Wallace's Moth and Darwin's Orchid

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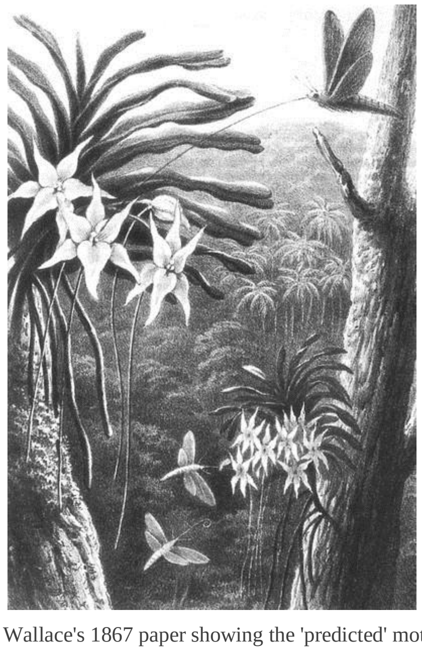
In January 1862 Charles Darwin was given a specimen of the Madagascan orchid *Angraecum sesquipedale* and was amazed by its spectacular flowers, which have a 30cm+ long hollow spur containing nectar near the bottom. He remarked in a letter to his friend Joseph Hooker "I have just received...a Box...from Mr Bateman with the astounding Angræcum sesquipedalia with a nectary a foot long— Good Heavens what insect can suck it". Later that year he published his book *On the various contrivances by which British and foreign orchids are fertilised by insects, and on the good effects of intercrossing* (Darwin, 1862) and predicted that a moth would be found in Madagascar with a proboscis long enough to reach the nectar at the end of the spur, a suggestion that some of his colleagues scoffed at. A few years later in 1867 Alfred Russel Wallace published an article in which he supported Darwin's hypothesis, remarking that the African hawkmoth *Xanthopan morganii* (then known as *Macrosila morganii*) had a proboscis almost long enough to reach the bottom of the spur. In a footnote to this article Wallace wrote "That such a moth exists in Madagascar may be safely predicted; and naturalists who visit that island should search for it with as much confidence as astronomers searched for the planet Neptune, -and they will be equally successful!" (Wallace, 1867).

It was only in 1903 that a population of *Xanthopan morganii* (commonly called Morgan's Sphinx Moth) with an especially long proboscis was discovered in Madagascar, and it was named subspecies *praedicta* by Rothschild & Jordan in honour of Wallace's (*not* Darwin's) prediction (Darwin's prediction was not even mentioned in their paper: see Rothschild & Jordan (1903)). Since Wallace predicted that the mystery pollinator would turn out to be a hawkmoth (he even included an illustration of a hawkmoth pollinating the orchid in his article - see image below), rather than simply a large moth as Darwin had suggested, and given that the subspecies name specifically refers to Wallace's speculations about it, I think that it would be appropriate if its common name was Wallace's Sphinx Moth. How fitting that Darwin's Orchid (as *Angraecum sesquipedale* is often called) should be pollinated by Wallace's Sphinx Moth!



The figure from Wallace's 1867 paper showing the 'predicted' moth. Note that this is a 'generalised' hawkmoth but is it recognizable as being of subfamily Sphinginae and tribe Sphingini. This is the tribe which *Xanthopan* belongs to (Ian J. Kitching, pers. comm., 2010).

Curiously enough it took until 1997 for someone to confirm that Wallace's Sphinx was indeed the pollinator of Darwin's Orchid (Wasserthal, 1997) and several mysteries still remain.

Darwin and Wallace proposed different evolutionary scenarios to explain why the orchid had evolved such a long spur and its pollinator a correspondingly long proboscis, and evolutionary biologists are still undecided as to the true explanation (see http://www.ncbi.nlm.nih.gov/pmc/articles/PMC2500161/).

This is what Darwin wrote about the moth and the orchid in his 1862 book:

> ...I must say a few words on the Angræcum sesquipedale, of which the large six-rayed flowers, like stars formed of snow-white wax, have excited the admiration of travellers in Madagascar. A whip-like green nectary of astonishing length hangs down beneath the labellum. In several flowers sent me by Mr. Bateman I found the nectaries eleven and a half inches long, with only the lower inch and a half filled with very sweet nectar. What can be the use, it may be asked, of a nectary of such disproportional length? We shall, I think, see that the fertilisation of the plant depends on this length and on nectar being contained only within the lower and attenuated extremity. It is, however, surprising that any insect should be able to reach the nectar: our English sphinxes have probosces as long as their bodies: but in Madagascar there must be moths with probosces capable of extension to a length of between ten and eleven inches!
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> ...I could not for some time understand how the pollinia of this Orchid were removed, or how it could be fertilised. I passed bristles and needles down the open entrance into the nectary and through the cleft in the rostellum with no result. It then occurred to me that, from the length of the nectary, the flower must be visited by large moths, with a proboscis thick at the base; and that to drain the last drop of nectar even the largest moth would have to force its proboscis as far down as possible... it cannot, I think, be doubted that a large moth must thus act; namely, by driving its proboscis up to the very base, through the cleft of the rostellum, so as to reach the extremity of the nectary; and then withdrawing its proboscis with the pollinia attached to it.
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> ...If the Angræcum in its native forests secretes more nectar than did the vigorous plants sent me by Mr. Bateman, so that the nectary becomes filled, small moths might obtain their share, but they would not benefit the plant. The pollinia would not be withdrawn until some huge moth, with a wonderfully long proboscis, tried to drain the last drop. If such great moths were to become extinct in Madagascar, assuredly the Angræcum would become extinct. On the other hand, as the nectar, at least in the lower part of the nectary, is stored safe from depredation by other insects, the extinction of the Angræcum would probably be a serious loss to these moths. We can thus partially understand how the astonishing length of the nectary may have been acquired by successive modifications. As certain moths of Madagascar became larger through natural selection in relation to their general conditions of life, either in the larval or mature state, or as the proboscis alone was lengthened to obtain honey from the Angræcum and other deep tubular flowers, those individual plants of the Angræcum which had the longest nectaries (and the nectary varies much in length in

> some Orchids), and which, consequently, compelled the moths to insert their probosces up to the very base, would be fertilised. These plants would yield most seed, and the seedlings would generally inherit longer nectaries; and so it would be in successive generations of the plant and moth. Thus it would appear that there has been a race in gaining length between the nectary of the Angræcum and the proboscis of certain moths; but the Angræcum has triumphed, for it flourishes and abounds in the forests of Madagascar, and still troubles each moth to insert its proboscis as far as possible in order to drain the last drop of nectar.

And this is what Wallace wrote in his 1867 paper "Creation by Law." (*Quarterly Journal of Science* 4: 471-488):

> I maintain...that the laws of multiplication, variation, and survival of the fittest, already referred to, would under certain conditions *necessarily* lead to the production of this extraordinary nectary. Let it be remembered that what we have to account for is only the unusual length of this organ. A nectary is found in many orders of plants and is especially common in the Orchids, but in this one case only is it more than a foot long. How did this arise? We begin with the fact, proved experimentally by Mr. Darwin, that moths do visit Orchids, do thrust their spiral trunks into the nectaries, and do fertilize them by carrying the pollinia of one flower to the stigma of another...In our British species, such as Orchis pyramidalis, it is not necessary that there should be any exact adjustment between the length of the nectary and that of the proboscis of the insect, and thus a number of insects of various sizes are found to carry away the pollinia and aid in the fertilization. In the Angræcum sesquipedale, however, it is necessary that the proboscis should be forced down into a particular part of the flower, and this would only be done by a large moth straining to drain the nectar from the bottom of the long tube.[1] Now let us start from the time when the nectary was only half its present length or about six inches, and was chiefly fertilized by a species of moth which appeared at the time of the plant's flowering, and whose proboscis was of the same length. Among the millions of flowers of the Angræcum produced every year some would always be shorter than the average, some longer. The former, owing to the structure of the flower, would not get fertilized, because the moths could get all the nectar without forcing their trunks down to the very base. The latter would be well fertilized, and the longest would on the average be the best fertilized of all. By this process alone the average length of the nectary would annually increase, because, the short ones being sterile and the long ones having abundant offspring, exactly the same effect would be produced as if a gardener destroyed the short ones and sowed the seed of the long ones only; and this we know by experience would produce a regular increase of length, since it is this very process which has increased the size and changed the form of our cultivated fruits and flowers.
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> But this would lead in time to such an increased length of the nectary that many of the moths could only just reach the surface of the nectar, and only the few with exceptionally long trunks be able to suck up a considerable portion.
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> This would cause many moths to neglect these flowers because they could not get a satisfying supply of nectar, and if these were the only moths in the country the flowers would undoubtedly suffer and the further growth of the nectary be checked by exactly the same process which had led to its increase. But there are an immense variety of

moths of various lengths of proboscis, and as the nectary became longer other and larger species would become the fertilizers, and would carry on the process till the largest moths became the sole agents. Now, if not before, the moth would also be affected, for those with the longest probosces would get most food, would be the strongest and most vigorous, would visit and fertilize the greatest number of flowers, and would leave the largest number of descendants. The flowers most completely fertilized by these moths being those which had the longest nectaries, there would in each generation be on the average an increase in the length of the nectaries, and also an average increase in the length of the proboscis of the moths, and this would be a *necessary result* from the fact that nature ever fluctuates about a mean, or that in every generation there would be flowers with longer and shorter nectaries, and moths with longer and shorter probosces than the average. No doubt there are a hundred causes that might have checked this process before it had reached the point of development at which we find it. If, for instance, the variation in the quantity of nectar had been at any stage greater than the variation in the length of the nectary, then smaller moths could have reached it and have effected the fertilization. Or if the growth of the probosces of the moths had from other causes increased quicker than that of the nectary, or if the increased length of proboscis had been injurious to them in any way, or if the species of moth with the longest proboscis had become much diminished by some enemy or other unfavourable conditions, then in any of these cases the shorter nectaried flowers which would have attracted and could have been fertilized by the smaller kinds of moths would have had the advantage. And checks of a similar nature to these no doubt have acted in other parts of the world, and have prevented such an extraordinary development of nectary as has been produced by favourable conditions in Madagascar only and in one single species of Orchid. I may here mention that some of the large Sphinx moths of the tropics have probosces nearly as long as the nectary of Angræcum sesquipedale.[2]

[Footnotes to Wallace's paper:]

1 It is a peculiarity of this species that the nectar only occupies a depth of one or two inches at the bottom of the nectary.

2 I have carefully measured the proboscis of a specimen of *Macrosila cluentius* from South America in the collection of the British Museum, and find it to be nine inches and a quarter long! One from tropical Africa (*Macrosila morganii*) is seven inches and a half. A species having a proboscis two or three inches longer could reach the nectar in the largest flowers of *Angræcum sesquipedale*, whose nectaries vary in length from ten to fourteen inches. That such a moth exists in Madagascar may be safely predicted; and naturalists who visit that island should search for it with as much confidence as astronomers searched for the planet Neptune, -and they will be equally successful!

In a 1991 article about 'Darwin's' prediction, Kritsky made one of his own: "Another Madagascan orchid, *Angraecum longicalcar* Bosser [now classified as *Angraecum eburneum* var. *longicalcar*], has been found with an even longer nectary than *A. sesquipedale*! This orchid's nectrary is nearly 40 cm long, 10 cm longer than that of *A. sesquipedale* (Bosser 1965). The search can begin again. For somewhere in Madagascar is a gigantic moth with a proboscis even longer than Darwin's Madagascan hawk moth!" Attractive as this hypothesis might be, there is at least one (even more intriguing!) possibility, which is that *Angraecum eburneum var. longicalcar* has evolved to mimic *A.*

sesquipedale and that its extremely long nectary fools Wallace's Sphinx into pollinating it without giving the moth a nectar reward (either because the nectar is too far down, or no nectar is produced). If this is really what is going on then the expectation is that *A. longicalcar* would be rare relative to *A. sesquipedale* (or the moth encounters the latter species more frequently than the former one). In any case it seems very unlikely that there is an undiscovered moth in Madagascar with a longer proboscis than Wallace's Sphinx Moth as the 'larger moth' fauna of the island is pretty well known. It is possible though, that there used to be such a species but it has now gone extinct and that the orchid now self pollinates.

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