fig. 10** *Angraecum compactum* visited by the pollinator *Panogena lingens* **a)** Male of the "short"-tongued form (tongue length: 6.6 cm) just before inserting its tongue, **b)** pushing its head into the spur mouth, **d)** withdrawal, tongue base with two sets of pollinaria, one set from a former visit.

Disadvantages of distal pollinaria attachment for flower and moth

Only illegitimate visitors carried pollinaria more distally on their probosces. In *X. morgani* and *C. solani* this was due to the fact that their tongues were much longer than the spurs of *A. compactum* which they visited. In these moths the distally attached pollinaria were scratched off by the forelegs when the moths were struggling during tongue withdrawal from *A. compactum* or during cleaning. None of the distally attached pollinaria were transferred to another flower and most were wasted within the following hours, whereas in *X. morgani* correctly attached pollinaria remained on the tongue for up to 25 days. A longer-lasting attachment of pollinaria is only possible at the proximal tongue base, which lies inside the cleaning radius of the forelegs. In the large *X. morgani* and *C. solani*, which have longer legs, the pollinaria are safely attached within the basal 11 mm of the tongue. Most pollinaria of 4 different angraecoid species transported on the tongue by the smaller *P. lingens* were placed within the basalmost 5 mm (Nilsson et al., 1987). This agrees with our findings for the same and three additional angraecoid species of similar size.

Also in one *P. lingens*, *A. sororium* pollinaria were found half way up the proboscis, although the spur length of this orchid is much longer than the proboscis. In this exceptional case the distal tongue coils were glued together permanently by the relatively large viscidia, making the tongue inoperative for further nectar uptake, because they could not be scraped off. This kind of illegitimate visit is a disadvantage not only for the flower but also for the moth.

Nectar content of Angraecum *spurs and nectar requirements of the pollinating hawkmoths*

The exploitable nectar quantity varied between 0 and 200 μl in *A. sesquipedale* and *A. sororium*. The proximal 13 cm of

A. sesquipedale and *A. sororium* spurs normally contain no nectar. Therefore, species other than *X. morgani* and *C. solani*, such as *P. lingens, A. convolvuli* and *C. mauritii* cannot exploit these flowers. On the other hand, a great volume of nectar cannot be exploited even by the long-tongued hawkmoths.

A. sesquipedale has a mean nectar content of 165 μl, whereas *X. morgani* with an average tongue length of 22 cm obtains about 50 μl during a single flower visit, while the 70% of nectar volume in the distal spur remains out of reach of the moth's tongue (Fig. **4**). In the flight tent, a maximum of three flowers were exploited per night per moth. The long-lasting exploitation of about 6 s suggests a rather high nectar volume in these flowers. With a nectar demand per individual ranging from about 400 to 1000 μl per night, 8 to 20 *A. sesquipedale* flowers would be needed by one active *X. morgani* each night with a maximum flight activity of 50 minutes. These data contradict the statement of Denso (1943) that the *Xanthopan* tongue would be too short to reach the nectar in the spurs. Such low nectar content has, however, been observed in our cultivated epiphytic *A. sesquipedale* greenhouse flowers.

The mean exploitable nectar volume of *A. sororium* was 107 μl, and with a mean tongue length of 19.2 cm *C. solani* would be able to obtain about 75 μl of nectar from the flowers (Fig. **6**). From the relatively short visiting time of *C. solani* of about one second at the virgin flowers offered in the flight tent, it is concluded that their nectar content was low. To satisfy its mean nectar requirement of about 3000 μl per night, *C. solani* has to visit about 40 flowers with a mean nectar content of 75 μl per night. *C. solani* should be a more efficient pollinator than *X. morgani,* due to a nectar demand which is three times higher and a flight activity which is 30 min longer per night. This advantage is, however, reduced by the frequently incomplete and short insertion of the tongue.

Unexpectedly, *A. sororium* flowers that had lost their pollinaria contained a higher, sometimes discontinuous fluid column than the unexploited blossoms at the peak of anthesis. The spurs of depollinated blossoms were always collected from exposed plants and the low sugar concentration suggests that rain or fog may have entered the spur and diluted the nectar residue.

The exploitation stay of *P. lingens* at *A. compactum* was relatively short, lasting about 1 s and suggesting the ingestion of only a small quantity of nectar per flower. This corresponds to the small nectar volume in the distal spur of 10 to 15 μl measured with the injection technique. In the greenhouse, *P. lingens* ingested a mean of 240 μl per night, if nectar was offered in artificial flowers *ad libitum*, but many individuals consumed only 10 μl or less. In fact, in the flight tent only a few unexploited intermediate orchids were visited in the course of each activity phase, after dusk and again before dawn. Because of its short nightly activity phases, *P. lingens* is probably a more stationary species than *X. morgani* and *C. solani*, and might thus contribute to the inbreeding of local orchid populations in isolated locations. As the only non-swing-hovering long-tongued species, *P. lingens* is capable of monopolizing orchids with spurs of intermediate lengths, including orchids with non-resupinate flowers. These are generally unexploitable for all other long-tongued moths, because these flowers cannot prevent the moth's swing-hovering behaviour. About half a dozen species of angraecoid orchids is known to be exclusively pollinated by *P. lingens* and all use its dorsal and ventral portion of the basal tongue and frons for pollinaria attachment (Nilsson et al., 1985, 1987).

Pollinator abundance and fruiting success

While *A. sesquipedale* is abundant in the area around Fort Dauphin, only two *X. morgani* could be captured in three weeks. The low fruiting success with one seed capsule in 200 *A. sesquipedale* flowers may also indicate that *X. morgani* is rare during the flowering period of *A. sesquipedale* in this area. Likewise, low fruiting success was observed in September 1993, with two fruiting plants on an isolated rock in coastal secondary vegetation (M. Kluge, personal communication). *Xanthopan morgani* must have already been rare in the years when fruiting success was high (about 75%: Denso, 1943). Denso captured only one individual in the location over two years and therefore supposed that different animals, perhaps *Nectarinia* birds might be the pollinators. The seed capsules, found in the garden of "Hotel le Dauphin" in the town of Fort Dauphin and in the coastal secondary vegetation by Kluge, must be attributed to pollination by a hawkmoth species capable of wandering from the natural environment into anthropogenous areas. Both *X. morgani* individuals were captured on a typical migratory route. As only sphingids which are known to be migrating and widely distributed species (Reinhardt and Harz, 1989) were captured here, the observations suggest that *X. morgani* is a migrating species too. According to Griveaud (1959) this powerful flying moth should be capable of covering long distances. The continental African subspecies *X. morgani morgani* is said to spread from the warmer coastlines inland (Pinhey, 1962). In combination with the long-lasting attachment of pollinaria for several weeks, this long-lived migrating hawkmoth might be of great importance for the pollination of distant orchid populations.

The high fruiting success of *A. sororium* observed over several years in the dense population of Angavokely, suggests the occurrence of an abundant and/or efficient pollinator. While Nilsson and Rabakonandrianina (1988) captured only one *X. morgani* and no *C. solani* in mid-March 1988 (at the end of the flowering period of *A. sororium*), we caught two male *C. solani* with pollinaria within only three evenings and observed one flower-visiting individual. As the hawkmoth is not common, pollination is probably performed by a few individuals which visit a great number of flowers owing to their high nectar requirements.

Incongruent distribution of generalist foragers and monophilous long-tubed flowers

The selective adaptiveness of sphingophilous characters in flowers has been convincingly documented (Gregory 1963–1964; Grant, 1983, 1993; Nilsson, 1988). A selective advantage of sphingid proboscis length in feeding has been implied by most investigators, but it is also appreciated that hawkmoths are not completely dependent on sphingophilous flowers. Hawkmoth flowers are assumed to provide a more reliable source than do less specialized flowers which can be exploited by other animals too. This reliability becomes more critical in seasons of general flower scarcity (Grant, 1983). In the vicinity of flowering *A. sesquipedale* and *A. sororium* there was, in fact, no excess of alternative nectar sources detectable. This might, however, be a consequence of habitat degradation.

On the other hand, *X. morgani* and *C. solani* were scarce in the habitats of the long-spurred *Angraecum* orchids. This may also, at least partly, be a result of the miniaturization and fragmentation of the primary forests with a reduction of the larval host plants. In contrast to this, both hawkmoth species have been captured more frequently on the borders of the forests of Périnet and Ambohitantely, where there is a lack of extremely long-spurred orchids, and this probably not just recently. Here the moths visited *Mussaenda*/Rubiaceae and the inflorescences with small flowers of *Clerodendron putre* and *Lantana camara*/Verbenaceae in the wild and in the flight tents (Wasserthal, 1993). *Crinum firmifolium* pollen was found on the tongues of some *X. morgani* and *C. solani* at Ambohitantely and Périnet (Walther and Wasserthal, in prep.). But even the longest corolla tubes of this amaryllidacean flower, ranging between 9 and 16 cm, are shorter than the mean tongue length of *X. morgani* and *C. solani* in the area. Thus, at the present time, it looks as if a sympatric abundance of extremely long-tubed flowers and extremely long-tongued hawkmoths does not exist even in the less degraded Malagasy areas. A more important nectar source for long-tongued hawkmoths might be offered by baobabs that do not withhold most of their nectar. Five of six Malagasy species are exploited by hawkmoths (Baum, 1995): *Adansonia rubrostipa* and *A. za* with brush-like anthers are pollinated by *C. solani* and *Adansonia perrieri* with a stalked bulbous androphor is pollinated by both *C. solani* and *X. morgani*. According to descriptions by Baum concerning the sites of these baobabs, the extremely long-tongued hawkmoths seem to be more abundant, but their appearance does not always coincide with the flowering period of the baobabs (Walther, 1995). In addition, for the exploitation of both types of *Adansonia* flowers, no extremely long probosces are required, indicated by the fact that the flowers are also exploited by shorter-tongued moths (Baum, 1995; Wasserthal unpubl.). In contrast to the tubular flowers, these open flowers do not restrict swing-hovering, rather they profit from it, when the moths swing with the body and wings over the horizontally exposed anthers and stigmata.

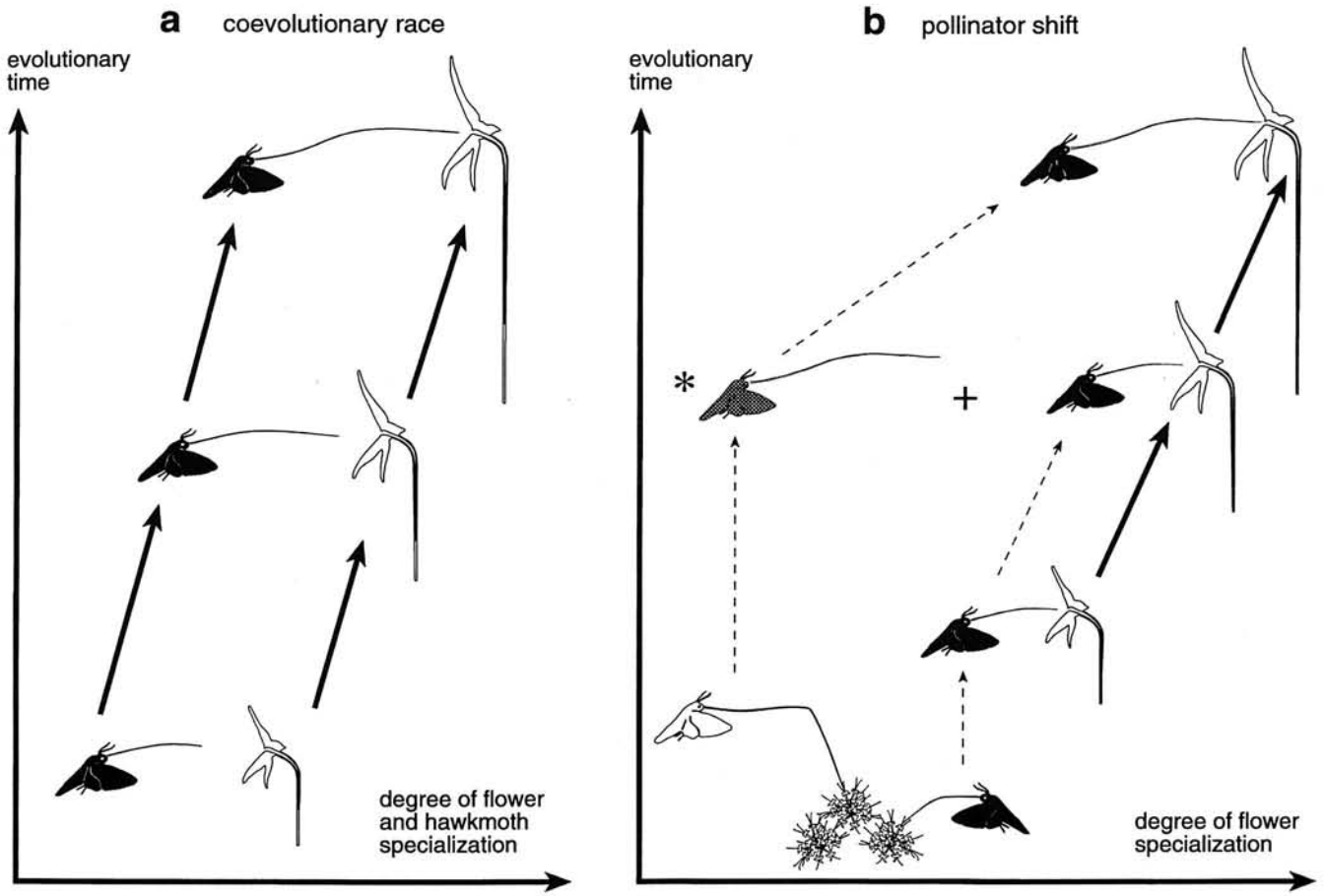


Fig. 12 Comparison of the "coevolution" model of Darwin 1862 (**a**) and the "pollinator shift" model (**b**) in orchid spur evolution. **a)** Evolutionary race between increasing spur length and increasing tongue length. **b)** Recruitment of generalist feeders with preadapted tongues of different lengths as pollinators by long-spurred angraecoid orchids and their gradual substitution. When spur enlargement driven by the primary visitor exceeds a certain diameter, the flower can be exploited by a longer-tongued illegitimate visitor (asterisk): Such a situation has recently been represented by the interaction of *X. morgani* and *C. solani* with *A. compactum*. The occurrence of the long-tongued species exerts an increase of selective pressure towards spur elongation on the orchid. When the spur size of the flower has reached a dimension so that the nectar column is out of reach for the primary pollinator, the flower may still be pollinated by this species but now acts as a deceptive flower. If an increase of overall dimension leads to pollinaria wastage by the shorter-tongued visitor, the selection favours further changes in the proportions of the flower's sexual organs so that pollinaria cannot be extracted by the shorter-tongued visitor. This is the case in *A. sesquipedale* and *A. sororium*. Black signature: orchid pollinator; grey: non-pollinating orchid visitor; white: moth incapable of exploiting orchid.

From the view of nectar availability it is therefore questionable if extremely long-tubed flowers could have exerted a driving selection pressure on the evolution of extremely long tongues.

Evolution of long-spurred orchids to fit the long tongues of preadapted hawkmoths

All *X. morgani* observed at Périnet, Ambohitantely and Fort Dauphin and all *C. solani* observed at Périnet, Ambohitantely and Angavokely exhibited the same swing-hovering flight, mainly spontaneously. Swing-hovering behaviour and long tongues have been interpreted as a predator-avoiding trait combination which occurs in several acherontiine genera (Wasserthal, 1993). The discovery of nocturnal heteropodid spiders, specialized to pursue and lie in ambush for flower-visiting moths, and the analysis of the efficiency of long-tongued and swing-hovering hawkmoths to escape from these predators' attacks, confirm the hypothesis of antipredator adaptations of long tongues and swing-hovering (Wasserthal, 1996 and unpubl.). Long tongues might thus have evolved before various plants such as *Angraecum* developed tubes with deeply hidden nectar to engage only a single extremely long-tongued hawkmoth species for pollination. The extremely long-tongued hawkmoths of the Old World are closely related to the New World genera *Amphimoea, Cocytius* and *Neococytius* with the longest probosces worldwide. These morphological characteristics, combined with the fact that the caterpillars of the longest-tongued species, from the New and the Old World, feed on annonacean trees, a family regarded to be a primitive angiosperm group of the old plant order Magnoliales (Gottsberger, 1988; Morawetz, 1988), characterizes these hawkmoths as an old monophyletic group with circumtropical distribution. If swing-hovering proves to be performed by the New World members of this group too, an additional argument would substantiate the hypothesis that long tongues evolved earlier than the various unrelated, extremely long-tubed flowers. The results of the present study confirm the view that plants and pollinators are selfish mutualists (Howe and Westley, 1986): moth foraging is only coincidentially associated with plant reproduction. It does not therefore seem astonishing that predator avoidance during flower exploitation is an important factor in this selfish interplay.

The question arises how a flower could develop an extraordinary long spur or nectar tube if there was no coevolutionary race between increasing spur length and tongue length as Darwin (1862) and Nilsson (1988) suggested. On the basis of the present results the coevolution hypothesis needs to be replaced by a pollinator shift hypothesis (Fig. **12**): the ancestors of the modern long-tubed flowers certainly had efficient pollinators at all phases of their spur evolution. With their gradually increasing spur length and diameter in response to the primary pollinator, the orchids became accessible at some stage to a preadapted, still longer-tongued illegitimate species. This exerted further selective pressure upon spur elongation, finally resulting in pollinator shift. The current spectrum of Malagasy hawkmoth species comprises orchid visitors with very different tongue lengths, some of which are known to pollinate less long-spurred orchids. *Cynorkis uniflora* with an operative flower depth of 6.2 cm is pollinated by *Nephele densoi* and *Hippotion geryon*, but much more frequently exploited by the longer-tongued *P. lingens* which does not normally transport pollinaria of this orchid (Nilsson et al., 1992). This example may serve as a model illustrating an evolutionary constellation where a preadapted longer-tongued visitor might exert high selective pressure upon the flower's morphology, in this example towards extreme elongation of pollinaria stalks.

Angraecum compactum is another living example which may presently pass through an early phase of an evolutionary shift from a medium long-tongued to an extremely long-tongued pollinator. The disadvantage of illegitimate visitors is greater in this orchid than in *Cynorkis*, because not only nectar but also pollinaria are lost. Therefore even a few visits by illegitimate visitors may reduce fruiting success. When this flower is frequently exploited by *X. morgani* and *C. solani* with wastage of the pollinaria, selective pressure towards further increase of the spur length should occur. Their influence would depend on visiting frequency relative to the primary pollinator. As the nectar demand and flight activity of both illegitimate species is much higher than that of the present legitimate visitor, their visiting frequency might be high even if they are less abundant than the primary visitor. If, during evolutionary spur elongation, the upper level of nectar in the spur becomes inaccessible to the tongue of the primary pollinator, the flower may still continue to profit for a while from its visits as a deceptive flower. Even the large *A. sesquipedale* and especially *A. sororium* are still attractive for these shorter-tongued hawkmoths, but the deceit no longer has an advantage for the flowers, because no pollinaria are transferred, or it is sometimes disadvantageous for both, orchid and moth, when pollinaria are wasted and the proboscis coils glued together.

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