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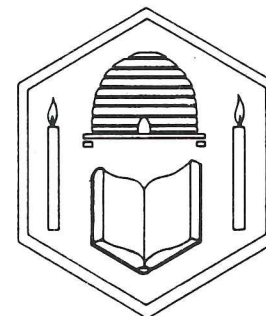
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THE BIOLOGY OF DEATH'S HEAD HAWKMOTHS, LEPIDOPTERAN KLEPTOPARASITES OF HONEY BEES



Ian J. Kitching

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THE BIOLOGY OF DEATH'S HEAD HAWKMOTHS, LEPIDOPTERAN KLEPTOPARASITES OF HONEY BEES

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A lecture given to The Central Association of Bee-Keepers on 13th March 2004

Introduction

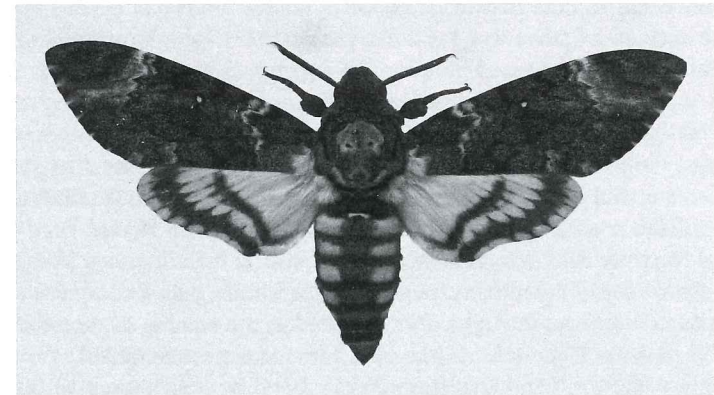


Figure 1. Adult male death's head hawkmoth, Acherontia atropos, from the Canary Islands.

The death's head hawkmoth, *Acherontia atropos* (Figure 1) has one of the direst and most fearsome reputations of all insects. First, there is that pattern on the thorax, which resembles a mask of death or a skull. Then there are the black and yellow bands on the abdomen that can be interpreted as "ribs". Finally, when the moth is at rest, its dark forewings are draped along either side of the body like a cloak. Add to this the high pitched squeak that the moth makes when disturbed, at the same time as which it hops around shrugging its wings up and down, and the result is more than sufficient to inspire fear and dread in the superstitious and

uneducated. The vernacular names applied to this moth across Europe all allude to its appearance: smrtihlav obecny (Czech), dødningehodesvermer (Danish/Norwegian), Doodshoofdvlinder (Dutch), tontsuru (Estonian), pääkallokiittäjä (Finnish), le sphinx à tête de mort (French), Totenkopfschwärmer (German), halálfejes lepke (Hungarian), zmora trupia-główka (Polish), mertvaya golova (Russian), cabeza de muerto (Spanish), Dödskallesvärmare (Swedish), and, of course, death's head hawkmoth (English). The moth was believed to be an evil omen: "It is regarded not as the creation of a benevolent being, but the device of evil spirits - spirits enemies to man - conceived and fabricated in the dark, and the very shining of its eyes is thought to represent the fiery element whence it is supposed to have proceeded. Flying into their apartments in the evening at times it extinguishes the light; foretelling war, pestilence, hunger, death to man and beast" (Harris, 1840). Newman (1965) noted a belief in central France that the "dust [scales] cast from its wings in flying through a room, produces blindness if it happens to fall upon the eyes". Even entomologists could not resist the lure of the moth's appearance when assigning names. The genus, *Acherontia*, derives from Acheron, the River of Pain in the underworld, and the species is named for Atropos, the Greek Fate who cuts the thread of life. The theme of death is continued in some of the named forms of *A. atropos*: *charon* (who ferried dead souls across the river Styx into Hades on payment of a bribe), *moira* (the Greek goddess of fate or necessity) and *sculda* (Skulda was the equivalent to Atropos in Norse mythology). It is repeated in the naming of the other two species in the genus: *lachesis* (the Fate who measures the thread of life and determines destiny) and *styx* (the principal and boundary river of Hades), with forms and synonymous names: *medusa* (the only mortal Gorgon), *circe* (the enchantress who informed Odysseus he would have to journey to Hades), *lethe* (another river in Hades, drinking the waters of which induced forgetfulness), *morta* and *satanas* (both of which are rather self-evident). Death's head hawkmoths have even entered into modern mythology. *Acherontia atropos* was sent by Count Dracula as food for his thrall Renfield, and in *The Silence of the Lambs*, the killer placed a pupa of *Acherontia styx* into the mouths of his victims.

Whatever the mythology and folklore surrounding the appearance of the death's head hawkmoth, it is nevertheless all the product of fanciful imaginations. The origin of the skull mark is very mundane. The basis of the skull mark is the pale mesothorax and clouded metathorax, which are bounded laterally by dark-scaled structures known as tegulae (these are

shield-shaped flaps that overlie and protect the delicate basal mechanisms used to move the wings). The two "eye-sockets" are simply dark spots. Similar spots occur in other hawkmoths (such as the American hawkmoth, *Manduca rustica*) but are much less conspicuous because of a more variegated thoracic pattern. Many hawkmoths have a series of lateral yellow spots along the abdomen, but in *Acherontia atropos* they are expanded into the rectangular patches, thus reducing the intervening dark areas to narrow "ribs".

Feeding biology of adult *Acherontia atropos*

However, the reality of the adult feeding biology of death's head hawkmoths is, perhaps, even stranger than the fiction associated with its appearance. Most moths and butterflies that feed as adults do so from flowers using a long, tubular "tongue" (proboscis) to drink nectar. Although there are a number of records of *A. atropos* visiting flowers for nectar (Tutt, 1904, and references therein; Pittaway, 1993), they are but few, and at least one of these records, of visits to tobacco, was not a conventional encounter, but rather one in which the moth robbed the flower of its nectar by piercing it near the base and drinking through the hole (A.R. Pittaway, personal communication). There have also been records of death's head hawkmoths feeding at damaged trees, drinking sap oozing from wounds in the bark, and also of being attracted to sugar bait, if honey has been added to the mixture (Bartel, 1899-1902). However, these moths are most famous for an entirely different and unique adult feeding strategy, namely visiting honey bee colonies for honey. This habit, perhaps in conjunction with the abdominal stripes, possibly gave rise to the archaic English vernacular name of "Bee Tiger" (Harris, 1766).

Raiding honey bee colonies and drinking honey directly from the comb would seem at first sight to be a distinctly suicidal life style for a large moth. However, adult *Acherontia* have numerous adaptations to help them survive their encounters with honey bees. The legs are short and stout, with well-developed claws, to facilitate movement among the combs. The pulvilli (thin, hairy lobes with a possibly sensory function located on the outside of the claws) and the arolium (a pad between the claws that facilitates grip on slippery surfaces) are both highly reduced and non-functional (*Figure 2, left*), possibly to prevent fouling by the sticky honey. The body is heavily sclerotized and covered in a dense pile of short, erect scales to help protect against the stinging attacks of worker honey bees. Heinig (1978) reported that the moths also appear to have some resistance

to honey bee venom. Finally, instead of being long and thin, the proboscis of a death's head hawkmoth is short, stout and apically pointed (*Figure 2, right*) to allow it to pierce capped honey cells and easily drink the viscous honey contained therein.

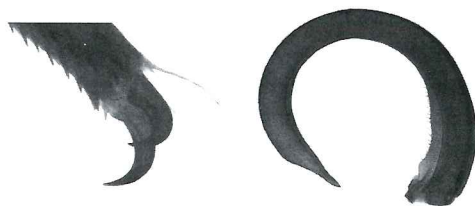


Figure 2. (Left) Vento-lateral view of the pretarsus of Acherontia atropos, showing large claws and lack of an arolium (adhesive pad) between them. (Right) Lateral view of the proboscis of Acherontia atropos (base to the right) showing the sharply pointed apex for puncturing capped honey cells and the large diameter suitable for ingestion of viscous honey.

However, the best-known behaviour of adult death's head hawkmoths is undoubtedly their ability to emit loud noises, referred to commonly as "squeaking". Certainly, the moths squeak loudly when disturbed or picked up (Pittaway, 1993), but they also make these noises when inside honey bee colonies (Tutt, 1904). These squeaks are said to bear some similarity to the piping sounds produced by queen honey bees (Rothschild, 1985), which, transmitted as vibrations through the honeycomb, elicit a "freezing" response in worker bees (Michelsen *et al.*, 1986). This has led to the claim that death's head hawkmoth adults are acoustic mimics of the queen honey bee and calm the worker bees by inducing this freezing reaction (Kettlewell, 1978; Rothschild, 1985). Moritz *et al.* (1991), however, doubted this explanation, as they never observed worker bees freeze in the presence of adult moths.

Many explanations, extensively reviewed by Tutt (1904) and Busnel & Dumortier (1959), have been proposed to explain how the moths produce these noises. However, it was the latter authors who finally determined the mechanism that produces the squeak and showed that the sound had two components. The structure responsible is a small chitinous flap called the epipharynx, at the base of the proboscis. The first element of the squeak is produced when the anterior part of the pharynx is dilated, drawing in air, while simultaneously the oral aperture at the base of the proboscis is rapidly opened and closed by rhythmic movements of the

epipharynx (*Figure 3*). This produces a rapid train of 40-50 distinct pulses each lasting about 160 ms. The air is then expelled while the epipharynx is held in the raised position, producing the second element of the sound, a single, sustained note lasting about 60 ms. This process is repeated 40-50 times to produce the whole squeak.

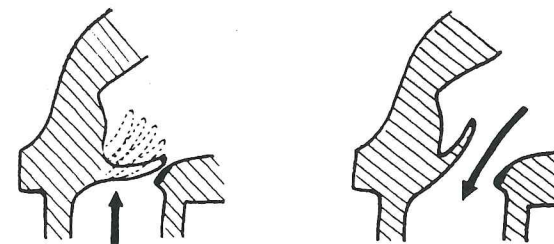


Figure 3. Squeaking mechanism in Acherontia atropos. The anterior part of the pharynx is dilated, air is drawn in and the epipharynx vibrates (left). When the air is expelled, the epipharynx is held up out of the way (right). The result is a series of rapid pulses followed by a single drawn-out note. This sequence is repeated 40-50 times to produce the full squeak. (Redrawn from Busnel & Dumortier, 1959: figure 7.)

There is some disagreement regarding the ease with which adult death's head hawkmoths gain entry to honey bee colonies and particularly how successful they are in their subsequent attempts to escape. Much of the literature (e.g. Tutt, 1904, and references therein; Newman, 1965; Kettlewell, 1978) maintains, or at least implies, that the majority of moths entering hives are attacked and killed, their bodies often then being entombed in wax or propolis by the bees. In contrast, Moritz *et al.* (1991) stated that *A. atropos* adults do meet some opposition from the guard bees on first attempting entry to a colony, but then, once inside, the defending workers rarely attacked them. Rothschild (1985) suggested the skull mark was actually the face of a worker bee (*Figure 4*). The dark tegulae represent the compound eyes of the bee and the paired black spots on the mesothorax are the antennal bases. The likeness is completed by the variegated pattern of the metathorax forming the bee's mouthparts. Rothschild argued that "in the obscurity of the hive, and seen from above by the guard bees, this combination must be quite impressive, for the 'face' set immediately above the brown and yellow striped segmented abdomen, topped by the bee's own antennae could give the impression of a huge

gravid queen bee; a super model, if ever there was one". Certainly, the thoracic pattern does make for a rather more convincing bee's face than skull, especially when viewed under ultraviolet light. However, it is difficult to see how the bees would be able to see the pattern, for not only is it dark inside the colony, but the moths raid at night. The available light of any wavelength would be extremely limited indeed. Interpreting the thoracic pattern as a bee's face is probably no less fanciful than imagining it as a skull.

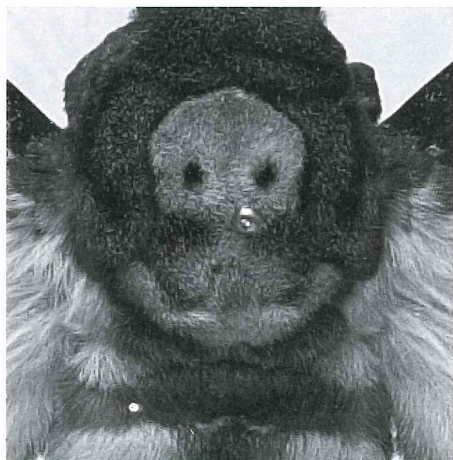


Figure 4. Close-up of the "skull-mark" of a death's head hawkmoth, *Acherontia atropos*.

Moritz *et al.* (1991) made extracts of the cuticular hydrocarbons of both honey bees and *Acherontia atropos* adults and compared them using gas chromatography. The honey bee extracts consisted of four compounds, two major components, the saturated fatty acids hexadecanoic acid (palmitic acid) and octadecanoic acid (stearic acid), and two minor components, the unsaturated fatty acids 9-hexadecanoic acid (palmitoleic acid) and 9-octadecanoic acid (oleic acid). The moth extracts were more complex, with many more compounds in the mix, but all four of the honey bee fatty acids were present and the fit between the two chromatograms for these four compounds ranged between 94% and 99%. The reason that death's head hawkmoths are not attacked once inside the colony thus appears to be because they smell like honey bees, and are thus chemically "invisible".

What has yet to be explained is why honey bees, whose odour sensitivity is such that they can distinguish between nest mates and non-nest mates, are fooled by such apparently gross and generalized chemical camouflage.

It is possible that many of the deaths reported in man-made hives are due to the moths finding it difficult to escape from the confines of these artificial structures within a reasonably short time. Newman (1965) reported that after drinking honey, only clicking sounds were emitted and the moth was unable to squeak again for five hours. This is only to be expected if the same structures are used for both squeaking and drinking – the moths simply cannot squeak with their mouths full! If the squeak does indeed act to pacify the bees, then any delay in leaving the colony when this mechanism is inoperative might give the workers sufficient time to realize that something is not quite right and react aggressively, with fatal consequences for the moths. Whatever the eventual fate of individual moths, they nevertheless cause sufficient damage within honey bee hives to be considered a major apicultural pest in countries as diverse as Italy (Patetta, 1982), Saudi Arabia (Al-Ghamdi, 1990) and South Africa (Buys, 1975).

Life history of *Acherontia atropos*

Otherwise, the life of *Acherontia atropos* follows the usual pattern for a moth, with four stages, egg, larva, pupa and adult. The egg, which is laid singly low down under old leaves of the food plant (Pittaway, 1993), is oval, pale green or bluish-green, and smooth to the naked eye. Under high magnification, a fine network of polygonal cells is seen covering the surface. It changes to a yellowish colour prior to hatching. The first instar larva is pale green with a disproportionately long, black, anal horn that has a slightly forked tip. In the second instar, the horn shortens and changes to a pale yellow colour, the surface of the horn and body become covered with minute pale tubercles and the oblique lateral stripes begin to appear. By the third instar (Figure 5), the seven lateral stripes typical of many hawkmoth caterpillars are fully developed. They are white, edged dorsally with blue-grey. The horn begins to recurve dorsally and the tubercles on it and the anterior part of the body become exaggerated. Overall, the colour of the caterpillar becomes more yellow. This yellow tone becomes much more vivid and the horn recurves more in the fourth instar, which is otherwise very similar to the preceding stage. In the fifth and final instar (Figure 6), the tubercles are lost except from the horn, which is now strongly recurved. The blue edging of the lateral stripes often becomes

more extensive, developing into a series of broad, V-shapes along the back. In addition to the usual yellow form, two more colour forms can occur in the final instar. One is not much different, with the yellow colour being largely replaced with green. The other form (Figure 7) is markedly different. The overall colour is a mottled brown, with no trace of the lateral oblique stripes. The thorax has a broad, whitish, dorsal patch and the whole effect is of a very large bird dropping.

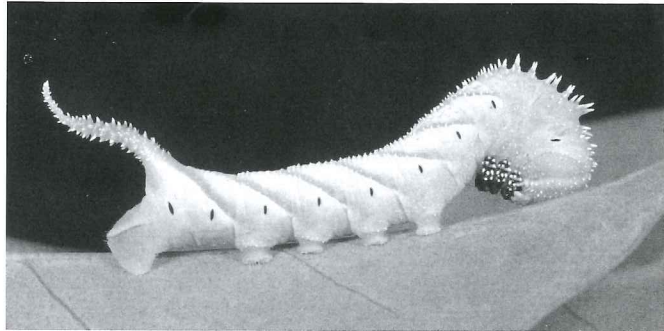


Figure 5. Third instar larva, *Acherontia atropos* (courtesy of P. Mazzei).



Figure 6. Fifth (final) instar larva, *Acherontia atropos*, yellow form (courtesy of P. Mazzei).

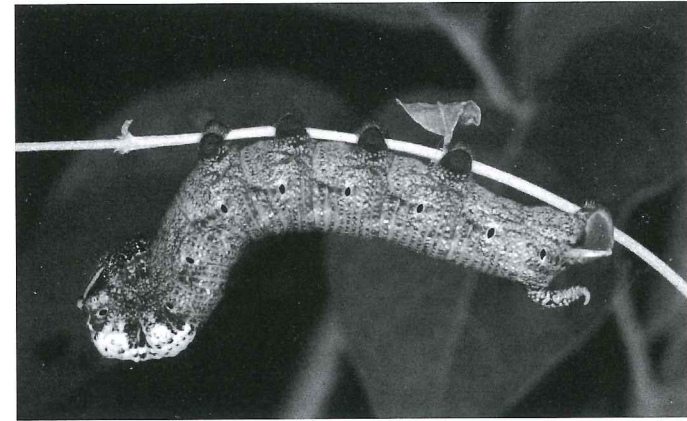


Figure 7. Fifth (final) instar larva, *Acherontia atropos*, brown form (courtesy of P. Mazzei).

When young, the larva rests along a vein under a leaf and nibbles small holes in the leaf surface. Later, its increased size and weight mean it has to rest on a leaf petiole or small branch. They are not very active, moving only to find a new leaf after the one they have been eating has been consumed, which leads to a characteristic pattern of damage to the plant. If disturbed, the caterpillars will gnash their formidable mandibles, making an audible clicking noise, and thrash back and forth in an attempt to bite their attacker.

The larvae of *Acherontia atropos* are highly polyphagous, but feed principally on plants of the orders Lamiales and Solanales. The former includes such families as Bignoniaceae, Oleaceae (privet and lilac are readily accepted in captivity) and Verbenaceae; the latter Solanaceae (larvae and pupae were often found in potato fields in former times, though rarely these days due to the combined effects of chemical sprays and mechanical harvesting). Overall, they have been recorded feeding on over 100 genera of plants, including cannabis (*Cannabis sativa*) and deadly nightshade (*Atropa belladonna*).

When fully grown, at a length of 12-13 cm, the caterpillar darkens and covers itself with a saliva-like secretion. It then wanders, often for considerable distances, in search of a pupation site. Once a suitable location has been found, the caterpillar burrows down to a depth of 15-40 cm and pupates in an oval, smooth-sided cavity that is lined with a little

silk to maintain the integrity of the walls. The pupa (Figure 8) is 7-8 cm long, smooth, deep chestnut-brown and very active, wriggling from side to side when disturbed. This is generally the overwintering stage but the pupa is not frost-tolerant; cold winters will kill it and it will rarely survive outdoors in the UK.



Figure 8. Pupa, *Acherontia atropos* (courtesy of P. Mazzei)

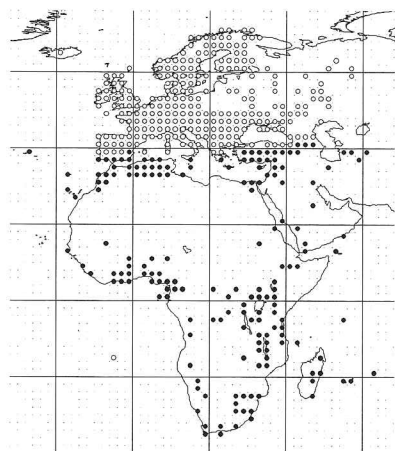


Figure 9. Distribution of *Acherontia atropos* plotted on a two-degree grid. Closed circles indicate resident breeding populations; open circles indicate non-resident breeding range, migrant and stray records. The northern edge of the permanent breeding range should be considered as being only approximate. Spots are based on published records and museum collections data and so lack of a spot from a given square should not necessarily be interpreted as absence of occurrence.

Acherontia atropos is essentially an Afrotropical species (Figure 9) that is also resident in the Mediterranean Basin and eastwards, through the Middle East and Arabian Peninsula, to the Caucasus and NE Iran. It is also resident on many islands, such as the Azores, Madeira, Canary Islands, Seychelles, Comoros, Madagascar, Mauritius and Réunion. It is a great wanderer and has been found throughout Europe, as far north as Scotland, Iceland and Scandinavia, both as moths and sometimes even caterpillars, if the weather has been warm enough. However, at these extreme latitudes, the species does not survive once the weather turns cold in winter.

Acherontia in Asia

Almost all that has been published on the biology of death's head hawkmoths refers to studies and observations made on *A. atropos*. However, the genus includes two other species, which are restricted to Asia. *Acherontia styx* (Figure 10) is superficially very similar to *A. atropos*, but slightly smaller. It differs mainly in the more uniformly coloured, pale brown mesothorax, which makes the skull mark more closely resemble a hooded head. A better character is found on the underside of the abdomen where the large black patches of *A. atropos* are reduced to small median spots. It ranges from the Persian Gulf, through South and Southeast Asia, to Japan, the Philippines, Sulawesi and Lombok (Figure 11). In the western part of its range, it has been recorded as a migrant as far west as Turkey, Syria and Jordan and has recently spread across the Arabian Peninsula to Jeddah (Pittaway, 1993). *Acherontia lachesis* (Figure 12) is a larger moth, immediately distinguishable from its two congeners by the black base to the hindwing and red coloration around the base of the skull mark. It has a similar range to that of *A. styx* but does not extend as far west or north, reaching only eastern Pakistan and southern Japan (Figure 13). However, *A. lachesis* is found much further east, where its occurrence in New Guinea is the result of a range expansion that has happened in only the last 25 years. Both *A. styx* and *A. lachesis* share many of the morphological adaptations of *A. atropos*, and honey feeding would seem to be a common feature of all three species. Few observations have been published on the adult feeding biology of the two Asian species. *A. styx* is recorded raiding honey bee hives in Oman (Pittaway, 1993), and I collected a moth in Thailand that regurgitated honey when handled. With regard to *A. lachesis*, Barlow (1982) simply stated "it is recorded as entering bee-hives to feed on the honey", and I found liquid honey still inside the abdomen of a male dissected for

morphological study, despite the moth having been collected over a decade earlier.

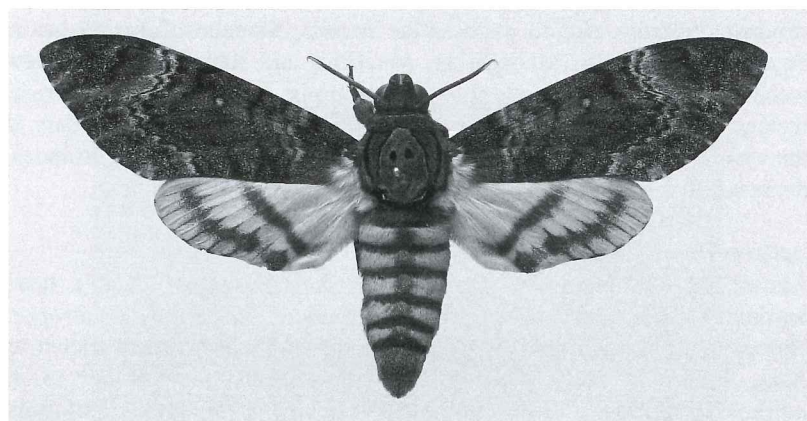


Figure 10. Adult male *Acherontia styx* from Karwar, SW India.

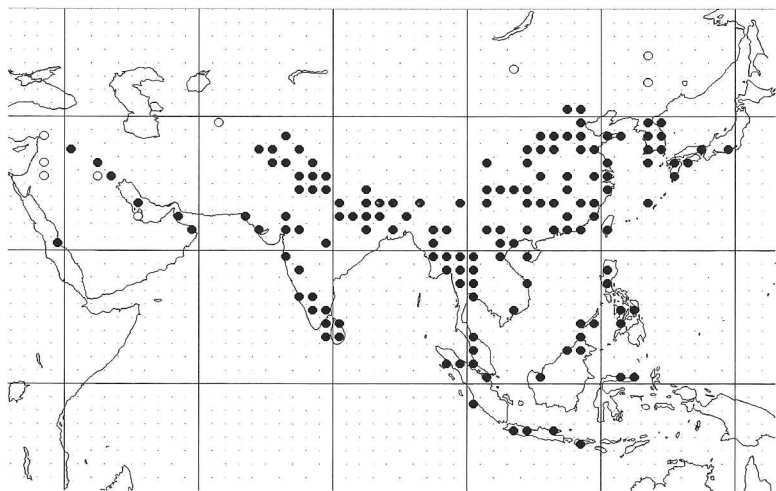


Figure 11. Distribution of *Acherontia styx* plotted on a two-degree grid. Symbols as Figure 9.

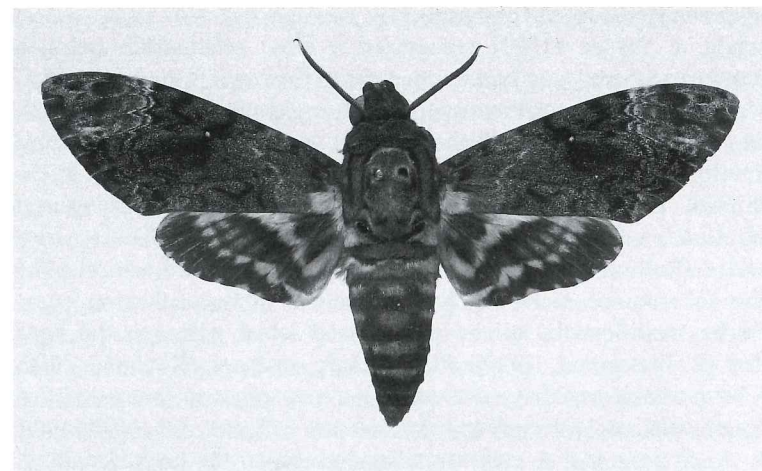


Figure 12. Adult male *Acherontia lachesis* from Shimla, NW India.

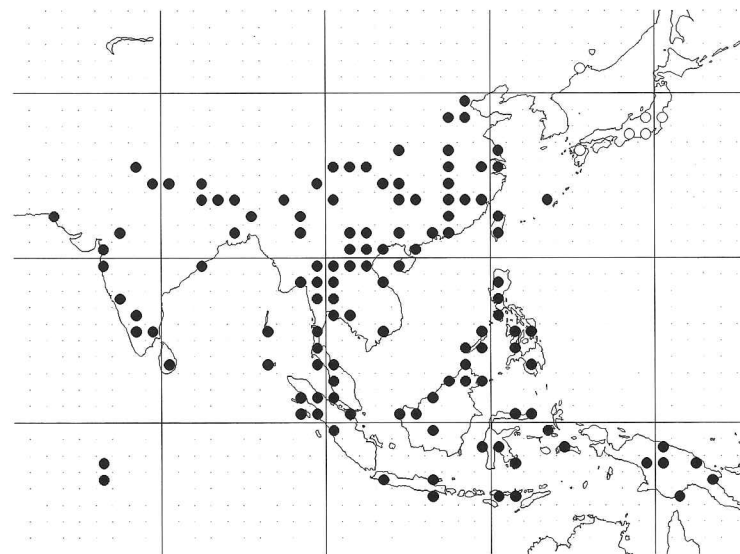


Figure 13. Distribution of *Acherontia lachesis* plotted on a two-degree grid. Symbols as figure 9.

Phylogenetic position of *Acherontia*

Rothschild & Jordan (1903) recognized a close relationship between *Acherontia* and three other hawkmoth genera. *Coelonia* is an Afrotropical and Madagascan genus of three species, while *Agrius* comprises six very closely related species, of which the most familiar is the convolvulus hawkmoth, *Agrius convolvuli*, which is a regular summer visitor to the British Isles. The third genus, *Megacorma*, includes a single Asian forest species. Later, a fifth genus, *Callosphingia*, from equatorial East Africa was added (Rothschild & Jordan, 1916). These five genera comprise the subtribe Acherontiina, members of which share an ultrasonic hearing organ formed by modifications of the pilifers and labial palps on the head (Gopfert & Wasserthal, 1999). Phylogenetic analyses (Kitching, 2002, 2003) have established that *Acherontia* is a monophyletic group and that its closest relative (sister-group) is *Coelonia* (Figure 14). Within the genus, *A. atropos* and *A. styx* are sister-species, to the exclusion of *A. lachesis*.

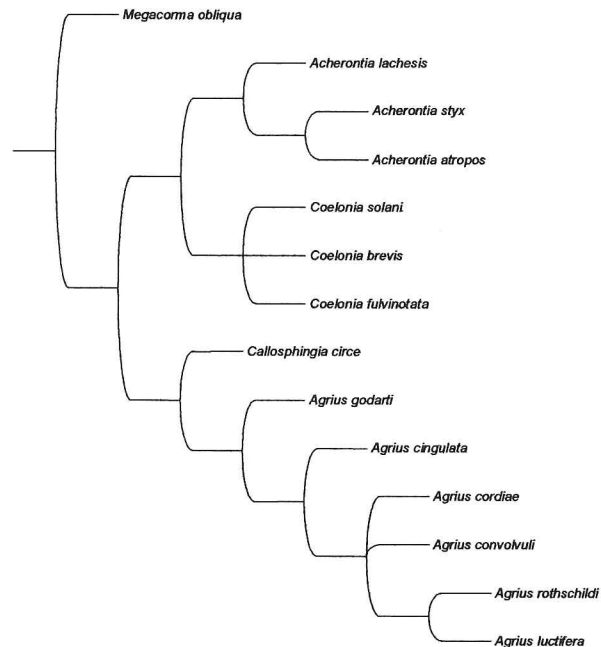


Figure 14. Phylogeny of the hawkmoth tribe Acherontiini (redrawn from Kitching, 2003).

Evolutionary and behavioural relationships of *Acherontia* and honey bees

It is well known that *A. atropos* attacks colonies of the honey bee, *Apis mellifera*, and a comparison of their respective distributions suggests that this may have been a long and close association. *Acherontia atropos* breeds throughout Africa and the Mediterranean area, across the Middle East as far as southern Turkmenistan and southwest Iran. Within this range, it is absent only from arid areas such as the Sahara Desert. *Apis mellifera* occurs throughout much the same region, but extends further north into colder regions of Europe, where *A. atropos* is absent except as migrant individuals. *A. mellifera* has its eastern limits near Mashhad and Bam in Iran. Thus, in tropical and subtropical areas, the two insects' distributions are remarkably coincident. Colony defence in honey bees is a complex system of mechanical, behavioural and physiological adaptations (Seeley *et al.*, 1982) and circumventing them will require finely tuned countermeasures. Moritz *et al.* (1991) demonstrated one such effective countermeasure, in which the cuticular hydrocarbons of *A. atropos* match those of the honey bee and thus act as a chemical camouflage. Squeaking may also have a role, although exactly how has yet to be determined. *Acherontia atropos* can be characterized as a kleptoparasite of *Apis mellifera*, albeit one that is not resident within the colony.

Little is known of the adult biology of the other two species of *Acherontia*. During fieldwork in Thailand in the 1990s, I observed that the squeaks of *A. lachesis* and *A. styx* differed from that of *A. atropos*. The sounds produced by *A. atropos* are what most people would think of as squeaks, being high-pitched and relatively pure in tone, very similar to those of rodents. In contrast, the squeaks of *A. styx* are hoarser, whereas the sound that *A. lachesis* produces has more of a rasping quality, rather than a squeak. If squeaking is one of the countermeasures that enable *Acherontia* adults to raid honey bee colonies successfully, then these observations suggest that both *A. lachesis* and *A. styx* may be adapted to attack honey bee species other than *A. mellifera*. Indeed, this must be the case, because until the advent of modern apiculture, which transported it around the world, the range of *A. mellifera* did not overlap significantly with that of either Asian moth.

Pittaway (1993) reported that *A. styx* was "an avid robber of honey in bee hives in Oman". Several species of honey bee are domesticated in Oman (which is also true for the rest of Asia). Inland at low elevation the usual species is *Apis cerana* and along the coast, *Apis dorsata* is also kept.

Apis mellifera apiculture is restricted to the mountains (A.R. Pittaway, personal communication). Of these, *Apis cerana* is the species most frequently attacked by *A. styx*. Comparison of the ranges of this bee and hawkmoth shows their remarkable coincidence. *Apis cerana* ranges from Iran, eastwards south of the Himalayas through China and Southeast Asia, to Japan, the Philippines and the Moluccas (Ruttner, 1988: fig. 9.1). This is almost exactly the range of *A. styx* (Figure 11) and provides strong circumstantial evidence that *A. cerana* is the host to which *A. styx* is most closely adapted.

There are no published records of the honey bee species attacked by *A. lachesis*. However, if a different squeak is indicative of a different host, then *A. lachesis* probably specializes on neither *A. mellifera* nor *A. cerana*. The distribution of *Acherontia lachesis* may provide a clue and a comparison with the ranges of the other honey bee species suggests that the best candidate is *Apis dorsata*. Its range, including all subspecies, is a reasonable match for that of *A. lachesis*, except that it is absent from most of China and Taiwan (Ruttner, 1988). However, the situation is now less clear-cut because in the last 20 years *A. lachesis* has dramatically expanded its range eastward across the whole of the island of New Guinea, where it is now well established and common (Moulds & Lachlan, 1998). However, there is no evidence of a similar range expansion in *A. dorsata*. Indeed, there are no native honey bees on New Guinea. There is, however, a thriving apicultural industry in Papua New Guinea based on *A. mellifera* (Kidd, 1979; Anderson, 1990), and in the late 1980s *A. cerana* escaped from its introduction site at Vanimo to establish feral colonies across the island (Anderson, 1989; Dunn, 1992). Perhaps *A. lachesis* has undergone a host shift and now uses these honey bees as alternative hosts.

The phylogeny of honey bees has been intensively investigated using both morphological and molecular sequence data (Alexander, 1991; Engel & Schultz, 1997). Both studies agreed on the same pattern of relationships among the three species, namely: *dorsata* (*mellifera* + *cerana*). If future studies do show that the hosts of *A. lachesis* and *A. styx* are *A. dorsata* and *A. cerana* respectively, then there will be a perfect match between the phylogenies of *Acherontia* and *Apis*, suggesting there may have been parallel evolution between the two genera. But even if this prediction regarding the hosts of *A. lachesis* and *A. styx* should prove incorrect, there are still fascinating biological questions to be addressed. For example, honey bees have a well-developed sense of hearing (Dreller & Kirchner, 1995) and both *A. cerana* and *A. dorsata* emit species-specific acoustic

signals when their nests are disturbed (Koeniger & Fuchs, 1972). In contrast, *A. mellifera* makes no such sounds. Given that the three *Acherontia* species each squeak differently, these sounds might be tuned to the defensive acoustics of their respective hosts. Moritz *et al.* (1991) reported that four cuticular hydrocarbons of adult *Acherontia atropos* were identical to those found on worker *Apis mellifera*. It is known that there are significant quantitative and qualitative differences among the extractable cuticular hydrocarbons of *A. cerana*, *A. dorsata* and *A. mellifera* (Francis *et al.*, 1985) and so the hypothesis that the cuticular hydrocarbon complements of adult *A. lachesis* and *A. styx* closely match those of their putative *Apis* hosts should be tested. There is still much exciting research yet to be undertaken into this unique kleptoparasite-host interaction.

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