SCIENTIFIC NOTE: FUNCTIONAL MORPHOLOGY OF MASQUERADING LARVA OF *CERATONYX SATANARIA* WITH NOTES ON HORNED SPANWORM, *NEMATOCAMPA RESISTARIA* (GEOMETRIDAE: ENNOMINAE)

Andrei Sourakov and Minna Stubina

McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, FL 32611; asourakov@flmnh.ufl.edu

Abstract - Morphological drawings and photographs are provided illustrating the unusual larval morphology, featuring long cervical horns or tubercles, of the geometrid moth *Ceratonyx satanaria* Guenée. In addition photographs of *Nematocampa resistaria* (Herrich-Schäffer) larvae, commonly known as a "horned spanworm" for its long abdominal tubercles, are also provided. The possible function of cervical horns is discussed in the context of predator-prey interactions. A survey of available photographs of geometrid larvae worldwide revealed cervical horns only in the genera *Ceratonyx* (Ennominae: Nacophorini) and in two Australian species of Geometridae: *Plesanemma fucata* (F&R 1875) (Ennominae: Nacophorini) and *Parepisparis lutosaria* (F. & R) (Oenochrominae).

Key words: anti-predator defenses, mimicry, camouflage, crypsis.

Larvae of Geometridae and genus *Ceratonyx*

The remarkable twig-like appearance of geometrid moth larvae, and in particular the polymorphism and effectiveness of this mode of defense against predators, has attracted much attention from researchers. While larval color can depend on diet, and hence can be regulated by environmental factors (e.g., Greene 1989), the number of tubercles that make caterpillars so realistically twig-like has been shown to be genetically determined (Bocaz et al. 2003). The evolution of this so-called 'masquerade' phenomenon (Skelhorn et al. 2010) is likely due to selection by birds (De Ruiter 1952).

The typical appearance of larvae in the subfamily Ennominae is illustrated by that of the maple spanworm, *Ennomos magnaria* Guenée, [1858] (e. g., Fig. 5A). Here we provide morphological drawings (Fig. 1) and photographs (Figs. 2-4) illustrating the unusual larval morphology of the geometrid *Ceratonyx satanaria* Guenée [1858]. Previously, a photo in Fig. 3A was published as an "unidentified geometrid" on the cover of the journal Tropical Lepidoptera Research (Sourakov 2010).

Ceratonyx satanaria is found throughout the southeastern United States, from Texas east to South Carolina and north Florida (Ringe 1975). Though Ringe (1975) lists the species as rare, Brou collected close to 400 individuals in his light traps in Louisiana, suggesting that this species is single-brooded, with flight peaking in mid-February (Brou 2012). In addition to the above distribution, Moth Photographers Group (2012) shows records for Kentucky, Oklahoma, and North Carolina.

Brou (2012) notes that only two females were collected, which probably suggests that the latter are poor fliers, or stay secluded from predators and are not attracted to light. It is very possible that this species is extremely local, which accounts for its apparent rarity. For instance, out of three separate moth surveys in the Gainesville area, the two that were relatively geographically broad detected *C. satanaria* (Austin 2009; Kons 2001), while one conducted at a fixed locality did not (Austin 2010), even though the latter survey was much more extensive than the two former surveys in terms of time (5 years), regularity of collecting (bi-weekly), number of species (ca. 1000), and number of individuals (ca. 40,000).

Morphology of *Ceratonyx* larvae

The larva illustrated in Figs. 1-2 was found on the ground in mid-April in Gainesville, Florida (Lat.: 29.6864; Long.: -82.3391"), and was preserved in 70% ethanol after boiling in water. It measures 33 mm long, with cervical horns 10 mm long, and head 3.5 mm wide. The adult in Fig. 2A was photographed the following year at the same location where the larva was found. Based on the photographs of the larva, David Wagner identified our specimen as *C. satanaria*. The identity is further confirmed by the description by Guenée (1857), which was based on an unpublished drawing by Abbot, that reads as follows: "…with a very long pair of prothoracic filaments, but has three small projections on the second abdominal segment and only a stump of the filament on the eighth abdominal segment. The body is gray, with the head, filaments, subdorsal line and all legs rusty red."

The curving of the cervical horns observed in *C. satanaria* larva found by Sourakov in 2010 (Figs. 2B-D, 3A-C) might be due to this particular individual being close to pupation (Noel McFarland, per.com.). Photographs of another larva, found by Donald Hall in Gainesville in April 2012 (which died as prepupa due to parasitism), show the cervical horns with tips being leaf-bud-shaped. Placing these photographs next to the twig of sweet gum *Liquidambar styraciflua* L. (Hamamelidaceae) (the hostplant listed for *C. satanaria* by Ringe (1975) and Heppner (2007)) suggests that this larva would be well masqueraded as an inedible object in its natural environment (Fig. 3D-F)). The lesser projections found on abdominal segments of *C. satanaria* mimic leaf scars and buds (Fig. 1(B-E)) and are covered with short sclerotized spines, which perhaps allow these cuticular flaps to maintain their shape, texture and color.

Ceratonyx satanaria is a member of a Neotropical genus comprising 12 species (Ringe 1975). Franclemont (1967) collected several *Ceratonyx arizonensis* (Capps, 1950) larvae on *Viguiera multiflora* (Nutt.) [Asteraceae] in Arizona and was able to use the unique immature stage morphology (cervical horns) to place this and other *Ceratonyx* species, including *C. satanaria*, into the correct genus, based on Guenée's larval description. The larva of *C. arizonensis* illustrated by Franclemont (1967) differs from ours in that its head is patterned with

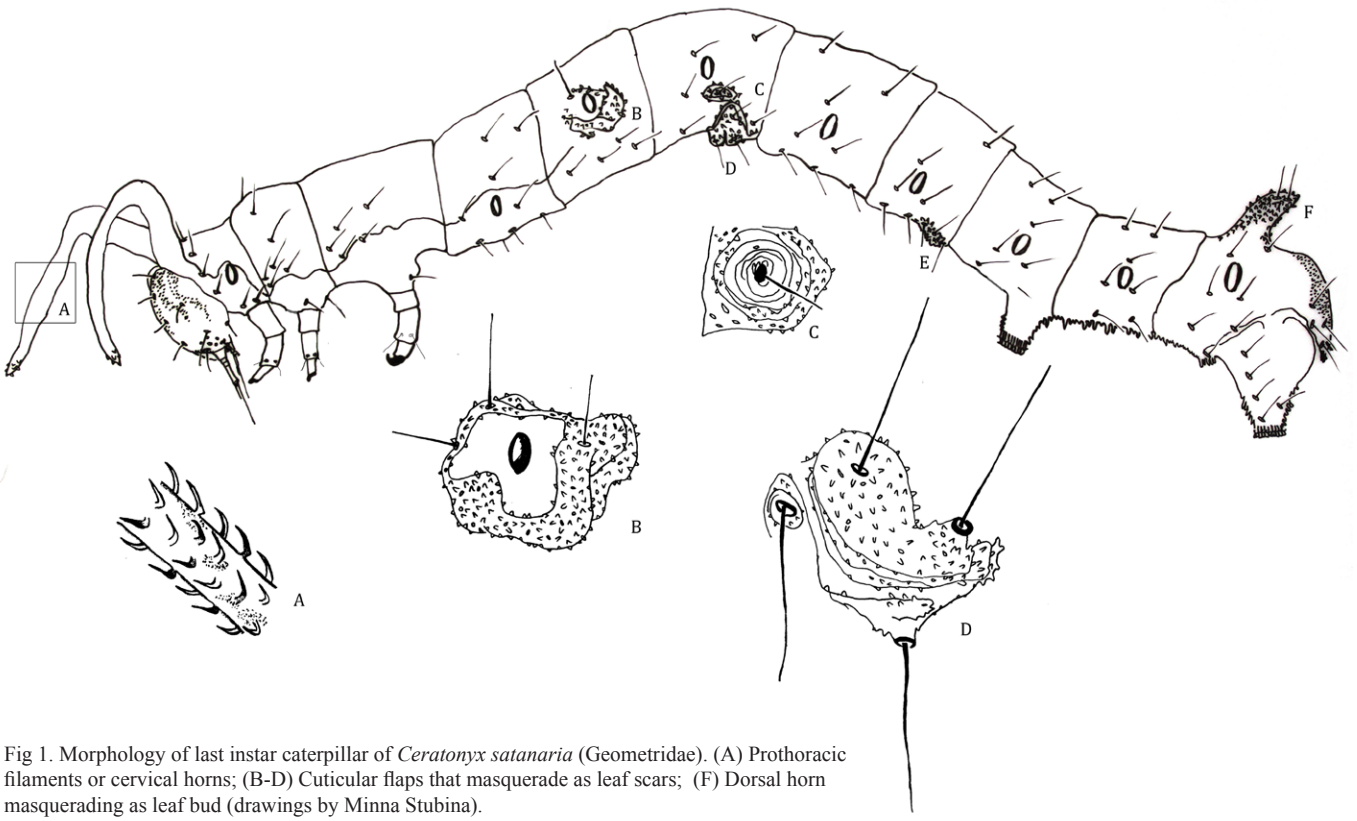

Fig 1. Morphology of last instar caterpillar of *Ceratonyx satanaria* (Geometridae). (A) Prothoracic filaments or cervical horns; (B-D) Cuticular flaps that masquerade as leaf scars; (F) Dorsal horn masquerading as leaf bud (drawings by Minna Stubina).

black dots and the body is striped (black subdorsal line, yellow stigmatal band and narrow black longitudinal stigmatal line). The dorsal horn on the penultimate abdominal segment of *C. arizonensis* is long, narrow and pointed, rather than bud-like as in *C. satanaria*.

Function of cervical horns

We propose that the function of the cervical horns in *C. satanaria* is mostly sensory, perhaps helping the larva to more quickly detect and hence avoid predators such as wasps. *Nematocampa resistaria* (Herrich-Schäffer [1856]), a North American geometrid whose larva is commonly known as "horned spanworm" for its long tubercles located on the abdominal segments, has very distinct (probably primary) setae at the tip of its filaments (Fig. 6), and it is likely that these setae located out at the tip of a long tubercle makes for a better vibration detector. The cervical horns or tubercles of *C. satanaria* that make its larvae so unusual among other twig-mimicking inchworms are covered with numerous outgrowths as well as secondary setae (Figs. 1A, 4B).

It has been shown that the monarch larvae, which have two pairs of long tentacles, react more strongly than larvae of other species lacking tentacles to sounds of buzzing wasps, bumble bees and passing aircraft (Rothchild and Bergström 1997). The monarchs in the latter study reacted by emitting noxious chemicals. Both *C. satanaria* and *N. resistaria*, as well as other caterpillars that masquerade as twigs, respond by "freezing" into a twig-like position when disturbed by a touch or a camera flash (Sourakov, pers. obs.). However, other types of defensive responses have been shown experimentally in the inchworm *Semiothisa (Macaria) aemulataria* (Walker, 1861), which drops off the plant and hangs by a silk thread upon detecting vibration produced by predatory wasps (Castellanos & Barbosa 2006). This study showed that defense responses are very predator-specific, with different responses to the approaching predatory Hemiptera and birds than to wasps. Potter or mason wasps (Vespidae: Eumeninae) commonly stuff their nests with geometrid larvae (Sourakov, pers. obs., e. g., Fig. 5B), and it would not be surprising if some species developed elaborate devices, such as tubercles, to detect and avoid them.

Cervical horns in larvae of other geometrid species

The cervical horns of *Ceratonyx* prove to be a rather unusual character for the geometrid family. Examination of ca. 7000 photographs of inchworms in Janzen and Hallwachs (2012) revealed many Neotropical species with sometimes dramatic abdominal projections, especially in the genera *Dichorda*, *Nemoria*, *Prochoerodes*, *Oxydia*, *Cathydata*, *Nematocampa*, *Tachychlora*, *Phrudocentrai*, *Tachyphyle*, *Synchlora*, *Melinodes*, *Opisthoxia*, and *Phyle*. However, we found no larvae with cervical horns among these photographs (very short tubercles exist in the prothoracic area of *Herbita medona* (Druce, 1892) and *Ischnopteris bifinita* (Walker, 1862)).

Worldwide, however, cervical horns were found in larvae of a eucalyptus-feeding Australian moth, *Plesanemma fucata* (F&R, 1875) (Young 2008), which belongs to the same tribe as *Ceratonyx* (Ennominae: Nacophorini). Even more similar is the larval morphology found in another Australian eucalyptus-feeding inchworm *Parepisparis lutosaria* (F. & R., 1875), which belongs to a different subfamily (Oenochrominae)

Fig. 2. *Ceratonyx satanaria* (Geometridae): (A) Adult male; (B-D) Caterpillar moving. (Gainesville, FL (A) Feb. 2011, (B-D) Apr. 2010, photos by A. Sourakov).

Fig. 3. *Ceratonyx satanaria* (Geometridae) masquerading as a twig (A) Ventral view; (B, F) Dorsal view; (C, D) Lateral view; (E) Twig of supposed host-plant, *Liquidambar styraciflua* (sweet gum). (Gainesville, FL) (photos A-C, E by A. Sourakov; D, F by D. Hall).

Fig. 4 *Ceratonyx satanaria* (Geometridae): (A) Prepupa; (B) Cervical horns of prepupa, close-up, showing numerous outgrowths; (C) Prepupa inside a cocoon that it made in leaf litter (photos by A. Sourakov, Gainesville, FL, Apr. 2012).

Fig. 5. (A) A typical stick-mimicking inchworm, *Ennomos magnaria*; (B) A dissected potter wasp nest with paralyzed geometrid caterpillars inside (photos by A. Sourakov, Aug. 2011 (A) Maine, (B) Florida).

(McFarland 1988). Ringe (1975) stated that "the tribal placement of *Ceratonyx* is in doubt" and was based primarily on a single character in the male genitalia (paired processes of the anellus). It is possible, that based on the present larval description and its similarity to *P. lutosaria* in Australia, the systematic position of *Ceratonyx* or *Parepisparis* should be reconsidered.

ACKNOWLEGEMENTS

We thank David Wagner for identifying the caterpillar and for suggesting an important reference. Noel McFarland in a letter to the first author suggested the similarity of *Ceratonyx* larva with *P. lutosaria*. Donald Hall kindly supplied a prepupa of *C. satanaria* and two photos of its larvae. Matthew Standridge found a larva of *N. resistaria* depicted in Fig. 6. The anonymous peer-reviews greatly improved the quality of this note.

Fig. 6. Horned spanworm, *Nematocampa resistaria*, another species of North American geometrid that posesses filaments: (A-B) Fourth instar, found on *Vaccinium* sp., nr. O'Leno State Park, FL, Apr. 2005; (C-F) Last instar, found on *Salix* sp. in Gainesville, FL, Apr. 2012. (photos by A. Sourakov).

REFERENCES CITED

Austin G. T.
2009. Inventory of moths (Insecta: Lepidoptera) of Paynes Prairie Preserve State Park, Alachua County, Florida. Interim Report under Research/Collection Permit Number 07070742.

Austin. G. T.
2010. Moth community from a northcentral Florida location – a taxonomic checklist. *Tropical Lepidoptera Research* 20(1): 41-44.

Bocaz P., L. E. Parra, and P.F. Victoriano
2003. Larval morphological variation and its relation to host plants in *Syncirsodes primata* (Lepidoptera: Geometridae). *Gayana* 67(1): 39-44.

Brou V. A. Jr.
2012. *Ceratonyx satanaria* in Louisiana (http://lsuinsects.org ; last accessed 5 April 2012)

Castellanos, I. and P. Barbosa
2006. Evaluation of predation risk by a caterpillar using substrate-borne vibrations. *Animal Behaviour* 72: 461-469. doi:10.1016/j.anbehav.2006.02.005

De Ruiter L.
1952. Some experiments on the camouflage of stick caterpillars. *Behaviour* 4: 222–232.

Franclemont, J. G.
1967. Identity of *Ceratonyx satanaria*, and the larva and pupa of *C. arizonensis* (Geometridae, Ennominae). *J. Lepidopterists' Society* 21: 11- 14.

Greene, E.
1989. A Diet-Induced Developmental Polymorphism in a Caterpillar. *Science* 243(4891): 643-646.

Guenée, A.
1857. [1858]. *Histoire naturelle des insectes. Species general des lepidopteres.* Paris, vol. 9, lvi+514 pp.

Heppner, J. B.
2007. *Lepidoptera of Florida, Part 1: Introduction and catalog. Arthropods of Florida and neighboring land areas, Vol. 17*. Florida Department of Agriculture. 670 pp.

Janzen, D. H. & W. Hallwachs
2012. Philosophy, navigation and use of a dynamic database ("ACG Caterpillars SRNP") for an inventory of the caterpillar fauna, and its food plants and parasitoids, of Area de Conservacion Guanacaste (ACG), northwestern Costa Rica (http://janzen.sas.upenn.edu). (last accessed 3-14-2012)

Kons H. L. Jr.
2001. Contributions Toward a Lepidoptera (Psychidae, Yponomeutidae, Sesiidae, Cossidae, Zygaenoidea, Thyrididae, Drepanoidea, Geometroidea, Mimalonoidea, Bombycoidea, Sphingoidea, & Noctuoidea) Biodiversity Inventory of the University of Florida Natural Area Teaching Lab. (www.natl.ifas.ufl.edu) (last accessed 3-15-2012)

McFarland, N.
1988. *Portraits of South Australian Geometrid Moths*. Allen Press. 400pp.

Moth Photographers Group
2012. http://mothphotographersgroup.msstate.edu (Last Accessed 7 May, 2012).

Rindge, F. H.
1975. A Revision of the Moth Genus *Ceratonyx* (Lepidoptera, Geometridae), *American Museum Novitates* 2564: 1-30 pp.

Skelhorn J., H. M. Rowland, and G. D. Ruxton
2010. The evolution and ecology of masquerade. *Biol. J. Linn. Soc.* 99: 1–8.

Sourakov, A.
2010. Back cover photo - unidentified geometrid larva. *Tropical Lepidoptera Research* 20(1).

Young C. J.
2008. Characterisation of the Larvae of Australian Nacophorini. *Zootaxa* 1862: 1–74.