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SOME ASPECTS OF THE EXTERNAL MORPHOLOGY OF
LARVAL OWLFIES (NEUROPTERA: ASCALAPHIDAE),
WITH PARTICULAR REFERENCE TO
ULULODES AND *ASCALOPTYNX*

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INTRODUCTION

It is widely known and accepted among evolutionary biologists that the selective pressures upon the immature stages of an organism may be very different from those upon the adult form. This principle is especially true of the endopterygote (holometabolous) insects: in these, there can be seen a nearly complete dissociation of the larva from the adult, manifested both biologically and morphologically. Thus it often happens that phylogenies based upon features of the immature endopterygote insect differ sharply from those constructed from the adult; ideally, both kinds of information should be available to and utilized by the taxonomist.

The Neuroptera** is thought to be the most generalized and primitive endopterygote order, and as such is considered to include forms that are closest to the common ancestor of all Endopterygota. Such families as Sialidae, Corydalidae and Raphidiidae express their primitive phylogenetic positions by the relatively small degree of biological and morphological divergence exhibited between larva and adult. Other families and complexes of families within the Neuroptera, notably the superfamily Myrmeleontoidea (ant lions and their relatives), are highly specialized, possessing larval forms that in no way resemble the adults. The larvae of most myr-

*Parts of this paper are adapted from a thesis submitted to the Department of Biology at Harvard University in partial fulfillment of the requirements of the PhD degree.

**This term is used in the wide sense, including suborders Megaloptera, Raphidioidea and Planipennia.

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meleontoid insects are cryptic in habits and coloration and often difficult to rear to adulthood. For these reasons, few have been reliably associated with adult forms, so taxonomic and phylogenetic studies have necessarily been based primarily upon the morphology of preserved imagos. In the myrmeleontoid family Ascalaphidae, larval-adult associations have been achieved for only five or possibly six of 65 described genera (MacLeod, 1970). Additionally, all of these published associations are within one of the two ascalaphid subfamilies, the Ascalaphinae; no neuroptyngine (=ascaloptyngine) larva has been formally described, despite the fact that nearly one third of ascalaphid genera are contained in the latter subfamily (Weele, 1908).

Only a few authors have made serious attempts to bring biological information about the immatures to bear upon the problems of phylogeny within the Neuroptera in general and Ascalaphidae in particular. The first of these was Hagen (1873), who described sixteen larval "types" within the Ascalaphidae and correctly assessed the taxonomic importance of numerous larval characters, but failed to establish strong evidence for larval-adult relationship in most cases. Navás (1914, 1915), like Hagen, stressed the importance of such larval features as the number and distribution of lateral abdominal scoli (extensions), particularly in separating the split-eyed (Ascalaphinae) from the entire-eyed (Neuroptynginae) ascalaphid subfamilies. However, his papers are crudely illustrated and suffer from the same (if not more) uncertainty of larval identity as do Hagen's; it is by no means certain or even likely that his assignment of several larvae to the subfamily Neuroptynginae is correct. Withycombe's work (1925) is far more ambitious, important, and accurate, assembling a large body of behavioral, physiological and morphological data on immature Neuroptera. Since he was not seeking evolutionary relationships within families like the Ascalaphidae but rather among all neuropteran families, Withycombe did not usually require or attempt species-level identifications. Finally, MacLeod (1964) produced a thorough, well-reasoned and superbly illustrated work on Neuroptera of a scope similar to that of Withycombe's but emphasizing comparative morphology of the larval head capsule rather than behavior and physiology. This is the first work to figure in detail the head capsule of an ascalaphid larva of the genus *Ululodes* [*U. quadrimaculata* (Say)] and to document, by rearing an adult association of a neuroptyngine ascalaphid larva [*Ascaloptynx appendiculatus* (Fabricius)]. Unfortunately, MacLeod's excel-

lent study remains unpublished, with only small parts appearing in abbreviated form in his 1970 paper on fossil neuropteran larvae.

A significantly larger number of authors have concerned themselves with evaluating the evolutionary relationships within and among neuropteran families through analysis of adult morphology and wing venation. The most important works of this type include the broad-based studies of Tillyard (1916, 1926), Adams (1958) and Shepard (1967) and the ascalaphid monographs of McLachlan (1871), Weele (1908), Navas (1913) and Orfila (1949). Papers of more limited scope on the immatures of particular ascalaphid species will be discussed in the concluding section of this study.

It is my intention eventually to re-assess the evolutionary patterns within the family Ascalaphidae, based upon morphological, behavioral, and life-cycle information pertaining to the immature stages of as many species as possible. Work toward this end was initiated in a comparative study of eggs, egg barriers (repagula) and early larval habits of two North American owlflies, *Ululodes mexicana* (McLachlan) and *Ascaloptynx furciger* (McLachlan), representing both ascalaphid subfamilies (Henry, 1972). The purposes of the present paper are (a) to provide formal generic and specific descriptions of the larvae of the above-named species, (b) to summarize key morphological differences between them and among other described forms, and (c) to suggest a tentative list of evolutionarily significant larval characters defining the ascalaphid subfamilies. The description of *Ascaloptynx furciger* is particularly useful as the first, to my knowledge, published description of a neuroptyngine (entire-eyed) owlfly larva.

Papers on the behavior and life history of *Ululodes mexicana* and *Ascaloptynx furciger* are in preparation.

ACKNOWLEDGEMENTS

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Living and preserved specimens were lent or given to me by Drs. Robert E. Silberglied and Thomas Hlavac (Museum of Comparative Zoology), M. A. Kolner and F. F. Hasbrouck (Arizona State University, Tempe), and James A. Slater (University of Connecticut); to these individuals I express great appreciation. In addition, warm thanks are extended to: Nancy F. Henry, for invaluable collecting assistance in the field and moral support at home; Mr. Vincent Roth of the Southwestern Research Station, for his advice on my field work in Arizona; M. Professeur A. Haget (Université de Bordeaux) for helpful suggestions pertaining to my collecting trips in France; and Drs. C. W. Rettenmeyer, C. W. Schaefer, and J. A. Slater (University of Connecticut) for their constructive comments on the manuscript.

Special thanks are extended to my colleague, friend and former advisor Professor Frank M. Carpenter, who has been consistently encouraging and helpful to me in my work on the Neuroptera.

METHODS AND MATERIALS

Ascalaphid larvae are extremely difficult to find in the field, even with intensive litter-sifting efforts. For this reason, field-laid eggs of the two owlfly species were collected, using techniques outlined in a previous paper (Henry, 1972). Eggs of *Ascaloptynx furciger* and *Ululodes mexicana* were found in abundance during August and September in the Chiricahua and Peloncillo Mountains, within a 25 mile radius of the Southwestern Research Station of the American Museum of Natural History (SWRS) in southeastern Arizona. Elevations of egg sites ranged from 1500 to 1800 meters (see Henry, 1972). Larvae hatching from these egg masses were maintained in 15 × 60 mm plastic petri dishes, one insect per dish, on a substrate of sterile sand (*U. mexicana*) or dried leaves of oaks native to Arizona egg sites (*A. furciger*). Each isolated larva received a letter and number designation and its movements, molts, etc., were recorded in chart form. Some dishes with larvae were kept in a one cubic foot wooden cabinet with regulated photoperiod but unregulated temperature regimen; others occupied a constant temperature and photoperiod Precision Scientific/GE Model 805 incubator. Temperature in the first chamber ranged from 30°C in the "day" to 22°C at "night;" the incubator was set for a constant 29°C. Light period was normally maintained at LD (light/dark) 16:8 hours.

Newly hatched larvae of both species were fed single live *Drosophila melanogaster* (Meigen) and *D. hydei* (Sturtevant) daily for the first week. They were later fed twice a week with first and second instar nymphs of *Blattella germanica* (Linn.). Each late third (last) instar ascalaphid was fed an adult female *B. germanica* roach once a week.

Larvae in various stages of development were killed in and initially fixed and injected with Bouin's solution. After 12 to 24 hours, specimens were transferred to 70 percent ethanol or, for mild clearing of sclerotized structures, to Weaver's dissection and preservation fluid: 2 parts 40% formalin, 1 part glacial acetic acid, 8 parts chloral hydrate, and 29 parts distilled water. When greater clearing was required, warm 10 percent potassium hydroxide or Nesbitt's solution (Nesbitt, 1945) proved adequate. Very small specimens and structures were run through dehydrating solutions of alcohol and xylene and mounted in Damar on depression slides. Observation, dissection and figuring of specimens involved use of a Wild M5 stereoscopic dissecting microscope equipped with integral camera lucida, and various Bausch and Lomb compound microscopes fitted with 10 × 10 micrometer eye-piece grids.

Most of the methods outlined above apply equally well to the collection, rearing, preservation and observation of other ascalaphid immatures used incidentally in this study, including an unidentified species of *Ululodes* from central Florida and *Ascalaphus libelluloides* (Schäffer) from south-central France. Large numbers of viable eggs of the latter European species were found on low herbiage clothing rugged hillsides near the Aveyron River outside the village of Penne, in the French district of Tarn-et-Garonne.

EXTERNAL MORPHOLOGY

The characteristics that define larvae of the extant Ascalaphidae and that set this family apart from other myrmeleontoid taxa like Psychopsidae, Nymphidae, Myrmeleontidae, Nemopteridae and Stilbopterygidae* have been discussed at length in the works of Withycombe (1925) and MacLeod (1964, 1970). These include (a) posterior margin of the head capsule strongly cordate, (b) pres-

*Larvae of this peculiar Australian and South American family are not sufficiently known to permit confident comparisons; immatures of Psychopsidae, Nymphidae and Nemopteridae are also poorly known.

ence of three true teeth on each mandible, (c) presence of seven lateral stemmata, one ventral and six dorsal, on each distinctly raised ocular tubercle, (d) lack of any pronounced prolongations of other specializations of the cervix, (e) presence of ten to nineteen pairs of finger-like or spatulate setose extensions called scoli, laterally fringing the thorax and abdomen, (f) ventral or lateral location of the spiracles of abdominal segments 3-8 and occasionally of all eight pairs of abdominal spiracles, and (g) fusion of the tibia and tarsus on each metathoracic leg. None of these features uniquely characterizes ascalaphid larvae to the exclusion of other myrmeleontoid families. For example, seven pairs of stemmata is typical of all Myrmeleontoidea except Psychopsidae (5) and possibly Nymphidae (6 in the larva of *Nymphes* sp.), while scoli are totally absent only in psychopsids and nemopterids. Additional characteristic ascalaphid features are shared with one to several other myrmeleontoid families: metathoracic tibio-tarsal fusion with all Myrmeleontidae and probably Stilbopterygidae (McFarland, 1968); simple cervical morphology with most nymphids, psychopsids and stilbopterygids; three mandibular teeth and raised ocular tubercles with many Myrmeleontidae and perhaps all Stilbopterygidae; and cordate head margin and spiracle pattern with a few nymphids. However, only owlflies display all of the above character states together in an unmistakable *gestalt*.

Ascalaphid larvae share with all other Myrmeleontoidea (a) a heavily sclerotized, roughly quadrate head capsule displaying a unique anteriorly-positioned, vertically oriented tentorium linking one pair of pits ("anterior" ones) on the dorsum with another pair of pits ("posterior" ones) on the venter (see figures 3 and 6, TAP and TPP); (b) robust, inwardly curved jaws with mandibular-maxillary sucking specializations typical of all planipennian Neuroptera; (c) relatively small, multisegmented, filiform antennae, each with enlarged scape and inconspicuous pedicel, usually originating from a small antennal tubercle; (d) labium distally divided into two large palpmere-like prelabia, each bearing a short, usually 3-segmented* palp (figures 3B and 6B, Plb, Prlb and Plp); (e) stout, ovoid body with varying tendencies toward dorso-ventral flattening, consisting of a thorax and 9-segmented abdomen bearing at

*2-segmented in some Nemopteridae and 4-segmented in *Psychopsis elegans*, according to MacLeod (1964).

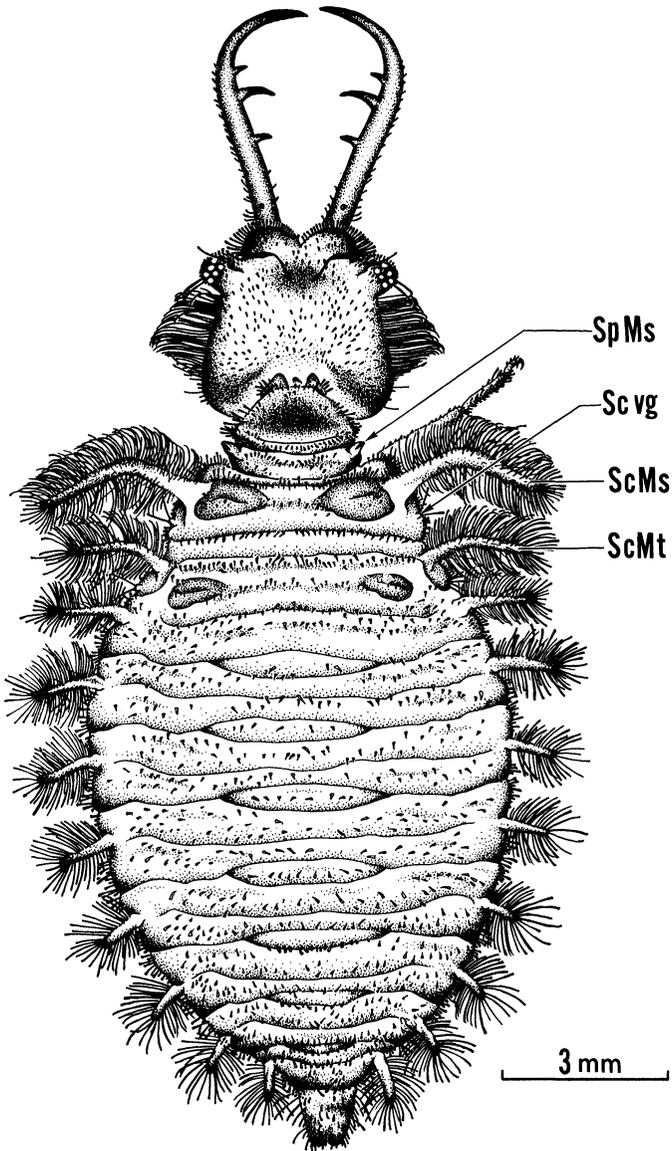


Figure 1. *Ululodes mexicana*, mature third instar larva. ScMs = mesothoracic scolus, ScMt = metathoracic scolus, Scvg = vestigial mesothoracic scolus, SpMs = mesothoracic spiracle.

its tip a retractile, tubular tenth segment that functions as a spinneret; (f) short, powerful walking legs; and (g) dolichasterine (trumpet-shaped) setae of diverse morphology over part or most of the body surface (figure 8). Like most Planipennia, ascalaphid larvae pass through three instars prior to pupation.

LARVA OF *ULULODES MEXICANA* (McLachlan)
(Refer to figures 1-4)

GENERIC DESCRIPTION: *Ululodes* Currie.

The following description is based upon examination of nearly 100 third instar specimens of *Ululodes mexicana* reared from egg to adulthood, together with 13 reared larvae of an unidentified species of *Ululodes* from Florida and two preserved third instar specimens representing a third unidentified species of the genus from Pima, Arizona. The generic diagnosis is also based on information presented in two excellent works: first, that of MacLeod (1964), describing the morphology of the head capsule and cervix of *Ululodes quadrimaculata* (Say) from Illinois, and secondly, that of McClendon (1902), describing the third instar larva of *Ululodes senex* Burmeister (described as *U. hyalina* Latreille) from Texas. I have chosen to follow the terminology used by MacLeod (1964, 1970).

Length: just prior to pupation, 13-19 mm, not including jaws.

Head: trapezoidal, approximately as wide as or slightly wider than long, broadest posteriorly and tapering evenly anteriorly; dorso-ventrally flattened but much thicker behind than in front. Cordate postero-lateral (occipital) margins. Labral margin (LmM) narrow and very strongly bilobed with a single wide deep notch at midline; labral lobes bulbous. Dorsum flat medially and convex laterally; ventral surface strongly convex with excavated antero-lateral margins permitting retraction of jaws beneath ocular tubercles (excv). Surface texture mildly rugose due to slightly raised bases of setae. Ocular tubercles (OT) large, prominent, approximately cylindroid but very slightly tapered distally and flattened dorso-ventrally; ventral stemma somewhat reduced in size compared with dorsal stemmata. Antennal tubercles (AT) prominent, cylindrical, nearly half length of ocular tubercles, appressed closely to bases of latter. Number of flagellomeres variable, usually 11 or 12, with tip of antenna projecting far beyond end of ocular tuber-

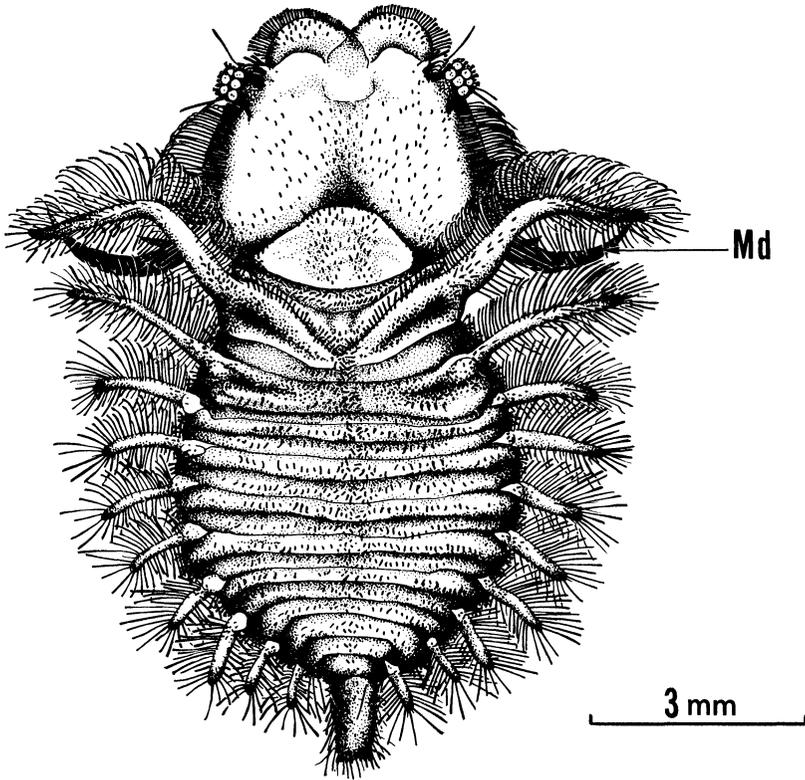
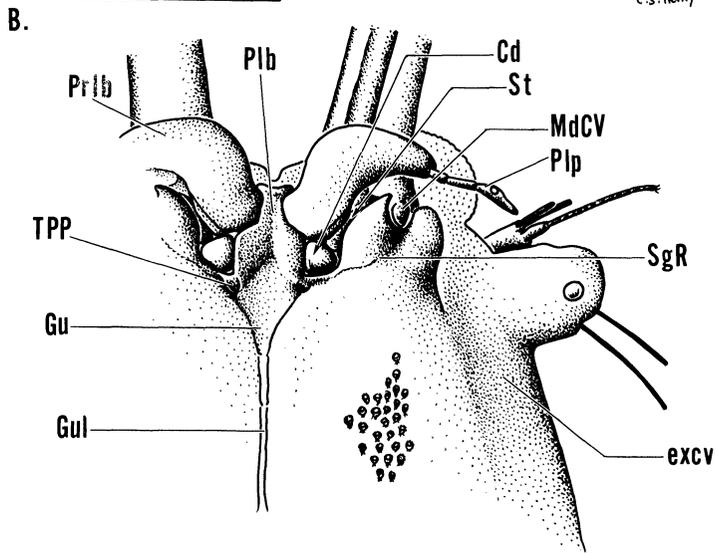
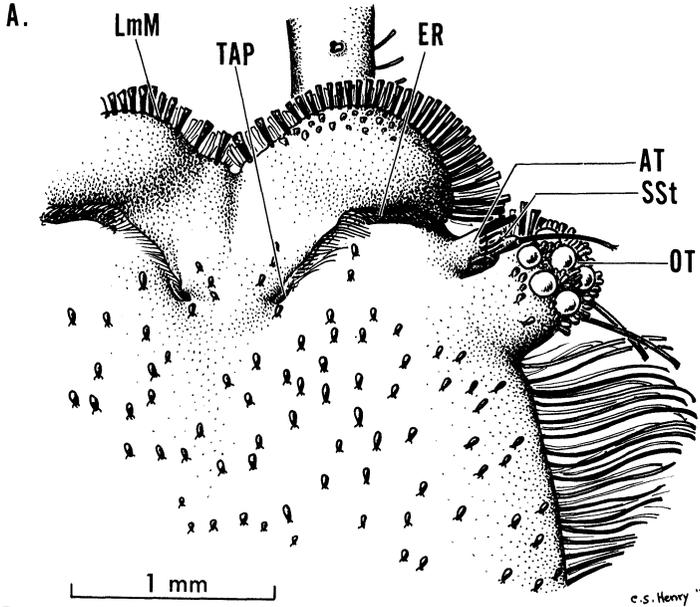


Figure 2. *Ululodes mexicana*, immature third instar larva with jaws in "trap" position. Md = mandible.

cle. Jaws falcate, smoothly tapering, and significantly longer than head capsule; they show a strong upward tilt in lateral view and are capable of being opened to an angle of 270 degrees or more (figure 2). First tooth always placed proximad of midpoint of mandible; central tooth much larger than the other two teeth and markedly curved; distal tooth unambiguously the smallest of the three and situated closely adjacent to central tooth. Ventral mandibular condyle (MdCV) positively contained within robust U-shaped socket formed from anterior ends of subgenal ridge (SgR — see figure 3B), the medial arm of which overgrows and nearly hides maxillary stipes (St). Postlabium (Plb) flask-shaped in outline



with very large, crescent-shaped, distally tapered prelabial lobes (Prlb) arising quite close to one another from sides of "neck" of postlabium. Terminal palpmere of labial palpus (Plp) nearly as long as first and second combined.

Body: elliptical in outline and not prominently flattened when mature. Prothoracic notum small, sclerotized, convex, roughly elliptical to triangular in outline and nearly twice as broad as long, bearing no scoli or tubercles. Remainder of body lightly sclerotized except for a pair of oval plates situated laterally in tergum of the mesothorax and a second smaller pair similarly located in metathorax. Lateral margins of each thoracic and abdominal segment (except terminal segments 9 and 10 of abdomen) prolonged into a pair of unflattened, finger-like setigerous scoli, ten pairs in all. Each mesothoracic scoli (ScMs) fully as long as head capsule, inclined forward basally and reflexed backward at its mid-point. Metathoracic scoli (ScMt) two-thirds as long as mesothoracic ones, less sharply reflexed; remaining 8 pairs of abdominal scoli straight, shorter than thoracic ones, and becoming gradually smaller toward rear. Minute pair of vestigial scoli (Scvg) present behind and slightly ventral to primary pair on both meso- and metathorax. Mesothoracic spiracles (SpMs) very large, borne dorso-laterally on cone-shaped sclerotized tubercles behind prothorax; all other spiracles smaller, ventro-laterally located, one pair for each of the first eight abdominal segments.

Chaetotaxy: Dense, double fringe of very long serrate setae present on lateral margins of head capsule and peripherally on all scoli. Single primary row of shorter, distally flared, serrate dolichasters (as in figure 8-a) closely set along entire anterior labral margin. Each ocular tubercle with still shorter, tightly packed dolichasterine setae over most of its distal surface, with two very large subequal setae projecting backward from the posterior outer margin. Antennal tubercle bearing a group of three (very rarely, four) slender, smooth setae with apical stellate enlargements (SSt and figure 8-d)

Figure 3. [opposite page] *Ululodes mexicana*, details of head capsule of mature third instar. A = anterior dorsal aspect, B = anterior ventral aspect. AT = antennal tubercle, Cd = maxillary cardo, ER = epistomal ridge, excv = lateral excavation, Gu = gular area, Gul = gular line, LmM = labral margin, MdCV = ventral mandibular condyle, OT = ocular tubercle, Plb = postlabium, Prlb = prelabial lobe, Plp = labial palp, SgR = subgenal ridge, SSt = stellate-tipped seta, St = maxillary stipes, TAP = anterior tentorial pit, TPP = posterior tentorial pit.

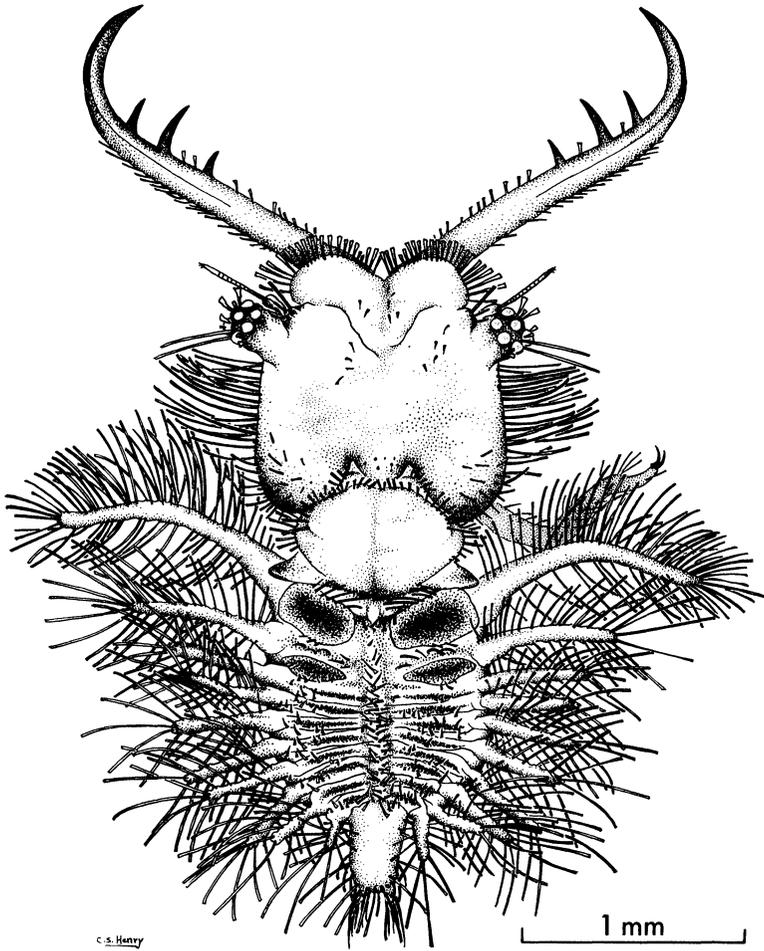


Figure 4. *Ululodes mexicana*, first instar larva at hatching.

that contact antenna scape, flanked anteriorly by two (very rarely, three) stout serrate setae and posteriorly by an enlarged dolichaster; a few other, smaller dolichasters may also be present on surface of the tubercle. Dorsum of head and body more or less clothed with small to medium sized dolichasterine setae; ventral surfaces bear more profuse, smaller dolichasters that are shaped like goblets (figure 8-c). Thick mat of very fine, tangled threads also present over entire dorsum of larva, including dorsal surfaces of all setal fringes on head and scoli. Four of five pairs of stout, tooth-like digging setae present terminally on ninth abdominal segment.

SPECIES DESCRIPTION: *Ululodes mexicana* (McLachlan), new larval association.

Measurements: Length of mature larva, 14.60-18.75 mm, mean length = 16.00 mm. Length of head capsule, 3.30-3.78 mm, mean = 3.54 mm; width of head capsule, 3.40-3.90 mm, mean = 3.60 mm.

Chaetotaxy: Setae composing fringes on lateral margins of head capsule and edges of scoli showing tendency toward gradual distal thickening with truncate tips (figure 8-a); not lanceolate. Ocular dolichasters projecting well beyond edges of stemmata and easily visible from above. Dolichasters on dorsal surface of head abundant, fairly evenly distributed, and cavitate (figure 8-b-2); never peg like (figure 8-b-1) or confined to occipital lobes. Dolichasters on dorsal body surface of the flared and curved type (figure 8-a), rarely parallel sided or pointed.

Pigmentation: Head with prominent but diffuse oval to heart-shaped spot of dark pigmentation centered just behind (but encompassing) anterior tentorial pits (TAP). Labral lobes, antennal tubercles, and tips of ocular tubercles also darkly pigmented. Occipital lobes noticeably more pale than the rest of the head capsule. Prothoracic notum without obvious pattern of pigmentation.

ONTOGENETIC VARIATION:

The first instar *Ululodes* larva (figure 4) differs considerably from the mature larva. The head capsule is more quadrate than trapezoidal. The antenna is more than twice the length of the ocular tubercle, bears 12 or 13 flagellomeres, and emerges from a poorly defined tubercle. The jaws are only slightly falcate, and the proximal tooth rather than the distal tooth is the smallest of the three. All setae are relatively longer and less numerous than in mature larvae: the central dorsal aspect of the head capsule in particular is nearly

devoid of setae in all forms studied. A single stellate seta rather than three (or four) is found on each antennal tubercle, flanked by (usually) one large stout seta anteriorly and one posteriorly. Terminal digging teeth on abdominal segment nine are lacking.

The second instar larva is intermediate between first and third instars with respect to most ontogenetically variable morphological features. Three stellate setae are borne by each antennal tubercle.

The generic discussion applies equally well to the species *U. mexicana*. It is considerably more difficult to distinguish among species in the first instar than in later instars, although the morphology of the long setae bordering the head and covering the body and scoli seems to separate first and second instar *U. mexicana* larvae from those of at least one undetermined species from Florida. Additionally, consistent differences in the pigmentation patterns of the dorsum of the head capsule can be found in early instars. However, other setal patterns uniquely characterizing mature *U. mexicana* larvae are absent or unreliably present in younger individuals.

LARVA OF *ASCALOPTYNX FURCIGER* (McLachlan)

(Refer to figures 5-7)

GENERIC DESCRIPTION: *Ascaloptynx* Banks.

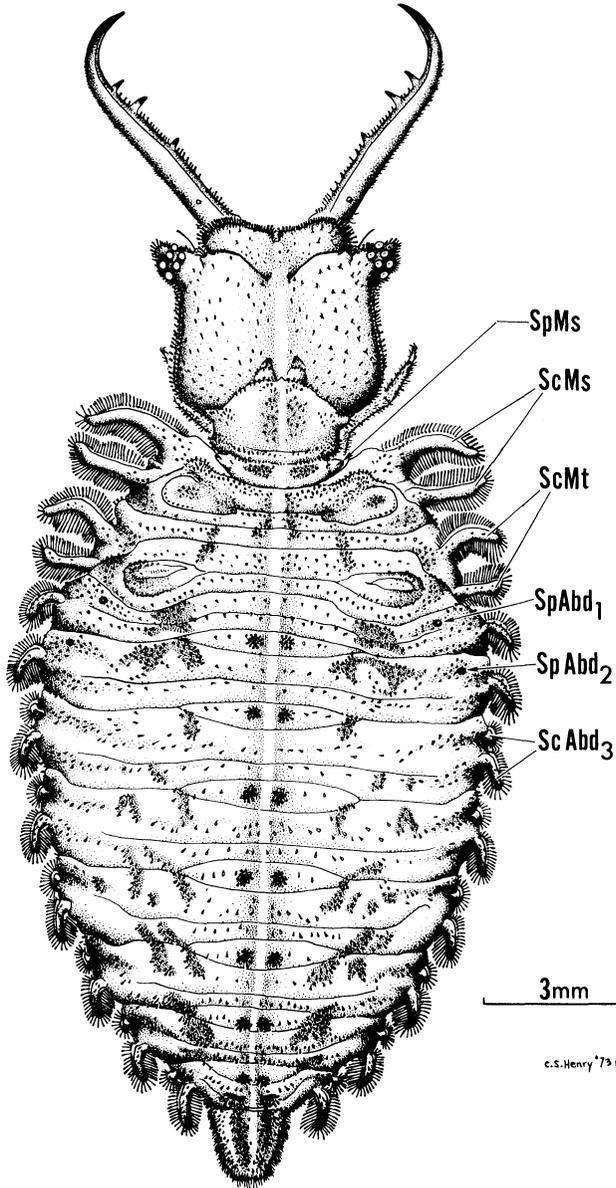
The following description is based upon examination of 67 third instar larvae reared from field-collected eggs that were morphologically matched with eggs obtained from females of *Ascaloptynx furciger*. *A. furciger* is the only species of the genus that has been sighted or collected from the vicinity of the egg collecting sites in the Chiricahua Mountains. Two additional specimens of an unidentified larva from Pima, Arizona that can be assigned with confidence to the genus on the basis of morphology were also available for comparison. In addition, the two figures published by Peterson (1953) are almost certainly of *Ascaloptynx* larvae, although the drawings are too schematic to contribute much morphological information.

Length: just prior to pupation, 16-22 mm, not including jaws.

Head: quadrate, slightly wider than long, slightly broader posteriorly than anteriorly but basically parallel sided; strongly flattened dorso-ventrally but thicker behind than in front. Moderately cordate postero-lateral (occipital) margins. Labral margin (LmM) wide and weakly bilobed with a narrow tubercle-flanked notch at

midline widening into a broad shallow central indentation; labral lobes dorso-ventrally flattened. Dorsum flat, ventral surface moderately convex with no lateral excavations for mandibles. Surface texture mildly rugose due to slightly raised bases of setae. Ocular tubercles (OT) large, prominent, unflattened, and tapering distally, each bearing a setigerous tubercle antero-laterally; ventral stemma somewhat reduced in size compared with dorsal stemmata. Antennal tubercles (AT) very small and inconspicuous compared with ocular tubercles, parallel sided to pedunculate, at least twice as broad as long. Antenna approximately three-fourths the length of ocular tubercle, bearing a variable number of flagellomeres (usually 12 or 13). Jaws only slightly falcate and significantly longer than head capsule, parallel sided to the level of proximal mandibular tooth and then tapering smoothly toward apices; they show a slight upward tilt in lateral view and are capable of being opened to an angle of 180 degrees. All teeth short and stout: proximal tooth smallest and situated barely basad of mandibular midpoint, central tooth largest and closely adjacent to distal tooth. Ventral mandibular condyle (MdCV) bounded medially by a very large curved arm formed from the anterior end of the subgenal ridge (SgR), but not contained laterally except by a low bump (see figure 6B); medial arm not appreciably overlapping stipes (St). Postlabium (Plb) broad, quadrate, articulating at its antero-lateral corners with widely separated prelabial lobes (Prlb) that are nearly straight and only slightly tapered distally; penultimate palpmere of labium medially constricted and longest of the three "segments" (Plp).

Body: elliptical in outline and not prominently flattened when mature. Prothoracic notum small, sclerotized, nearly flat, roughly pentagonal in outline and broader than long, bearing a pair of prominent setigerous tubercles at its antero-lateral corners. Remainder of body lightly sclerotized except for a pair of large oval tergal plates placed laterally on mesothorax and metathorax and a third pair of much smaller plates on eighth abdominal tergum. Body laterally fringed by 12 pairs of primary and six pairs of secondary (smaller) setigerous, dorso-ventrally flattened scoli: meso- and metathorax each bearing two pairs of primary scoli (ScMs and ScMt), with anterior pair curving gently posteriad and posterior pair curving anteriad; abdominal segments one through eight each bearing one pair of basally constricted and posteriorly directed primary scoli; additional pair of much smaller mushroom-shaped



c.s. Henry '73 (75)

secondary scoli present on abdominal segments three through eight immediately anterior to each primary pair (ScAbd). Anteriormost pair of body scoli longest, measuring half the length of head capsule; primary scoli become progressively smaller posteriorly, then subequal from first to eighth abdominal segments. Mesothoracic spiracles (SpMs) very large, borne dorso-laterally on cone-shaped sclerotized tubercles behind prothorax; all other spiracles smaller, those of first two abdominal segments dorso-lateral (SpAbd 1 & 2), remaining six pairs ventro-lateral.

Chaetotaxy: Dense fringe of serrate dolichasters present on lateral and labral margins of head capsule and peripherally on ocular tubercle, prothoracic shield and tubercle, ninth abdominal segment, and all scoli; longest on scoli, lateral margins of labral lobes and anterior margins of ocular tubercles. Antennal tubercle bearing a group of three small slender setae with apical stellate enlargements (SSt and figure 8-d) that contact antennal scape, flanked anteriorly by one to several stouter, serrate setae. Dorsum of head and body more or less covered by complex but minute scale-like setae (Scl and figure 8-e) interspersed with medium-sized dolichasters, the latter aggregated into pairs of tight clumps (one pair per segment) on middorsal surfaces of abdominal segments one through seven; setae nearly absent from midline of body. Ventral surface of body uniformly and thickly clothed with small, sharply flared dolichasters which become more peg-like or lanceolate on head capsule. A single long, lanceolate seta present on ventral surface of each trochanter; other, shorter lanceolate setae profusely present on ninth abdominal sternum, nearly obscuring the five terminal pairs of tooth-like digging setae.

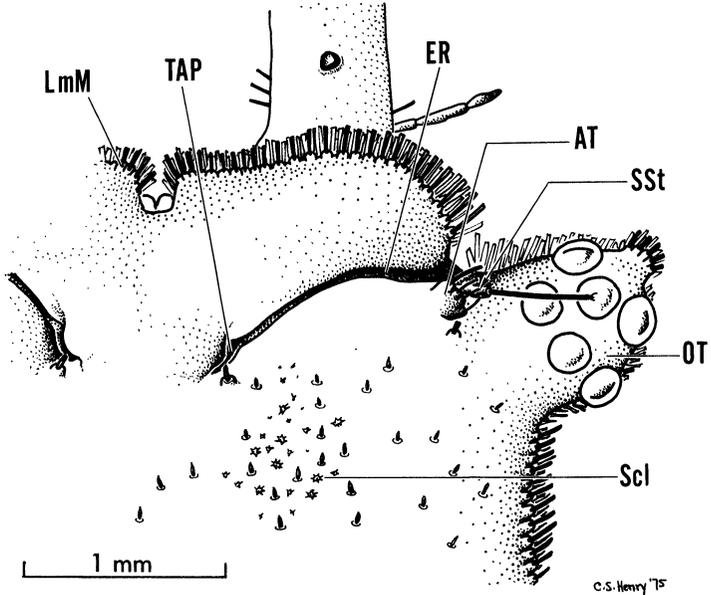
SPECIES DESCRIPTION: *Ascaloptynx furciger* (McLachlan), new larval association.

Measurements: Length of mature larva, 16.80-21.80 mm, mean length = 19.25 mm. Length of head capsule, 4.00-4.50 mm, mean = 4.35 mm; width of head capsule, 4.37-4.90 mm, mean = 4.57 mm.

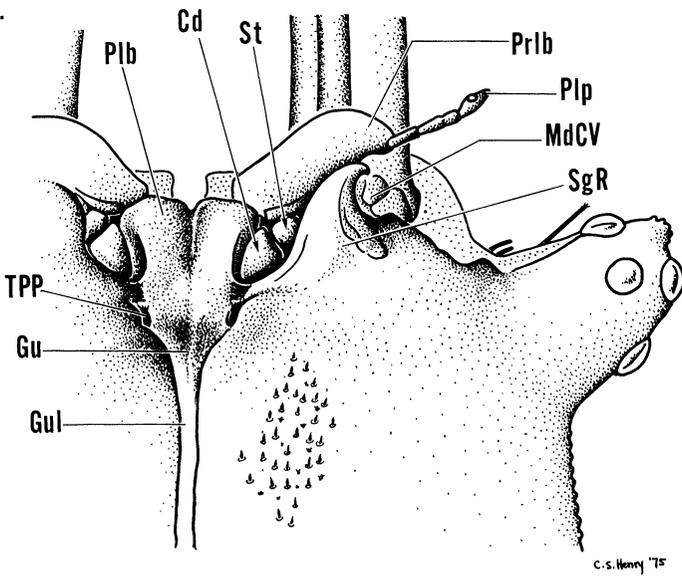
Chaetotaxy: Dolichasters on lateral margins of head capsule short and stout; those on dorsal aspect of head with closed tips.

Figure 5. [opposite page] *Ascaloptynx furciger*, mature third instar larva. ScAbd₃ = scoli of third abdominal segment, ScMs = mesothoracic scoli, ScMt = metathoracic scoli, SpMs = mesothoracic spiracle, SpAbd₁ and ₂ = spiracles of abdominal segments one and two.

A.



B.



Setae on anterior and distal margins of primary scoli stout and flared (figure 8-a); postero-basal setae on each scolus are longer, sharp-tipped, and more nearly plumose than serrated (figure 8-f). Non-scale-like setae mostly dark pigmented except all pale on labral margin and predominantly pale on margins of body scoli; several to most dolichastes on anterior distal half of anteriormost scolus prominently darkened.

Pigmentation: Head uniformly dark brown, entire body light brown to reddish brown; darker tints present dorsally in cuticle beneath clumps or thick patches of setae. Overall dorsal pattern exhibits longitudinal medial stripe, transverse segmental bands, and mid-lateral patches that strongly suggest the venation of a small dead leaf.

ONTOGENETIC VARIATION:

The first instar *Ascaloptynx* larva (figure 7) differs from the mature larva in several obvious respects. The ocular tubercle is pedunculate and nearly ovoid rather than tapered and bears a poorly developed setigerous secondary tubercle. The antenna is relatively large, projecting well beyond the tip of the ocular tubercle, but arises from a "tubercle" that can be identified as such only by the presence of stellate-tipped setae; nine flagellomeres are typically present rather than 12 or 13. The jaws are not falcate and bear relatively long mandibular teeth. Primary body scoli show little dorso-ventral flattening and no tendency toward basal constriction; the secondary scoli are inconspicuous and resemble small tubercles. All setae are relatively longer, less numerous, and of fewer morphological types than in mature larvae: the distally flared dolichaster predominates, and no minute scale-like setae are present. Two stellate setae rather than three are more likely to be found on each antennal "tubercle," with stout serrate setae usually absent from this structure. Terminal digging teeth on abdominal segment nine are also lacking.

The second instar larva more nearly resembles the third than it does the first, although its antennae are still relatively large and the ocular tubercle remains somewhat pedunculate. Additionally, constriction of the bases of the abdominal scoli is not so marked as it will become in the mature larva.

Figure 6. [opposite page] *Ascaloptynx furciger*, details of head capsule of mature third instar. A = anterior dorsal aspect, B = anterior ventral aspect. Sc1 = scale-like seta; other labels as in figure 3.

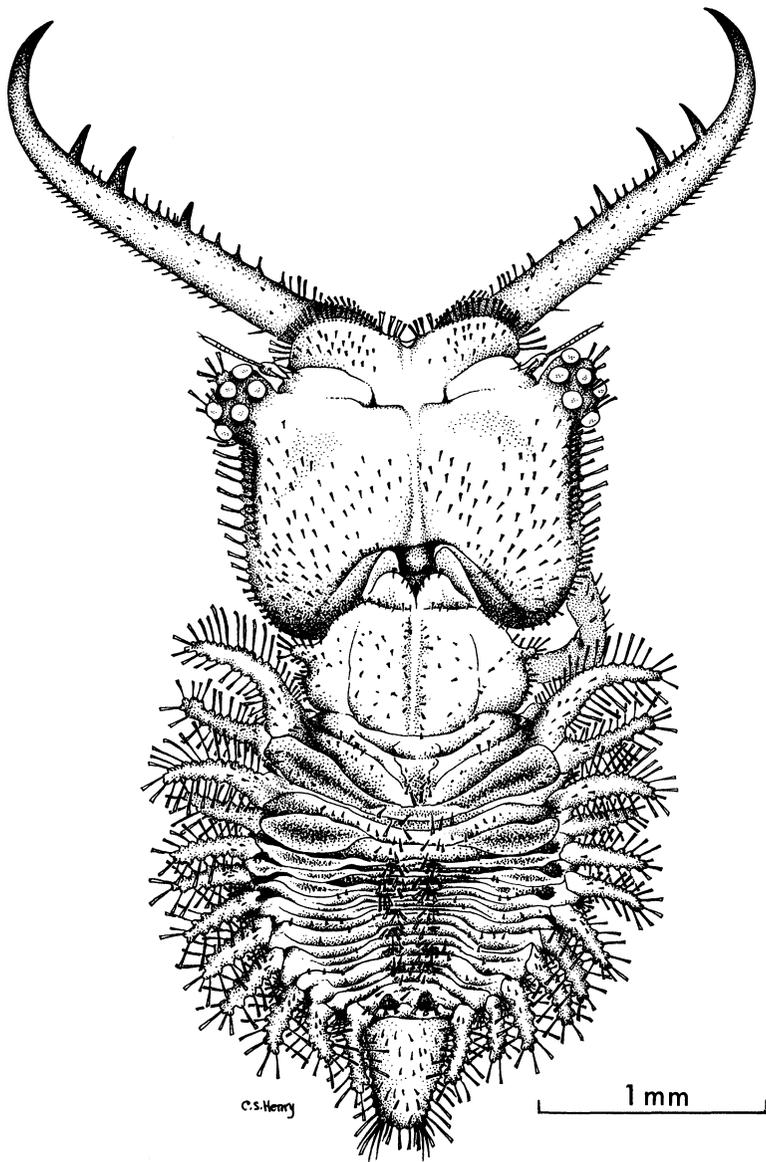


Figure 7. *Ascaloptynx furciger*, first instar larva at hatching.

DISCUSSION

Works on the morphology and biology of the immatures of Ascalaphidae other than *Ululodes* and *Ascaloptynx* include those by Westwood (1888) and Ghosh (1913) on the Asian genus *Helicomitus* McLachlan; Froggatt (1900, 1902) and Tillyard (1926) on the Australian forms *Acmonotus* McLachlan and *Suhpalacsa* Lefebvre; Gravely and Maulik (1911) on the Asian *Pseudoptynx* Weele; and Brauer (1854), Zaki (1917), Rabaud (1927), Withycombe (1925) and Rousset (1973) on various European species of *Ascalaphus* Fabricius. Xambeu (1904), Fraser (1922), Withycombe (1925), von Someren (1925) and Wheeler (1930) have contributed valuable notes on true ascalaphid larvae of uncertain taxonomic affinities. Purely morphological works on the family and general phylogenetic treatments of higher groupings within the Neuroptera have been mentioned in the introductory section of this paper.

Morphological features of owlfly larvae that have been thought to be of special evolutionary and taxonomic importance include the shape of the head capsule, the form and dentition of the jaws, the details of the ventral mandibular articulatory structure, the size, number and degree of flattening of the lateral body scoli, and the placement of the first two pairs of abdominal spiracles (Hagen, 1873; MacLeod, 1964, 1970). To this list may be added the shape and width of the labral margin (LmM), the relative size and shape

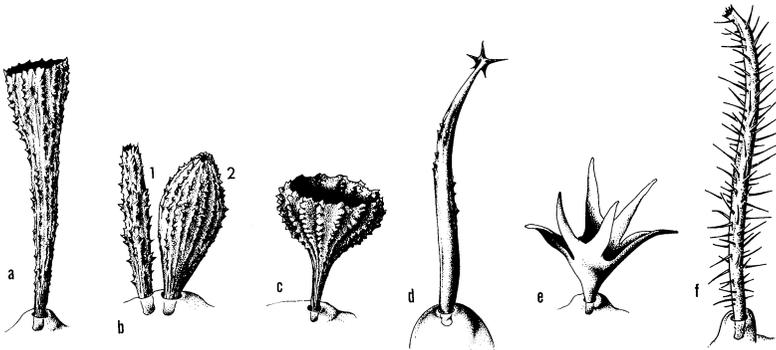


Figure 8. Ascalaphid setal types. a = typical dolichaster, b = clavate dolichasters, c = goblet-shaped dolichaster, d = stellate-tipped seta, e = scale-like seta, f = plumose seta.

of the antennal and ocular tubercles (AT and OT), the morphology of the labium (Plb and Prlb), the shape of the pronotum, and the structure and placement of setae — particularly those located peripherally and on the ocular and antennal tubercles and those forming distinct dorsal patterns.

There is some evidence from both adult and larval morphology that the Nymphidae of Australia is closer to the ancestral taxon leading to the Ascalaphidae (and to the closely related Stilbopterygidae) than any other myrmeleontoid family (Withycombe, 1925; Tillyard, 1926; and MacLeod, 1970). Thus, many of the features of certain described larvae within the Nymphidae, particularly of the Oligocene ? *Pronymphes* sp. and the extant *Nymphes* spp. (MacLeod, 1970), are thought to represent shared specializations of the ascalaphid-nymphid (*et al.*) evolutionary branch and hence to typify the generalized condition in the Ascalaphidae. In addition, the generalized condition is presumed by MacLeod (1970) to predominate in the Oligocene fossil ascalaphid larva *Neadelphus protae* MacLeod; I have carefully examined and figured the specimen from which MacLeod wrote his description, and I can attest to the nearly perfect state of its preservation in amber (figure 9).

It may be suggested tentatively, then, that generalized character states in owlfly larvae could include quadrate head with weakly cordate posterior margin (*Nymphes* and *Pronymphes*); long, non-falcate jaws bearing subequal teeth (*Neadelphus*); simple and loose ventral articulation of the mandible against a medial strut of the anterior terminus of the subgenal ridge (*Nymphes*); a dorsal and ventral series of unflattened, finger-like setigerous scoli of short to moderate length (*Pronymphes*); and all abdominal spiracles oriented co-linearly on the sides of the body (*Neadelphus* and *Pronymphes*). In addition, like *Neadelphus*, the primitive larva should probably display a wide, weakly bilobed labral margin, small antennal tubercles, cylindroid ocular tubercles, postlabium with broad anterior margin, ellipsoidal pronotum bearing small lateral tubercles, and relatively unmodified setae of moderate length clothing most body surfaces.

According to the above criteria, we may state that the genus *Uluodes* is a generalized one with respect to its unflattened scoli, cylindroid ocular tubercles and ventrally situated (and linear) abdominal spiracles. However, in certain major respects, it is highly specialized. First, the *Uluodes* larva shows no obvious

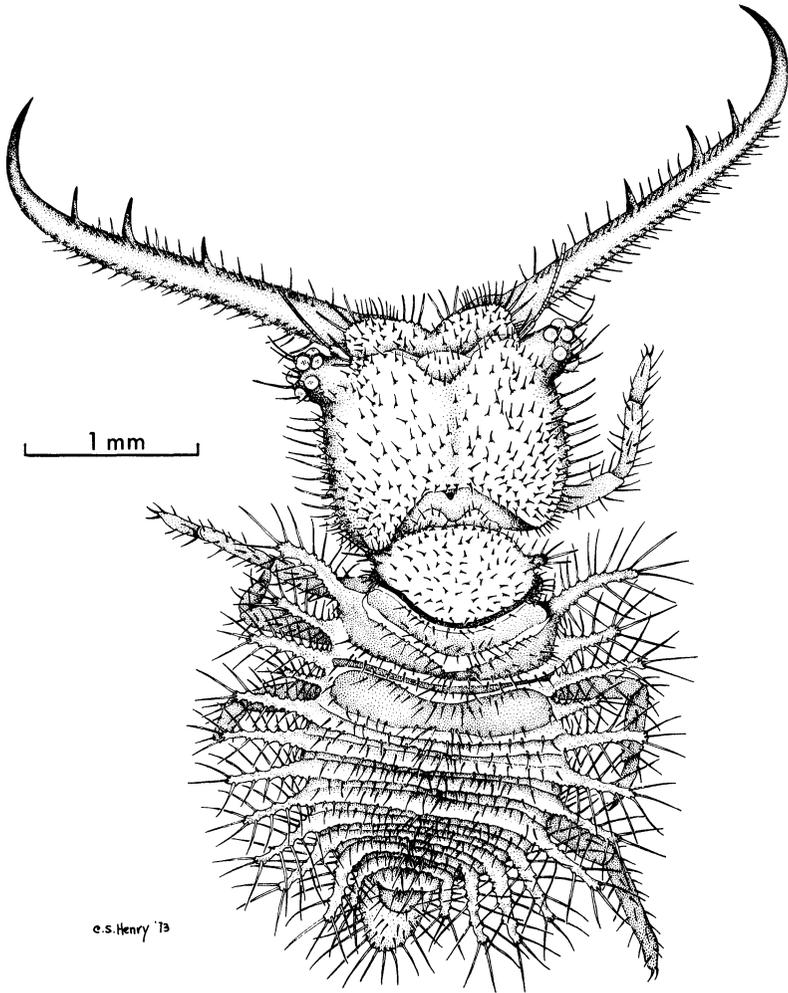


Figure 9. *Neadelphus protae* MacLeod. Baltic Amber (Oligocene). MCZ.

trace of the ventral series of body scoli; it is characterized by ten lateral extensions, all presumably dorsally derived. Secondly, it lacks any trace of pronotal tubercles. Thirdly, it has relatively much larger antennal tubercles and longer antennae than our hypothetical generalized ascalaphid. Fourthly, the setae situated laterally on the head, peripherally on the scoli, and postero-laterally on the ocular tubercles are longer than one would expect to find in a generalized form. Finally, it is characterized by a constellation of specializations associated with its method of prey capture. The strongly falcate, long-toothed and upwardly tilted jaws, the trapezoidal, strongly cordate head with concomitantly small postlabium and narrow bilobed labral margin, the ventro-lateral excavations of the head capsule, and the massive bifurcate socket that receives and tightly locks the ventral mandibular condyle are all secondary expressions of the ability of the *Ululodes* larva to draw its jaws far back alongside the body in the 270 degree "trap" position.

Ascaloptynx appears to have retained a more generalized complex of feeding-related head and jaw adaptations than has *Ululodes*. In addition, the double row of scoli has been retained from the mesothorax to the end of the abdomen, except for abdominal segments one and two. However, the two series of scoli have moved into a common horizontal plane, losing their dorsal and ventral relationship to one another; this must be considered a derived characteristic. Correlated with co-planar location of all scoli is dorso-ventral flattening of the *Ascaloptynx* larva, particularly evident in the extreme flattening of the head capsule and of each thoracic and abdominal scolus: this is also a specialization. Additional derived traits include the scale-like setal modifications and, presumably, the dorsal location of the first and second pairs of abdominal spiracles.

To assess the significance of generalized and specialized traits of *Ululodes* and *Ascaloptynx*, one must compare these genera to other described ascalaphids of known subfamilial affinity. From such an analysis emerges the view that many of the specializations of the *Ululodes* larva are, as previously mentioned, related to its method of prey capture: in this respect it most closely resembles the Indian form *Pseudoptynx* (Gravely and Maulik, 1911) among the Ascalaphinae. Larvae of other split-eyed types like *Ascalaphus*, *Acmonotus* (Froggatt, 1902), *Suhpalacsa* (Tillyard, 1926), *Helicomitus* (Westwood, 1888; Ghosh, 1913) and some unidentified

Australian and African forms in my possession* display the more widespread and plesiomorphic pattern of head and mouthpart morphology characteristic of *Ascaloptynx*. Several additional specializations of *Ululodes* seem to be unique to the genus (or to its tribe, Ululodini, confined to the New World): for example, ventral scoli, entirely lacking in *Ululodes*, are retained on the meso- and metathoraces of all known ascalaphine types and on a number of anterior abdominal segments in *Ascalaphus*, *Helicomitus* (Ghosh, 1913), and several distinct but unidentified species from South Africa and Australia. Other features that are more extreme in *Ululodes* than in other Ascalaphinae include the length of the anteriormost body scoli, the prominence of the antenna and its tubercle, the degree of reduction in the size of the prothoracic tubercles, and the length of lateral head and body setae. On the other hand, *Ululodes* shares with all other known Ascalaphinae such plesiomorphic traits as cylindroid body scoli and relatively unflattened head capsule; prominent, cylindrical ocular tubercles of the *Ululodes* type are also characteristic of most ascalaphines, but *Pseudoptynx* (Gravely and Maulik, 1911) is exceptional in possessing a somewhat flattened, nearly sessile ocular area. Finally, the positioning of abdominal spiracles presents an ambiguous picture in the subfamily. Spiracles are placed ventrally in *Ululodes* and in the extinct genus *Neadelphus*. However, a tendency can be noted in *Ascalaphus* (figure 10) that becomes more pronounced in several Australian and African forms toward lateral or even dorsal placement of the first pair of abdominal spiracles; in extreme cases, the second pair may also be involved in this dorsal migration, although never to the same extent as the first.

Comparison of the *Ascaloptynx* larva with two unidentified Central American neuroptyngines in my possession** suggests that extreme dorso-ventral flattening of the head and scoli may be a universal specialization within the New World Neuroptynginae that is perhaps least developed in *Ascaloptynx*. In conjunction with this flattening, all three types bear "dorsal" and "ventral" series of scoli together in a common plane; the number of scoli in each series is also constant within the group, insofar as our limited sample permits us to generalize. Other specializations shared by

*All Australian owlflies are ascalaphines.

**A description of these forms is in preparation.

the known New World forms include prominent dorsal placement of the first and second pairs of abdominal spiracles and modification of some setae to form pigmented scales; in this latter respect, they all resemble an arboreal African larva tentatively assigned by Withycombe (1925) to the neuroptyngine genus *Tmesibasis* McLachlan, which is described as possessing conspicuous swatches of white scale-like setae on its otherwise dark body. On the other hand, those aspects of New World neuroptyngine head and mouthpart morphology that are functionally associated with prey capture fit the generalized pattern seen in most ascalaphines. However, one of the Central American forms shows a slight modification of the ventral mandibular articulation that may be associated with its proven ability to open its jaws slightly beyond 180 degrees. This tendency toward a *Ululodes* type of specialization is much more completely expressed in Withycombe's "*Tmesibasis*" just mentioned. The plesiomorphic complex of head features, then, may not be any more characteristic of Neuroptynginae than it is of Ascalaphinae.

In summary, it appears that we are dealing here with two genera, *Ululodes* and *Ascaloptynx*, that seem to have acquired numerous specializations independently of one another and of other Old World members of their respective subfamilies. In view of the distinctiveness of the New World owlfly fauna (Weele, 1908; Orfila, 1949), it is probably safe to assume that the American radiations of both subfamilies are old ones and that many of the basic traits that ancestrally defined the subfamilies have been partially obscured or modified. Thus, it is extremely difficult, given the present state of our knowledge, to separate unequivocally the larvae of split-eyed owlflies from those of entire-eyed ones. Equally difficult is assessing which of the two subfamilies displays the more specialized complex of larval traits. We have seen that feeding-related adaptations of the head and mouthpart region are of the same basic, generalized sort in the majority of known representatives of both subfamilies, with presumably independent evolution of the specialized constellation of characters at least twice in the Ascalaphinae and once in the Neuroptynginae. Other evidence presented in this paper suggests that the placement and degree of flattening of the body scoli may be more reliable indicators of subfamily affinity than head features: known neuroptyngines have flattened scoli with the secondary series coplanar with the primary series, while ascala-

phines display cylindroid scoli with the secondary abdominal scoli, when present, situated beneath the primary extensions. However, we may be dealing with specializations of the New World neuroptyngines that do not characterize the subfamily as a whole: were one analogously to base his conclusions solely upon New World ascalaphines, he might wrongly interpret the extreme specializations of the Ululodini (10 scoli, 270 degree jaw trap position, etc.) as basic larval features of all split-eyed owlflies. In addition, I have seen bizarre unassociated larval ascalaphids from South Africa that bear flattened co-planar scoli on the thoracic segments and two complete series of non-co-planar cylindroid scoli on the abdominal segments!

Spiracle placement also seems to be intimately associated with scoli evolution and can be more easily understood in this context. Examination of many different ascalaphid forms has convinced me that the ancestral condition in the family is lateral placement of all abdominal spiracles between a fully-developed dorsal and ventral series of scoli. Ventral location of spiracles, as in *Ululodes*, results from retention of the dorsal scoli only — or, as in *Ascaloptynx* and its American relatives, perhaps from dorsal migration of the ventral scoli of abdominal segments three through eight to positions immediately behind the dorsal ones. Dorsal location

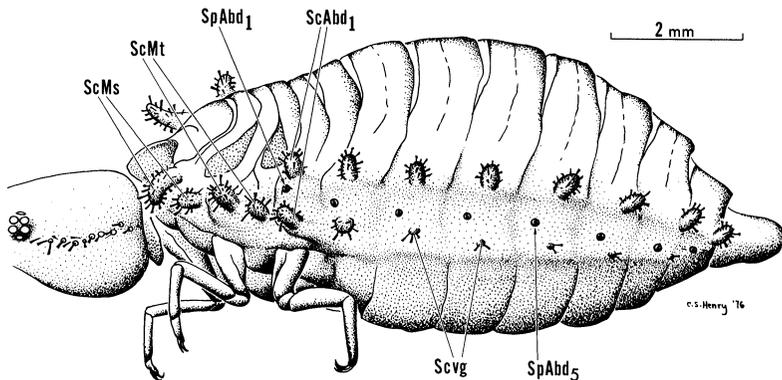


Figure 10. *Ascalaphus libelluloides*, lateral aspect of body of mature third instar larva. Scvg = vestigial abdominal scoli of ventral series; other labels as in figures 1 and 5.

of spiracles, as seen on the first and second abdominal segments of known neuroptyngine larvae, can be thought of as a consequence of total loss of the dorsal scoli of these segments. Support for this view of spiracle placement can be found in the European genus *Ascalaphus* (figure 10) and in several African and Australian forms already mentioned, in which intermediate stages in the loss of the anteriormost dorsal abdominal scolus can be seen to be correlated with dorsad migration of the associated spiracle. However, none of these ascalaphine forms carries this tendency to the second abdominal segment: here, the situation is exactly the opposite of that seen in Neuroptynginae, since the ventral rather than dorsal scoli suffer reduction (figure 10, Scvg). Note that acceptance of the above interpretation of scolus/spiracle evolution forces us to accept the larger ("primary") scoli on abdominal segments three through eight in New World neuroptyngines as derivatives of the ventral rather than dorsal series; this view gains additional support from the relative shapes of the various scoli in *Ascaloptynx* (figure 5), but compels us to consider the "primary" abdominal scoli of ascalaphines and neuroptyngines as non-homologous.

A final point concerns the chaetotaxy of the various larvae and some associated behavior patterns. None of the known neuroptyngines is a debris carrier: protective coloration is achieved through the presence of cuticular or epidermal pigments and clumps of colored, often scale-like setae. The one larva of possible neuroptyngine affinities that has been described in the literature, "*Tmesibasis*" from Africa, shares with *Ascaloptynx* and its Central American relatives similar pigmented setal scales (Withycombe, 1925). On the other hand, littering of the dorsum is widespread in the Ascalaphinae, having been described in such distantly related forms as *Ululodes*, *Ascalaphus* (Brauer, 1854; Withycombe, 1925); and personal observation), *Helicomitus dicax* (Ghosh, 1913), and several unassociated Australian species. It may be that the absence of littering may simply be correlated with arboreal or leaf-associated habits: several primarily arboricolous or litter-dwelling ascalaphines apparently remain naked (Westwood, 1888; Froggatt, 1902; Gravely and Maulik, 1911; Fraser, 1922; and Tillyard, 1926), as do a number of unassociated forms resembling bark, lichens and green leaves (von Someren, 1925; Withycombe, 1925; Wheeler, 1930). However, the possibility remains that the ability to place and secure items of sand or debris on the body has evolved entirely

within the subfamily Ascalaphinae, with the Neuroptynginae pursuing a different evolutionary route toward setal specialization.

From the preceding discussion we may conclude, tentatively;

(a) Ascalaphines show varying tendencies toward loss of the ventral scoli, while neuroptyngines retain the ventral scoli as the primary series on the abdomen.

(b) As a result of scoli modifications, full dorsal placement of the first and second pairs of abdominal spiracles has occurred in Neuroptynginae but not Ascalaphinae.

(c) Only ascalaphines systematically litter the dorsum with sand or debris — though not all species within the subfamily possess the ability.

As more of an impression than established fact, I suggest that the Ascalaphinae share with the hypothetical ancestral type a larger number of plesiomorphic larval character states than do the Neuroptynginae. Retention of primitive traits does not require close relationship between ascalaphines and ancestral ascalaphids. In fact, such a relationship is unlikely in view of indisputably derived adult features like the divided compound eye and specialized cervix (Shepard, 1967) of the Ascalaphinae. Data presented in the present work point to the many difficulties in deriving either larval type from the other; it is more convincing to invoke long separate evolutionary histories for the two subfamilies. In keeping with such an interpretation, it should be noted that the oldest known fossil ascalaphid larva, *Neadelphus protae*, is easily assignable to the subfamily Ascalaphinae (MacLeod, 1970). Another paper, by Adams (1958), adds further support to our interpretation by pointing to the impossibility of deriving the venational pattern of the Ascalaphinae from the highly specialized venation of known neuroptyngines. It is hoped that greater efforts will be made by future workers to associate, by rearing or other valid means, immature and adult ascalaphid material. A peripheral benefit of such efforts will be the accumulation of valuable information on the biology of these insects that will add additional pieces to the puzzle of their evolutionary history.

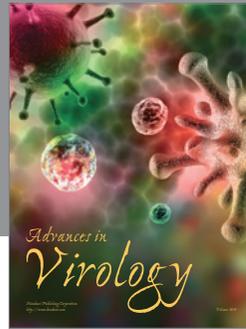
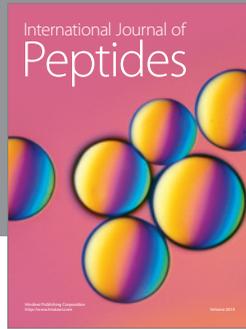
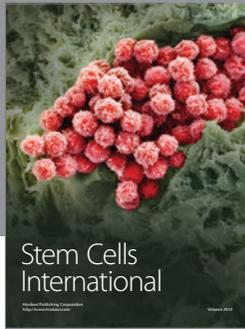
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