



**Journal of Vasyl Stefanyk
Precarpathian National
University. Biology**

V.12 (2025) pp. 106-116

DOI: 10.15330/jpnubio.12.106-116

UDC: 595.788:57.017:574.5

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ISSN(Online): 3083-662X
ISSN(Print): 3083-6611

Conservation Biology and Phylogeny of *Acherontia atropos* (Death's-Head Hawkmoth): Ukrainian Distribution and Illumination Effects

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Abstract

This article addresses the problem of the disappearance of the unique tropical species *Acherontia atropos* (Death's-head Hawkmoth) from the fauna of Ukraine. The main focus of this article is the study of the anatomical and physiological features of this species, its ecological connections, and its distribution in Ukraine and globally. As a result of investigating the influence of illumination on the ontogenetics of this species, we can conclude that constant artificial lighting has a positive effect on the larvae (caterpillars). Other ontogenetic stages could not be investigated, as the larvae perished during pupation, which may have been caused by a bacterial disease or unfavorable weather conditions during transportation. In the resulting phylogenetic analysis of *Acherontia atropos*, we note that all representatives originated from a common ancestor. *Acherontia styx* and *Acherontia lachesis* are sister species, while *Acherontia atropos* is a collateral lineage within the genus. The study of the distribution of *Acherontia atropos* revealed that the species has a large global range, but is rare in Ukraine.

Keywords: *Acherontia atropos*, distribution range, phylogenetics, species' ecological connections.

1. INTRODUCTION

1.1. Systematic Analysis of the Genus *Acherontia*

Based on the Lifemap platform, we can distinguish the following taxonomic classification:

Kingdom: Animalia

Phylum: Arthropoda

Class: Insecta

Order: Lepidoptera

Superfamily: Bombycoidea

Family: Sphingidae

Subfamily: Sphinginae

Tribe: Acherontiini

Genus: *Acherontia* (LifeMap, 2025).

The studied species, *Acherontia atropos*, is one of the three representatives of the genus *Acherontia*. All representatives share common characteristics, namely a massive streamlined body, a characteristic skull-like pattern on the abdomen, and others. Together with the genera *Coelonia*, *Agrius*, *Megacorma*, and *Callosphingia*, the genus *Acherontia* belongs to the tribe Acherontiini. In addition to the species *Acherontia atropos*, the species *Agrius convolvuli*, a representative of the genus *Agrius*, is also typical in the fauna of Ukraine.

The tribe Acherontiini belongs to the family Sphingidae (Hawkmoths/Sphinx moths), which in turn belongs to the superfamily Bombycoidea (Bombycoid moths). This taxon also includes the following families: Lasiocampidae (Lappet moths), Saturniidae (Giant silk moths), Sphingidae (Hawkmoths), Apatelodidae (American silk moths), Endromidae (Kentish glory moths), Eupterotidae (Eupterotid moths), and Phiditiidae (Phiditiid moths). This superfamily is very interesting and one of the most studied among the order Lepidoptera (Butterflies and Moths), comprising more than 3,500 species. The superfamily unites large moths with diverse coloration and characteristic features. The best-known representatives are the Hawkmoths, Silkmoths, and Giant Silk Moths (LifeMap, 2025).

The superfamily Bombycoidea belongs to the order Lepidoptera (Moths and Butterflies), which in turn belongs to the class Insecta (Insects).

1.2. Physiology and Anatomy *Acherontia atropos*

Acherontia atropos (Linnaeus, 1758) is a large hawkmoth, with a wingspan ranging from 95 to 125 mm (Pittaway, 1993). It is easily recognized by the characteristic human skull-like pattern on the dorsal side of the thorax and its yellow-crimson abdomen (Moulds et al., 2020). The body is massive and streamlined; the forewings are narrow and elongated, while the hindwings are significantly smaller. The abdomen is robust (up to 60 mm long and 20 mm in diameter) (de Freina, & Witt, 2001) yellow with black rings and a broad bluish-grey longitudinal stripe along the centre. Sexual dimorphism is minimally expressed.

The adult imago possesses a well-developed siphoning proboscis adapted for feeding on liquid substrates such as floral nectar, tree sap, and honey (Moulds et al., 2020), and it is capable of piercing soft fruits to obtain juice. A unique feature is its ability to produce sound using a chitinous outgrowth on the upper lip (epipharynx), which mimics a cry (UCL, 2025). The head features large compound eyes, enabling nocturnal vision, and sensitive antennae for detecting odors, including pheromones and food sources.

The internal anatomy of the imago includes powerful thoracic musculature that enables intensive flight, and a digestive system with a well-developed midgut for efficient nectar and honey assimilation (Moulds et al., 2020). In the larval stage, the digestive system is adapted for leaf consumption (esophagus, stomach, hindgut with Malpighian tubules), but the intestine is significantly shorter in the adult. Respiration occurs via tracheae that open through spiracles (stigmata) along the sides of the body, ensuring highly efficient oxygen delivery required for adult activity.

A. atropos possesses an open circulatory system, where haemolymph (functions: transport of nutrients, hormones, and thermoregulation; does not carry oxygen) circulates within the body cavity, bathing the organs. The dorsally located heart contracts rhythmically. The central nervous system consists of the brain (with well-developed optic lobes) and the ventral nerve cord. In larvae, the suboesophageal ganglion is well-developed, coordinating feeding and movement. The excretory system is composed of Malpighian tubules which open into the intestine, regulating osmotic balance and eliminating nitrogenous waste products. The male and female reproductive systems consist of

testes and ovaries, respectively, connected to ducts and accessory glands; reproduction is sexual with internal fertilization (Donahue, 1995, Chapman, 1998, Holub, 2012, Chown, & Nicolson, 2004).

1.3. Behavioral Characteristics

Acherontia atropos is a striking example of nocturnal activity among Lepidoptera, exhibiting peak flight periods at dusk and during the night. One of the most intriguing features of their behavior is their cleptoparasitism towards honey bees (*Apis mellifera*). Adults are capable of entering beehives, where they feed on honey, often remaining unnoticed or provoking minimal aggression from the bees (Photo 1) (Pavlovic et al., 2024).



Photo 1. Imago of *Acherontia atropos* in an *Apis mellifera* hive (Photographer: Santi Longo)

In fact, these moths calm the bees by releasing chemical substances that mask their own scent (chemical mimicry). These include four fatty acids: palmitoleic, palmitic, stearic, and oleic, which are found in the same concentration and ratio in honey bees. Furthermore, the moths have low sensitivity to bee venom and have been shown in experiments to withstand up to 5 bee stings (Moritz et al., 1991). Nevertheless, beekeepers occasionally find mummified bodies of the hawkmoths encased in propolis within the hives. There is evidence that consuming 10g of honey can cause the adult moth to perish. The sounds produced by the moths inside the hive may also play a role in their interaction with bees.

Acherontia atropos larvae demonstrate polyphagy, feeding on the leaves of a wide spectrum of plants, including representatives of the Solanaceae family (e.g., potato, tobacco), Oleaceae family (e.g., jasmine), Fabaceae, and others (Pittaway, 1993). However, research has shown that unlike some other Lepidoptera, *A. atropos* larvae are unable to sequester alkaloids (such as atropine) from their host plants, and thus do not acquire chemical defense. Their survival strategy is instead based on a nocturnal lifestyle and cryptic behavior (Petzel-Witt et al., 2023).

Adult moths are also known for their ability to migrate over significant distances. Observations using photographic identification can help track their movements and understand population dynamics (Ruiz de la Hermosa et al., 2022).

2. MATERIALS AND METHODS

2.1. Phylogenetic Research Method

For this study, 18 sequences representing the genus *Acherontia* were identified in the GenBank database, including 5 sequences of the species *Acherontia atropos*, 8 of *Acherontia styx*, and 5 of *Acherontia lachesis*. The access codes for the sequences in the GenBank database are listed in the table (Tab. 1).

Table 1. Accession Codes and Origin Information for *Acherontia* DNA Sequences in the GenBank Database Used for Phylogenetic Analysis

| | Species | Accession Codes | Country | Date |
|----|---|-----------------|---------|------------|
| 1 | Death's-head Hawkmoth (<i>Acherontia atropos</i>) (Linnaeus, 1758) | JF853604 | Canada | 22.04.2011 |
| 2 | | HM871673 | Canada | 23.07.2010 |
| 3 | | MK187699 | France | 16.11.2018 |
| 4 | | JN677647 | Canada | 15.09.2011 |
| 5 | | HQ992062 | Canada | 25.01.2011 |
| 6 | Death's-head Hawkmoth, Styx (<i>Acherontia styx</i>) (Westwood, 1847) | MG783940 | India | 12.01.2018 |
| 7 | | MG783935 | India | 12.01.2018 |
| 8 | | KC182151 | Canada | 19.11.2012 |
| 9 | | KC182150 | Canada | 19.11.2012 |
| 10 | | KC182149 | Canada | 19.11.2012 |
| 11 | | KC182148 | Canada | 19.11.2012 |
| 12 | | HQ990987 | Canada | 25.01.2011 |
| 13 | Death's-head Hawkmoth, Lachesis (<i>Acherontia lachesis</i>) (Fabricius, 1798) | JN677649 | Canada | 15.09.2011 |
| 14 | | MG783981 | India | 12.01.2018 |
| 15 | | JN677648 | Canada | 15.09.2011 |
| 16 | | KC182147 | Canada | 19.11.2012 |
| 17 | | KC182146 | Canada | 19.11.2012 |
| 18 | | HQ558303 | Canada | 02.11.2010 |

For conducting the research, we chose the FASTA format. Using the GenBank database and the available accession codes, we generated sequences from different countries in FASTA format for each species of the genus *Acherontia*. To perform the phylogenetic analysis of the genus *Acherontia*, we applied the specialized program Seaview 5.0 for Windows (Gouy et al., 2021, Edgar, 2004).

The next step involved loading the FASTA files from the GenBank database into the working window of the Seaview 5.0 application. We performed sequence alignment using the MUSCLE (Multiple Sequence Comparison by Log-Expectation) algorithm. Following the alignment, we checked its quality by manually removing regions that were not aligned or were aligned incorrectly. Alignment is a mandatory element of any phylogenetic study. To construct the phylogenetic trees of the genus *Acherontia*, we used the PhyML algorithm, which is integrated into SeaView 5.0 (Gouy et al., 2021, Guindon et al., 2010).

2.2. The Influence of Light Regimes on the Ontogenesis of *Acherontia atropos*

For the research conducted in this study, we acquired three specimens of the Death's-head Hawkmoth (*Acherontia atropos*) from a specialized breeding facility. The larval stage was the focus of investigation in this scientific work. Each caterpillar was kept in a specialized container featuring the following: a feeding area at the top containing the feed, a mesh screen to simulate plant stems, openings on the walls for oxygen access, and a detachable bottom section to maintain comfortable conditions for the larvae (Photo 2). The container dimensions were: $h = 12$ cm, $l_1 = 14.5$ cm, $l_2 = 9.5$ cm, $V = 1000$ mL. The feed composition included: agar-agar, water, wheat germ, sugar, inorganic phosphates, chlorides and sulfates, soy flour, yeast, a vitamin complex, phytosterols, ascorbic acid, sorbic acid, and streptomycin. The typical conditions maintained for each caterpillar were a dry room with an average temperature of 20–22 °C and humidity of 40–45%.

During their development, the caterpillars were maintained under different light regimes, namely natural light (14L:10D), darkness (0L:24D), and constant light (24L:0D). A 10 W LED desk lamp was used to provide the constant illumination.

Conditions were checked and maintained daily. Temperature, air humidity, and lighting were adjusted as needed.

We received the *Acherontia atropos* caterpillars on April 16th, took the initial measurements (Photo 3), and placed them into the required conditions. On April 19th, the caterpillar reared under constant illumination became ready for pupation; specifically, it moved to the bottom of the container, secreted some fluid, and curled up, though it still reacted to touch. On April 20th, the caterpillars reared under natural light and in darkness also prepared for the pupation process. We transferred all caterpillars into small boxes filled with paper, where the animals found concealed spots and began the pupation process. This process occurs in darkness.

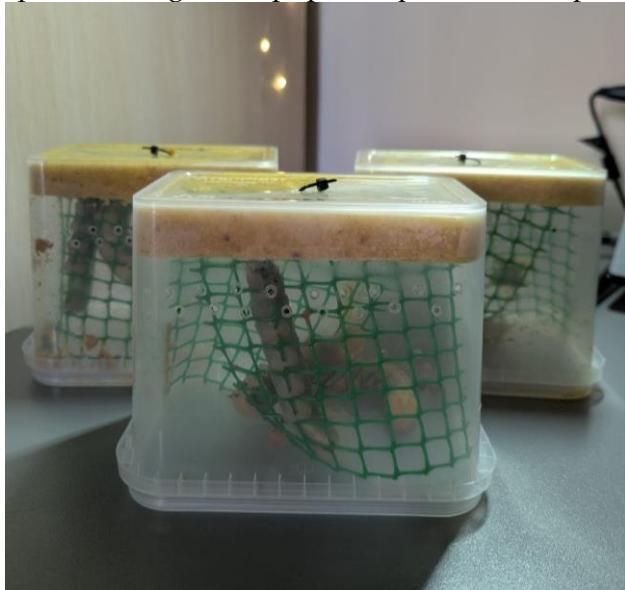


Photo 2. Containers for Rearing the Caterpillars



Photo 3. Photo of Measurements Being Taken on an *Acherontia atropos* Larva

3. RESULTS AND DISCUSSION

3.1. Distribution Analysis of *Acherontia atropos*

The iNaturalist platform provides an opportunity for every user to document important data on the modern distribution of species (iNaturalist, 2025). Analyzing the global distribution map (Fig. 1) one can notice that this species has been most frequently observed in European and African countries, specifically: Spain, Portugal, Andorra, Monaco, France, Switzerland, and South Africa.

It is important to note that *A. atropos* is also distributed on islands distant from the continents: Madeira, Cape Verde, Réunion, Mauritius, and others. The Death's-head Hawkmoth is known to be a skilled flier and capable of covering great distances, although it is possible that the species was introduced to the islands via maritime transport.

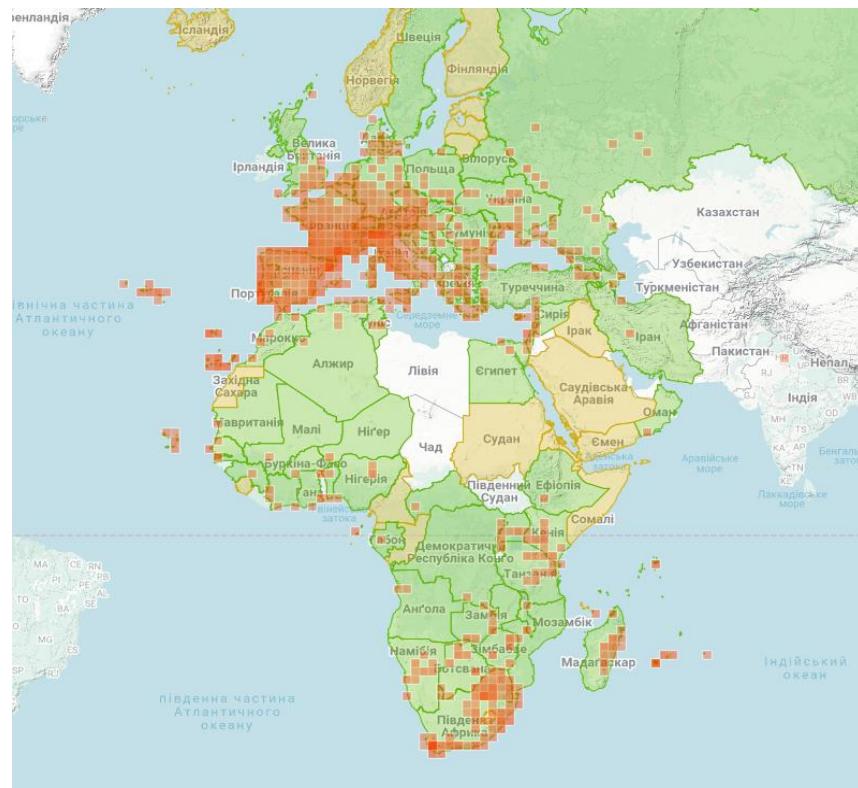


Fig. 1. Global Distribution of *A. atropos* (Source: inaturalist.com)

When analyzing the distribution map of the hawkmoth in Ukraine (Fig. 2), it can be noted that the majority of specimens were observed in the central and southern parts of the country, specifically in the following regions: Odesa, Mykolaiv, Kherson, the Autonomous Republic of Crimea, Kyiv, and Cherkasy (Khalaime, 2022). There were also single sporadic findings of *A. atropos* in the western part of the country, namely in the Zakarpattia and Lviv regions.

We also want to note that, given the occupation of the eastern regions and military aggression over three years, we do not have accurate data on the population of the Death's-head Hawkmoth in Ukraine, and we also believe that ecological changes resulting from the Russian-Ukrainian war have significantly affected the distribution of *A. atropos* in the country.

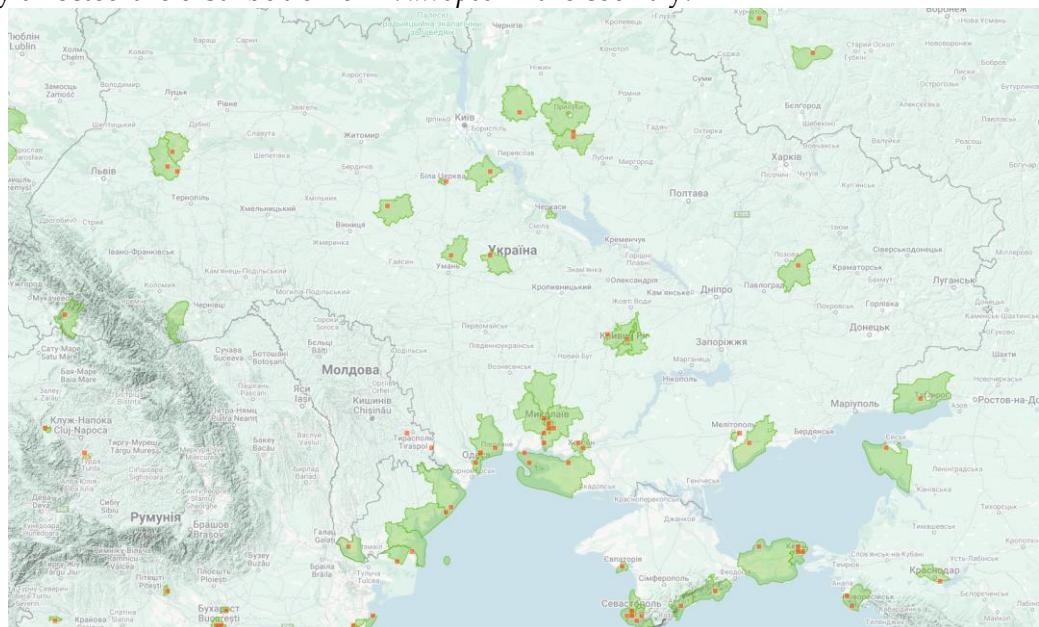


Fig. 2. Distribution of *A. atropos* in Ukraine (Source: inaturalist.com)

3.2. Phylogenetic Analysis of *Acherontia atropos*

For the study of the genus *Acherontia*, we selected sequences of each species from various countries, specifically: *Acherontia atropos* – Canada (4 units), France (1 unit); *Acherontia styx* – India (2 units), Canada (6 units); *Acherontia lachesis* – India (1 unit), Canada (4 units). Sampling sequences from different countries allows us to cover genomic diversity within the species.

As we can see in the overall phylogenetic tree of the genus *Acherontia*, all representatives originated from a common ancestor. We can also conclude that *Acherontia styx* and *Acherontia lachesis* are sister species, while the species *Acherontia atropos* is a collateral lineage within the genus (Fig. 3).

Analyzing the phylogenetic tree of *Acherontia atropos*, we observed genomic relatedness among the specimens from Canada, while the representative from France constitutes a collateral lineage (or outlying branch). It should also be noted that the sequences from Canada were generated between 2010 and 2011, whereas the sequence from France was uploaded to the GenBank database in 2018.

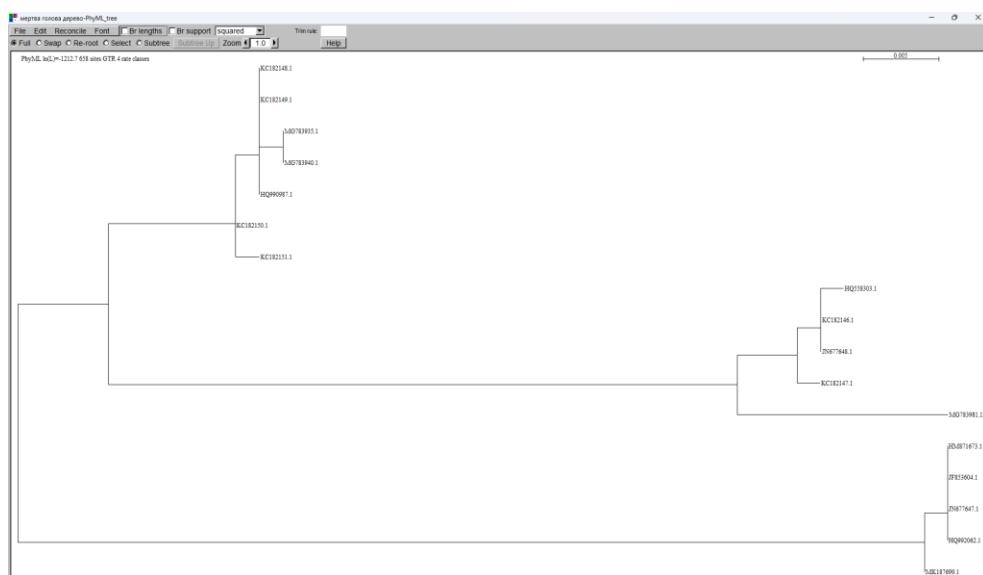


Fig. 3. Phylogenetic Tree of the Genus *Acherontia*

An interesting situation is observed in the phylogenetic tree of the species *Acherontia styx*. The sequences with accession codes MG783940 and MG783935 from India are related and were generated on the same day, 12.01.2018. It is visible that they are included in a branch with specimens from Canada, which were generated on 19.11.2011 and 25.01.2011. This may indicate that the Canadian specimens or their descendants could have been introduced to India by humans. It is also interesting that two Canadian specimens form a separate branch, although they were also generated on 19.11.2011 (Fig. 4).

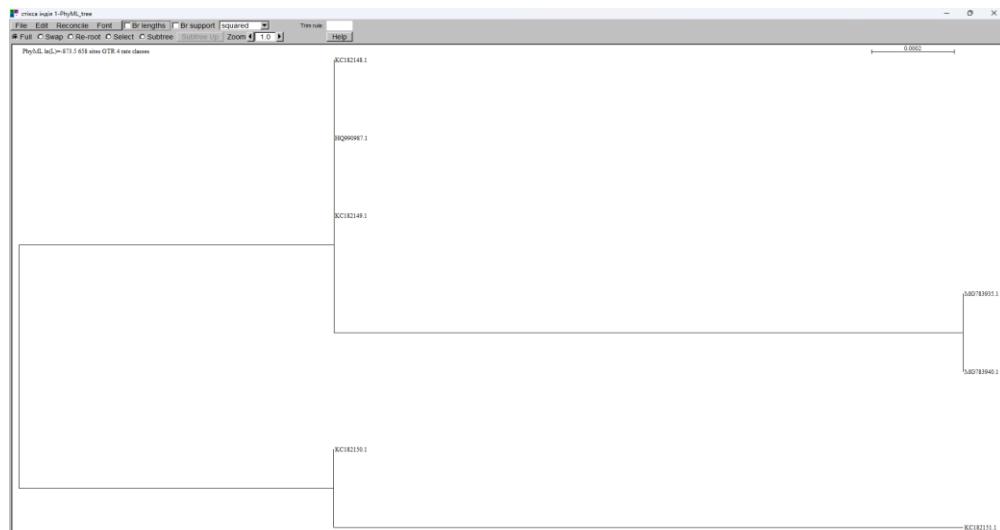


Fig. 4. Phylogenetic Tree of the Species *Acherontia styx*

Analyzing the phylogenetic tree of the species *Acherontia lachesis*, we observed that three representatives belong to one clade (or branch). The genetic distance between the clades (indicated by the scale) shows the level of evolutionary divergence. In this branch, the scale points to evolutionary divergence between sequences generated in different years. It is also interesting that a collateral branch is formed by a representative from Canada, whose sequence was generated on the same day as the representative in the preceding branch. Another branching event is created by the sequence of a specimen from India.

3.3. The Influence of Light regimes on *Acherontia atropos* Larvae

We conducted a study on the effect of illumination on the development of *Acherontia atropos*, starting from the larval stage. Although we adhered to all necessary rearing conditions and provided the larvae with everything essential, they unfortunately perished during the pupation process (Fig. 5).



Fig. 5. Larvae that Perished During the Pupation Process

The premature death of these specimens might have been caused by a bacterial disease or stress due to weather conditions during transportation, specifically due to light frost. This failure limits our ability to draw definitive conclusions about the influence of light regimes on the entire ontogenesis, as successful pupation is a critical bottleneck stage. The observed stress may have disrupted the delicate hormonal balance (e.g., ecdysteroids and juvenile hormones) required to successfully initiate and complete metamorphosis.

Nevertheless, as a result of the comparative observations, we can state that constant illumination (24L:0D), provided by a 10 W LED lamp, resulted in the fastest onset of pre-pupal behavior. The caterpillar under constant light was the first to cease feeding and prepare for pupation.

This preliminary finding suggests that the absence of a dark phase (scotophase) may accelerate the development rate towards metamorphosis in *A. atropos* larvae. Further research is required to determine the optimal photoperiod for survival and successful completion of the life cycle.

Before the start of the experiment, we took measurements of the caterpillars, which are presented in Table 2.

Table 2. Initial Morphometric Parameters of *Acherontia atropos* Larvae

| | Length (cm) | Width (cm) | Weight (g) |
|---------------|-------------|------------|------------|
| Caterpillar 1 | 8.3 | 2.3 | 15 |
| Caterpillar 2 | 9.2 | 2.1 | 16.2 |
| Caterpillar 3 | 10 | 2.5 | 17 |

CONCLUSIONS

The comprehensive research conducted yielded a number of key conclusions regarding the systematics, ecological connections, and the influence of light regimes on the ontogenesis of *Acherontia atropos*. The phylogenetic analysis of the genus *Acherontia*, performed using GenBank sequences, confirmed the origin of all three representatives from a common ancestor. *Acherontia styx* and *Acherontia lachesis* were established as sister species, while *Acherontia atropos* acts as a basal lineage within the genus. Analysis of the phylogenetic trees of individual species revealed genetic divergence between samples collected across various countries and years (Canada, India, France), which suggests potential anthropogenic influence on the dispersal of this migratory species. *Acherontia atropos* exhibits a wide global range, emphasizing its outstanding migratory capabilities. The species is rare in Ukraine, with findings concentrated in the southern and central regions. Given the ongoing military aggression, it is hypothesized that the resulting ecological changes have significantly impacted the species' population and distribution. The unique adaptation of the species involves cleptoparasitism in *Apis mellifera* hives, utilizing chemical mimicry (fatty acid secretion) and acoustic signals for concealment. This reliance on behavioral camouflage is necessary because, as suggested by literature, the species does not acquire chemical defense through alkaloid sequestration, depending instead on its nocturnal lifestyle and cryptic coloration. Preliminary observations on the influence of light regimes on the larval stage showed that constant artificial illumination (24L:0D) resulted in the fastest onset of the pre-pupal stage. However, despite adherence to all rearing conditions, all individuals perished during the pupation process. The most likely causes of mortality are attributed to bacterial disease or stress from unfavorable weather conditions (light frost) during transportation, which prevented a full analysis of the light regimes' effect on the entire ontogenesis. In conclusion, *Acherontia atropos*, a unique and rare representative of the family Sphingidae in Ukraine, requires focused conservation efforts to preserve the species diversity of the region. We hope that the data collected and research conducted will aid domestic scientists in protecting this species from local extinction.

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Анотація

Дана стаття присвячена проблемі зникнення унікального тропічного виду *Acherontia atropos* з фауни України. Головна увага у даній статті присвячена вивченняю анатомо-фізіологічних особливостей даного виду, екологічних зв'язків та поширення даного виду в Україні та світі. У результаті дослідження впливу освітлення на онтогенез даного виду, ми можемо стверджувати що постійне штучне освітлення позитивно впливає на гусінь. Інші стадії онтогенезу дослідити не вдалось, адже гусінь загинула в процесі лялькування, що може бути зумовлено бактеріальним захворюванням або ж несприятливими погодними умовами під час транспортування. У результаті філогенетичного аналізу виду *Acherontia atropos* зазначаємо, що усі представники пішли від спільного предка. *Acherontia styx* та *Acherontia lachesis* є сестринськими видами, тоді як вид *Acherontia atropos* є побічною гілкою в роді. У результаті дослідження поширення виду *Acherontia atropos* з'ясували, що вид має великий ареал поширення у світі, проте в Україні є рідкісним.

Ключові слова: *Acherontia atropos*, ареал поширення, філогенетика, екологічні зв'язки виду.