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## Deep flowers for long tongues

Key words: Coevolution Blütenbesuch Räuber

In 1862 Charles Darwin proposed that the evolution of flower depth and insect tongue length is driven by natural selection due to mutual gain from the plant-animal interaction<sup>1</sup>. His partial evidence for such coevolution was the star orchid of Madagascar *Angraecum sesquipedale*, with a nectariferous flower spur '11½ inches long'. But no insect with a matching long tongue for nectar extraction was known. Darwin simply predicted the existence of a giant pollinator hawkmoth in Madagascar that was, tongue-wise, capable of handling the orchid's extraordinary nectar position. His prediction was ridiculed by entomologists. In response, the star orchid-hawkmoth interaction was discussed in greater detail in 1867 by Alfred Russel Wallace in his supportive paper 'Creation by law' defending the theory of natural selection (Fig. 1)<sup>2</sup>.

Fritz Müller (dubbed 'the Duke of Observation' by Darwin), who had emigrated to Brazil in 1852, showed in 1873 via his brother Hermann that hawkmoths with tongues capable of sucking such deep-seated nectar existed<sup>3</sup>. The pollinator candidate hawkmoth of the star orchid of Madagascar was later recovered and described in 1903 under the history-associative name *Xanthopan morgani praedicta*<sup>4</sup>. However, while the relationship between shorter-spurred *Angraecum* orchid species and shorter-tongued hawkmoth species in natural populations in Madagascar has been verified<sup>5</sup>, Darwin's famous predicted interaction between *Angraecum sesquipedale* and its pollinator hawkmoth, although continuously revolving in the scientific literature, has eluded empirical documentation.

In a recent report in *Botanica Acta*, based on analyses of flower-visits by caged *X. m. praedicta* hawkmoths to flowers of *A. sesquipedale*, L.T. Wasserthal not only describes the pollination mechanism, but also challenges Darwin's theoretical model for the flower depth-tongue length evolution<sup>6</sup>. Wasserthal's main contention is that *praedicta*'s impressive tongue length (up to 25 cm, Fig. 2) does not reflect coevolution with plants, as proposed by Darwin and Wallace, but evolution for avoidance of predators. In Wasserthal's model, *praedicta*'s tongue elongation has primarily evolved to increase distance-keeping and sideways oscillating hovering against predators that ambush at visited shallow flowers of other nectariferous plant species. According to this model, the star orchid has been driven to great flower depth not by a coevolutionary race with

*praedicta* but by a pollinator shift to it—that is, one-sided plant adaptive evolution.

Wasserthal's report increases our knowledge about the possible natural interactions substantially. However, evidence for the proposed predator-avoidance hypothesis is not unequivocal. In particular, quantitative data showing that systematic predator-ambushing for large hawkmoths at flowers exists have never been reported. At most, single large mantids or spiders

have been observed occasionally to capture smaller species<sup>7,8</sup>. Furthermore, the endemic Malagasy race *praedicta* belongs to a species that consists of two recognized races. The second race, *morgani*, is widely distributed over tropical Africa. In Madagascar, the guild of long-tongued hawkmoths is greater than in Africa (five species compared to three species with average tongue length >9 cm), and the Malagasy hawkmoth *Coelonia solani*, which is absent from Africa, almost matches *praedicta* in tongue length<sup>5</sup>. Thus, it seems more likely that *praedicta*'s long tongue has originated by a coevolutionary race between hawkmoths competing for nectar.

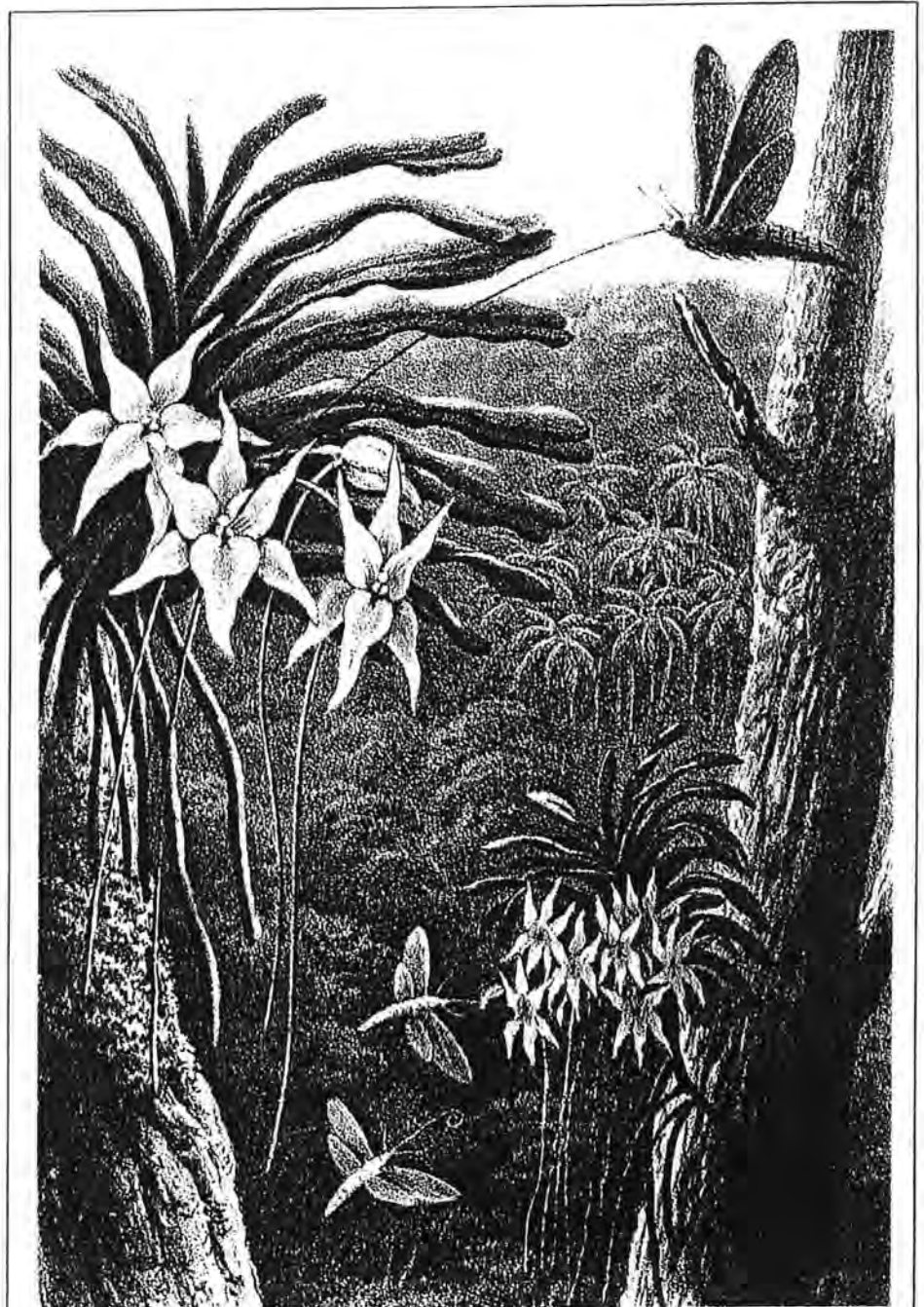


Fig. 1. Natural selection at its famous extreme. Darwin's predicted pollination of the star orchid of Madagascar as illustrated in Wallace's article<sup>2</sup>.



Fig. 2. Madagascar's *Xanthopan morgani praedicta*, the longest-tongued hawkmoth of the Old World. Photo by Börge Pettersson and L. Anders Nilsson.

The world's most long-tongued species of hawkmoths, one of which is *X. morgani praedicta*, are also among the largest and/or heaviest and most primitive (i.e. exhibiting the lowest number of specialized traits) within the Sphingidae<sup>4</sup>. Their primitiveness also probably includes physiological traits for flight and behaviour, and so there may be reason to believe that these hawkmoths are particularly susceptible to energy-limitation and thus prone to an evolutionary race in tongue length for more nectar.

In Madagascar there is a guild of more or less unrelated plant species (one of which is *A. sesquipedale*) whose flower depth fit *praedicta*'s average tongue length. Similar pollinator-matching plant guilds exist in other parts of the world with

long-tongued hawkmoths, such as the Neotropics<sup>9,10</sup>. Extreme tongue length is clearly not a shared derived character among the hawkmoth species<sup>4</sup>; it has arisen within several geographically separate lineages (one of which is *X. morgani praedicta*). That evolution for the avoidance of (still unknown) predators would, in multiple, geographically separate lineages, result in extreme tongue elongation, and in turn in extreme flower depth guilds by pollinator shift, seems improbable. Finally, Wasserthal's pollination mechanical data appear to contradict his own pollinator-shift hypothesis: pollen for transfer and adaptive spur evolution can only be carried at the basalmost portion of the tongue, whereas hawkmoths with tongues considerably longer than the flower depth (as in the case of a proposed shift to a suddenly great tongue length evolved for predator avoidance) receive distally attached pollen that becomes wasted. There is merely a mechanical constraint against great shifts in exploited tongue length. On balance, the evidence still suggests that the star orchid has been evolutionarily driven to great flower depths according to Darwin's classical model of a coevolutionary race, whereby the hawkmoth visitor is compelled to insert its tongue into the very base, and thus to selectively pollinate, deeper flowers than its tongue reach<sup>11</sup>.

The new hypothesis on the evolution of long tongues and deep flowers remains to be tested in the field. Wasserthal's evidence for interaction in the wild between *X. m. praedicta* and *A. sesquipedale* was a single viscidium of a pollinarium discovered on the tongue of a field captured male introduced into the flight tent. What is still needed after 135 years is quantitative observational data of *X. m. praedicta* pollinating *A. sesquipedale* in natural populations. This magnificent orchid grows epiphytically in the coastal rainforest of Eastern

Madagascar, a disappearing unique habitat. To explore Darwin's prediction is indeed a race against time. Wasserthal's study serves commendably to highlight the irreparable losses under way – losses that will only be mitigated through cooperation with local researchers.

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## Deep flowers for long tongues

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Darwin<sup>1</sup> explained deep-spurred flowers as adaptations to long-tongued pollinators. This spur elongation model was experimentally tested in some European orchids with rather short spurs<sup>2</sup>. The reciprocal effect in the coevolutionary race model<sup>1</sup>, postulating that the long tongues evolved as adaptation to exploit long-tubed flowers – favoured in Nilsson's news & comment article<sup>3</sup> about my paper<sup>4</sup> – has never been confirmed. The pollinator shift model<sup>4</sup> is a modification of the spur elongation model, entailing the 'driving force' of a nectar-exploiting competitor with a longer tongue than the 'legitimate' pollinator(s). It was established after the following facts and arguments favouring the hypothesis that long tongues evolved for predator avoidance<sup>5-7</sup>:

- Individuals of European long-tongued hawkmoths (*Agrius convolvuli*) exhibited a swing-hovering behaviour and were incapable of inserting their tongues into long-tubed tobacco flowers<sup>5</sup>.
- Swing-hovering has been discovered in almost all long-tongued Malagasy hawkmoths and recently in several related Central/South American species<sup>5,6</sup>.
- In primarily nonswinging individuals, swing-hovering could be induced by simulated predator stimuli<sup>5</sup>.
- Heteropodid spiders in Madagascar and ctenid spiders in Costa Rica systematically pursue and jump at shivering or hovering moths<sup>7</sup>.
- Long-tongued hawkmoths are generalist feeders; they skilfully exploit small and shallow flowers (e.g. of Verbenaceae<sup>5</sup>).
- The Old World *Xanthopan* and the New World *Cocytius* are regarded as close relatives, with their very long tongue being a basic trait of ancestral Sphingicae and Acheronticae<sup>8</sup>.
- Their hairy caterpillars feed on primitive angiosperms (Annonaceae)<sup>7,9</sup>.
- The sphingophilous long-tubed flowers, especially the orchids, are of more recent origin, and the ancestors of their modern pollinators visited less-specialized flowers of older plant families<sup>10</sup>.

When extremely long tongues are old adaptations against ambushing predators, they cannot have been evolved in a race with long-tubed flowers. No data confirm the obligatory synchrony and syntopy of *Xanthopan morgani praedicta* and *Angraecum sesquipedale* necessary



for a coevolutionary race<sup>4</sup>. Why should a spur increase its length further after having reached an optimal length with regard to its present pollinator(s) without interference with an additional longer-tongued competitor? The documented visits of *Xanthopan* to *Angraecum compactum* under wastage of pollinaria may serve as an example of a pollinator shift in its early stages; it is not a sudden event but a long-term process<sup>4</sup>.

The pollinator shift model is based on more examples (e.g. *Coelonia solani* and *Angraecum sororium*) and field data than mentioned by Nilsson<sup>3</sup>. When he suggests<sup>3</sup> that 'quantitative observational data of *X. m. praedicta* pollinating *A. sesquipedale* in natural populations are still needed after 135 years ... to explore Darwin's prediction' he seems to have overlooked that this was the intention and part of my study! However, with fewer than one fruit among 200 examined flowers and two captured *Xanthopan* within one month it is hopeless to observe even one pollinator interaction in the habitat. It was rather good luck to find a viscidium at all! In 1943, when in the same location the fruit setting was about 75%, Denso<sup>11</sup> captured only one *Xanthopan* and observed no pollinators over three years.

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In a recent *TREE* article<sup>1</sup>, L.A. Nilsson describes the fascinating coevolution between tropical deep corolla flowers and their pollinators the 'long-tongued' hawk-moths, drawing attention to an old controversy in evolutionary biology. Nilsson attributes adaptations in the feeding apparatus of the moths and the spurs of the flowers to coevolution, hence following the interpretation of Darwin and Wallace. He doubts Wasserthal's recent suggestion<sup>2</sup> that a long tongue is an anti-predator adaptation, pointing out that 'quantitative data showing that systematic predator-ambushing for large hawk-moths at flowers exists have never been reported'<sup>1</sup>.

However, there is no reason to expect ambushing predation, implicating spiders and mantises, nor that the predation has to be systematic. First, mantids and spiders are probably minor predatory groups on hawk-moths compared to flying vertebrates such as birds and bats. Second, predation differs from other selective agents in that it only has to occur once. There is indirect evidence that the long-tongued hawk-moths (subfamily Macroglossinae), illustrated by the elephant hawk-moths *Deleiphila elpenor* and *D. porcellus*, are subject to predation from both birds and bats while feeding on flowers. Adults of these species occur in June and July in the northern Palearctic. They start to feed shortly after sunset, while there is still a fair amount of light, and continue until midnight<sup>3</sup>, and are thus exposed both to birds and bats successively.

*Deleiphila elpenor* is brightly coloured in pink red and olive green. Its beauty, the real adaptive significance of which can only be appreciated when the moth is seen in its natural surroundings, is simply a camouflage when the moth is feeding on its preferred pink flowers (e.g. *Lychnis viscaria*) dispersed among green leaves and stalks. This presumably works as a protection from birds.

Members of the subfamily Macroglossinae possess ultrasonic bat-detecting organs consisting of modified labial palps<sup>4</sup>. *Deleiphila elpenor* feeding at *L. viscaria* in southern Sweden (57°N) responds strongly to ultrasonic pulses (26 kHz, 100 dB SPL at 1 m) delivered at distances of 1–20 m. They either leave the flower rapidly or they freeze while still attached to it (J. Rydell and M.G.E. Svensson, unpublished). Both responses are highly adaptive defences against echolocating bats. We have argued elsewhere<sup>5</sup> that a crepuscular activity pattern typical of many moths is in itself an anti-predator behaviour. It minimizes the exposure to birds on the one hand and bats on the other.

Predation is a very strong selective force, as a mistake may be deadly. The fact that no predation attempts have been observed in the case of hawk-moths cannot be used to argue that the observed trait is not an effect of predation. We provide three pieces of evidence that feeding is a dangerous business for hawk-moths, and therefore provide support for Wasserthal's interpretation<sup>2</sup>. The vast richness of colours and forms of animals in nature can surprisingly often be explained as adaptations against predation.

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Nilsson<sup>1</sup> presents a cogent argument in support of Darwin's classic model of a coevolutionary relationship between long moth-tongues and deep corollas. This is no mean feat on the part of the moth. *Convolvulus* hawks (*Herse convolvuli*) in South Africa insert their 10 cm tongues within a fraction of a second, hover for less than 3 seconds and then move to the next flower. The tongues are indeed inserted so that the head is close to the corolla opening. It is done with such accuracy and speed that strong selection pressures are presumably at work. Several hundred flowers from various individual plants are visited in one night. A dozen or so moths may be in the local area for two or three nights and then all the moths move on to a new site.

Can we exclude predation as a selective force in this behaviour? Might current behaviour be a ghost of past selection pressures? *Convolvulus* hawkmoths hover steadily; there is no side-to-side movement – indeed, they appear almost fixed. A solid-substrate based predator like a mantid or spider would have to find purchase in order to strike, and it would not have a firm foothold on a flimsy corolla. Much more likely is predation from flying predators – bats. But can such a predator approach the feeding prey unhindered? On balance, Nilsson<sup>1</sup> is probably correct in that the primary driver has been coevolution between plant and moth, but if it were not for flying predators, the interaction might not have the exquisite elegance we see today.

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### Editor's note

A reply from Nilsson will appear in a subsequent issue of *TREE*.

## Reply from M. Heino, J.A.J. Metz and V. Kaitala

Éva Kisdi clarifies the relationships between frequency dependence, optimization and ESSs. We basically agree with all her comments. However, some further clarification may be useful.

In the first paragraph of Kisdi's letter, ESSs and optimal strategies are seemingly opposed by saying that 'finding an optimal strategy is a considerably stronger result than finding an ESS'. Although this statement is factually correct, it might engender a suggestion that is slightly wrong. Conceptually, ESSs are always primary: only ESSs matter from the viewpoint of long-term evolution. Optimization is secondary only, and must be justified by an ESS argument that explicitly accounts for the ecology in which the evolutionary problem is embedded. When we approach the problem from this angle it is found that there exist special ecological circumstances for which the ESSs satisfy an optimization principle (that is, the rather exceptional one-dimensional environments).

Kisdi characterizes one-dimensional environments by assuming that 'fitness is an increasing function of a single environmental factor'. Since precision matters here, mainly for technical reasons<sup>1</sup>, we suggest rephrasing this statement as 'fitnesses depend uniformly monotonically on a single environmental factor'. Dependence on the environment is 'uniformly monotonic' only if it is monotonic in the same direction for every possible value of the evolutionary trait. This condition is both necessary and sufficient for the ESS to be characterizable by an optimization principle.

To conclude, we agree that the analysis of certain simple models can be done by optimization arguments in place of an ESS analysis. Since optimization tools are usually easier to use, such methods are preferable whenever they are appropriate. But considerable care is needed, as the conditions under which optimization methods apply are ecologically a lot more restrictive than is commonly realized.

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## Deep flowers for long tongues: reply from L.A. Nilsson

The core for disagreement about the tongue-flower elongation, coevolution versus non-coevolution, is whether a long hawkmoth tongue is used primarily for feeding or for predator avoidance. Wasserthal<sup>1</sup> considers his predation hypothesis for tongue length confirmed, but his three cited papers lack quantitative data on natural predation. Svensson *et al.*<sup>2</sup> argue in support of his interpretation by anecdotal evidence. They miss the flight-elongation focus. However, I agree with them and with Samways<sup>3</sup> that major predation on large hawkmoths is expected from flying vertebrates, not arthropods in ambush à la Wasserthal.

Nectar-extracting mouthparts have attained impressive extremes in euglossine bees (4 cm), nemestrinid flies (8 cm) and hummingbirds (10 cm), each set of taxa using/pollinating a unique guild of deep-flowered plants<sup>4,5</sup>. Nothing suggests that predator avoidance has influenced the elongation (co)evolution. Long-tongued hawkmoths and their deep flowers, although displaying world records (30 cm and 40 cm, respectively), are hardly exceptions in this respect. The various very deep-flowered angiosperms (e.g. *Epiphyllum* in neotropical Cactaceae) are probably coevolved with hawkmoth tongues.

Hawkmoth flight repertoires include 'on-the-spot' hovering as well as 'swing-hovering' during flower-visits. Also, hummingbirds, long-tongued solitary bees (euglossines, anthophorids) and long-tongued flies (horseflies, nemestrinid and bee flies) hover on-the-spot. No doubt this behaviour favours targeting and insertion precision with the extended mouthparts into narrow nectariferous structures. Extremely long-tongued hawkmoths probably require even more precision control. Added swing-hovering may increase visual and/or olfactory information about the position of the flower. Anti-predator adaptations, on the other hand, are to be expected among other traits.

Basal hawkmoth clades contain the long-tongued taxa<sup>6</sup>. But modern phylogenetic analyses (so badly needed!) are likely to show a very long tongue to be a derived, relatively late trait within several lines (e.g. *Amphimoea*, *Coelonia*). Furthermore, very long-tongued hawkmoths might not be true generalists but instead might have guild constancy under natural, undisturbed conditions. Their opportunistic exploitation of pantropical weedy *Lantana*<sup>7</sup>, a lepidopteran-adapted species, is hardly surprising.

Wasserthal's argument that 'obligate synchrony and syntopy' of *Xanthopan morgani praedicta* and *Angraecum sesquipedale* would have been required

for coevolution is flawed. These interactors are participants of coevolving guilds<sup>8</sup>. Various pollinator shifts may well have occurred, as are commonplace in the history of orchids and other angiosperms<sup>9,10</sup>. Coevolution and shifting occur by relatively 'better' pollinators. The basis for Darwin's reciprocal-effect model is that a competitive visitor with a non-bottom-reaching tongue better contacts the flower's pollination organs<sup>11</sup>. The depth of spur and the length of reward-extracting organ become inter-dependent and matching at the population level<sup>12</sup>. A consistently bottom-reaching, although competitive, hawkmoth tongue excludes pollinator shifts, as indicated by *Xanthopan* on *Angraecum compactum*<sup>7</sup>. Some 100 Madagascan angraecoids have demonstrably retained adaptation to medium-tongued hawkmoths. *Angraecum sesquipedale*, guild-member angiosperms, *Xanthopan* and major hawkmoth competitors are evidently coevolved.

The intention of Wasserthal's study has not been overlooked, nor has the difficulty of obtaining natural interaction data. Our team still recorded frequent pollination of *A. sesquipedale* in 1983 and 1986. Wasserthal's study of the same populations, species and systems in Madagascar has partly led to more questions than answers, and he has yet to adopt a plausible evolutionary interpretation of his observations.

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## Letters to TREE

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Kura makes some calculations which he believes show that the benefits (gained by *C. briggsae* as a result of outcrossing) accrue to the species or to the deme and not to the individual. I fail to see how they lead to the conclusion he draws. Kura then asks why the hermaphrodites intensely resist the X chromosome of males, or something to that effect. I don't see any evidence that they do so. It is difficult to explain why the X chromosome of *C. elegans* is also not selfish; such overtly selfish elements do seem to be rather rare, for reasons that we do not fully understand. But, in any case, I do not see what local mate competition has to do with it.

Kura's question as to which is more advantageous – self-fertilization or meiotic drive – is misleading. Such questions cannot be answered unless we specify from whose point of view we are thinking of the advantage. Moreover, there is probably no meiotic drive here; gametic selection is sufficient to explain the observed phenomenon. I have argued that one should expect the hermaphrodite to cooperate in suppressing the male's null-X sperm<sup>6</sup>. This is quite correct, but it does not mean that the cooperation of the hermaphrodite is essential; gametic selection on the male's selfish X chromosome may be sufficient to produce the observed phenomenon even without the cooperation of the hermaphrodite.

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## Deep flowers for long tongues: a final word

Ever since it was coined by Ehrlich and Raven<sup>1</sup>, the term 'coevolution' has often been used indiscriminately in interpretations of insect–plant relationships, although in the meantime it became more precisely defined. To avoid misleading interpretations, it is advisable to restrict the use of this term to cases in which 'reciprocal evolutionary change in interacting species'<sup>2</sup> can be proved at least by circumstantial evidence. Reciprocal evolutionary changes occur in two interacting organisms, if symmetrical selection pressures act, that is, if a change in the traits of organism A selects the organism B for a corresponding change. This happens if the existence (the overall fitness) of organism A depends on the coexistence of organism B, and vice versa. Fig species and most fig wasp species are the textbook examples of such symmetrical interactions, as neither would exist without the other.

In contrast, the relationship between the orchid *Agraecum sesquipedale* and its pollinator the hawkmoth *Xanthopan morgani* *predicta*, discussed recently by Nilsson<sup>3</sup> and in subsequent correspondence in *TREE*<sup>4,5</sup> is clearly asymmetrical. There is no mutual dependence between the two partners, since the orchid's existence (fitness) fully depends on the coexistence of the extremely long-tongued hawkmoth, while the moth could exist in the absence of deep flowers because it is also able to feed on different shallow flowers. Nilsson's argument that 'these hawkmoths are particularly susceptible to energy-limitation and thus prone to an evolutionary race in tongue length for more nectar', that is, that *X. m. predicta* has been selected by nectar competitors for a long tongue, is speculation that would need thorough quantitative field studies on the flower-visiting behaviour of the coexisting hawkmoth and other pollinator species before it could be accepted. Wasserthal's<sup>6</sup> hypothesis, questioned by Nilsson, that predation has selected the moth for long tongue also needs more supporting evidence. So, at present there is no convincing explanation for the adaptive significance of *X. m. predicta*'s long tongue – if there is any (see Gould and Lewontin's<sup>7</sup> often-forgotten criticism of the adaptationist view).

Yet, there is an important point that should be considered. The special characteristic of hawkmoth feeding behaviour – sucking nectar while hovering over the flowers – is possible only because the moths have relatively long tongues and, vice versa, long tongues enable the moths to feed during hovering. That means that a long tongue is a fundamental family character of sphingids independent of the morphology of flowers on which the various hawkmoth species feed. This morphological character might have evolved earlier than the flowers with extremely long spurs<sup>6</sup>. (It would be ridiculous to look for the adaptive advantage of hovering over the feeding behaviour of other lepidopterans.) This explains why there are long-tongued hawkmoth species in regions, like Central Europe, where deep-flowered plant species are scarce.

Variation in tongue length among hawkmoth species may result from genetic changes in the process of moth speciation. Extremely long-tongued hawkmoths then could select flowers for extremely long spurs and so provide reproductive isolation among plant lines differing in spur length as expounded by Wasserthal<sup>6</sup>. In the end, this could foster plant speciation without any evolutionary feedback to the moths.

In conclusion, deep flowers are for long tongues, otherwise such flowers could not exist. Long tongues, however, are not for deep flowers, as feeding with long tongues is possible also on shallow flowers. Thus, Wasserthal's opinion that great flower depth is the result of a one-sided plant adaptive evolution is more plausible than Nilsson's evoking the ghost of coevolution past for explaining the origin of this plant–pollinator relationship.

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