# On the evolution of diversity of sexual and protective characters in neotropical Ctenuchinae (Lepidoptera: Arctiidae)

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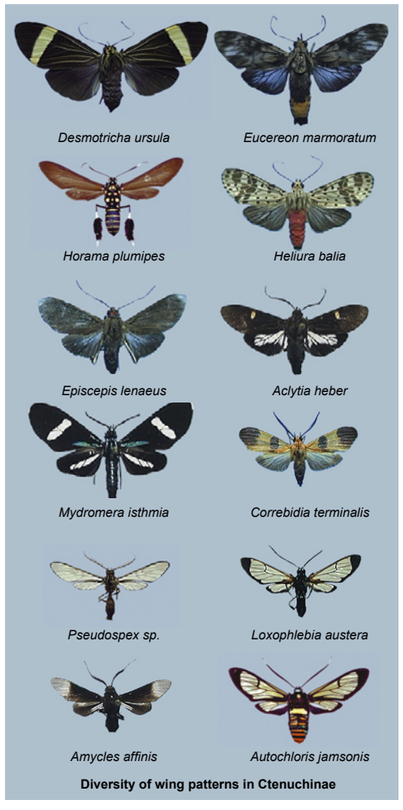
The Ctenuchinae (= Syntominae) are a subfamily of the Arctiidae (tiger moths) which comprises mostly small to medium sized, often conspicuously colored moths. It contains wordwide ca 2,000 species distributed throughout tropical and subtropical areas, with the great majority of species occurring in the neotropical region from where currently about 1,800 species are described.

The group is exceptionally diverse with respect to morphological characters (tymbal, tympanal and androconial organs), behavioural (PA-pharmacophaguous, protective) and ecological (cryptic, aposematic, mimicry) features.

In South America, ctenuchines occur in all biogeographic zones throughout in considerable abundance, several taxa being widespread and others having a limited distribution range. There are day-flying as well as nocturnal species which can be quite simply surveyed in the field (by netting / at light traps / at selective (PA-)baits). Thus, Ctenuchinae can be considered to represent a key group for assessing biodiversity in the neotropics.




**Diversity of wing patterns in Ctenuchinae**

*Horama oedippus* displaying its aposematic characters.

In a long-term research project we aim to understand the many ecological adaptations and their linkages as well as the evolutionary significance of the diversity of protective mechanisms and androconial systems realized in this fascinating group of Lepidoptera by undertaking morphological, ecological and systematic studies but also ethological and chemical investigations. Here, we present an overview on some aspects of our study.

## Mimetic and defensive characters

Many ctenuchine species are exceptionally colourful exhibiting aposematic patterns (see figs). Several genera (Sphecosoma, Macrocneme, Isanthrene, Pseudosphex) perfectly resemble wasps or other aculeate Hymenoptera and provide classical text book examples for Batesian mimicry („wasp moths"). However, most Ctenuchinae are quite well self-defended by distastefulness through sequestered secondary plant compounds, the production of ultrasonic clics, frothing and extrusion of defensive processes – many are thus rather Mullerian than Batesian mimics. Mimetic associations also involve beetles (e.g., Lycidae), but faunistic studies on mimicry rings are missing.

## Systematics

The Ctenuchinae (Ditrysia; Macrolepidoptera; Noctuoidea; Arctiidae) are currently divided into three tribes: Amatini, Ctnenuchini, and Euchromiini of which only the latter two are represented in the New World.

The last monographic treatments are by Draudt (1916-1919) and Hampson (1914, 1920) and most taxa are in need of a thorough revision; for several genera it is yet unresolved if they belong to Ctenuchinae or Arctiinae. Part of our project is the compiliation of a comprehensive, illustrated catalogue of all nominal taxa in the Ctenuchinae based on examination and verification of original descriptions and type specimens.

## Chemical ecology

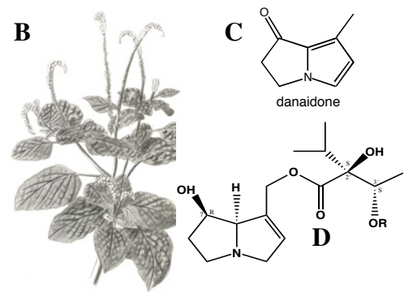
Chemoecological studies include qualitative and quantitative analyses of sequestration of plant chemicals and of volatiles emitted from androconial organs as well as studies on host plant relationships.

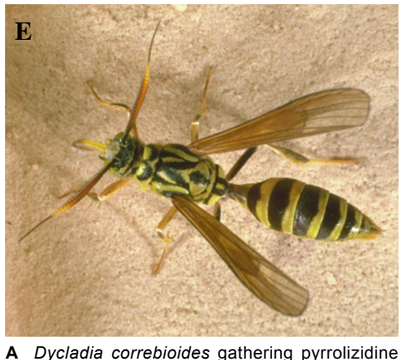
## Pharmacophagous relations to plants containing pyrrolizidine alkaloids (PAs)

Many Ctenuchinae are pharmacophagous with respect to PAs, i.e., they gather these secondary plant chemicals independent of nutritional requirements to increase their fitness. This syndrome is found in several other Lepidopteran taxa (Danainae, Ithomiinae, Arctiinae, Agaristinae) but also in the Coleoptera (Alticinae: *Gabonia*), Orthoptera (Pyrgomorphidae: *Zonocerus*) and Diptera (Chloropidae).

Natural sources of PAs are certain Boraginaceae (e.g., *Heliotropium*), Asteraceae and Fabaceae. Adult moths gather PAs exclusively from withered or dry parts of PA-plants. With their proboscides they apply a fluid onto the dry plant material to extract PAs for uptake as solution. The same behaviour can be elicited by pure PAs, showing that the target compounds also represent the source of the luring stimulatory cues and that there are no other chemicals involved in eliciting this response; long-range attraction is mediated by volatile breakdown products of the non-volatile PAs. Pure PAs are equally attractive, i.e. baits made of PAs can be used for selective baiting.

Of some ctenuchine taxa only males visit dry PA-plants, of others both sexes or females only exhibit pharmacophagy.

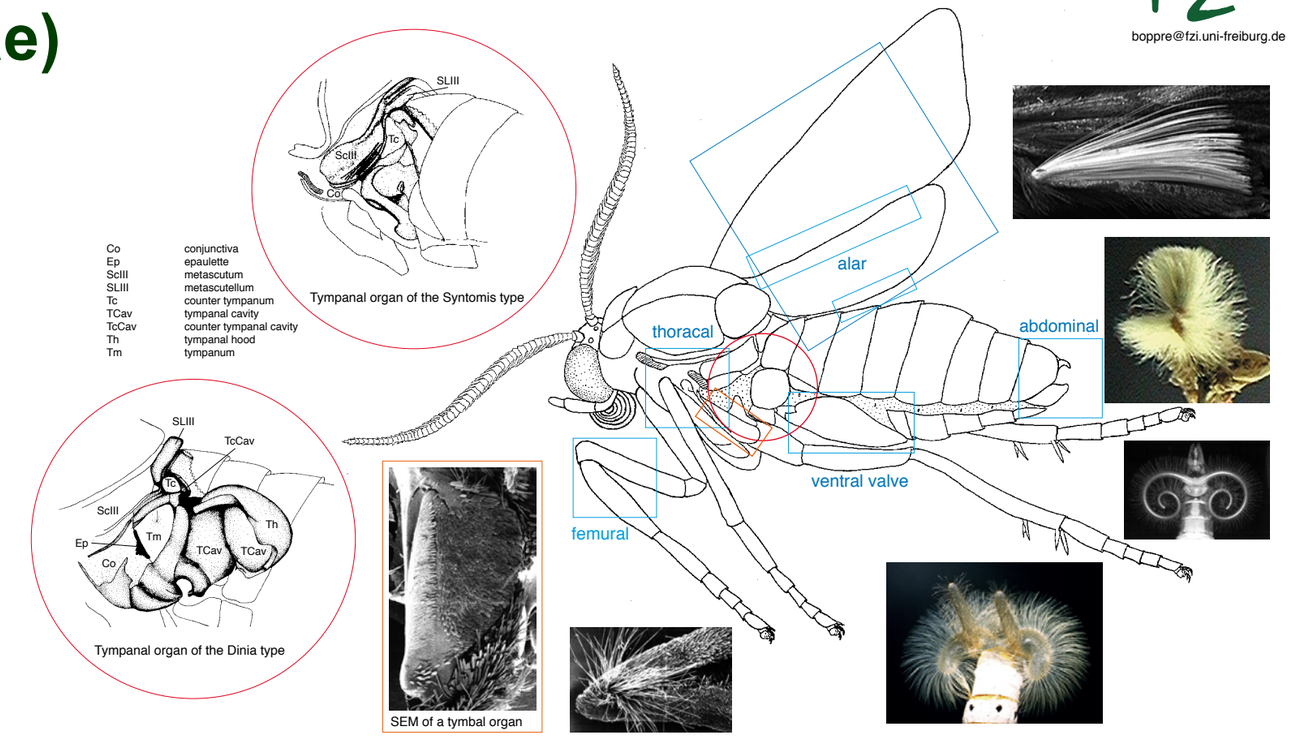




**A** *Dycladia correbioides* gathering pyrrolizidine alkaloids (e.g., heliotrine: **D**) from drying seeds of *Heliotropium* (**B**); C dihydropyrrolizine pheromone component derived from PA; **E** *Pseudosphex* sp. gathering crystals of PAs from a dish

PAs are generally repellent to non-adapted animals and serve as protective devices for the plants that produce them. By sequestration and storage of PAs many, if not all, PA-pharmacophagous taxa gain protection from predators, and this is reflected by the aposematic coloration and lifestyle of many of the species in question. In addition, males of several lepidopterans – including Ctenuchidae – use PAs as precursors for the biosynthesis of sex pheromone components required for the acceptance of a courting male by a female. Such sexual communication can also relate to chemical defence: with his spermatophore a male can transfer large amounts of PAs as a nuptial gift to the female, which then gains protection for herself and also protects her offspring by incorporating PAs into the eggs.

Characters: PA-gathering diurnal or nocturnal, male or female biased / storage of converted or unconverted PAs / use of PAs for male pheromone biosynthesis / ...

Of some ctenuchine species the larvae use PA-plants as primary host plants. This again is a parallel to other Lepidoptera (Arctiinae, Danainae) and Coleoptera (Alticinae) which gene-rates exciting evolutionary questions.




## Tymbal and tympanal organs

Production of ultrasonic clicks by tymbal organs located at the metathorax is common in Ctenuchinae. There are well or poorly sclerotized types with or without microtymbals in different numbers.

At least, six types of tympanal organs can be recognized differing with respect to presence or absence of tympanum, counter tympanum, attachment of scoloparium, expression of prespiracular hood, and tympanal cavity.

Functionally, the clicks are employed in sexual communication but also to gain protection from bats; they interfere with bats' ecolocation system and/or are acoustic aposematic characters.

## Behaviour

Protective behaviour not only involves aposematic colours, sounds and lifestyle but also characteristic patters of escape behaviours.

Sexual behaviour is quite poorly understood in Ctenuchinae and only a few species have been studied with respect to mate-finding and mate choice although androconial organs suggest complex courtship behaviours.

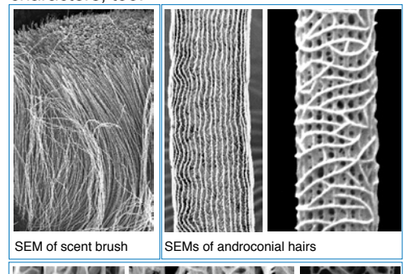
Because PA-pharmacophagy is not related to primary metabolic processes and ordinary host plants, qualitative as well as quantitative manipulations of defensive potency and/or pheromonal outfit are possible without any artificial disturbance of the insects – this enables experimental approaches to the role(s) of pheromones but also to (Mullerian / Batesian) mimicry.

## Additional morphological characters

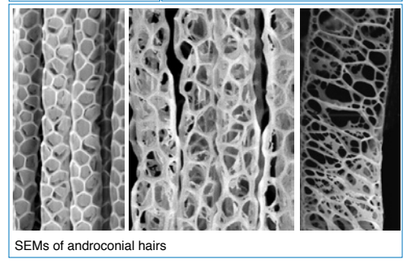
Expression of proboscis / palps / antennae / various larval characters / pupal cocoons / ...

## Androconial organs

Sexual communication involves male courtship pheromones emitted from androconial organs which occur in a striking structural diversity in Ctenuchinae. Large protrudable and expandable abdominal scent organs are found as well as brush-like structures on the wings, the legs, at the thorax and in a ventral abdominal pouch. The androconial hairs exhibit diagnostic characters, too.



SEM of scent brush | SEMs of androconial hairs



SEMs of androconial hairs

## Prospects

By recording, evaluating and interlinking data on the variety of morphological, chemical, behavioural and ecological features Ctenuchinae provide, we expect to gain deep insight into ecological factors governing evolution of defensive and sexual communication mechanisms and strategies.