Nota lepid. 10 (3) : 183-192 ; 31.X.1987 ISSN 0342-7536

The defensive biology of the larvae of *Amata (= Syntomis) phegea* L. and *Amata (= Syntomis) kuhlweinii* Lef. (Lepidoptera, Ctenuchidae)

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Zusammenfassung

Die Wehrhaftigkeit der Imagines und Larven der Ctenuchiden wurde aus Literaturdaten zusammengefaßt und das Wehrsystem der Larven zweier *Amata*-Arten beschrieben. Die Larven besitzen ein für Vögel als Freßfeinde höchst unschmackhaftes Wehrsekret. Bei einem Angriff setzen die Larven dieses Sekret in Tropfen durch eine spezielle Struktur, eine Sollbruchstelle am caudalen Ende der großen dorsalen Haarwarzen, frei.

Summary

The defensive properties of Ctenuchid moths and their larvae are reviewed and the defensive system of two species of *Amata* larvae are described. The larvae contain a defensive secretion which is highly unpalatable to avian predators. When attacked these larvae are able to release droplets of this secretion from a specialized structure, a small rupture situated in the caudal part of the large dorsal warts.

Introduction

Moths of the family Ctenuchidae Kirby, 1837 are known to possess effective defensive properties. Müller (1874) described the release of offensively smelling substances from the coremata of South American Ctenuchid moths, and this is also recorded for *Delphrye rubricincta* Hampson by Blest (1964). The unpalatability of these moths has been shown in feeding experiments with *Scepsis fulvicollis* (Hübner), *Syntomeida epilais* Walker, *S. ipomoeae* (Harris) and *Lycomorpha pholus* (Druce) (Jones 1932, 1934). Hitherto several compounds causing this unpalatability have been identified : pyrazines in *Amata* species from Australia (Rothschild et al. 1984), cardiac glucosides in the body tissues of *Syntomeida epilais* Walker (Rothschild et al. 1972), a histamine-like compound in *Amata phegea* (L.) and pyrrolizidine alkaloids in Ctenuchid moths from Southern America (Boppre 1984). There is little information about the way these substances are sequestered, stored or utilized, but species, such as *Histaea cepheus* CRAMER from Trinidad can exhibit reflex-bleeding from the thorax, when attacked (BEEBE & KENNEDY 1964).

In several cases it can be shown, that the larval foodplants are the source of these substances. *Syntomeida epilais* larvae feed on *Nerium oleander* (Apocynaceae) and *Echites* sp. and store their cardiac glucosides Oleandrin and Nerigosid (ROTHSCHILD et al. 1972). Similar data are available for other Ctenuchid moths. Many of them seem to have a preference for foodplants containing cardiac glucosides or pyrrolizidine alkaloids (BEEBE & KENNEDY 1957, ROTHSCHILD et al. 1972, PLATT 1921, PINHEY 1979).

Some Ctenuchids, however, such as *Balacra rattray* from India or the European *Amata* species, feed on plants that do not contain any substances known to be pharmacologically active, nevertheless they are well protected. The larvae of *Balacra* are reported to cause severe urtications when rubbed against the skin (JACKSON, 1931), and *Amata phegea* and the allied European species are thought to form the models for a MÜLLERIAN mimicry ring in the Mediterranean area, together with the Zygaenid moth *Zygaena ephialtes* (L.) (BULLINI et al. 1969, SBORDONI & BULLINI 1971, SBORDONI et al. 1979, TURNER 1971).

Until now only very few species have been investigated in order to identify the mechanisms which produce these defensive properties. For example, specialized morphological structures must be related to the reflex-bleeding of *Histaea cepheus*. In *Homoeocera stictosoma* males, BLEST (1964) described a "ventral valve", from which the secretions are released, but he does not give any further details. The larvae especially have never been investigated properly, although they have effective defensive properties as well (JACKSON 1931).

As an example of such larval defensive mechanisms, the exudation of defensive fluid by *Amata* larvae and the corresponding morphological structures are described in this paper.

Materials and methods

The following species were examined: *Amata phegea* from Italy (Friaul, Monte Simeone) and *Amata kuhlweinii* from South Africa (Cape Province, East London). The larvae were fed exclusively on *Plantago longifolia*.

The fourth and fifth larval instars of each species were examined by using the following techniques: histological cross-sections and longitudinal sections, SEM of the surface structures and whole mounts of the larval cuticle after maceration in 10% aqueous KOH.

Results

Larvae of the two *Amata* species examined release droplets of a secretion if they are irritated (fig. 1). These droplets only occur in the region of the large dorsal warts ("I" according to Hampson 1898, fig. 4) and consist of a viscous fluid that can be reabsorbed into the body after a few seconds.

Feeding experiments with hand-raised starlings (*Sturnus vulgaris* L.) proved that the larvae are highly unpalatable to these birds. Twelve individually caged starlings were used as predators in this experiment. They were fed with different kinds of prey objects like mealworms, flies, larvae of tipulids and butterflies. Usually they pecked at the offered larvae immediately and ate them without hesitation. After a period of three days each bird received the usual feeding bowl with a mixture of prey objects and one *Amata* larva. All prey objects were eaten as usual, and even the *Amata* larva was pecked at the first approach, but none of them was really harmed as the birds dropped them immediately after pecking and showed obvious signs of distress like shivering, intensive beak wiping, and nervousness. During the next five days the birds always had a *Amata* larva among their food mixture, but after the first experience the starlings never attacked any of them again.

A second experiment, with another group of starlings, was conducted under identical conditions, but using *Amata* larvae whose hairs were carefully

Fig. 1. Larva of *Syntomis kuhlweinii* with droplet of defensive secretion after pinching with tweezers.

removed. The starlings reacted in the same way as quoted above, and after their first experience they always rejected these larvae.

The structures that are significant for this function are localized in a small zone situated at the caudal end of the dorsal warts I (fig. 3, 5). As shown by SEM investigation, this region consists of very smooth cuticle which lacks setae or microtrichia (fig. 4). When the larva is attacked, it raises its internal pressure by contracting the body musculature. With increase of pressure the thin zone breaks open and releases the droplet. When the pressure falls after relaxation of the muscles, a part of the droplet is reabsorbed and a little remains on the surface and closes the fissure by coagulation.

More details are shown in the histological sections (fig. 2, 6). The cuticle in the region of the rupture is extremely thin and has an undulated surface which lacks microtrichia.

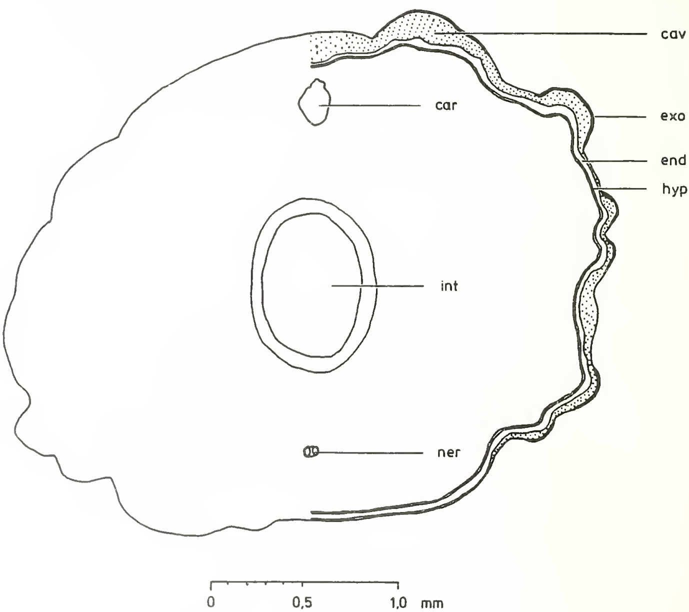

Fig. 2. Cross-section of *Syntomis kuhlweinii* larva. The marked region shows the cavity with defensive secretion. Mag. × 40.
cav = cavity, exo = exo- and mesocuticle, end = endocuticle, hyp = hypodermis, car = heart, int = gut, ner = nervous chord.

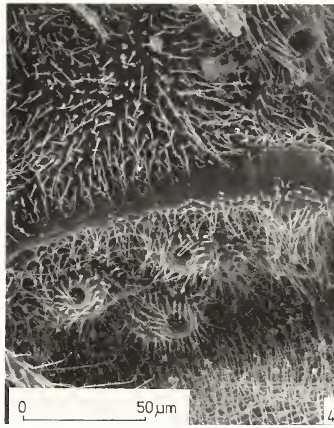

Fig. 3. *Syntomis kuhlweinii*, SEM of the dorsal region of the 4th abdominal segment showing the dorsal warts. The marked area is shown in detail in fig. 4.
Fig. 4. *Syntomis kuhlweinii*, detail from fig. 3, showing the region of the rupture. Smooth cuticle without microtrichia or setae.

The cross-sections of the *Amata* larvae show one single large cavity within the cuticle of each segment ; this cavity is filled with a coagulating substance that definitely differs from the haemolymph. It is not divided to form several separate cavities as in *Zygaena* larvae (Franzl 1980, Franzl & Naumann 1984) ; instead, there is one large undivided cavity extending from the region of the proleg on one side of the larval body to the other (fig. 2). The main part of the secretion is stored beneath the hairy warts (characteristic for all Ctenuchid larvae) (Friese 1959, Hampson 1898, Jackson 1931, Sevastopoulo 1941, 1942)) and the dorsal part of the cuticle.

The longitudinal extension of the cavities is shown in figure 6. For a larva in the last instar the cavities have the following size (all data approximate) :

Longitudinal extension in fourth abdominal segment :	3800 µm
Average height of cavity in the dorsal region :	12 µm
Length of rupture in the cuticle of the wart :	250 µm
Average height of rupture :	15 µm

Preliminary studies of the chemical composition of the defensive secretion revealed the occurrence of at least three different proteins and three free amino acids in an aqueous medium. Pyrrolizidine alkaloids or cyanide

-containing compounds, which were shown to be the repellent agencies in many other defensive secretions, could not be found so far, but the chemical analysis of the secretion will be continued.

Discussion

The presence of hairy warts on all body segments of Ctenuchid larvae was described a long time ago. A closer investigation of the defence mechanism

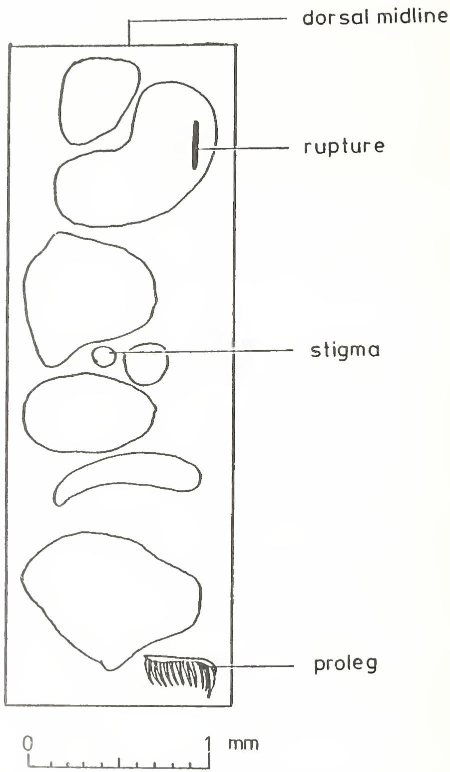

Fig. 5. Diagram of *Syntomis kuhlweinii* last instar larva cuticle, 4th abdominal segment. Only the warts are outlined, leaving out the bases of the setae. KOH-macerate, stained with Chlorazol-black. Mag. × 20.

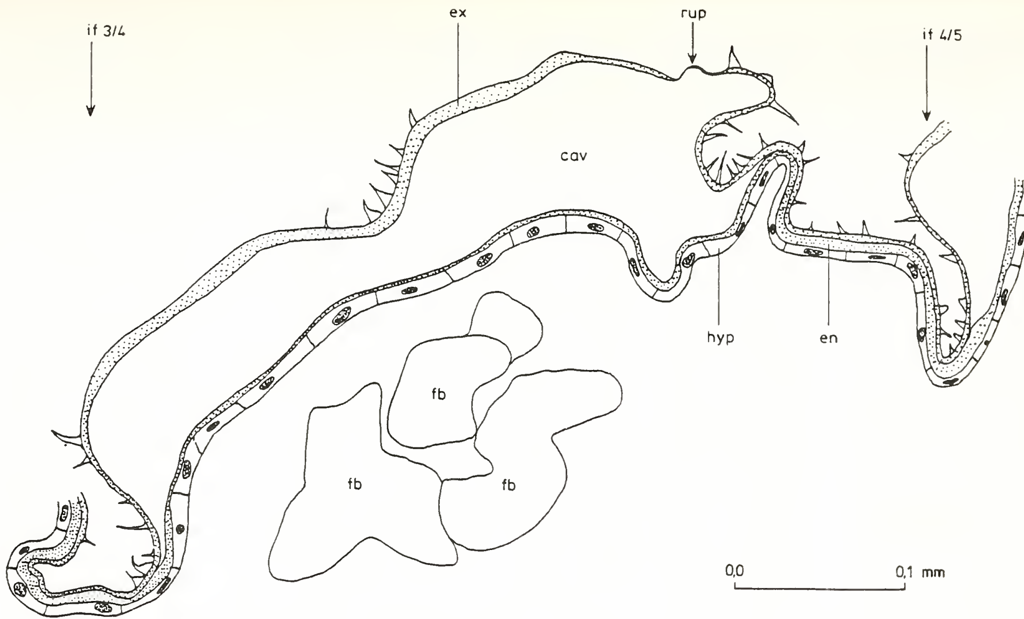

Fig. 6. *Syntomis phegea*, last instar, 4th abdominal segment, longitudinal section, showing the longitudinal extension of the cavity. The region of the fission is marked by an arrow. It is characterized by the very thin exocuticle without setae or microtrichia and by the pleated condition of the surface. Staining Azan, mag. × 400.
cav = cavity, en = endocuticle, ex = exocuticle, fb = fat body, hyp = hypodermis, if 3/4, if 4/5 = intersegmental folds.

in the larvae of two species of *Amata* has revealed a structure in the dorsal warts which enables the larvae to release a droplet of a secretion when attacked. The occurrence of hairy warts on the larval segments is not unusual. Comparable structures can be found, among others, on larvae of Arctiidae, Lymantriidae, Megalopygidae, Noctuidae and Notodontidae (Fracker, 1915). All of the groups cited above, however, possess urticating hairs or spines (Gilmer 1925). A special structure within the cuticle has so far only been described for Zygaenid larvae (Franzl 1980, Franzl & Naumann 1984).

In the present case it was also shown that the secretion is a very important factor in defence and that the defence mechanism still functions even when the setae are removed. This is demonstrated by the fact that larvae without setae are obviously as unpalatable to the starlings as are those larvae with hairs. This may be an important discovery, because larvae that are due to moult within the next 24 hours lose almost all their hairs before they move to a hiding place for moulting.

The question arises whether it is an advantage for the larvae to exude the secretion when attacked instead of just storing it within the body.

It is possible that the secretion contains additional substances which are offensive when smelled. These could warn those predators that are guided by olfaction and even prevent them from biting into the larva.

Also, insectivorous birds usually keep their prey in the beak for a while before swallowing it or feeding it to their young. This is especially true, if they have found a novel prey object and are still testing its taste (Coppinger 1969, 1970, Schuler 1980, 1982). If the larva is not harmed by cautious pecking and it could not exude its secretion, the bird would not experience the foul-tasting substance unless it killed the larva. The reactions of the starlings, however, show that the larvae are highly unpalatable, and as no larva was really injured, the rejection must have been caused by the exuded secretion of the larva.

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