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Poisonous setae on a Baltic amber caterpillar

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ABSTRACT

The knobbed setae on a small caterpillar in 45–55 million years old [Eocene] Baltic amber were studied and characterized as urticating, with evidence of liquid release implying the production of poisons. It is presumed that the caterpillar had been disturbed just prior to falling into the resin, as some of its setae showed defensive responses. The swollen tips of the setae are equipped with “trip hairs” and when disturbed, the tips release liquid deposits, some of which contain rod-like bodies. These setal responses to a disturbance are the first report of poisonous setal defense mechanisms in a fossil insect.

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1. Introduction

The presence of poisonous, urticating setae in many lepidopterous caterpillars is assumed to have evolved as a defense against predators, even though there is scant evidence for this assumption (Smedley et al., 2002; Murphy et al., 2009; Greeney et al., 2012; Pentzold et al., 2016). In humans, these setae can cause what is referred to as “caterpillar dermatitis” or “lepidopterism” (Maier et al., 2003; Hossler, 2010a, 2010b; Seitz et al., 2019). For extremely susceptible individuals, there can be prostration, renal failure, shock, breathing difficulties and even intracerebral bleeding (Bowles et al., 2018; Villas-Boas et al., 2018). Some caterpillars of *Hemileuca* Walker, 1855 (Lepidoptera: Saturniidae) can become so abundant in cattle pastures that they essentially poison the range, as the cattle become injured by ingesting the living larvae as well as their cast skins (Gilmer, 1925; Beavis et al., 1981).

Urticating setae occur globally in a number of lepidopteran larvae as well as in adults (Battisti et al., 2011). Some 12 families of Lepidoptera have caterpillars with poisonous hairs (Murphy et al., 2009; Villas-Boas et al., 2018). Basically, the poison apparatus (*sensu* Gilmer, 1925) consists of a trichogen cell that forms the seta and an associated poison gland cell that supplies the toxic material. Both of these cells are normally adjacent and located in the hypodermis. Several variations of this basic type occur when the poison gland cells shift their position from the hypodermis upwards into the setae (Gilmer, 1925).

Baltic amber was formed in tropical and subtropical forests covering a large part of northern Europe for ca. 10 million years during the early Tertiary. Much of it was eroded from the original accumulation and re-deposited in marine sediments referred to as the “blue earth” layers in the Samland Peninsula (Poinar, 1992). Age estimates of amber from this region range from 35 to 55 million years (Larsson, 1978) to 45–55 million years (Wolfe et al., 2016).

Detailed studies on the body covering of fossil insects are rare, but due to the preservative qualities of amber (Poinar and Hess, 1985), it has been possible to obtain detailed views on various setal features of insects (Poinar and Poinar, 2016).

The present study demonstrates the presence of poison setae on a fossil caterpillar in 45–55 million years old [Eocene] Baltic amber. While basically similar to the structure of poison setae in some extant caterpillars, the fossil seta presents some interesting modifications. This is the first detailed analysis of poison setae on a fossil insect.

2. Materials and methods

The amber specimen was obtained from an unknown collector from deposits along the southern shoreline of the Baltic Sea. A Nikon SMZ-10 R stereomicroscope (Nikon Instruments, Tokyo) and a Nikon Optiphot microscope (Nikon Instruments, Tokyo) with magnifications up to 800 X were used for observing and

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photographing the specimen. Photos were stacked using Helicon Focus Pro X64 to improve clarity and depth of field.

The specimen is deposited in the Poinar amber collection maintained at Oregon State University under accession number L-3-43.

3. Results

Determination that the fossil larva is a lepidopteran was based on morphological characters such as its prognathous head with a distinct head capsule, mandibular mouth parts, 3-segmented antennae inserted at the base of the mandible, 4-segmented thoracic legs, each bearing a single claw, an adfrontal suture and ventral prolegs bearing crochets on segments 3, 4, 5, 6, and 10 (Fig. 1). Placement in a specific family was difficult since many of the fine features are not visible; however, based on the characters that are present, the fossil appears to represent a first instar noctuid larva (Lepidoptera: Noctuidae) (Chu, 1949; Peterson, 1956).

The specimen measures 1.7 mm in length and 0.6 mm in greatest width. The entire dorsal and lateral surface of the body is covered with long single (non-plumose) setae (Figs. 1 and 2). At the base of each seta is a sclerotized projection on an elevated process (chalaza; Fig. 2A). The setae are straight, ranging from 400 to 480 μm in length and 13–19 μm in width. Each seta bears a terminal swelling (knob) approximately 26 μm in greatest diameter (Fig. 2B–F). A series of stages involving the release of secretions from the swollen tips were recorded. In non-disturbed setae, one or two "trip hairs" (Fig. 2B, C) extended apically from the closed swollen tips. When disturbed, liquid deposits could be seen emerging from the swollen tips (Fig. 2D). In some setal heads, along with the liquid deposits, were short, rod-shaped particles (Fig. 2E). In some cases, liquid deposits were ejected through an opening in the swollen tip (Fig. 2F).

4. Discussion

The secretions produced by the fossil caterpillar are considered to be poisons rather than venoms. This is based, in part, by the definition of these terms by Nelsen et al. (2014). The latter authors define venom as a toxin delivered via a mechanical trauma produced by a structure that results in a wound while a poison is transferred from one organism to another without mechanical injury.

Determination that the projections on the caterpillar are setae and not spines is based on the definition of setae as sclerotized hair-like projections of cuticula arising from a single trichogen cell and surrounded at the base by a small cuticular ring (Gilmer, 1925). Spines are multicellular, thorn-like outgrowths of the cuticula without any separating cuticular rings (Nichols, 1989). An example of an extant caterpillar with setae is shown in Fig. 3A and an extant one with spines in Fig. 3B.

It would appear that the caterpillar had been disturbed just prior to its fall into the resin and some of its setae responded to the disturbance. There is also the possibility that the hairs were triggered by the fall itself into the resin.

The primitive type of poison seta on lepidopterous larvae is a seta formed by a trichogen cell in the hypodermis. Adjacent to the trichogen cell is a poison gland cell that produces cytoplasm that passes through the lumen of the seta and is released at the tip when the seta is broken (Gilmer, 1925; Snodgrass, 1935; Nichols, 1989).

Normally, setae on extant caterpillars are pointed at the tip and in some cases have developed into thick protective spines without the need to produce any associated fluid poisons. However, in some caterpillars of *Vanessa* Fab. (Lepidoptera: Nymphalidae) and members of the Saturniidae, the poison gland cell shifts its position

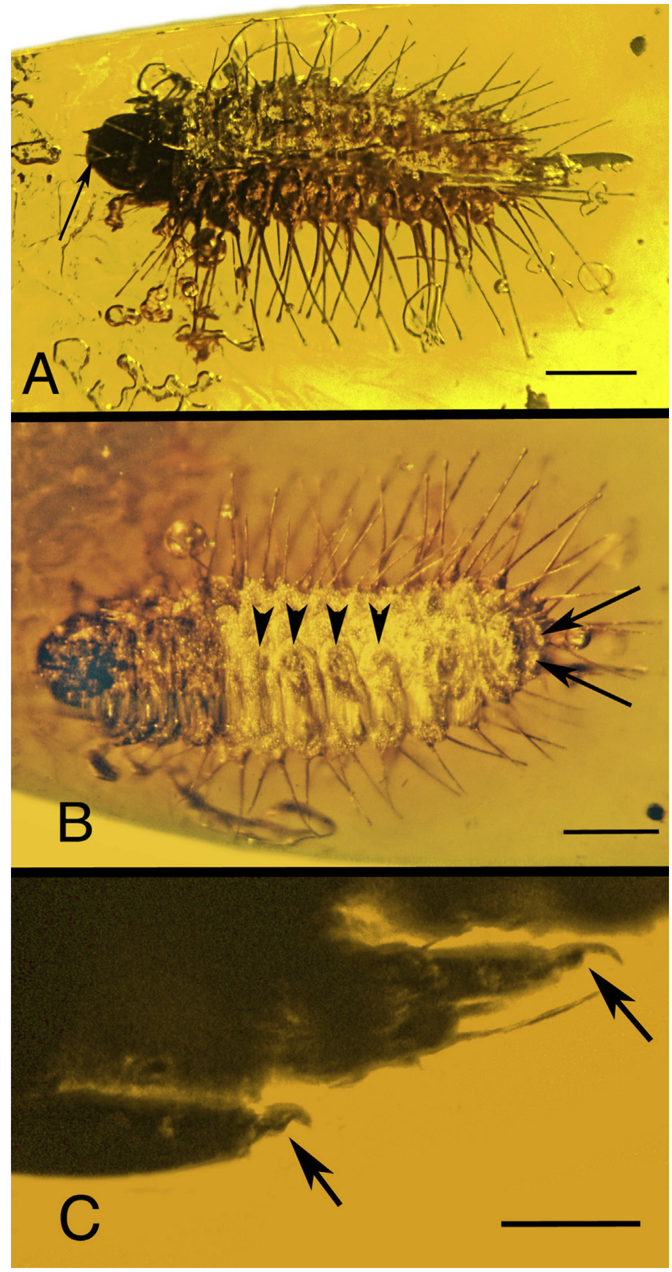

Fig. 1. A. Dorsal view of setaceous caterpillar in Baltic amber. Note adfrontal suture (arrow) on head. Scale bar = 340 μm. B. Ventral view of setaceous caterpillar in Baltic amber. Arrowheads show prolegs bearing crochets on abdominal segments 3–6. Arrows show prolegs on segment 10. Scale bar = 300 μm. C. Single claw (arrows) on middle and hind legs of the setaceous caterpillar in Baltic amber. Scale bar = 85 μm.

from above the body wall into the lumen of the seta (Gilmer, 1925). Such a migration of the poison gland cell to a site in or just beneath the expanded tips of the seta appears to have occurred in the fossil. The released liquid is a product of the cytoplasm of the gland cell, whose nuclei can vary from round to branched or bluntly lobate (Gilmer, 1925).

The hairs arising from the knobbed apex of undisturbed setae probably serve as "trip hairs" or mechanosensory hairs used for detecting approaching predators. After the setal tips are tripped, they began to release fluid (Fig. 2D) produced by gland cells, possibly representing toxic material similar to that found in extant

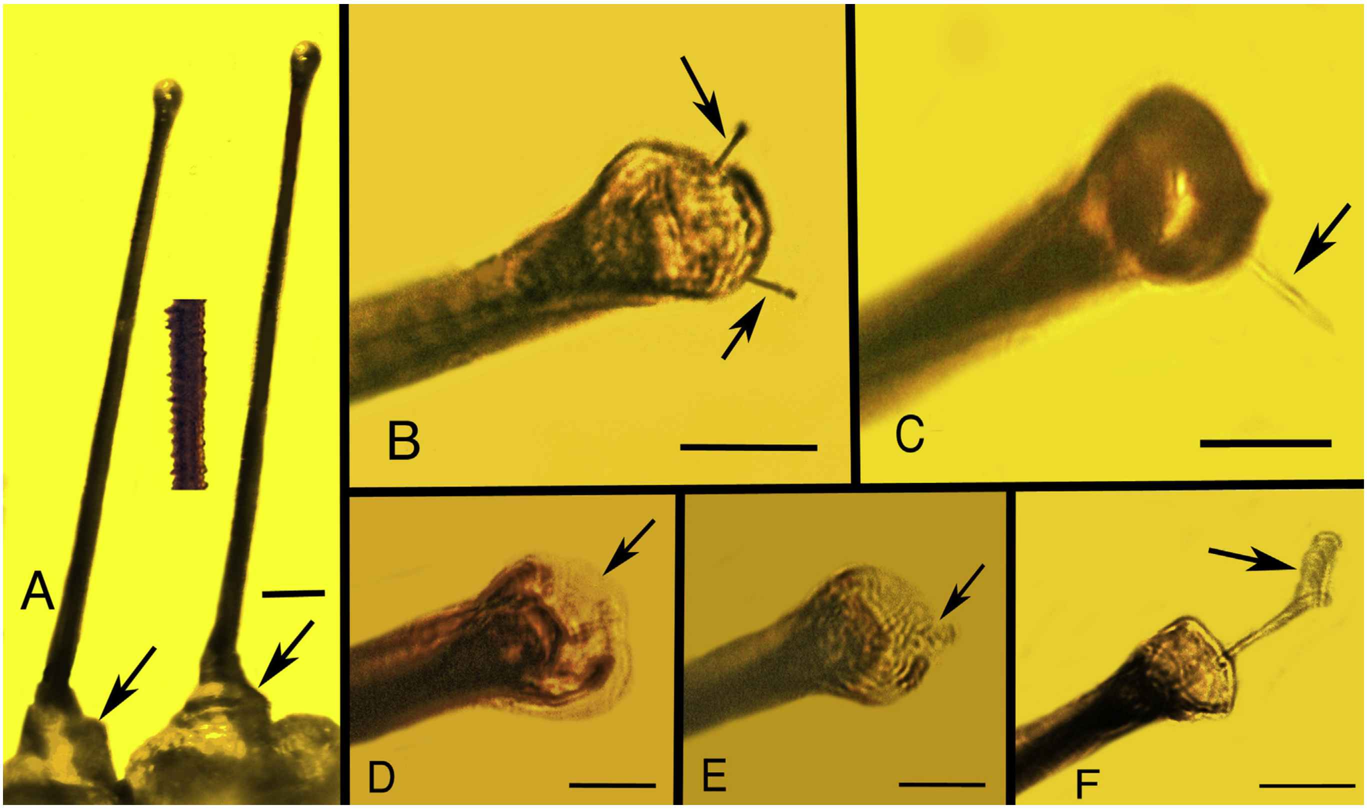

Fig. 2. A. Two poisonous setae with swollen tips on the abdomen of the setaceous caterpillar in Baltic amber. Detail view of ridged setal stalk shown in middle of photo. Arrows show chalazae at base of setae. Scale bar = 42 μm. B. Two "trip hairs" (arrows) extended apically from the closed swollen setal tip on the setaceous caterpillar in Baltic amber. Note possible gland cell nucleus in swollen tip. Scale bar = 19 μm. C. Single "trip hair" (arrow) extended apically from the swollen setal tip on the setaceous caterpillar in Baltic amber. Scale bar = 20 μm. D. Liquid deposit (arrow) emerging from the swollen tip of a disturbed seta on the setaceous caterpillar in Baltic amber. Note likely gland cell nucleus in swollen tip. Scale bar = 13 μm. E. Short, rod-shaped particles (arrow) associated with the liquid deposit expelled from the swollen tip of a disturbed seta on the setaceous caterpillar in Baltic amber. Note likely gland cell nucleus in swollen tip. Scale bar = 17 μm. F. Liquid deposit (arrow) ejected from the swollen tip of a disturbed seta on the setaceous caterpillar in Baltic amber. Scale bar = 21 μm.

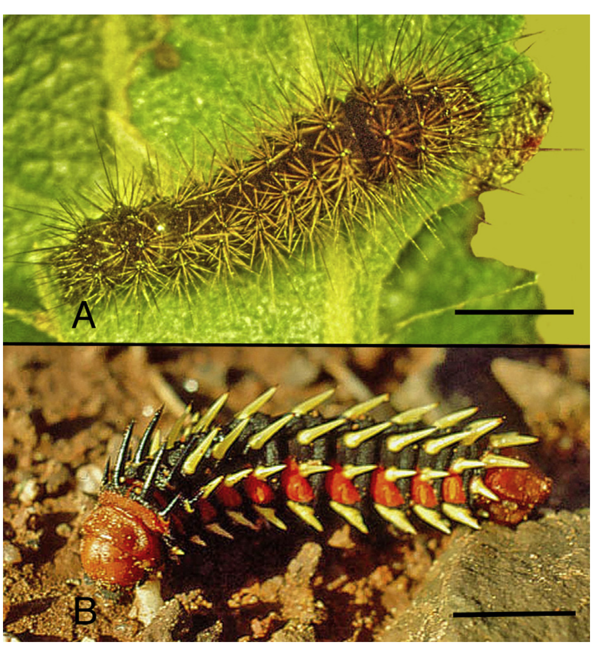

Fig. 3. A. Pointed setae on a caterpillar of *Grammia* sp. (Lepidoptera: Noctuidae) on a willow (*Salix* sp.) leaf in Oregon. Photo by G. Poinar (October 17, 1999). Scale bar = 8 mm. B. Pointed spines on a caterpillar of *Bunaea alcinoe* (Stoll) (Lepidoptera: Saturniidae) from an African mahogany tree (*Khaya senegalenisis*) in Burkina Faso, West Africa. Photo by G. Poinar (August 17, 1976). Scale bar = 16 mm.

caterpillars (Gilmer, 1925; Snodgrass, 1935; Nichols, 1989; Bowles et al., 2018). It is unknown if the secretion by itself repels potential predators or if the protective elements are a combination of secretions with other sticky substances. The nature and function of the rod-like particles in the released secretions (Fig. 2E) are unknown. They could be analogous to the minute granules reported in the glandular poison cells of *Parasa latistriga* Distant (Lepidoptera: Limacodidae) (Gilmer, 1925).

In extant caterpillars, most setae (Fig. 3A) and spines (Fig. 3B) are pointed at the tips and function as mechanical protection as well as poison release in some species. This is in contrast to the rounded tips of the setae of the fossil. The deposits on the tips of the fossil setae are somewhat similar in general appearance to the glandular hair types of the cabbage butterfly, *Pieris rapae* (L.) (Lepidoptera: Pieridae) (Smedley et al., 2002). These hairs bear droplets of an oily secretion at their tips. Similar deposits are found in the caterpillar of *Zygaena filipendulae* (L.) (Lepidoptera: Zygaenidae) (Pentzold et al., 2016). However, these "viscous defense droplets" that act as a glue on the appendages of potential insect or arachnid predators differ in structure from those on the fossil and are not accompanied by "trip hairs".

While some extant noctuid larvae are known to possess setae with knobbed apices (Peterson, 1956), none of these, to our knowledge, have been examined regarding the presence of poison glands.

This discovery provides an early record of poisonous setae of lepidopterous larvae that were used for defense some 40–50 million years ago.

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