PSYCHE

EGGS AND RAPAGULA OF *ULULODES* AND *ASCALOPTYNX* (NEUROPTERA: ASCALAPHIDAE): A COMPARATIVE STUDY*

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I. INTRODUCTION

Ascalaphidae is a fairly large family of planipennian Neuroptera, encompassing perhaps 300 species in 65 genera, yet relatively little is known of the biology of its various representatives. Although several systematic monographs concerned exclusively with the family have been published (Lefebvre, 1842; Rambur, 1842; McLachlan, 1871; Van der Weele, 1908; Navás, 1913), attempts to discern the true phylogenetic relationships among the various genera and other taxa must necessarily await studies of life-history and behavior. In fact, definite larva-adult associations are lacking for a great majority of ascalaphid species. Larvae have been reliably identified only for the genera *Ascalaphus* Fabricius, *Helicomitus* McLachlan, *Pseudoptynx* Weele, *Suhpalacsa* Lefebvre, and *Ululodes* Currie, all belonging to the "split-eyed" subfamily Ascalaphinae; of the "entire-eyed" subfamily Neuroptynginae, only *Ascaloptynx* Banks has been associated with a larval type (MacLeod, 1970: p. 155).

I have succeeded in rearing an additional species of *Ululodes* from egg to adult: *Ululodes mexicana* (McLachlan), common in northern Mexico and southern Arizona and New Mexico. I have also been able to compare the form and habits of the various life stages of this species with those of a sympatric neuroptyngine species, *Ascaloptynx furciger* (McLachlan). The identity of this last-named species is inferred, but based upon various types of evidence: (1) third-instar larvae, raised from field-collected eggs, were positively identified by Dr. Ellis G. MacLeod (University of Illinois) as those of *Ascaloptynx;* (2) the only species of the genus *Ascaloptynx* — or, for that matter, of subfamily Neuroptynginae — ever taken at the

collecting sites in question is *furciger;* (3) males and females of *Ascaloptynx furciger* were captured in fair abundance in the same areas and at the same time of year that eggs and young larvae were collected; (4) dissections of gravid *A. furciger* females revealed eggs and egg-attendants (see text) that were in every respect identical to field-laid eggs that yielded *Ascaloptynx* larvae.

The first student of ascalaphid life-history was the Reverend L. Guilding, whose 1827 account of the various life stages of *Ululodes macleayana* (Guilding)* from St. Vincent's Island in the West Indies remains one of the best such studies ever published. In describing the eggs of this species, he noted the presence of curious rod-shaped structures encircling the twig beneath the egg-mass. He called these egg-attendants "repagula,"** meaning "barriers," because he believed that they prevented ants and other predators from approaching and destroying the eggs and newly hatched larvae; conversely, he felt that the repagula discouraged the larvae from leaving their twig "until they have acquired strength to resist . . . [their] enemies." McClendon (1901) also noted repagula accompanying the eggs of *Ululodes hyalina* (Latreille) [believed by MacLeod (1964) to be *Ululodes senex* (Burmeister)] from Texas; he confirmed Guilding's description of these structures and concluded from his dissections of gravid female ascalaphids (unfortunately unillustrated) that certain ovarioles ("tubercles") were specialized for the production of repagula. Thus it was shown that repagula were in fact abortive eggs. Seventy years later, New (1971), apparently overlooking the papers of Guilding and McClendon, re-introduced the concept of ovariolar dimorphism in his cursory study of the eggs and repagula of eight species of Ascalaphidae from central Brazil. New's paper is important, nonetheless, for two reasons: first, it proved that repagula-formation is not unique to the genus *Ululodes* but is also found in the closely-allied genera *Colobopterus* Rambur, *Ascalorphne* Banks and *Cordulecerus* Rambur, and in the neuroptyngine genera *Byas* Rambur and *Episperches* Gerstaecker; secondly, it suggested that the repagula of neuroptyngine species are fundamentally different in form from those of ascalaphine species — the former type more nearly resembling fertile eggs than the latter type.

The functional significance of repagula has not been investigated. Most authors (Imms, 1957, for example) have accepted Guilding's "ant guard" view. New (1971) intimates that repagula and eggs

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*Guilding's name for this species was *Ascalaphus macleayanus.*
**singular = repagulum.

alike of *Ululodes* were carried off by ants in Brazil, but admits that more controlled experimentation is needed to assess the effects of the repagula on egg or larval survival. Through my studies of the life-histories of *Ululodes mexicana* and *Ascaloptynx furciger,* I have been placed in a unique position to verify or disprove experimentally the ant-guard hypothesis, as it applies to these representative species of two taxonomically distant genera. Especially important is the fact that *Ululodes* is an ascalaphine genus while *Ascaloptynx* is a neuroptyngine one, thus encouraging direct comparison of the functional significance of the morphologically disparate repagula characteristic of the members of these subfamilies. In the remainder of this paper, I intend (1) to describe the eggs and repagula of *Ululodes mexicana* and *Ascaloptynx furciger,* (2) to outline the procedures and results of several simple experiments undertaken to test the protective importance of the repagula of both species, and (3) to discuss the functional significance of the ascalaphine type of egg and repagula as compared to that of the neuroptyngine type.

II. Acknowledgements

Figure 1. Typical sites for oviposition, *Ululodes mexicana* (1-a) and *Ascaloptynx furciger* (1-b).

III. METHODS AND MATERIALS

Eggs of both *Ululodes mexicana* and *Ascaloptynx furciger* were collected during August and September in the southeastern part of Arizona, within a 25-mile radius of the Southwestern Research Station of the American Museum of Natural History (SWRS). All egg-masses, 25 of *Ululodes* and 35 of *Ascaloptynx*, were taken on shrubs in the arroyos and canyons of the Chiricahua and Peloncillo Mountains, at elevations of 4700 to 5700 feet (1500-1800 meters). Several egg-masses were left *in situ* and visited twice daily; others

were placed twigs and all in 2.5 cm × 9.0 cm glass screw-top vials and transported carefully to the research station laboratory. There, the egg-bearing twigs were taped in their "natural" positions, covered with large glass jars for observation and situated in a southwest window shielded by heavy curtains form the vicissitudes of indoor artificial light. Complete records from oviposition through hatching to descent of larvae were obtained for seven egg-masses of *Ululodes* and eight of *Ascaloptynx*. Additional egg-clumps of both species of Ascalaphidae were exposed to several natural and exotic insect predators (mostly ants) under various experimental conditions, to ascertain the effectiveness of the repagula. In each experiment, for each ascalaphid species, two normal egg-masses and one egg-mass stripped of its repagula were mounted (on their respective twigs) in the vicinity of foraging ants, in such a manner that the bottom-most egg of each clump was positioned 16 cm above the ground. The behavioral details and success of each foray of an ant (or other insect) up an egg-bearing twig were carefully noted. Similar experiments were carried out using hatched egg-masses, prior to descent of the larvae from their twigs.

Closer observation and dissection of eggs, repagula, and gravid female ascalaphids were undertaken beneath a Wild M5 stereoscopic dissecting 'scope outfitted with an integral *camera lucida* attachment; most of the illustrations included with this paper were rendered with the aid of this precision imaging device. Extremely small specimens and structures were treated with xylene and mounted in Damar on depression-slides and observed at higher magnification using a Bausch and Lomb stereoscopic compound microscope with one ocular fitted with a 10 × 10 micrometer grid to insure accurate drawings.

IV. DESCRIPTIONS OF EGGS AND REPAGULA

A. *Ululodes mexicana* (McLachlan)

Adults of *U. mexicana* appear in large numbers in southeastern Arizona at the beginning of August, and remain abundant until the time of first frost — mid or late October. Males apparently die off by early September, while females, which individually may live three months or more under laboratory conditions, begin laying eggs at the start of the dry season in September and continue ovipositing far into October. Females display great selectivity in their choice of sites for oviposition, but are quite unselective of the particular species of plant: eggs are laid probably at dawn on the thin peripheral dead twigs of any two or four foot deciduous shrub growing
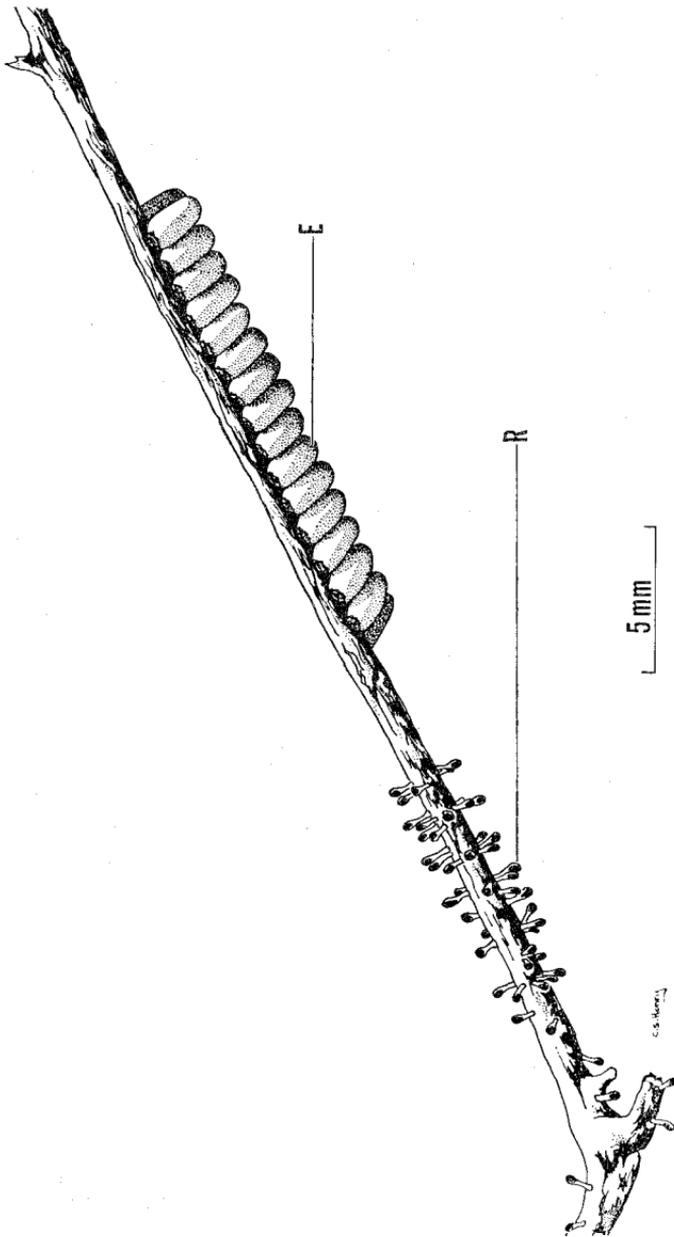
Figure 2. Egg-mass of *Ululodes mexicana*. Fertile eggs (E) and repagula (R) in natural position.

on totally exposed, south-facing embankments of dry arroyos and canyons (figure 1-a). The insects always seem to choose inclined rather than vertical twigs, and seek out the downhill sides of the bushes in preference to any other spots; this latter choice gives the hatched larvae an unobstructed fall of 50 to 85 cm (18-30 inches) to the crumbling rocky substrate below.

U. mexicana eggs are laid on the undersides and towards the tips of their twigs, in two long interdigitating rows together totalling 30 to as many as 52 eggs (figure 2). Each freshly laid egg is light grey or cream-grey in color and oblong in shape, averaging 1.6 to 2.0 mm in length and 0.8 to 1.0 mm in diameter; all the eggs in a given egg-mass will be of roughly equivalent size, but different egg-masses will vary considerably in their egg dimensions. The eggs are laid on end, inclined slightly toward the tip of the twig. They are attached to the substrate by a shiny reddish-brown glue. Each egg possesses two identical, pale micropyles, about 0.1 mm in diameter, axially located one at each end; high power examination reveals the micropyle to be saucer-shaped, constructed of approximately twenty ribs or channels radiating from a central depression (figure 3-A). Except for the micropylar sculpturing and a very slight graininess to the balance of the egg surface, the *Ululodes* chorion displays no elaborate fine-stucture.
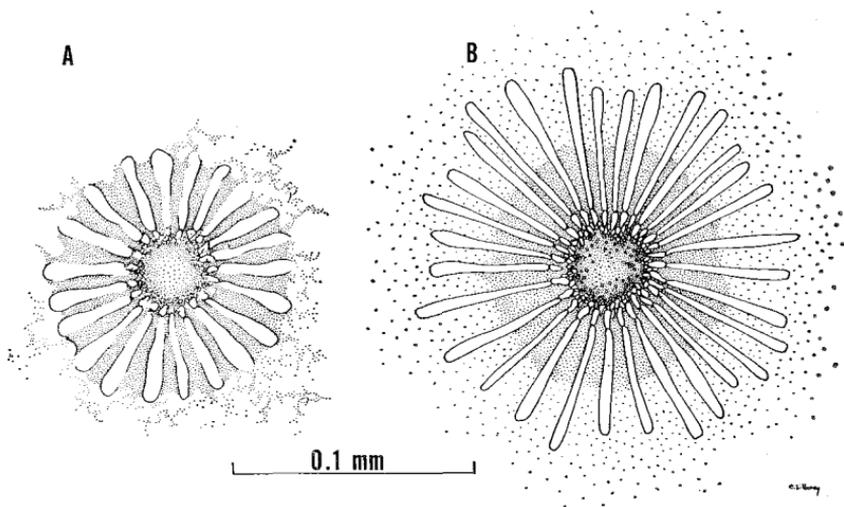

Figure 3. Micropyles of *Ululodes mexicana* (A) and *Ascaloptynx furciger* (B) eggs.

Three to four days after oviposition there appears a diffuse whitish line nearly girdling the egg a short distance from its distal pole (figure 4). This line circumscribes an arc of 270 degrees and marks the line of weakness along which the egg will split as the larva emerges; the extent of the weakened area and the positioning of each egg at the time of laying assures that the "cap" of each egg will remain attached to the main egg body by a "hinge" and will flip toward the midline of the egg-mass at the time of hatching. It can be seen (figure 4) that the developing embryo conforms to no strict rule of position within the egg except to have its head end toward the egg's distal pole. A few days prior to hatching, the whitish outline of the embryo disappears and the sides of the egg cave in slightly; the egg progressively darkens to a slate-grey color and hatches on the fifteenth or sixteenth day after oviposition.

The repagula of *Ululodes mexicana* do not resemble the eggs at all. They are rod- or club-shaped structures, reddish-brown and shiny in apperance, surrounding the twig bristle-like five to ten millimeters below the egg-mass (figure 2). Sometimes they are arranged in a series of neat rings but more usually are rather irregularly placed. Each repagulum is approximately two-thirds the length of a normal egg, measuring 1.2 to 1.4 mm in length and 0.25 to 0.30 mm at its widest point; it appears to lack any vestige of a micropyle, despite its ovariolar origin. It is characterized by a small, round, light-colored basal swelling and a larger, oblong, darker distal swelling, joined by a thin translucent stem (figure 5-B). The over-all reddish hue is apparently imparted by the shiny fluid coating each repagulum. This non-sticky fluid should not be confused with the hard brownish glue that secures both eggs and repagula to the stem: it neither hardens upon nor evaporates from the repagulum surface for at least three to four weeks after oviposition. Long after the true eggs have hatched, these strange barriers gradually collapse, their surfaces choked with debris.

Apparently the repagula are extruded from the female's body after she has deposited her eggs, since in laboratory situations repagula are often found glued randomly to the surfaces of the eggs. Thus it would seem that the *Ululodes* female oviposits progressively from the tip of the twig towards its base, with her head oriented downward; such a view agrees with what we know of the standard rest-posture of Ascalaphidae. Typically, four of the twelve ovarioles in each of the female's ovaries are modified for the production of repagula (figure 6). However, the insect is nevertheless capable
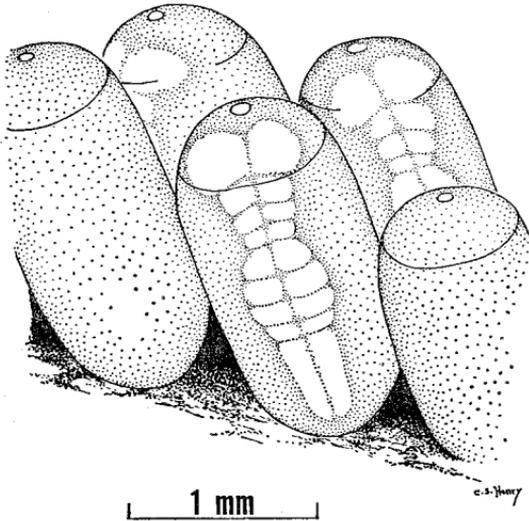
Figure 4. Detail of eggs of *Ululodes mexicana,* three to four days old.

of depositing as many as or more repagula than eggs at any given time, since each modified ovariole can store many more "mature" repagula than a normal ovariole can eggs. Stored repagula show no trace of the reddish color characteristic of oviposited repagula, suggesting that the red fluid is secreted by some accessory gland at the time of deposition.

B. *Ascaloptynx furciger* (McLachlan)

Adults of *Ascaloptynx furciger* are active earlier in the summer than *U. mexicana,* seemingly being most abundant in southeastern Arizona during the rainy season, from early June to early September. As in *Ululodes,* males become less common in the latter half of this time period. Eggs are in greatest evidence during August, with chalcidoid parasitism destroying 95 percent of the egg-masses deposited after September 1. Again like *Ululodes,* ovipositing *Ascaloptynx* females are extraordinarily habitat specific, yet display little preference for particular plant species: eggs are laid on the thin terminal dead twigs of any one to two foot perennial or grass clump growing in protected semi-shaded locales in the foothills of the mountains, where rainfall is relatively great and scrub oak (*Quercus emoryi* and *Q. arizonicus*) and juniper (*Juniperus deppeana*) abound. In contrast to *Ululodes,* vertically oriented twigs
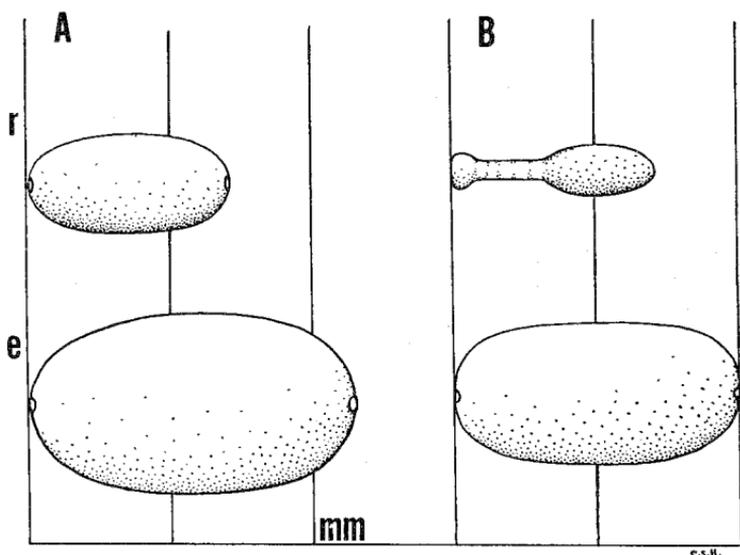
Figure 5. Comparison of the repagula (r) and eggs (e) of *Ascaloptynx furciger* (A) and *Ululodes mexicana* (B).

or grass-stems are always selected (figures 1-b); the substrate beneath the egg-clumps is nearly always densely strewn with dry oak litter.

Ascaloptynx furciger eggs are laid in dense clumps completely surrounding their twigs, near the tips of the stems, perhaps 22 to 55 cm (8 to 18 inches) from the ground. The structure of the egg-mass suggests that it might consist of several long, parallel, tightly-spiraling rows of eggs. These clumps typically include 35 to 45 ovoid eggs, each one glued by its mid-section to its twig with its longer dimension oriented nearly horizontally (figure 7). The freshly laid *Ascaloptynx* egg is bright yellow-ochre in color, averaging 2.1 to 2.4 mm in length and 1.2 to 1.3 mm in diameter; it is thus larger and proportionally less elongate than that of *Ululodes*. It possesses two axially located micropyles, about 0.15 mm in diameter, identical to those of *Ululodes* in all respects except size (figure 3-B). The chorion of the egg displays no sculpturing.

As in *Ululodes,* several days after oviposition a whitish girdling line appears at the "head" end of the egg, outlining the extent of the egg cap (figure 8). In *Ascaloptynx,* positioning of the eggs on the twig assures that every egg cap will flip downward on its hinge;

in fact, the cephalic (cap) pole of each egg is slightly lower than its opposite pole and related to the cephalic poles of its neighbors in such a way that no larva interferes with another during hatching. It is of interest that in *Ascaloptynx* the whitish outline of the developing embryo always appears on the dorsal surface of the egg. As in *Ululodes,* this outline disappears as the egg gradually darkens to a muddy brownish-yellow color and acquires a semi-collapsed appearance several days before hatching; eclosion occurs a minimum of 14 days after oviposition.

The repagula of *Ascaloptynx furciger* appear to be miniaturized versions of fertile eggs: each is identical to a full-sized egg in color, proportion, micropylar structure, and orientatation (figure 5-A). Typically, a repagulum in this species measures 1.3 to 1.4 mm by 0.65 to 0.70 mm; it has no fluid of any kind on its surface. In all egg-masses examined, repagula occurred in a small group immediately below (and continuous with) the main egg clump, and in a larger group about 10 cm further down the twig; frequently, one or two additional, smaller masses of repagula would be present, spaced varying distances below the largest clump (figure 7, "R_3"). Usually the masses of repagula surround the twig in the same manner as fertile eggs, but occasionally, especially on large stems, the repagula are deposited in an obvious spiral pattern. Dissections of *Ascaloptynx* females reveal an arrangement of specialized ovarioles similar to that in *Ululodes;* however, poor preservation prevented reliable conclusions as to numbers of ovarioles present and modified. Field-collected egg-masses always exhibit slightly higher numbers of fertile eggs than of repagula.

V. Predation Experiments

Experimental exposure of the eggs and repagula of both ascalaphid species involved three situations: (1) natural predation by *Dorymyrmex pyramicus, Formica* sp. and *Pogonomyrmex* sp. at the site of the Southwestern Research Station (5400 feet); (2) natural predation by *Pheidole* sp., *Paratrechina* sp., *Crematogaster* sp., *Dorymyrmex pyramicus,* and *Formica* sp. at a typical egg-collecting site near Crystal Cave in the Chiricahua Mountains (5700 feet); and (3) artificially-induced predation by *Monomorium* sp. introduced to the Harvard Biological Laboratories (Cambridge, Massachusetts) from Brazil.

A. *Ululodes mexicana*

In all experimental situations, *Ululodes mexicana* eggs protected
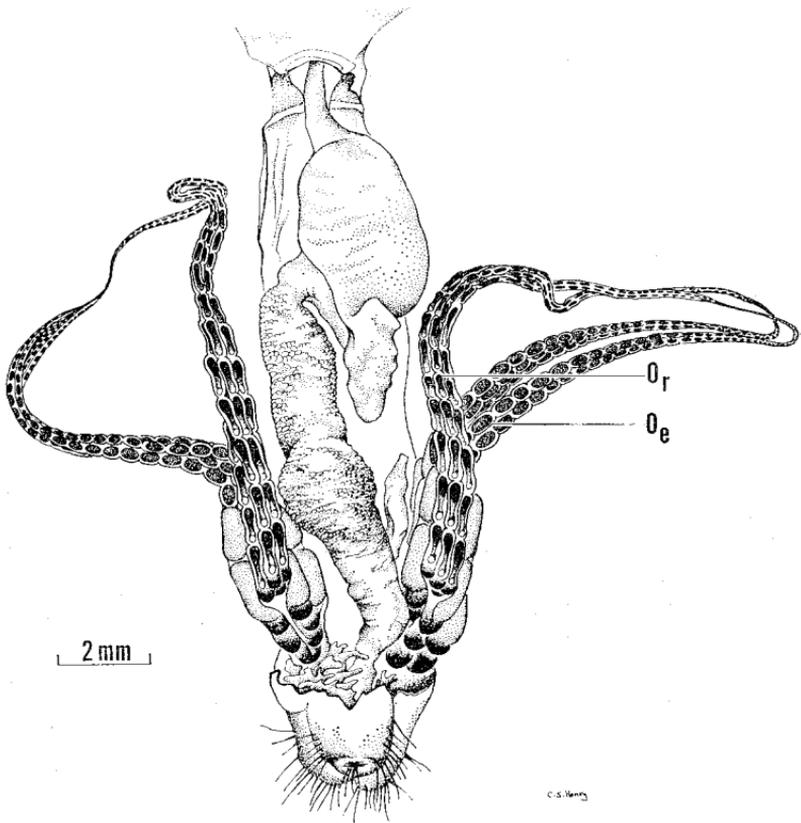
Figure 6. Ventral dissection of gravid female *Ululodes mexicana,* show-ing normal ovarioles (O_e) and those specially modified for the production of repagula (O_r).

by their repagula were unassailable by any species of ant, even large ($\geqslant$ 5mm) *Formica* sp. (see Table 1); on the other hand, unprotected eggs were quickly discovered and carried off by all ant species tested. Ants ascending the twigs and touching the repagula with their antennae would immediately and violently withdraw, occasionally falling to the ground. An intense period of antenna-cleaning, lasting from 15 to 60 seconds, always followed such con-tact. Experiments under laboratory conditions using the exotic Brazilian ant *Monomorium* sp. (2 mm long) indicated that con-tact with one repagulum alone was sufficient to discourage an ant from ascending the twig. Artificial "repagula" made from short

ANT SPECIES TESTED	R E S U L T	EXPERIMENT 1 SWRS grounds, Portal, Arizona						EXPERIMENT 2 Natural Egg-habitat, 1/2 mi. from SWRS						EXPERIMENT 3 Laboratory: Cambridge, MA.					
		Ululodes mexicana egg-mass:			Ascaloptynx furciger egg-mass:			U. mexicana egg-mass:			A. furciger egg-mass:			U. mexicana egg-mass:			A. furciger egg-mass:		
		a	b	contr.	a	b	contr.	a	b	contr.	a	b	contr.	a	b	contr.	a	b	contr.
Dorymyrmex pyramicus	succ.	0	0	15	7	9	4	0	0	4	22	18	9						
	fail	19	7	0	4	2	0	5	3	0	14	3	0						
Formica sp.	succ.	0	0	6	5	7	8				1	0	0						
	fail	3	2	0	0	1	0				0	0	0						
Pogonomyrmex sp.	succ.	0	0	0	15	11	7												
	fail	1	0	0	4	0	3												
Pheidole sp.	succ.							0	0	0	3	4	2						
	fail							2	1	0	1	4	0						
Paratrechina sp.	succ.							0	0	0	6	10	8						
	fail							7	5	0	7	4	0						
Crematogaster sp.	succ.							0	0	1	1	2	1						
	fail							3	0	0	1	0	0						
Monomorium sp.	succ.													0	0	35			
	fail													27	15	0			

Table 1. Tabulation of the susceptibility of *Ululodes mexicana* and *Ascaloptynx furciger* egg-masses to attack by various species of ants. Succ. = successful attack, defined by ant ascending 16 cm of twig to bottom-most true egg. Fail = unsuccessful attack: ant does not reach bottom-most egg. a and b = field-collected egg-masses, complete with protective repagula. contr. = control, field-collected egg-masses stripped of their repagula.

threads coated with mineral oil were partially effective as guards against *Monomorium,* but induced in the ant simple avoidance rather than active withdrawal; a single artificial "repagulum" proved totally inadequate for protecting an egg-clump.

Our field data is most complete and convincing for the ground- and low-bush-foraging species *Dorymyrmex pyramicus* (3 to 4 mm long). This is fortunate in the sense that *pyramicus* appears to be quite abundant in areas normally chosen by *Ululodes* for ovi- position; however, *Formica* sp., *Crematogaster* sp., and several other undetermined species of bush-foraging ants are also potentially important egg predators and should be more extensively tested.

The ant-fences of *Ululodes* are equally effective against ant predators after hatching has occurred and the larvae are sitting in a group on their eggshells; in fact, repagula remain full and fluid- covered even three weeks after eclosion, while the larvae apparently rest on the twigs for no more than ten days. Insect predators or other disturbances introduced artificially elicit no defensive reactions from the larvae during their gregarious phase. Instead, upset larvae simply drop to the ground, suspended at first on silken threads two to three centimeters long.

B. *Ascaloptynx furciger*

The repagula of *Ascaloptynx furciger* seemingly serve no dis- cernable protective function. No species of ant tested (see Table 1) displayed any pronounced or consistent negative reaction to the repagula. However, despite the accessibility of the main egg-mass to ant predators, no eggs were broken or carried off in the course of these experiments. Ants were observed to probe and bite the eggs, but even robust specimens of *Formica* sp. and *Pogonomyrmex* sp.* seemed unable to pierce the shells. Repagula, too, for the most part remained unharmed; in the one case where a *Formica* sp. crushed a repagulum in its jaws, the ant showed no further interest in eating the structure or retrieving it for the colony. Admittedly, our sample- sizes are quite small and incomplete so far as ant species are con- cerned, but the contrast between the reactions of ants to *Ululodes* eggs and repagula compared with their reactions to those of *Asca- loptynx* is striking.

The repagula of recently hatched *Ascaloptynx* egg-masses always appear to be shriveled or collapsed, almost as if the abortive eggs had been consumed by predators. Observations of the activities of

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Pogonomyrmex is not normally a twig-forager: the egg-mass was thrown directly on to the nest mound, at midday.
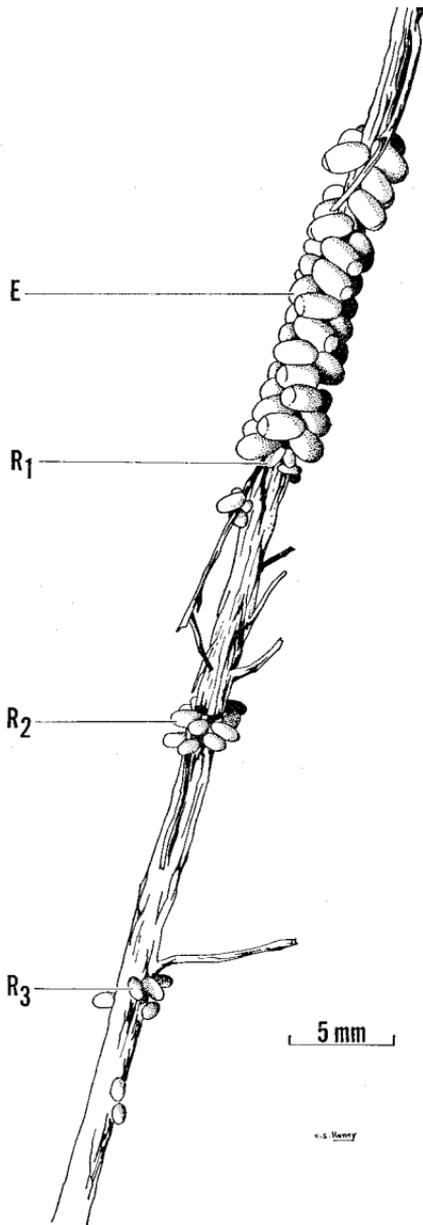
Figure 7. Egg-mass of *Ascaloptynx furciger*. Fertile eggs (E) and repagula (R_1, R_2, R_3) in natural position.

newly hatched larvae reveal that each *Ascaloptynx* larva, within three hours of eclosion, descends the twig to the level of one or another of the rings of repagula and feeds upon the contents of one or two abortive eggs. The repagula are punctured by the sickle-shaped sucking mouthparts. No attempt is made to pierce fertile, unhatched eggs. Perhaps 75 percent of the brood obtain a first meal in this fashion; then, all return back up the twig and settle head-downwards on and above the empty eggshells, overlapping like shingles in such a manner that only the heads and jaws of individual larvae are visible (figure 9). Unlike *Ululodes* larvae, *Ascaloptynx* larvae actively defend themselves against predators during the seven to ten days spent on the twig: small invaders like fruit-flies or midges will be captured and eaten by individual larvae, but larger predators or ants induce a mass response consisting of head-rearing and rapid snapping of the jaws (figure 9). This reaction has been seen to discourage wasps (15 mm) and caterpillars (25 mm) and presumably would be effective against a wide array of enemies; however, more intense and persistent disturbances cause the larvae to drop from their twigs to the ground. It should be noted here that the first-instar larvae of neither *Ascaloptynx* nor *Ululodes* can individually resist attacks by even small ants like *Monomorium* sp.; second- and third-instar larvae of both species seem to be less vulnerable.

VI. DISCUSSION

It is difficult meaningfully to compare the eggs and repagula of *Ululodes mexicana* and *Ascaloptynx furciger* with those of other types of owlflies, largely because our ignorance of the biology of other ascalaphids is so profound. Only the eggs of ascalaphine species have been described in any kind of detail. New (1971) observed the eggs and repagula of two species in the neuroptyngine genera *Byas* and *Episperches,* but his descriptions are by no means complete. Despite such difficulties, we will attempt some comparisons of our findings with those of other workers, and will emphasize wherever possible the phylogenetic implications of these comparisons, especially as they bear upon the relationship between the Ascalaphinae and Neuroptynginae.

A. THE EGG

In general form, color, and size the eggs of *Ululodes* and *Ascaloptynx* resemble those described for other ascalaphids: European *Ascalaphus macaronius* (Scopoli) (Brauer, 1854) and *Ascalaphus*
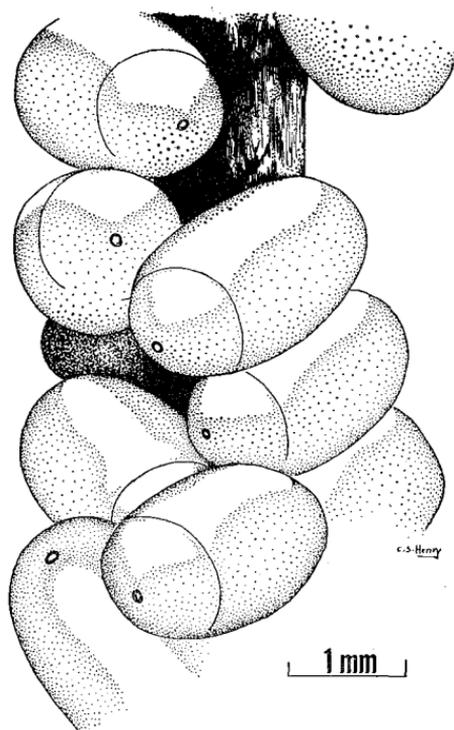
Figure 8.   Detail of eggs of *Ascaloptynx furciger,* three to four days old.

longicornis Linnaeus (Ragonot, 1878) ; Indian *Helicomitus insimu-lans* (Walker) (Westwood, 1888) and *H. dicax* (Walker) (Ghosh, 1913) ; Central and South American *Colobopterus* sp. (Withycombe, 1925) and *C. dissimilis* McLachlan (New, 1971) ; American *Ululodes* (various species, described by Guilding, 1827; McClendon, 1901; New, 1971) ; Madagascan *Balanopteryx umbraticus* Fraser (Fraser, 1957) ; and Brazilian *Byas* sp., *Episperches arenosus* (Walker), *Ascalorphne impavida* (Walker), and *Cordulecerus alopecinus* (Burmeister) (New, 1971). Those of *Ascaloptynx furciger* seem to be larger and more colorful than most, rivaling in size the eggs of the neuroptyngine genus *Byas* (New, 1971) and in color the yellowish eggs of *Ascalaphus* (Brauer, 1854; Ragonot, 1878; Navás, 1915). The structure and placement of the micropyles observed in both Arizona species are basically the same as in other species of Ascalaphidae and Myrmeleontidae (Withy-
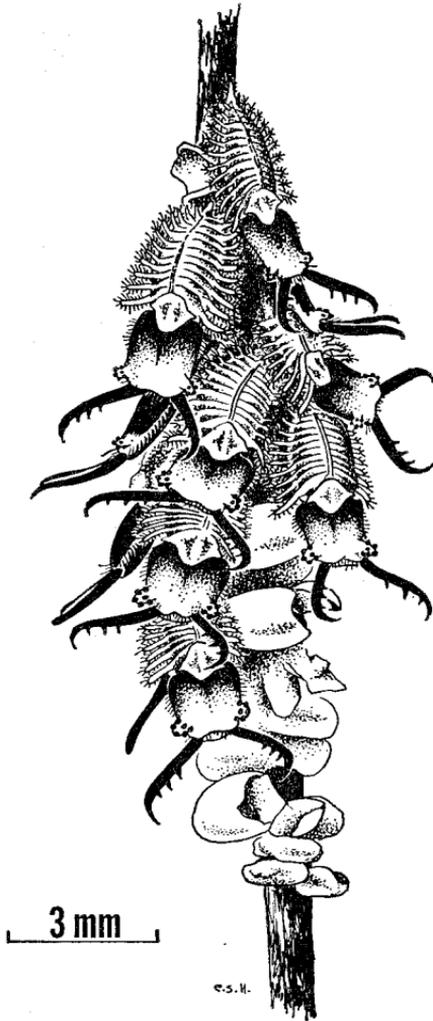
Figure 9.   Mass defensive reaction by newly hatched, gregarious larvae of *Ascaloptynx furciger*.

combe, 1925). *Ululodes* and *Ascaloptynx* also share with other owlflies and antlions the presence of a line of weakness girdling the cephalic pole of the egg; Brauer (1854) and Ragonot (1878) were familiar with this "egg cap" and with its function during eclosion in the genus *Ascalaphus,* but did not elaborate upon its formation or orientation.

Placement of eggs in linear rows on sprigs of grass or foliage is apparently widespread in the Ascalaphidae and even Nymphidae (Gallard, 1935). Surrounding the twig with eggs, as is done by *Ascaloptynx furciger,* has been reported only by Tillyard (1926) for various unidentified Australian ascalaphine species. Tillyard also reports masses of 50 to 100 or more eggs laid on one twig by one female; observations of other authors tally more closely with my own — thirty to fifty eggs for most species studied, except up to 60 in *Ascalorphne impavida* and 75 in *Ululodes macleayanus* (Guilding, 1827; New, 1971). Just as *Ascaloptynx* is exceptional in its oviposition of eggs around twigs, so *Ululodes* is exceptional in placement of its eggs on end; all other ascalaphids studied glue the mid-sections of their eggs to twigs, like *Ascaloptynx.* Obviously, without further information about many more ascalaphid species, one cannot decide from what we know of egg form and oviposition habits which conditions represent specializations. In fact, representatives of neither the Ascalaphinae nor the Neuroptynginae (as represented by *Ascaloptynx*) display any features of egg or oviposition that uniquely characterize one subfamily to the exclusion of the other.

B. THE REPAGULA

Repagula have been reliably reported only in New World ascalaphid species — in the ascalaphine genera *Ululodes, Colobopterus, Ascalorphne,* and *Cordulecerus* (all in the tribe Ululodini), and in the neuroptyngine genera *Byas, Episperches,* and now *Ascaloptynx* (New, 1971). Dissections of gravid females of several species of *Ascalaphus* — a European-Asian ascalaphine genus presumably closely related to *Ululodes* — seemingly confirm the absence of repagula: only egg-producing ovarioles are present in the ovaries (Brauer, 1854; Dufour, 1860). Unfortunately, dissections of other Old World Ascalaphidae have not been undertaken.

Previous studies of the repagula of several species of *Ululodes* (Guilding, 1827; McClendon, 1901; New, 1971) reveal little interspecific variation in the form and arrangement of the repagula

within the genus. Whether this homogeneity in repagula morphology extends to other genera within the Ululodini cannot be said: unfortunately, New (1971) does not clarify this point with regard to the genera *Ascalorphne, Colobopterus* and *Cordulecerus,* except to say that repagula of these last-named groups were observed to be "glossy castaneous" like those of *Ululodes.* We have shown that it is this very "glossy castaneous" appearance of the *Ululodes* repagulum that is most significant in terms of ant-repulsion; it seems likely that the shiny repagula of these other Ululodini are also fluid-covered and similarly serve to protect the eggs and brood from predators.

Interpretation of repagula function in the other subfamily, the Neuroptynginae, is ambiguous. New (1971) describes for *Episperches* spp. (Neuroptynginae) a type of repagulum which is quite similar to, though simpler than, that of *Ululodes* spp. in its rod-like form and glossy surface texture; *Byas* sp., on the other hand, displays an unspecialized egg-like repagulum very similar to that of *Ascaloptynx furciger.* Seemingly, the *Episperches*-type of repagula could serve as an antguard in the same manner as the *Ululodes*-type; however, our experiments suggest no such function for the abortive eggs of *Ascaloptynx* and, probably, *Byas* as well. Instead, the newly hatched gregarious larvae of *Ascaloptynx* — and perhaps of *Byas* — utilize the repagula as food. It is tempting to view the condition seen in *Episperches* as intermediate between relatively unspecialized or "primitive" neuroptyngines like *Byas* and *Ascaloptynx* and specialized ascalaphines like *Ululodes:* parental provision of food for the hatchlings in the form of abortive eggs can be interpreted as preadaptive to the construction of an ant-fence, in the sense that coating an abortive egg with insect-repellent fluid effectively converts that egg into a true "repagulum" or barrier. Once their protective function has been established, true repagula may lend additional, less obvious advantage to the species: (1) loss of the need for the heavy, ant resistant eggshell, (2) loss of the need for robust newly hatched larvae that are capable of group defense — correlated with reduction in the size of individual eggs, increase in clutch-size, or both, and (3) reduction in the size of energy-consuming repagula, since protection of larvae negates the need for providing them with food.

Conclusions concerning the relationship of the New World Ascalaphidae to those of the Old World, based upon egg and repagula morphology, cannot be justified. Repagula have not been

demonstrated in Old World owlflies, and active defense of the twig by the gregarious larvae of Old World species appears to be the norm, even among ascalaphine genera (Westwood, 1888, on *Helicomitus insimulans;* Froggatt, 1900, on *Acmonotus sabulosus;* Ghosh, 1913, on *Helicomitus dicax;* and Tillyard, 1926, on *Suhpalacsa* spp.). The need for detailed studies of the life histories of certain key groups within the various subfamilies and tribes is very great.

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