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Daniel K. Young
University of Wisconsin

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CANTHARIDIN AND INSECTS: AN HISTORICAL REVIEW

Daniel K. Young¹

ABSTRACT

The defensive role played by cantharidin in meloid and oedemerid beetles has been well documented. However, several groups of insects are known to orient positively toward the chemical or to the beetles which produce it: Miridae (Hemiptera); Pyrochroidae, Anthicidae (Coleoptera); Ceratopogonidae, Anthomyiidae (Diptera); and Braconidae (Hymenoptera). Literature citations are summarized for each of these taxa using current nomenclature and indicating the nature of the association.

While reviewing literature pertinent to research on the systematics and bionomics of the genus *Pedilus* (Coleoptera: Pyrochroidae), an intriguing association with a blister beetle (Meloidae) came to my attention. It involved the type specimen of *P. impressus* which was found attached to the side of a *Meloe angusticollis* (Say 1827).

Subsequent reading revealed that several groups of insects have been observed in association with meloids. The primary stimulus involved in every case appears to be cantharidin, the blister-causing compound evolved by the Meloidae as a chemical defense mechanism. Although long thought to be a bicyclic monoterpene, recent research has shown that farnesol is the biosynthetic precursor of cantharidin (Sticher 1977). Thus, cantharidin must be considered a sesquiterpenoid derivative.

Cantharidin was first isolated from *Lytta vesicatoria* (L.), the green Spanish-fly, by Robiquet in 1810. The creature is actually not a fly at all but a rather common European blister beetle. Beauregard (1890) stated that cantharidin was produced in the third pair of seminal vesicles of the adult male and in the copulatory vesicle and ovaries of the adult female. While both sexes contain the compound, data have been presented to suggest that biosynthesis takes place primarily in the accessory glands of the adult male (Sierra et al. 1976). The compound may also be produced by the larval stages (Meyer et al. 1968), but Sierra's group found that cantharidin biosynthesized in males was transferred to females, which were unable to biosynthesize cantharidin from any terpenoid precursors. The chemical is known to occur in all developmental stages of the majority of meloids analytically examined (Mayer & Johansen 1977, and references cited therein).

Cuenot (1890) was probably one of the first to recognize cantharidin's probable defensive function. He noted that when provoked or attacked, *Meloe proscarabeus* L. exuded cantharidin-containing hemolymph from the tibiotarsal articulations. He further observed that most reptiles and carnivorous insects disliked the substance intensely and hypothesized that such an effective means of defense might compensate for the short elytra and general soft-bodiedness of *Meloe* and other vesicating species. Such an evolutionary strategy is perhaps analogous to the repugnatorial stink glands of cantharids (Sulc 1949), another generally soft-bodied, "loosely-constructed" group. When applied to certain insects, cantharidin reportedly acts as a potent nerve poison; its potential as an insecticide has been discussed by Görmitz (1937). Carrel and Eisner (1974) also demonstrated cantharidin to be a potent feeding deterrent to insects, with concentrations effective at 10^{-2} M. Further expression of the defensive role cantharidin plays in meloids is manifest in their characteristic aggregating behavior (Selander & Mathieu 1969:45), which strongly

¹Department of Entomology, University of Wisconsin, Madison, WI 53706.

resembles the behavioral strategy described by Eisner and Kafatos (1962) for the aposematic and distasteful *Lycus loripes* (Chevrolat).

Even with the evolution of this elaborate chemical defense mechanism there occur in nature several paradoxes. Members of six families representing four orders have been attracted to meloid beetles, cantharidin, or both.

HEMIPTERA

MIRIDAE

Cantharidin-orienting Hemiptera belong to the Miridae or plant bugs, which are primarily a phytophagous group as the common name suggests. However, whether mirids are primitively phytophagous is a matter of some controversy (see Wheeler 1976 for discussion and references cited therein), as is the same question when asked of the order as a whole (Cobben 1979, Sweet 1979). Miller (1956) pointed out that some mirid species are oligophagous.

Orthotylinae

Hadronema bispinosa Knight, on *Epicauta andersoni* Werner and *E. ventralis* Werner (Pinto 1978).

H. militaris Uhler, on *Lytta nuttalli* Say (Fox 1943, Selander 1960, Church and Gerber 1977) and *L. viridiana* LeConte (Church and Gerber 1977).

H. uhleri VanDuzee, on *L. moerens* (LeConte), *L. croichi* (Horn), *L. stygica* (LeConte), *Tegrodera erosa* LeConte, and *Cordylospasta opaca* (Horn) (Pinto 1978).

Hadronema sp., at cantharidin (Pinto 1978).

Bryocorinae

Halticotoma nicholi Knight, on *Megetra cancellata* (Brandt and Erickson) and *Meloe laevis* Leach (Pinto 1978).

Sixeonotus sp., at cantharidin (Pinto 1978).

COLEOPTERA

PYROCHROIDAE

As was mentioned in the introduction, the first account of a pediline-meloid association was that of Thomas Say (1827). Although he could detect no damage to the meloid, several authors have observed that other meloid's elytra had been chewed by *Pedilus* (Leech 1934, Pinto and Selander 1970, LeSage and Bousquet 1983).

Pyrochroinae

Neopyrochroa flabellata (Fabricius), at cantharidin (Young 1984b).

Pedilinae

Pedilus elegans (Hentz), on *Meloe niger* Kirby (Harrington 1894).

P. impressus (Say), on *M. angusticollis* Say (Say 1827).

P. labiatus (Say), near caged *Epicauta fabricii* (LeConte) (Abdullah 1964a).

P. lugubris (Say), on *M. angusticollis* (LeSage and Bousquet 1983).

P. terminalis (Say), on *M. americanus* Leach and *M. angusticollis* (Pinto and Selander 1970).

Pedilus sp. nov. (cited as *P. monticolus*), on *M. niger* (Leech 1934).

Anisotria shooki Young, at cantharidin (Young 1984a).

ANTHICIDAE

Most of the published observations dealing with anthicid-meloid or anthicid-cantharidin associations have come from Europe and North America.

- Acanthinus scitulus* (LeConte), at cantharidin (Chandler 1976).
Anthicus aubei LeFerté, on *Meloe majalis* L. (Pic 1897).
A. biauriculatus Pic, on *M. erythrocnemus* Pallas (Chobaut 1923).
A. chobauti Pic, on *M. majalis* (Pic 1897).
A. cincturus Marseul, on *M. majalis* (Pic 1897).
A. fairmairei Brisbane, on *M. rugosus* Marsham (Chobaut 1895), and on *M. violaceus* Marsham (Theodorides and Dewailly 1951).
A. insignatus Lucas, on *M. corallifer* Germar (Sanz de Diego 1880, Bolivar y Urratia 1896), and on *M. cavensis* Petagona (Rotrou 1941).
A. lutulentus Casey, on dead meloids (Werner 1964).
A. nanus LeConte, on dead meloids (Werner 1964).
A. obscuripes Pic, on *M. autumnalis* Olivier (Normand 1918).
A. panousei Pic, on *Meloe cavensis* (Dewailly and Theodorides 1952).
A. pumilis Baudi, on *M. majalis* (Pic 1897).
A. tortiscelis Marseul, on *M. cavensis* (Rotrou 1941).
Mecynoiarsus balsasensis Werner, at cantharidin (Chandler 1976).
Notoxus anchora Hentz, at cantharidin (Chandler 1982).
N. calcaratus Horn, at "chemical traps" (presumably cantharidin or dead meloids) (Blaisdell 1936), and at cantharidin; on dead meloids (Chandler 1976, 1977).
N. celatus Chandler, at cantharidin; on dead meloids (Chandler 1977).
N. caudatus Fall, at cantharidin (Chandler 1982).
N. cavicornis LeConte, at cantharidin (Chandler 1982).
N. conformis LeConte, at cantharidin (Chandler 1982).
N. constrictus Casey, "chemical traps" (Blaisdell 1936), and at cantharidin; on dead meloids (Chandler 1976, 1977).
N. desertus Casey, "chemical traps" (Blaisdell 1936).
N. denudatus Horn, at cantharidin (Chandler 1982).
N. hageni Chandler, at cantharidin (Chandler 1982).
N. hirsutus Champion, at cantharidin (Chandler 1976, 1977).
N. intermedius Fall, at cantharidin (Chandler 1982).
N. lateralis Chandler, at cantharidin (Chandler 1977).
N. marginatus LeConte, on dead meloids (Chandler 1976, 1977).
N. mauritanicus LaFerté, on *Lytta vesicatoria* (L.) (Chobaut 1897).
N. mexicanus Champion, at cantharidin; on dead meloids (Chandler 1976, 1977).
N. monoceros L., on dead *Lytta vesicatoria* (Bedel 1895, Kieffer 1922), on *Meloe proscarabeus* L. (Richards 1928), on *Meloe* spp. (Tylden 1865, Traizet 1896), on "oil beetles" (presumably *Meloe*) (Hacker 1899), on "Miakafer" (presumably *Meloe*) (Geilenkeuser 1908, Folwaczny 1937), and at cantharidin (Görnitz 1937; Abdullah 1964a, 1964b, 1965, 1969).
N. monodon (Fabricius), at cantharidin; on dead meloids (Chandler 1976).
N. montanus Casey, at cantharidin (Chandler 1982).
N. murinipennis (LeConte), on dead meloids (Chandler 1976, 1977).
N. nevadensis Casey, at cantharidin (Chandler 1982).
N. nuperus *haustus* Chandler, on dead meloids (Werner 1964, Chandler 1977).
N. pictus Casey, at cantharidin (Chandler 1982).
N. pygidialis Chandler, at cantharidin; on dead meloids (Chandler 1977).
N. robustus Casey, "chemical traps" (Blaisdell 1936).
N. serratus (LeConte), at cantharidin (Chandler 1982).
N. sparsus LeConte, "chemical traps" (Blaisdell 1936).
N. spatulifer Casey, at cantharidin (Chandler 1982).
N. ialpa LaFerté, at cantharidin (Chandler 1976, 1977).

N. toltectorum Chandler, at cantharidin; on dead meloids (Chandler 1977).

N. whartoni Chandler, at cantharidin (Chandler 1982).

N. youngi Chandler, at cantharidin (Chandler 1982).

N. zapotecorum Chandler, on dead meloids (Chandler 1977).

Tomoderus spp., on dead meloids (Chandler 1976).

Vacusus infernus (LaFerté), at cantharidin (Chandler 1976).

Relative to the above accounts, Chobaut (1897) was first to speculate on a possible mechanism for the unusual behavior observed. He believed that the attraction was due to sight and odor, especially the latter, pointing out that another group of beetles, the Cantharidae, produce a strong odor. No attempt was made to ascertain why the anthicids were attracted. The mechanism of attraction was not dealt with further until 1928 when Richards suggested that the behavior might be related to the presence of cantharidin in the meloids. To test his hypothesis, several workers used either cantharidin powder, ground up meloid beetles (Fey 1954), or dead meloids which had been treated with a cantharidin solvent such as acetone (Hille 1954). In several experiments, Görnitz (1937) used cantharidin powder which attracted nearly 700 *Notoxus monoceros*; he noted that the substance remained an active attractant at concentrations of as low as 10^{-7} g. Geiler (1953) used cantharidin powder obtained from *Lytta vesicatoria* to collect 374 *monoceros* in one year, noting that the most intense activity occurred from April to May and again in July.

Several experiments and additional hypotheses accompanied the above findings. Görnitz attempted to demonstrate that cantharidin was either a nutritive necessity or the major stimulus for feeding behavior in *N. monoceros*. He noted that specimens taken at cantharidin powder appeared to feed upon it. In addition, anthicids were known to feed upon adult and larval Meloidae and sometimes were found to contain cantharidin themselves in the adult stage (Fey 1954). However, Flach (1887) and Korschefsky (1937) observed that *monoceros* fed upon groups of insects not known to contain cantharidin as well. Analyses of gut and fecal contents in several cantharidin-orienting anthicids have shown them to be polyphagous, the diet consisting of fungi, insects, and unknown materials (Görnitz 1937, Fey 1954). Furthermore, Görnitz found that *monoceros* was sometimes present in large, gregarious populations even when meloids were lacking. And, since anthicids are not known to be cannibalistic, there would be no available sources of cantharidin. To circumvent this fact, Görnitz speculated that many other insects might contain cantharidin, but this has yet to be demonstrated.

Görnitz was apparently the first to recognize a difference in the ratio of males to females attracted to cantharidin. Of his collections, 642 specimens were males, while 51 were females. In Africa, Hille (1954, 1961) collected only males of *Anthicus* and *Notoxus* at cantharidin. A close examination of the specimens revealed that the apices of their elytra were modified, forming a dorsal cavity which opens to the exterior. He considered it likely that the structures represented chemical sense organs. Based in part on his observations relative to *N. monoceros*, Abdullah (1965) suggested that cantharidin might serve as an aggregation pheromone and sex attractant.

OEDEMERIDAE

While no member of this family is known to orient to cantharidin, several lines of evidence suggest that oedemerids produce cantharidin.

Several species of ceratopogonid flies orient to cantharidin (see section dealing with Diptera). One of these, *Atrichopogon oedemerarum* Storå, was described from a specimen attached to a museum specimen of the oedemerid *Oedemera flavescens* (L.). Subsequent field studies in Finland showed that *A. oedemerarum* is associated with *O. flavescens* as well as two other species of Oedemeridae: *Chrysanthia viridis* Schmidt and *C. viridissima* (L.) (Storå 1937). Since the same ceratopogonid has been associated with the meloid *Epicauta fabricii* (LeConte) via a cantharidin stimulus (Wirth 1956a), deductive logic would support the hypothesis that these oedemerid beetles also possess cantharidin or a closely related compound.

Additional support comes from observations of vesication of human skin caused by

contact with certain species of Oedemeridae (Herms 1925, Vaurie 1951). Britton (1970:605) speculated that cantharidin was the cause. Finally, the dermatitis-causing substance of one oedemerid, *Xanthochroa waterhousei* Harold, was clearly identified as cantharidin (Kurosa & Watanabe 1958).

Recalling that cantharidin is utilized for defensive purposes in the Meloidae in conjunction with aposematic coloration, it is interesting to note that many oedemerids have evolved striking color patterns as well. It seems likely that aposematic coloration has also coevolved with a cantharidin chemical defense mechanism in the Oedemeridae.

DIPTERA CERATOPOGONIDAE

Species of "no-see-ums" (actually, only the females) attacking man and other warm blooded animals belong to the genera *Leptoconops* Skuse, *Culicoides* Latreille, and *Forcipomyia* Meigen (subgenus *Lasiohelea* Kieffer) (Wirth 1952). However, most of the species in the subfamily Forcipomyiinae have been observed to feed on a wide variety of other insects, as summarized by Wirth (1956b). The subfamily Forcipomyiinae is divided into the genera *Atrichopogon* Kieffer and *Forcipomyia* Meigen.

Melohelea was erected as a subgenus of *Atrichopogon* by Wirth (1956a) to include four species which were said to be unique because of their meloid-attacking habit and unusually upcurved mouthparts. In the same paper, Wirth presented a fairly complete history of the various published accounts of these species feeding upon meloid and oedemerid beetles. Numerous misidentifications in the literature as well as taxonomic problems have rendered these accounts useless. Fortunately, these problems have been dealt with in some detail (Wirth 1979) and the summary of meloid associations has been revised (Wirth 1980).

ANTHOMYIIDAE

Two references in the European literature reported the association of *Anthomyia plumialis* L. with cantharidin (Görnitz 1937, Fey 1954).

HYMENOPTERA BRACONIDAE

Cantharidin orientation was first recorded for the European *Perilitus plumicornis* Ruthe, which was "attracted" to cantharidin powder (Görnitz 1937). Görnitz stated that *plumicornis* was a parasite of adult *Notoxus monoceros*. Smith (1953) restated this record, noting that *plumicornis* probably belonged in the genus *Microctonus* rather than *Perilitus*. Both genera are parasitoids of adult Coleoptera.

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