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The Ctenoid Form of the Noctuid Epaulette

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The tympanic membrane of noctuid moths, in its typical form, is an exceedingly thin and delicate structure of circular or semicircular outline, bounded laterally by a more or less thickened and pigmented ridge, epimeral in origin (figs. 1, 7). This ridge was designated by Eggers (1911, 1919) as the "epaulette." It is referred to in the publications of Forbes (1923) and of Richards (1933) as the "nodular sclerite," while Kiriakoff (1948) proposes for it the Latin term "nodulus." Because the structure is not always nodular and is sometimes difficult to recognize as a distinct sclerite, it would seem that appropriateness as well as priority should cause the term of Eggers to be preferred. The epaulette is said to be wanting in primitive noctuoids such as the Diopitidae, Notodontidae, and Thaumtopoeidae. According to Richards it reaches its highest development in the quadrid Noctuidae, where it varies considerably in form, but, as far as Richards checked, is constant within a given species.

In certain trifold species the epaulette is armed with an array of comb-like teeth projecting mediocaudally so as to form a grill, more or less completely screening the tympanic membrane from the exterior. In some forms the teeth are simple; in others they are many-branched and antler-like (fig. 5). This ctenoid modification of the epaulette was described (Treat, 1954) in certain species of *Lacimipolia*, with the very tentative suggestion that the structure might serve as a barrier to the moth ear mite, *Myrmonyssus phalaenodectes* Treat, which occasionally invades the tympanic air sacs and associated cavities of these and several other noctuid moths. The present paper presents new evidence regarding the occurrence, variation, and significance of the ctenoid epaulette.

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The anatomical and distributional studies were made chiefly at the American Museum of Natural History, through the courtesy of Dr. Frederick H. Rindge, whose help is here gratefully acknowledged. The experimental work was done at the author's summer laboratory in Tyringham, Massachusetts. As far as practical, every species of Nearctic and Palearctic noctuid in the Museum collection was examined, together with scattered representatives from other geographical regions. The figures were drawn directly from pinned specimens. The species chosen for illustration were considered representative of the general range of variation in the ctenoid form of the sclerite. The necessity of avoiding damage to the specimens made it impractical to draw all figures to the same scale or from the same angle.

DISTRIBUTION

Listed below are the Nearctic species in which the ctenoid form of epaulette has been found. Names are given as they appear in the collection of the American Museum of Natural History, the arrangement in general following that of McDunnough (1938). The letter r following a name indicates that in that species the teeth, though present, are so short as to be considered rudimentary.

ACRONYCTINAE

Acronycta tritona Hübner r, *grisea* Walker r, *grisea revellata* Smith r, *albarufa* Grote, *mansueta* Smith r, *superans* Guenée r, *hasta* Guenée r, *thoracica* Grote r, *strigulata* Smith r, *morula* Grote and Robinson r, *pruni* Harrison, *exilis* Grote, *ovata* Grote, *clarescens* Guenée, *inclara* Smith, *inclara constans* Smith, *tristis* Smith, *hamamelis* Guenée, *increta* Morrison, *afflicta* Grote, *afflicta* form *schmalzriedi* Lemmer, *brumosa* Guenée, *brumosa persuasa* Harvey, *brumosa liturata* Smith, *marmorata* Smith, *lithospila* Grote r

HADENINAE

Lacinipolia meditata Grote, *determinata* Smith, *lustralis* Grote, *rubrifusa* Hampson, *imbuna* Smith, *vicina* Grote, *vicina acutipennis* Grote, *pensilis* Grote, *basiplaga* Smith, *spiculosa* Grote, *lepidula* Smith r, *erecta* Walker, *olivacea* Morrison, *olivacea lucina* Smith, *olivacea altua* Smith, *olivacea petita* Smith, *comis* Grote, *comis obnigra* Smith, *comis rectilinea* Smith, *laudabilis* Guenée, *marinitincta* Harvey, *explicata* McDunnough, *implicata* McDunnough, *illaudabilis* Grote, *illaudabilis alboguttata* Grote, *consimilis* McDunnough, *lunolacta* Smith, *quadrilineata* Grote
Lasionycta raineri Smith
Trichorthosia parallela Grote, *ferricola* Smith
Mimobarathra antonito Barnes
Homorthodes communis Dyar, *fractura* Smith, *fractura mecrona* Smith
Morrisonia diplogramma Schaus

CUCULLIINAE

Lithomoia solidaginis germana Morrison, *solidaginis albertae* Strand
Xylena nupera Lintner, *brucei* Smith, *thoracica* Putnam-Cramer, *cineritia*
Grote, *cineritia martena* Smith

Among Palearctic species, ctenoid epaulettes were found in the following:

ACRONYCTINAE

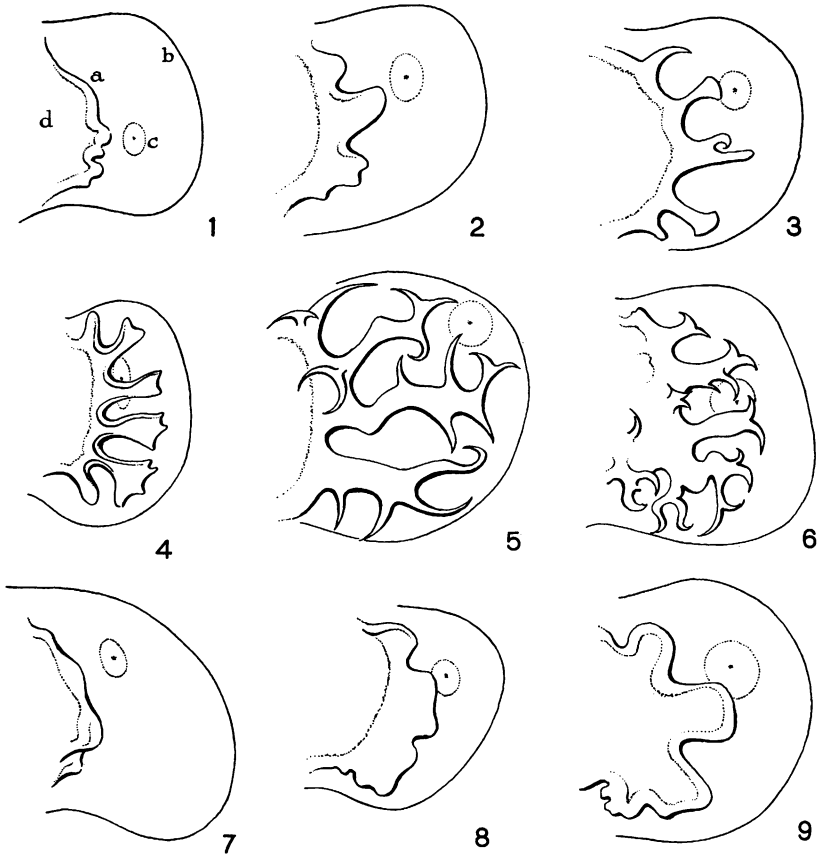
Canna sugitanii Nagano, *malachitis* Oberthur
Acronycta alni Linnaeus

CUCULLIINAE

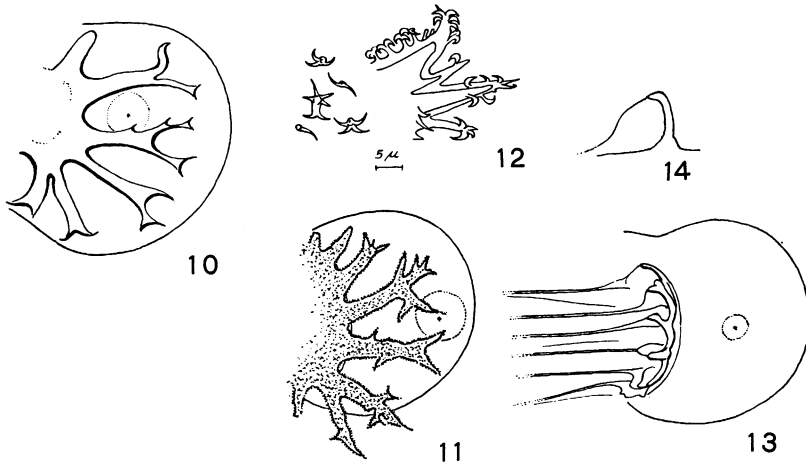
Chloantha (= *Lithomoia*) *solidaginis* Hübner
Xylena vestuta Hübner, *exoleta* Linnaeus, *formosa* Butler
Orbona fragariae Esper

The sole example of a ctenoid epaulette thus far discovered outside the Noctuidae occurs in the African agaristid *Daphoenura fasciata* Butler, of which a single specimen exists in the American Museum collection. The sclerite in this specimen bears an array of two unbranched teeth and three teeth with flat, pointed, secondary branches. Among other agaristids the epaulette is commonly an erect, palisade-like structure of contiguous vertical lamellae. It is of interest that in Richards' phylogenetic scheme, the Agaristidae are derived from Acronyctinae along with the other trifold subfamilies, in which, alone, the ctenoid form of epaulette appears to occur.

Serial examination of many specimens of a single species shows that the ctenoid modification is not an individual aberration but a definite species character. In no instance has any specimen of a series been found to lack the structure while the others possess it. On the other hand, the ctenoid form is subject to individual variations of the same order of magnitude as those that affect other anatomical features. For example, in a series of 29 males and one female of *Laciniipolia m. meditata* collected in Tyngham, Massachusetts, during the summers of 1954 and 1955, the number of primary teeth (i.e., those originating directly from the base of the sclerite) ranged from four to six, averaging five. There were variations in the relative sizes of the teeth and in the number and position of the secondary branches. Among 33 males and three females of *Laciniipolia o. olivacea* collected during the same period at the same station, the usual number of primary teeth was four, with a single specimen showing three and several having five. In this species there were also variations as regards the shape and position of the primary teeth, the



FIGS. 1-9. Left tympanic membranes and associated external structures in various noctuid moths, showing range of variation in ctenoid form of epaulette as compared with unmodified sclerite. 1. *Laciniipolia renigera* Stephens, male. Abbreviations: a, epaulette of unmodified form for comparison with other figures; b, boundary of tympanic membrane; c, area of attachment of chordotonal organ; d, conjunctiva. 2. *Laciniipolia lepidula* Smith, male; rudimentary form with unbranched teeth. 3. *Laciniipolia pensilis* Grote, male; one branched, four unbranched teeth. 4. *Laciniipolia spiculosa* Grote, male; flattened teeth with rudimentary branching. 5. *Laciniipolia m. marinitincta* Harvey, male; advanced form with primary and some secondary branching. 6. *Laciniipolia o. olivacea* Morrison, male; advanced form with extensive secondary branching. 7. *Acronycta vinnula* Grote, male; rudimentary form, for comparison. 8. *Acronycta hasta* Guenée, male; rudimentary, plate-like teeth. 9. *Acronycta tritona* Hübner, female; intermediate form with plate-like teeth.



FIGS. 10-14. Left tympanic membranes and associated external structures in various noctuid moths. 10. *Acronycta albarufa* Grote, male; advanced form with elongate, branching teeth. 11. *Trichorthosia parallela* Grote, female; caltrop form as seen under low magnification. 12. At right, portion of a tooth, highly magnified, of specimen shown in figure 11, showing secondary branching, hollow interior, and caltrop-like spines. At left, caltrop spines on conjunctiva as seen from above. 13. *Mimobarathra antonito* Barnes, male; exceptional form showing recurved and winged teeth. 14. A single tooth of specimen shown in figure 13 in side view. Parallel ridges in conjunctiva may be result of drying and shrinkage.

number and position of the secondary teeth, the presence or absence of accessory teeth on the conjunctiva, and the pigmentation of the entire structure. No sexual dimorphism was found, nor was there any obvious correlation with color, wing pattern, or other characters.

Although reasonably constant for a given species, the epaulette shows great intrageneric variation. This is illustrated in figures 1 through 6 for the genus *Laciniipolia* and in figures 7 through 10 for the genus *Acronycta*. Both of these genera include some species in which the sclerite is wholly without teeth, and others in which the teeth are very highly developed. Gradations may be found from "rudimentary" teeth, which are little more than enlarged nodules, to elongated and slender types with primary and secondary branching. The bizarre form represented by *Trichorthosia parallela* Grote (figs. 11, 12), and seen also in *Morrisonia diplogramma* Schaus, may be called the "caltrop" type. In these moths both the sclerite itself, with its branching teeth, and the entire surface of the conjunctiva are thickly studded with minute knobs bearing one to four or more hook-like blades. This may be taken as an

extreme of the ctenoid development. It is curious that both examples of the caltrop type were found in moths from Arizona, and that congeneric with the second example is a species, *Morrisonia evicta* Grote, of wide distribution, which lacks the ctenoid modification entirely. An unusual form of the sclerite is found in another hadenine genus, *Mimobarathra*, of which the sole species, *antonito* Barnes (fig. 13), possesses a row of recurved teeth bearing thin, wing-like vanes continuous (in the dried specimens examined) with folds or ridges in the conjunctiva.

In the genus *Acronycta*, forms possessing the ctenoid modification represent approximately 38 per cent of those studied. In *Laciniipolia* the proportion was 60 per cent. No seasonal or geographic correlation was noted that might lend significance to this distribution. In western Massachusetts, *Laciniipolia renigera*, *L. olivacea*, and *L. meditata* can be taken at light throughout August, the first-named also appearing earlier in the summer. In *L. renigera* the epaulette is virtually unmodified (fig. 1), while in the other two species it is of the highly developed, antler-like form (figs. 5 and 6).

Forbes (1954) divides the genus *Apatela* (= *Acronycta*, *Acronicta*) into five groups, partly on the basis of larval characteristics. In his Group I (*rubricoma* through *leporina*) the ctenoid modification does not occur; in Group II (roughly *Cuspidia* of Chapman, but less extensive) the modification is well developed only in *clarescens* and *hamamelis*, absent or rudimentary in the other species; in Group III it is well developed in both the included species, *afflicta* and *brumosa*; it is well developed throughout Group IV (*Lepitoreuma* Grote) except in *retardata* which lacks it entirely; it is absent throughout Group V (*Pharetra* Hübner, *Eulonche* Grote, *Viminia* Chapman).

It should be clear from the foregoing that useful taxonomic inferences from the ctenoid epaulette are not easily drawn.

BIOLOGICAL SIGNIFICANCE

That so extraordinary a structure is without adaptive significance would be hard to believe. That it does not serve for camouflage or for ornamentation is shown by the fact that the sclerite is not usually visible from the exterior of the moth without manipulation or removal of hair or scales. That it is not essential to audition is suggested by its absence in most sound-sensitive species, and can be shown experimentally, at least in *Laciniipolia meditata*, by removal of the teeth without damage to the tympanic membrane. A moth so prepared responded as vigorously as before the operation to crystal-generated ultrasonics ranging in frequency from 20 to 120 kcps.

The thorny, hedge-like character of the epaulette in moths such as *Laciniipolia meditata* and *L. olivacea*, together with the discovery that these insects are occasionally subject to attack by the moth ear mite, gave rise to the conjecture (Treat, 1954) that the structure might act as a barrier to the adult female mite, which normally gains access to the tympanic air sac by perforating the tympanic membrane.

At the time of writing, nine natural and 12 experimental infestations with the moth ear mite have been studied in moths of the two species named above. More than 1000 cases have been examined in other noctuids, not possessing the ctenoid modification. Except where the ctenoid epaulette is present, the tympanic membrane is invariably destroyed. On the other hand, six of the nine naturally infested moths having the modified form of the sclerite escaped all damage to the tympanic organ, although in several instances the mites established mature and populous colonies in the external tympanic area. In two moths there was slight damage to the tympanic membrane, doubtfully attributable to the mites. In only one instance were the mites clearly able to pass the barrier; in this moth the abdomen appeared to be abnormally relaxed, so that non-engorged mites were able to force their way between the tips of the teeth and the median wall of the inner tympanic recess. Of seven experimentally infested moths with the epaulette intact, five sustained no damage to the tympanic organ; one suffered only a minute perforation of the membrane, presumably by a mite that was able to reach the membrane with its feeding organs but was unable to force its way past the teeth of the epaulette and enter the air sac. One moth showed extensive, though possibly post-mortem, destruction, doubtfully attributable to the mites.

In five experiments, mites were introduced into the tympanic recesses of moths from which either the teeth of the epaulette or the entire structure had previously been removed with a fine, hooked needle. In all instances the mites entered the tympanic air sacs, and in three, remained there to deposit eggs. In most of these cases the mites probably gained access through rents in the conjunctiva produced accidentally during the removal of the epaulette, but in one where the integument was spared during the operation, the tympanic membrane was later perforated by the mite.

Three essential facts are thus established: (1) moths of the species studied are susceptible to attack by the moth ear mite; (2) they are physiologically acceptable as hosts to the mite; (3) they are at least partly and more often wholly protected by the teeth of the epaulette from the usual damage to the tympanic organ experienced by infested moths

which lack the ctenoid modification. If it be assumed that the auditory sense is of selective advantage to the moths, either in the avoidance of bats or in some other context, these facts would indicate a positive survival value for the toothed form of the sclerite, as a barrier to mites or to other possible invaders of the tympanic organs. The possibility of other functions is not excluded, nor is there a ready explanation for the sporadic distribution of the ctenoid structure among closely related species of the same or nearly the same habitat.

That barrier-like structures of this type have arisen independently in various lines of descent is suggested by their discontinuous occurrence in three of the four tritid subfamilies and in the above-mentioned agaristid *Daphoenura fasciata*. A similar conclusion must be drawn from the curious fence-like screens, first noted by Jordan (1923), which separate the inner from the outer parts of the tympanic recess in certain Indo-Australian noctuids such as *Speiredonia helicina* Hübner, *S. martha* Butler, *Calliodes* sp., *Nyctipao leucotaenia* Guenée, *Maxula capensis* Herrich-Schaeffer, and *Hypopyra extricans* Walker. In these insects there is a row of thin, hair-like bristles, some with terminal branches, extending towards but not quite to the lateral margin of the tympanic membrane from points of origin on the posterior wall of the tympanic recess. Although the grill-like effect resembles that of the ctenoid epaulette, the peculiar aspect of the bristles and their origin from the abdominal rather than from the metathoracic integument make it clear that the two structures are not to be homologized.

It is perhaps significant that although the "barrier" is well developed in certain of the Acronyctinae, moths of this subfamily are not known to be hosts of the moth ear mite, and an attempt to produce an experimental infestation in a moth of this group was unsuccessful. Mites of other species are occasionally found as transients, however, in the external tympanic recesses of many noctuids, though none thus far is known to destroy the tympanic membrane or other essential structures. In one instance an undetermined dipterous larva has been found attached to the conjunctiva of a female of *Porthetria dispar* Linnaeus. It is therefore not necessary to suppose that barrier-like structures have been evolved in exclusive response to a particular species of parasite.

If one accepts the barrier hypothesis to account for the adaptive evolution of the ctenoid epaulette, he is certain to be puzzled by those forms in which the teeth are rudimentary. In these instances it would seem that invading parasites could be little if at all deterred from attacking the tympanic membrane, for the teeth do not form an impenetrable screen between the inner and outer portions of the recess. A selective advantage

in relation to mites or other invaders is hard to envision. Unless a wholly different function is assumed to exist, the alternatives appear to be either (a) that the "rudimentary" form is actually an unused vestige of a more elaborate primitive structure, or (b) that the evolution of the advanced types has been either haphazard and non-selective or else orthogenetic, and that in any event the barrier function was not acquired until the fully developed form had been attained. Neither alternative is attractive.

SUMMARY

1. The ctenoid form of the epaulette (nodular sclerite) occurs in scattered representatives of three trifold subfamilies: Acronyctinae, Hadeninae, and Cuculliinae. It occurs also in at least one agaristid. More or less similar but not homologous structures are found in certain other noctuids.

2. The ctenoid modification varies from a "rudimentary" type possessing short, simple teeth, to an advanced form having long, branched teeth studded in some species with caltrop-like spines.

3. Experimental evidence indicates that the ctenoid epaulette is not essential to audition and that it can serve as a barrier protecting the tympanic membrane from destruction by parasitic mites or other invaders.

4. The barrier hypothesis does not account for the taxonomically scattered distribution of the structure, nor for its occurrence in the "rudimentary" form.

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