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EVOLUTION OF LONG-TONGUED HAWKMOTHS AND POLLINATION OF LONG-SPURRED *ANGRAECUM* ORCHIDS

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Since Darwin the extremely long tongues of tropical hawkmoths have been interpreted to be the result of a coevolutionary race with long nectar spurs of orchids. However, extremely long-proboscis hawkmoths are not restricted to the exploitation of highly specialized sphingophilous flowers. Due to their long tongues and a swing-hovering flight they avoid ambush predators such as huntsman spiders, which lurk among flowers. However, swing-hovering hinders full insertion of the proboscis into the long spurs of orchids. Some orchids prevent the moths from the swinging flight by forcing them to land on their protruding labellum. This is the case with *Angraecum sesquipedale* and *Xanthopan morgani praedicta*. Illegitimate visitors with tongues longer than the orchid spurs can exploit the nectar or even waste the pollinaria, thus exerting selection pressure towards spur elongation with the consequence of pollinator-shift from shorter- to longer-tongued moths.

Introduction

After having inspected one specimen of the long-spurred orchid *Angraecum sesquipedale* Darwin (1862) predicted a pollinating moth with a long proboscis, which could reach the nectar hidden deeply in the spurs. This assumption was supported by Wallace (1867). Rothschild and Jordan in their revision of Sphingid moths (1903) had a choice between two Malagasy hawk moths with such long tongues, *Xanthopan morgani* and *Coelonia solani*. They attributed the "job" of pollinating the long-spurred *Angraecum sesquipedale* to *Xanthopan morgani* and called the endemic Malagasy race *praedicta* with reference to Wallace's prediction. Since then, the extremely long tongues of hawkmoths have been interpreted to be the result of a coevolutionary race with long nectar spurs or tubes of plants as suggested by Darwin and Wallace. Fruit set in European *Platanthera* orchids with long spurs was shown experimentally to be higher in specimens with spurs

slightly longer than the moth's tongue (Nilsson, 1988). There is, however, no evidence for the correlated nutritional dependence of the moths on the orchids, which could exert a high selection pressure on length increase of the moth's tongue. The extremely long-tongued hawkmoths from Madagascar and the tropics of South America are not restricted to an exploitation of highly specialized sphingophilous flowers. They also visit less specialized flowers such as inflorescences of *Lantana camara* or *Clerodendron putre*, Verbenaceae (Wasserthal, 1993).

Flowers, Pollinating Moths and Predatory Spiders

Extremely Long Tongues and Swing-Hovering: Adaptations for Predator Avoidance

With their long tongues and a swing-hovering flight during visits to flowers the hawkmoths

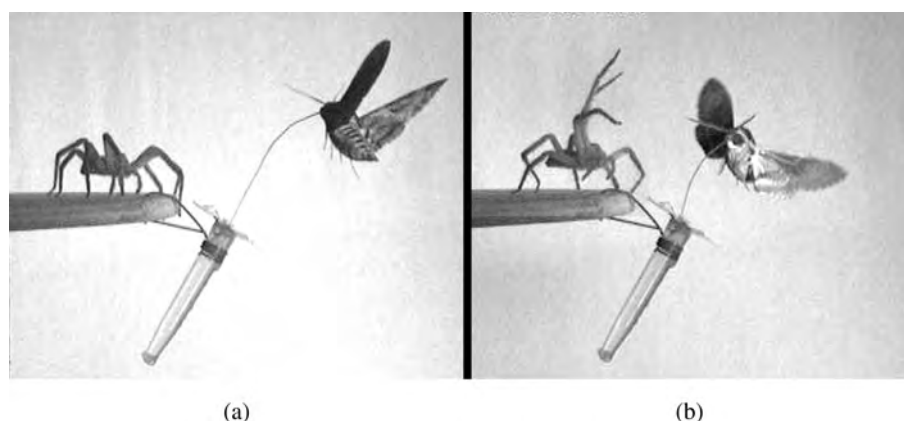


Fig. 1. A *Cupiennius coccineus* spider changes from lurch (a) to attack position (b) without jumping at the hovering *Agrius cingulatus* moth, which is swinging in front of an artificial blossom between position (a) and (b). From Wasserthal (2001).

avoid predators such as huntsman spiders, which produce no webs but locate and catch their prey in vegetation (Wasserthal, 1993, 1996). They sense the wing vibrations of the moths from distances of up to 3 m. The long tongues allow the moths to maintain a safe distance from most flowers they visit and the swing-hovering prevents the predators from targeting the moths and finding the proper moment for an attack (Wasserthal, 2001; Fig. 1). Swinging flight and long tongues are assumed to be very old traits. Hunting spiders existed as far back as the Carboniferous (Kittel, 1910). When hawkmoths appeared on the evolutionary stage they were confronted with predators such as hunting spiders and evolved their long tongues. The long-spurred orchids thus profited from the availability of diverse pre-adapted moths with different tongue lengths. They recruited for the transfer of pollinaria species with tongues best fitted to their actual spur length.

The hypothesis that extremely long tongues evolved as an adaptation to predators was countered with the argument that hunting spiders were not observed in the wild to capture large hawkmoths (Nilsson, 1989). However, these interactions occur in the dark. Also, most flowers are in the canopy of the rainforest, where there is little chance of observing them. Our confrontation experiments with diverse hawkmoths species in the field and greenhouse cages with Malagasy spiders of the family Sparassidae and Costa Rican Ctenid spiders showed that they target and approach the shivering or hovering moths at night (Wasserthal, 1998). Moreover, the longest tongued hawkmoth species occur in the new world tropics with sphingophilous flowers in plant families

other than orchids. Some sphingophilous flowers are suspended in a manner, which allows the moths to swing-hover together with the blossom while their proboscises are fully inserted into the nectar tubes.

How is Angraecum Sesquipedale Pollinated Despite the Impediment of Swing-Hovering?

It was hypothesized that the swing-hovering hawkmoths are incapable of inserting their tongues deeply enough into the spurs of *Angraecum* orchids to obtain nectar and remove the pollinaria, which become attached to the proper (basal) area of the proboscis. To test this hypothesis the visits of *Xanthopan morgani* to *A. sesquipedale* were observed and documented with infrared videos in southeastern Madagascar in 1992. As *Xanthopan* proved to be rare in that area, we introduced two captured individuals into a large flight tent installed in the field above flowering *A. sesquipedale*. The captured male moth already carried at its tongue a viscidium and nectar remnants from the wild. This was the first proof of the pollinator role of *Xanthopan* for *A. sesquipedale*. In the flight tent the male and a female repeatedly visited the flowers. Both stopped the initial swing-hovering when they established leg-contact with the protruding labellum and thus fully inserted the tongue into the spur. They removed the pollinaria and transferred them later to other blossoms (Wasserthal, 1997 and Fig. 2).

A similar interaction exists between *Angraecum sororium*, which also has a protruding

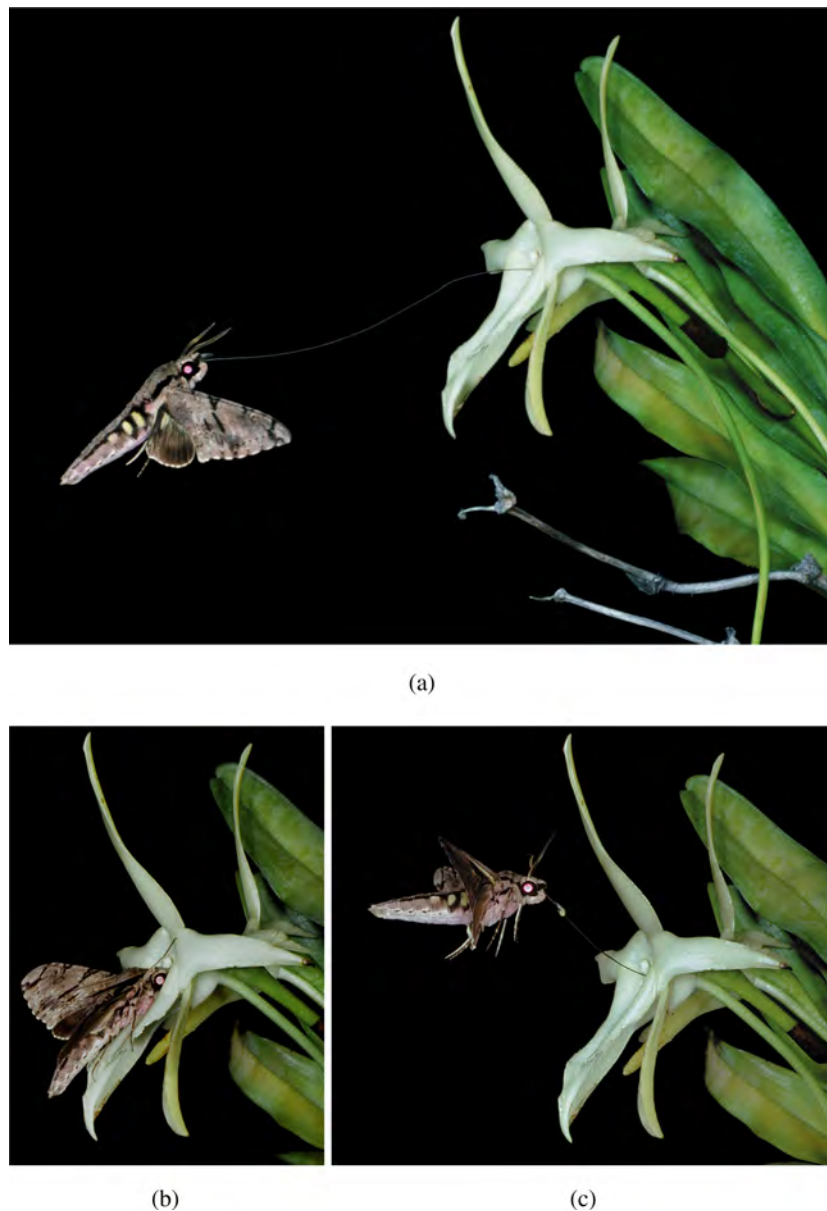


Fig. 2. *Xanthopan morgani praedicta*, first photographic documentation for it as the pollinator of *Angraecum sesquipedale*. (a) Tongue insertion, (b) Landing on the protruding labellum (c) Backwards and upwards flight with pollinarium on the tongue base. From Wasserthal (1997).

labellum and the swing-hovering *Coelonia solani*. One moth species of this guild (*Panogena lingens*) never swing-hovers. This is why they can pollinate orchids with upright rather than protruding labella like *Angraecum arachnites* or species with intermediately long or narrow spurs like *A. compactum* and *A. teretifolium*, which are not pollinated by related species with swing-hovering flight. This confirms observations by Nilsson *et al.*, (1985, 1987) who detected pollinaria of these and other species on different sites on the basal tongue of *Panogena lingens*. Moths with tongues longer than the spurs can become illegitimate visitors and exploit

the nectar without transferring pollinaria, which may even be wasted. This exerts selection pressure towards spur elongation with the consequence of pollinator-shift from shorter tongued moths to longer tongued ones (Wasserthal, 1997; Fig. 3).

***Angraecum longicalcar* — Lack of a Landing Platform as an Obstacle to Successful Pollination**

Angraecum longicalcar is another extremely long-spurred orchid (up to 32 cm in length), which can have as many as 10 blossoms per panicle.

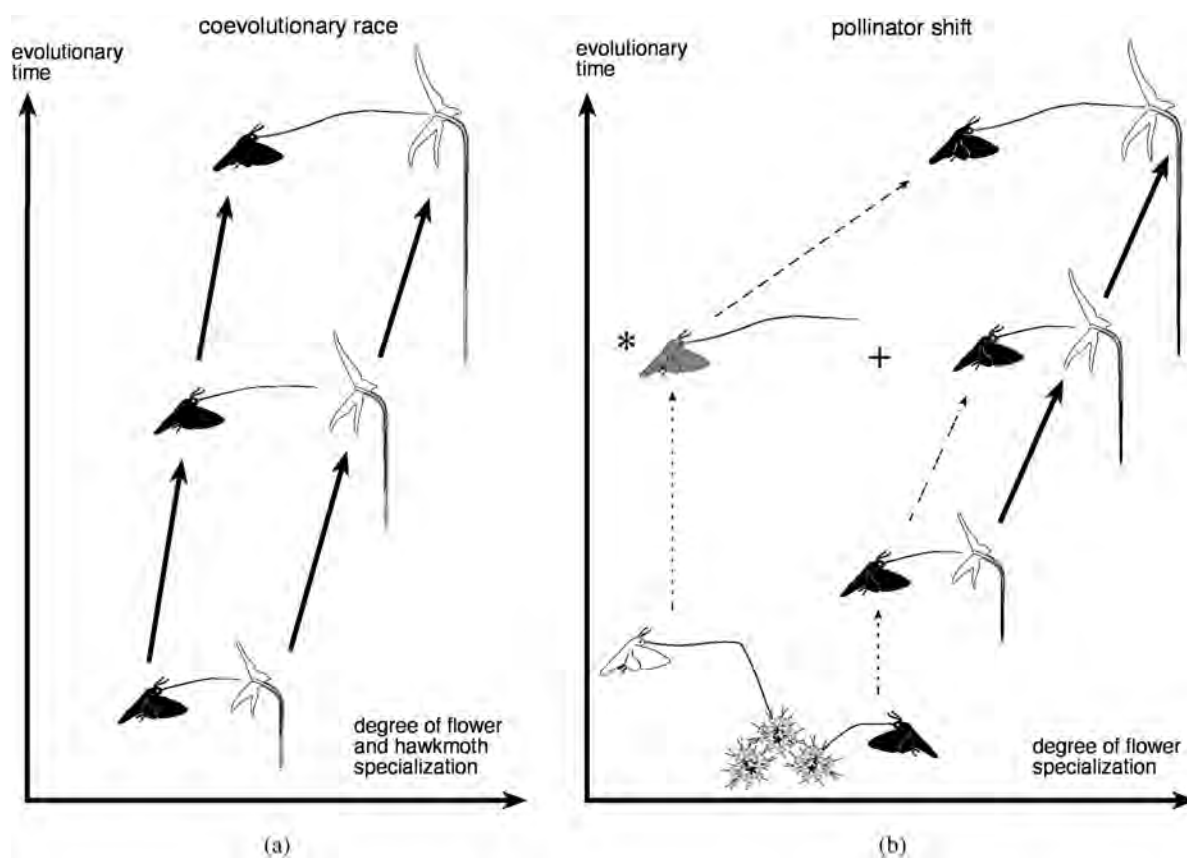
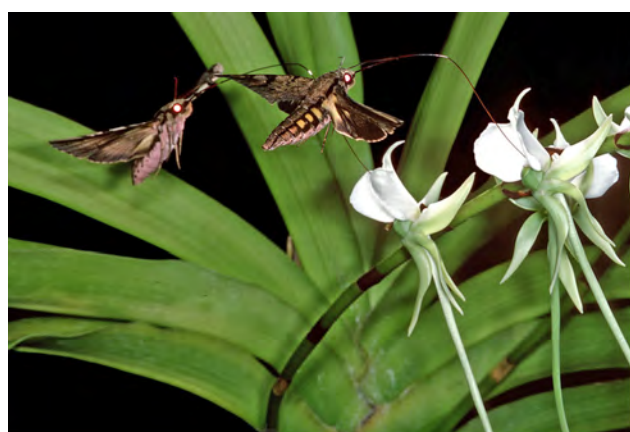
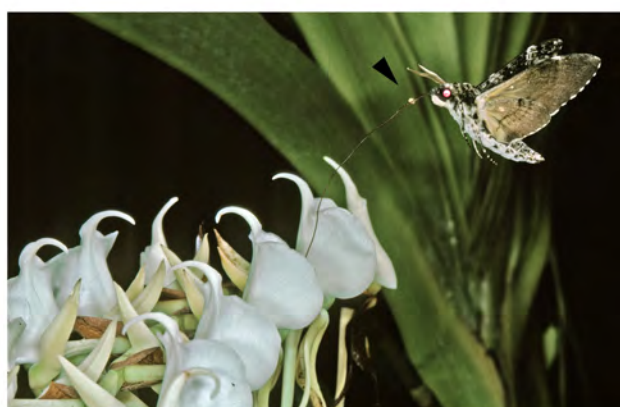


Fig. 3. Comparison of the “coevolution” model of Darwin 1862 (a) and the “pollinator shift” model (b) in orchid spur evolution. (a) Evolutionary race between increasing spur length and increasing tongue length. (b) Recruitment of generalist feeders with preadapted tongues of different lengths as pollinators by long-spurred angraecoid orchids and their successive 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 been represented by the interaction of *X. morgani* and *C. solani* with *Angraecum compactum* (Wasserthal, 1997). When the spurs have reached a length longer than the extremely long tongues of the moths, these become the regular pollinators. When the spur of the flower reaches a size which places the nectar column out of reach for the primary pollinator, the flower may still be pollinated by this species but it now acts as a deceptive blossom. Black: orchid pollinator; grey: non-pollinating orchid visitor; white: moth incapable of exploiting the orchid. From Wasserthal (1997).



(a)



(b)

Fig. 4. (a) Two *Xanthopan morgani praedicta* swing-hovering in front of *Angraecum longicalcar* without an attempt to fully introduce extended tongues into the spur. The moths did not obtain access to the nectar column and did not remove the pollinaria. (b) An unusual not spontaneously swing-hovering female *Coelonia solani* removed and transferred the pollinaria at the base of the proboscis (arrowhead). This is the first documentation of a successful visit to *Angraecum longicalcar* by an extremely long-tongued hawkmoth.

It has an upright labellum, not appropriate for landing. This Malagasy endemic orchid has vanished from its natural habitat. We obtained plants from Marcel Lecoufle in Paris in 1994 and cultivated them until now. In addition, we bred all relevant long-tongued hawkmoths species in our Erlangen greenhouse in a subtropical climate. We synchronized the eclosion of the moths with the flowering season of the orchids between 1995 and 2009. In confrontation experiments with 21 *Xanthopan morgani praedicta* all proved to be unable to introduce their tongues deeply enough into the spurs to obtain nectar because the labellum is upright and the blossom structure is such that the moth could not land. Thus the moths swing-hovered and moved restlessly from blossom to blossom without a chance of coming close enough to obtain nectar, which is in the distal half of the spurs (Fig. 4a). The other Malagasy Sphingid with an extremely long tongue, *Coelonia solani*, was also confronted with this orchid and one individual of seven with a tongue length of 19 cm removed and transferred the pollinaria (Fig. 4b). It was an individual which was exceptional in not exhibiting spontaneous swing-hovering. All 19 tested *Panogena lingens* were not capable of obtaining nectar, as their tongues (maximum length between 7.4 and 11.5 cm) were too short to reach it. None of the moths removed the pollinaria, although they inserted the tongue fully into the spur. Perhaps the dimension and proportions of this orchid are too large for the slender tongue of *Panogena*.

The observed interactions of angraecoid orchids with sphingid moths confirm Darwin's hypothesis that these flowers are dependent on moths with correspondingly long proboscises for their pollination. These moths "pay" for the nectar reward with impaired mobility. Long tongues and the swing-hovering behavior are pre-adapted to avoid predator attacks. The orchids take advantage of the extremely long-tongued and big moths, which consume large volumes of nectar due the high energy demands of their powerful flight.

Acknowledgements

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