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SOUND PRODUCTION IN PUPAE OF LYCAENIDAE

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Most of the research being undertaken on sound production in insects involves only the adult stage. Perhaps this is due to the obvious nature of the noise in adults of certain groups, for example, cicadas, crickets, and even mosquitoes, as well as the ease with which certain behavioral activities (e.g., courtship) can be related to sound production. Significantly less information is available on sound production and reception in immature stages. For example, we were amazed to note during this study that the pupa of the common monarch butterfly, *Danaus plexippus* (Linn.), makes a very audible clicking sound at certain times. Since this species has probably been reared more often than any other Nearctic butterfly, and is often used in texts to illustrate life history stages, one would think that this aspect of its behavior would surely have been reported. However, it appears no one has previously noted sound in monarch pupae, let alone in less commonly reared species. Since the pupal stage is inactive in most butterflies, showing little or no external response to stimuli, the question of how and why noises are produced is perplexing.

It is the purpose of this paper: 1) to bring together the scattered information on sound in pupae of Lycaenidae; 2) to note the occurrence of the organs which produce sound in a great number of species and, equally important; 3) to record those species which lack stridulatory devices; 4) to describe and compare the sound producing structures within the family, correlating findings with previous taxonomic arrangement as determined by adult taxonomy; and 5) to present some inferences on the origin and function of pupal sound in Lycaenidae.

Frings and Frings (1960) provide a valuable bibliography on sound production and reception in insects. They list 24 orders, and over 280 families about which some information is available. Somewhat surprising is the fact that representatives of at least 40 families of Lepidoptera produce sound at one stage or more in their life cycles.

According to Prell (1913: 500), Kleeman in 1774 was the first naturalist to record that a lycaenid pupa could produce sound. Over 100 years passed before Schild (1877) also reported slight noises from pupae of the same species, *Callophrys rubi* (Linn.). DeNiceville (1900) noted that "creaking noises" are commonly produced by lycaenid pupae, but he only mentioned one species directly, *Rapala lankana* Moore. Most references to sound-producing pupae are scattered in the vast literature dealing with life histories of various species, and for the most part, they consist of brief statements that sound was heard. Since 1900 a chronological arrangement of authors noting sound would include: Bethune-Baker (1905), Prell (1913), Dodd (1916), Roepke (1918), Bell (1919a, b, c, 1920), Thorn (1924), Jackson (1937), Carter (1952), Clench (1961), and Downey and Strawn (1963).

Two workers have made very substantial contributions to the knowledge of pupal sound in the Lycaenidae. Prell (1913) described the noise in *Thecla quercus* (Linn.) and discussed the structures involved. His very accurate drawings of the stridulating devices in that species provide an excellent foundation on which to add our observations. Although Prell quoted earlier workers in stating that *C. rubi* produced sound, and added that he heard the noise in *Strymonidia spini* Schiff., no details concerning these species were given. Hinton (1948) summarized the general literature on pupal sound in the Lepidoptera, and presented four types of mechanisms involved: 1) body knocked against substrate or walls of pupal cell; 2) one or more pairs of abdominal segments rubbed together; 3) abdomen rubbed against proboscis; and 4) ridges or tubercles of pupa rubbed against walls of cocoon. Thirteen Lycaenidae, all previously reported, were included in Hinton's categories one and two above.

The sound produced by lycaenid pupae have been described variously as "chirping," "creaking," "ticking," "buzzing," "humming," or "clicking" noises. We first noted the sound in 1962 after placing in a single vial two dozen pupae of *Lycaena thoe* Guer. The container acted as a reflecting surface and the sounds produced were distinctly audible. Subsequently we were forced to use small vials held close to the ear, often in a closet or room where ambient noises were reduced, to detect the subtle noises produced by single individuals of other species. We were able to associate the sound with extremely rapid movements of abdominal segments, particularly posterior to segment five, and our attention was drawn to the distinct intersegmental region between abdominal segments five and six (see Plate I, Fig. 1). Slide preparations of sections from this region disclosed the mircoscopic stridulatory organs described below. Having thus associated sound with the structures involved, it was then possible to examine a cast pupal skin often retained with the adult in reared material, and make a judgment whether or not sound could be produced by the living pupa.

Table I is a list of all Lycaenidae which were found to have stridulating devices in the pupae or which have been reported as sound producers. For the sake of completeness, all references have been included in addition to columns indicating whether the sound was heard, or only the stridulating structures observed. The organs were noted for the first time in three species (*Strymon melinus*, *Strymonidia spini*, and *S. w-album*) which were previously reported as sound producers. As indicated in Table I, all records are new for the subfamily Riodininae and for the tribes Gerydini, Lycaenini, and Plebejini in the subfamily Lycaeninae. The addition of 57 species to the 25 previously reported represents a considerable increase in our knowledge of the occurrence of pupal stridulation in the family.

Sound producing structures were not found in all species examined. *Glaucopsyche lygdamus* Dbldy., *Philotes mohave* Wats. & W. P. Comst., and *P. rita* B. & McD., lacked the structure. Since these species belong to the same tribe (Glaucopsychini) it is strongly suspected that other related genera, i.e., *Phaedrotes*, *Iolana*, and *Maculinea*, may also lack sound-producing organs. However, the presence of the structures in 40 genera of rather diverse taxonomic subgroups suggests that the occurrence of sound production is widespread within the family.

Statements and drawings in published accounts of life cycles gave us evidence that other lycaenids have sound-producing structures although stridulation was not mentioned. Photographs of the pupae of *Gerydus boisduvali* Moore by Roepke (1918) and *Agriades escheri* Hbn. by Chapman (1916), and a drawing of *Liphyra brassolis* Westw. by Bethune-Baker (1924) all show either a prominent dorsal ridge on the fifth tergite or a marked depression between abdominal segments 5 and 6, or both. In addition, statements in other papers are highly suggestive of stridulatory movements. Zikan (1935: 411) noted that pupae of *Nymula brennus* Stichel were able to execute lateral movement between the fifth and sixth abdominal segments. Dickson (1952: 455) wrote that the abdomen of *Phasis zeuxo zeuxo* L. has a limited degree of flexibility. He stated that when a pupa was touched, the portion of the abdomen beyond the fourth segment was seen to move with a "rapid, almost trembling motion." Perhaps these workers noted only the movements, but did not check for sound and consequently missed slight noises involved. Even though highly suspected, the above species have not been considered as sound producers in Table I.

Six species belonging to the genera *Hypolycaena*, *Iolaus* (both subgenera *Argiolaus* and *Epamera*), and *Narathura* have pupae which will hammer rapidly against a leaf or twig substrate with their anterior end. Presumably the flexibility permitting this hammering is between abdominal segments. Jackson (1937: 214) indicates that when alarmed the pupa can make sufficient noise, by hammering, to frighten away a small predator. Dodd (1916) has reported that an Australian species of *Narathura* stridulates, while Bell (1919b), who was well acquainted with both types of noise making, noted only hammering in an Oriental *Narathura*. Perhaps both types of noise production are possible in a single species with extremely flexible abdominal segments, and it would not surprise me to find stridulatory organs in pupae of all six species reported as hammerers in Table I.

For convenience in the following discussion only the trivial scientific name of the lycaenids will be used. The generic name and author of each species is given in Table I. Two other usages should be noted. I have followed Mosher (1916) in saying that a particular abdominal segment is movable when motion is possible between its sclerotized caudal margin and the segment posterior to it. Snodgrass (1935, Fig. 39: 77) indicates that it is the posterior part of each segment which forms the infolded conjunctival membrane in typical secondary segmentation. The true intersegmental groove in primary segmentation does not usually coincide with the extant intersegmental membrane but is often posterior to it. Whatever the nature of origin, I will be assigning the entire intersegmental region to the segment anterior to it, regardless of any possible ontogenic contribution of the posterior segment. "Membrane 4" as used below refers then to the usually infolded intersegmental region between segments 4 and 5. It should also be pointed out that certain sclerites of the pupae are ill-defined and the use of the morphological term "tergite" is for convenience; the stigmatal lines (an imaginary line between adjacent abdominal spiracles) are directly lateral of the "tergite" as that term is herein used.

SOUND-PRODUCING STRUCTURES

The external structures involved in sound production are located on membrane 4 and 5 of the pupal abdomen. They may completely encircle the pupa, but are generally limited to the dorsal region, usually the tergite. All specimens possessing stridulatory structures had them on membrane 5, and members of the subfamily Riodininae had, in addition, a distinct and equally functional apparatus on membrane 4.

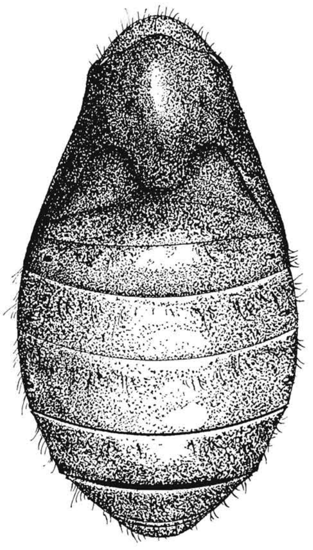

FIG. 1

FIG. 2

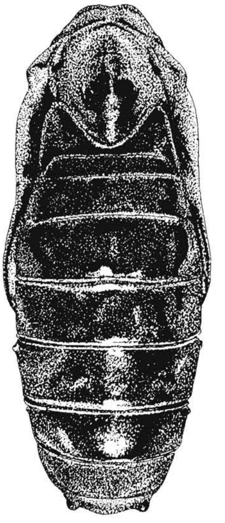

FIG. 3

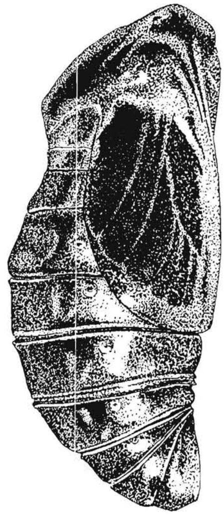

FIG. 4

EXPLANATION OF PLATE 1

Pupae of Lycaenidae with prominent stridulating regions. Figs. 1, 2. Dorsal and lateral view of the Nearctic *Callophrys* (*Incisalia*) *henrici* Grote & Robinson, a rather rigid pupa. The microscopic stridulating organs are limited to the dorsal intersegmental cleft between abdominal segments 5 and 6. Figs. 3, 4. Dorsal and lateral view of the Australian *Ialmenus evagoras evagoras* (Don.), which has greater flexibility of abdominal segments. The organs are found only between segments 5 and 6, but they extend completely around the segment.

TABLE 1. LYCAENIDAE WITH SOUND-PRODUCING PUPAE

Species	Realm	Type	Sound Heard	Organs Noted	Reference
Riodininae					
Ancylurini					
Anatoli rossi Clench	Neo.	Str.		X	new
Apodemia mormo virgulti (Behr)	Nea.	Str.		X	new
A. m. deserti (B. & Mcd)	Nea.	Str.	X	X	new
Lephelisca wrighti (Holl.)	Nea.	Str.		X	new
Lycaeninae					
Miletini					
Allotinus horsfieldi Moore	Or.	Str.	X		Roepke, 1918
Gerydini					
Feniseca tarquinius (Fabr.)	Nea.	Str.		X	new
Lycaenini					
Lycaena (L.) *helloides* (Bdv.)	Nea.	Str.		X	new
L. phlaeas (Linn.)	Nea.	Str.	X	X	new
L. thoe Guer.	Nea.	Str.	X	X	new
L. virgaureae (Linn.)	Pal.	Str.		X	new
L. (*Tharsalea*) *arota* (Bdv.)	Nea.	Str.		X	new
Plebejini					
Brephidium exilis (Bdv.)	Nea.	Str.		X	new
Everes argiades Pall	Pal.	Str.		X	new
E. comyntas (Godt.)	Nea.	Str.	X	X	new
Leptotes marina (Reakirt)	Nea.	Str.		X	new
Lysandra coridon Poda	Pal.	Str.		X	new
L. thersites Cant.	Pal.	Str.		X	new
Plebejus (Icaricia) *acmon* (West & Hew.)	Nea.	Str.	X	X	new
P. (I) *icarioides* Bdv.	Nea.	Str.	X	X	new
P. (Lycaeides) *argyrognomon* Brgster.	Pal.	Str.		X	new
P. (L.) *melissa* Edw.	Nea.	Str.		X	new
P. (*Plebejus*) *argus* (Linn.)	Pal.	Str.		X	new
P. (*P.*) *saepiolus* Bdv.	Nea.	Str.	X	X	new
P. (*Agriades*)*glandon* (Prunner)	Nea.	Str.		X	new
Zizeeria labradus Godt.	Aus.	Str.		X	new
Lampidini					
Ialmenus evagoras Don.	Aus.	Str.		X	new
I. ictinus Hew.	Aus.	Str.		X	new
Jamides celeno Cram.	Or.	Str.	X		Bell, 1919a
Ogyrini					
Ogyris geneoveva gela Waterh.	Aus.	Str.		X	new
O. hewitsoni Waterh.	Aus.	Str.	X		Beth.-Bak., 1905
O. hymetus taygetus Feld.	Aus.	Str.		X	new
O. olane Hew.	Aus.	Str.	X		Thorn, 1924
O. orates Hew.	Aus.	Str.	X		Beth.-Bak., 1905
O. zosine Hew.	Aus.	Str.	X		Beth.-Bak., 1905
Theclini					
Atlides halesus (Cram.)	Nea.	Str.	X	X	new
Callophrys (*Callophrys*) *rubi* (L.)	Pal.	Str.	X		Kleeman, 1774
C. (*C.*) *sheridani* (Carpenter)	Nea.	Str.		X	new
C. (*C.*) *viridis* (Edw.)	Nea.	Str.		X	new
C. (*Incisalia*) *fotis* (Strecker)	Nea.	Str.		X	new

TABLE 1. Continued.

Species	Realm	Type	Sound Heard	Organs Noted	Reference
C. (*I.*) *henrici* (Grote & Rob.)	Nea.	Str.	X	X	new
C. (*Mitoura*) *gryneus* (Hbn.)	Nea.	Str.	X	X	new
C. (*M.*) *hesseli* Raw. & Zieg.	Nea.	Str.		X	new
C. (*M.*) *johnsoni* (Skin.)	Nea.	Str.	X	X	new
C. (*M.*) *loki* (Skin.)	Nea.	Str.		X	new
C. (*M.*) *nelsoni* (Bdv.)	Nea.	Str.		X	new
C. (*M.*) *spinetorum* (Hew.)	Nea.	Str.	X	X	new
C. (*Sandia*) *macfarlandi* Ehr. & Cl.	Nea.	Str.		X	new
Calycopis beon Cram.	Neo.	Str.	X	X	new
Chrysophanus titus (Fabr.)	Nea.	Str.	X		Clench, 1961
Dolymorpha jada (Hew.)	Nea.	Str.		X	new
Eumaeus debora Hbn.	Nea.	Str.		X	new
E. minyas Hbn.	Nea.	Str.		X	new
Habrodais grunus (Bdv.)	Nea.	Str.		X	new
Hypaurotis crysalus (Edw.)	Nea.	Str.	X		Clench, 1961
Hypolycaena philippus Fabr.	Eth.	Ham.	X		Clark & Dickson, unpubl.
Iolaus (*Argiolaus*) *silas* Westw.	Eth.	Ham.	X		Jackson, 1937
I. (*Epamera*) *alienus* Trim.	Eth.	Ham.	X		Clark & Dickson, unpubl.
I. (*E.*) *mimosae* Trim.	Eth.	Ham.	X		Clark & Dickson, unpubl.
I. (*E.*) *sidus* (Trim.)	Eth.	Ham.	X		Jackson, 1937
Narathura araxes eupolis Miskin	Aus.	Str.	X		Dodd, 1916
N. centaurus F.	Or.	Ham.	X		Bell, 1919b
Eupsyche m–album (Bdv. & LeC.)	Nea.	Str.	X	X	Clench, 1962
Pratapa blanka argentea Aur.	Or.	Str.	X		Bell, 1919b
P. deva Moore	Or.	Str.	X		Bell, 1919b
Rapala lankana Moore	Or.	Str.	X		deNice, 1900
R. Manea schistacea Moore	Or.	Str.	X		Bell, 1920
R. varuna Horsf.	Or.	Str.	X		Bell, 1920
Rathinda amor (Fabr.)	Or.	Str.	X		Bell, 1919c
Satyrium acadica (Edw.)	Nea.	Str.		X	new
S. adenostomatis (H. Edw.)	Nea.	Str.		X	new
S. auretorum (Bdv.)	Nea.	Str.		X	new
S. behrii (Edw.)	Nea.	Str.		X	new
S. saepium (Bdv.)	Nea.	Str.		X	new
S. sylvinus (Bdv.)	Nea.	Str.		X	new
Strymon melinus Hbn.	Nea.	Str.	X	X	Clench, 1961 new
Strymonidia acaciae (Fabr.)	Pal.	Str.		X	new
S. pruni Linn.	Pal.	Str.		X	new
S. spini Schiff.	Pal.	Str.	X	X	Prell, 1913 new
S. w–album Knoch	Pal.	Str.	X	X	Carter, 1952 new
Thecla quercus (Linn.)	Pal.	Str.	X	X	Prell, 1913
Tmolus echion (Linn.)	Neo.	Str.		X	new
Curetini					
Curetis thetis Drury	Or.	Str.	X		Bell, 1919a

Lysandra thersites also had the stridulatory devices on membrane 4, although they appeared slightly smaller than the same structure on 5. Such species as *coridon, debora,* and *minyas* had roughened surfaces on membrance 4, rather different than the apparent noise-producing structures on membrance 5, so that their functional nature remains in doubt. It is to be expected that other species, particularly those with flexible abdomens, will be found to have at least two intersegmental regions equipped with stridulating mechanisms.

The sound-producing region may be divided into an anterior stridulating plate (Schrillplatte of Prell, 1913), a median region consisting of a rather transparent membrane, and a posterior file (Reibplatte of Prell, 1913). The relative position of these components can be seen on Plate II, Fig. 1, where the external parts of segments 5 and 6 have been separated to show the intersegmental region. In the normal infolded position, the stridulating plate or grating surface is directly opposed to the file with its numerous teeth. Sound is produced by the frictional mechanism of drawing the projecting teeth across the irregular surface of the plate. This "file" and "scraper" method of noise production is very common in insects and no doubt every external part of an insect body which is normally subject to friction on an adjoining surface may cause some sound.

It is assumed that the integument vibrates as each tooth in a file receives the impact of friction against the irregular surface of the scraper. The speed with which the surfaces contact as well as the resonance of the vibrating integument appear to effect the pitch of the sounds emitted. Rather complex modulated sounds result from these frictional devices in other insects, and we have some evidence, presented below, which indicates the complexity of the sound in the lycaenids.

The following observations call attention to similarities and differences in the stridulating devices of various species. These remarks are arranged by the major subdivisions of the sound-producing organ.

Stridulating Plate.

The stridulating plate is always just posterior to the sclerotized abdominal segment. Whereas the latter may have setae, microtrichia, and lenticels and otherwise be variously sculptured, the plate is usually rather uniform in structure. In fact, the regularity of the roughened surface of the stridulating plate may impart its distinctive nature and add to the impression that it is a band or "plate."

In many species the plate is heavily sclerotized. This hardening is usually indicated by the amount of pigment deposited in the integument. The rigid, exposed, anterior part of each abdominal segment serves as

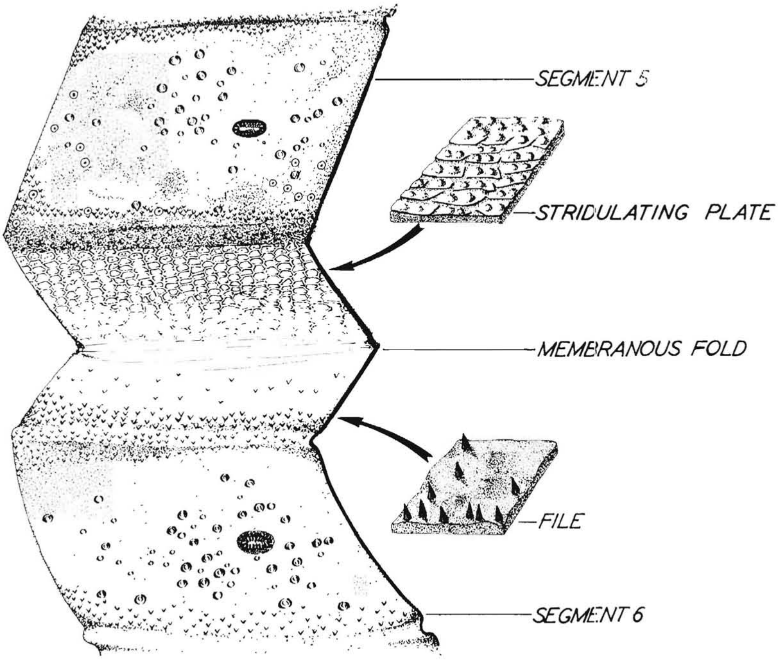

FIG. 1

FIG. 2

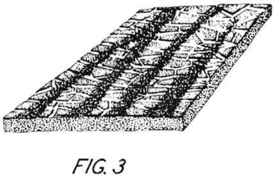

FIG. 3

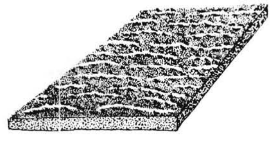

FIG. 4

EXPLANATION OF PLATE 2

Partially diagrammatic drawings of the pupal integument showing stridulating organs. Fig. 1. Dorsal view of membrane 5 (see text) in the region of the spiracles in *Apodemia mormo virgulti* (Behr). Segments 5 and 6 have been separated so that the infolded stridulating plate and file are no longer in juxtaposition. Inserts represent enlargements of plate, showing tubercles on the grainy reticular surface, and the file with teeth and small protuberances. Figs. 2–4. Highly schematic enlargement of the stridulating plate; Fig. 2, *Strymonida spini* Schiff. with longitudinal ridges; fig. 3, *Atlides halesus* (Cram.) with reticular surface and sclerotized longitudinal bands; fig. 4, *Lysandra coridon* Poda with an irregular, aciculate surface.

a handy reference point for determining degrees of sclerotization in the stridulating plate. Ordinarily, the plate is not as heavily sclerotized as the segment. This is the case in most species of Plebejini, including *exilis* and *labradus*. On the other hand, the plate is often darker than the anterior part of the segment in species of Theclini, as well as *debora* and *coridon*. Or, the two areas may have about the same degree of sclerotization, as is the case in *halesus* and *jada*. Only the protuberances on the plate contain an appreciable amount of color in some species, so that the tubercles in *thoe* are the easiest means of delineating the plate. The anterior and posterior limits of the grating surfaces, which are not sclerotized, are usually indefinite.

As indicated above, the plate may extend completely around the segment in certain species, i.e., *evagorus, mormo, rossi*, and *wrighti*. In most species, however, the stridulating plate terminates laterally, at, or just beyond the stigmatal line. It may also end a substantial distance beyond this line (*acadica, beon, argus*, and *tarquinius*) or stop short of the spiracles (*adenostomatis, debora, genoveva, labradus*, and *marinus*). It was noticed that there was some intraspecific variation in the termination of the plate. One specimen of *henrici* had the dorsal grating surface end short of the stigmatal line, while the termination in at least six other specimens had a more typical terminus beyond the spiracles. This suggests a need for some caution in the taxonomic use of this character.

The anterior–posterior length of the stridulating plate, measured at the midline of the dorsal surface, was usually less than 0.15 millimeters. As might be expected, large pupae tended to have large plates, particularly in the Theclini. Correspondingly, one of the smallest pupae examined was *comyntas* whose plate measured 0.04 mm. An exception to this generalization was *Eumaeus*. Both *E. debora* and *E. minyas* have very large pupae, although the stridulating plates in both species were of only average length. The plate seemed to be the longest at the middorsal line, which at least in preserved material, was also the region of greatest possible movement. In species such as in the Riodininae where the plate completely encircled the pupa, there is less variation in length.

The type of grating surface on the stridulating plate is ordinarily distinctive and rather variable from species to species. Three basic types commonly observed are designated as 1) tubercles, 2) reticulations, and 3) ridges. A few surfaces did not fit any of these categories. These types are discussed below.

Tubercles are protuberances whose apices are not sufficiently sharp that they could be confused with teeth, nor sufficiently flat that they could be mistaken for flat-topped plates. Generally tubercles are pimple-like structures varying in size from tiny ill-defined roughenings on an otherwise flat membrane, to rather large well-formed knobs. These roughenings are present in most species and often occur on other types of surfaces. It is almost impossible to assess the possible contribution tubercles might play in sound production when they occur in areas other than the stridulating plate. They can be noted on surfaces that normally do not contact other parts, as well as on intersegmental membranes other than those involved in sound production. The tubercles on the plate, however, are either sufficiently numerous, or large and clustered, in opposition to the file, that their part in stridulation appears more obvious.

Tubercles can best be observed where their structure is not obscured by pigments, ridges, or other sculpturing. Most Lycaenini have well-defined tubercles situated on a nonsclerotized reticulated surface (see below) which has a transverse orientation. This arrangement makes the tubercles also appear to be in obscure transverse rows. Both *phleas* and *thoe* exhibit this condition.

The tubercles may vary in density, size, or shape on a single specimen. Plate II, Fig. 1, illustrates the large knobby structure of the tubercles toward the anterior part of the plate in *mormo*. The opposite situation occurs in *beon* where small tubercles are located anteriorly, and large protuberances are posterior on the plate. Strawn (1964) measured the smaller tubercles in four different areas (anterior and posterior part of the plate in a mesal and lateral position) on nine species. Her figures indicate that while the average diameter of the base of the tubercles is greater toward the anterior area of the plate and toward the mesal area in the specimens examined, the size range of the tubercles (2–7 microns) was approximately the same for all areas from all species. Strawn also found interspecific variation in the number of tubercles per unit area. While this may be a real difference, attention has already been called to the variability in the clustering and number of tubercles in different areas on one plate, consequently extreme care must be taken to insure unbiased samples.

Cast pupal skins of 11 male and 14 female *thoe* were compared by Strawn (1964). She could not detect any differences between the sexes of *thoe* in regards to stridulating devices, particularly the average size of the tubercles.

Reticular surfaces on the stridulating plate consist of a series of prominences which, while actually subequal and irregular in size, are relatively uniformly arranged so that their longitudinal axes are roughly parallel. Thus the description applies not so much to a single protrusion as to a series of peaks and valleys whose surface texture can be compared to grainy leather. This appearance is in large measure due to the net-like, interconnecting depressions between the prominences. In fact in some species, like *evagorus*, which lack tubercles on the prominences, it appears that the reticuliform valleys provide the functional grating surface. The reticular depressions may also impart a degree of flexibility on the surface, with the flection at right angles to the longitudinal axis of the grain. In most species with a pronounced reticular surface, the grain is transverse to the longitudinal axis of the pupa. Such a surface would appear to be more efficient as a grating device if the opposing file were drawn across the grain in the same direction as the body of the pupa.

The entire integument appears reticulate in *rossi*, yet in the region of the stridulating plate the prominences undergo anterior–posterior compression so that they are transversely elongate. Each elevation or "grain" in the plate has tubercles so that its surface is rougher and consequently much more distinct. Tuberculate grains are illustrated in *mormo* on Plate II, Fig. 1.

The nature of the plate surface in some species reinforces certain taxonomic conclusions made on adult specimens. The reticulate–tuberculate plate in *grunus* would seem to justify its placement in the separate subtribe (Thecliti) distinct from other Theclini (subtribe Strymoniti) as Clench has recently done (*in* Ehrlich and Ehrlich, 1961). The Strymoniti lack reticulations, and have distinctive longitudinal ridges.

Ridges on the stridulating plate are distinctive in having a rather pronounced crest with two or more sloping surfaces. Some ridges with numerous branching and anastomosing surfaces, as in *acaciae*, may be confused with those which are reticular. Usually, however, the valleys between ridges are very different in size and do not exhibit the general consistency of pattern that can be observed in the reticuliform types. Also, plates with ridges never appear to be flexible as do more granular surfaces. The ridges may have had their evolutionary origin in a reticular surface having been compressed in such a way that the integument folded vertically, with a subsequent obliteration of any reticular depressions along the axis of the fold. Regardless of origin, in most species with a pronounced series of ridges, the crests tend to run in the same direction as the longitudinal axis of the pupa. Thus oriented, they would appear to be more efficient as a grating surface if the teeth were drawn across them in a transverse direction, at right angles to the main axis of the crests.

As can be noted in the drawing of *spini*, Plate II, Fig. 2, the ridges form the only functional grating surface. They do not have tubercles or uneven areas other than those of the sides and crests of the ridges themselves. Other Strymoniti may have a few small roughened areas, but the strongly sclerotized longitudinal ridges of the plate characterize this group.

The stridulating plates of some species contain folds, which are not artifacts of slide preparation, whose relationship to the more prominent ridges with which they are grouped is not clear. In *beon,* for example, there are very regularly spaced tubercles which no doubt form the main frictional devices on the plate, but there are also very slight longitudinal folds. It would seem that such wrinkling of the surface, even though very slight, would tend to keep the teeth on the file away from tubercles in the valleys between the folds. Since the juxtaposition of plate and file in the living pupa is not known, speculation on the functional relationship between these folds and the tubercles is unwarranted.

As shown in Plate II, Fig. 3, *halesus* also has longitudinal sclerotized areas superimposed on a reticular surface which seems to be the functional area. The pupae of both *Eumaeus* examined, *minyas* and *debora*, are similarly unique because the ridges on the plate occur only on the lateral parts of the intersegmental region. Elsewhere, the surface may be sclerotized, but no tubercles, reticulations, or ridges can be observed and a distinct stridulating plate is lacking.

The stridulating surface of some species could not be grouped as consisting of tubercles, reticulations, or ridges. Plate II, Fig. 4, shows such a condition in *coridon.* The plate itself in *coridon* is heavily sclerotized, narrow and band-like in gross view. Its surface appears as if it were scratched and gouged with needles (aciculate), the resultant furrows have a transverse orientation. The prominences between the scratches cannot be properly designated as ridges or tubercles. The irregularity of the surface, however, makes it an excellent grater.

Membranous Region.

Between the stridulating plate and the file is a nonpigmented subdivision of the intersegmental membrane. This area is devoid of common structural features and for this reason appears transparent and much the same in all species. In its normal position the membranous region is folded so that the plate and file are in contact. In slide preparations it is extremely difficult to stretch the membrane flat; consequently, many fine transverse folds occur, which may give the impression that the surface is striated. It is to the lateral areas of the membranous region that longitudinal muscles and attachments are fixed in some species (see below). The remnants of such attachments are found in many cast pupal skins. The place of attachment of the muscles prompted Prell (1913) to designate a "Prasegmentalleiste" in *quercus*, which he illustrated (1913: 498) as a series of transverse lines in the center of the membrane. I concur that the attachment of the muscles to this area indicates it is the region of primary intersegmental folding but feel that Prell's drawings make the area much more obvious than it is. No doubt the membrane and stridulating plate anterior to this primary fold belong to the anterior tergite, while the membrane and file posterior to the muscle attachment are derived from the adjacent posterior tergite. The only unusual feature is that the muscles appear not to be attached to heavily sclerotized plates but to a seemingly flexible conjunctiva.

The membranous area of cast pupal skins may contain artifacts such as adult scales and detritus, "accidentally" caught in the numerous folds.

File.

The posterior subdivision of the stridulating region is designated as the file. In most species it is not distinct except for conspicuous sharply pointed protuberances, or "teeth." The latter may have originally developed from smaller tubercles; a suggestive sequence of sclerotized tubercles grading into more elongate teeth is still retained in the Australian *hymetus*. Small tubercles also occur on files in other species such as *henrici*, but they probably do not play a part in sound production. Interspecific variation in characteristics of the teeth is often marked. The following conditions of the teeth were noticed with species or groups having the condition placed in parentheses: Sclerotized (*hymetus*), nonsclerotized (most species); small, indistinct (*comyntas*), large, well-defined (most Theclini); tendency for pairing (*hymetus*); irregular distribution (*mormo*, see Plate II, Fig. 1); tendency for clustering (*comyntas*), arranged in regular rows (*gryneus, acadica*); transverse rows of 4 to 5 (*exilis*); oblique rows (*fotis, sheridani, sylvanus*); and serpentine rows laterally (*johnsoni*).

Teeth are very common on other parts of the integument, particularly on the anterior margin of each segment. Most often these teeth do not appear in a position where they would contact another surface. However, they do occur on posterior parts of the intersegmental membranes, in a position corresponding to the file on the sound-producing membrane. Although they are not opposed by obvious surfaces like the stridulating plate, it is possible that the teeth in other movable intersegmental areas also contribute some sound when they are rubbed against the integument.

The anterior–posterior length of the file is very difficult to measure because of the irregular placement of teeth and tubercles. In general it can be said that the length of the file is smaller than the length of its corresponding plate. The file, however, always extends further laterally than the plate, except in those species where both structures encircle the pupa.

A few species have files which were considered less typical than others. For example, while the teeth of *adenostomatis* did not differ from those of other Theclini, the region of the file was very obvious as a sclerotized band. The file of *tarquinius* lacks teeth and consists only of irregular nonsclerotized tubercles. Although equipped with small teeth and sclerotized tubercles, the file of *labradus* has a slightly granular surface.

Movements Associated with Sound.

As mentioned earlier, the file and stridulating plate are brought into contact by rapid dorsoventral movements of the abdomen. Since the stridulating plate *in situ* is not perpendicular to the body axis but projects caudoventrally from the tergite, the direction of the stridulating movements might be more accurately described as a cephalodorsal drawing of the file across the stridulating plate. Since the file and plate also arch with the segments from one lateral surface to the other over the rounded dorsum, the angle of movement of the teeth across the grating surface is slightly different from area to area.

Movement is made possible through contraction of longitudinal muscles in the dorsal abdominal region which, according to Prell (1913), attach to the "Prasegmentalleiste" on the intersegmental membrane in *quercus*. Contraction causes the file to slip forward over the plate. Strawn (1964) found a pair of longitudinal muscle bands attached to the intersegmental region in *thoe*, *debora,* and *henrici,* although the insertion in these species was lateral in position. I have been able to trace the muscle bands thought to be involved in *sheridani* pupae, from an origin on the anterior margin of tergite 3 to their insertion on the posterior intersegmental membrane between tergites 5 and 6. The latter insertion appeared to be as much on the anterior margin of segment 6 as on the membrane itself, which would agree with the muscle attachment concept in primary segmentation (see Snodgrass, 1935). Each of the two muscle bands was about one millimeter wide and located on the lateral surface midway between the spiracular line and the midline. These muscles were found, in segments of the adult (see below), and a short ligament connected the adult integument with the pupal fifth intersegmental membrane. Strawn (1964) found these ligaments, which she called stridulating attachments, in sectioned pupae, but they are also visible with ordinary dissecting procedures. We were not able to locate scars or rudiments of the ligament on adults, even freshly emerged specimens.

We did not locate any muscles which seem to work antagonistically to the longitudinal pair, and therefore assume that the elastic nature of the pupal integument, or fluid pressure in the adult body, may return the file to a "resting" position where it is not in contact with the plate.

There is some question as to which stage of the life cycle is involved in these movements. Snodgrass (1935: 64) points out that whereas the length of a developmental stage may be measured from the time exuviae are shed, as is done in "life history" studies, physiologically it should be calculated from the time the old cuticula is loosened from the epidermis. Hinton (1946) likewise points out that the precise discrimination of instars is of considerable importance, particularly when dealing with the imaginal stage. Hinton proposes the name "pharate" (= cloak) to designate the phase of an instar which is enclosed within the cuticle of the previous instar and considers that, for instance, most records of "hibernating" pupae are pharate adults. It has been regarded as axiomatic, particularly by many students of Lepidoptera, that adult life commences with its emergence from the pupal case. In spite of certain objections (see Tutt, 1900), there is some justification for the belief that many individuals ordinarily called pupae are in reality pharate adults, and that adult life in butterflies may have two stages, a pharate stage and a stage capable of flight. In certain cases the onset of the pharate adult stage may coincide with the elaboration of a pupal case; it may also occur at a much later time, perhaps after an extended diapause.

Thus considered, the stridulating response in Lycaenidae, and the movements responsible, may be limited to pharate adult behavior. The real pupal stage would then have to be considered as occurring during that brief quiescent period ordinarily thought of as a "pre-pupal" interval. The real pupa may be capable of some limited movements owing to the fact that some abdominal muscles are carried over from the larvae. Most "pupal" movements, however, seem to be those of the pharate adult. It perhaps matters little whether we call this stage a physiological adult or a pupa as long as it is understood that the muscles and the instigating sensory apparatus are still present in the emerged adult while the stridulatory devices seem to be limited to the pupal integument. It may also be of significance in the function of sound that it is limited to this particular stage, regardless of name. To prevent confusion in subsequent discussion, the term pupa will still be used in the broad sense in referring to the stage which is surrounded by a pupal skin containing the stridulating organ.

Sounds Produced.

The sound of 12 Nearctic and 1 Neotropical species detected during this study could all be described as slight, rapidly repeated, creaking noises. A squeaking door analogy might be used for comparison, provided we lessen the amplitude of the noise and move the door with a series of short pulls rather than a steady motion. As indicated above, we often had difficulty hearing the noise unless the pupae were contained in a sound reflecting device such as a vial. On the other hand, in some species, such as *thoe,* the sounds were sufficiently loud so that at least two types of noises could be detected; a distinct chirp and a slight humming noise. It is thought that noises of the former type are produced by the stridulating devices, while the latter type may be caused by other as yet undetected movements of the integument.

With some difficulty, we were able to tape-record the sounds of Illinois *thoe* and *henrici.* Strawn (1964) was able to feed these tape outputs into an oscilloscope and obtain a graphic representation of the sounds produced. There were differences in both the intensity and frequency of the noises of the two species, which helps verify the slight differences between species noted by the unaided human ear. At least one other author noted interspecific differences in the sounds: Dodd (in Bethune-Baker, 1905) reported that although *Ogyris oraetes* Hew. and *O. hewitsoni* Waterh. produced the same "tick" as *O. zosine* Hew., the ticks were not as frequent or as loud.

Sound was detected at various times throughout the pupal period in several species, including *phleas, thoe, gryneus, henrici, melinus,* and *comyntas.* In *thoe* the earliest sound detected was within minutes after the last larval skin was shed. An individual of the same species was also heard to stridulate up to the time of eclosion of the adult. In almost all cases the sound was elicited by external agitation, usually by shaking or finger-thumping a vial containing the pupa. Only occasionally were we able to detect spontaneous stridulation. The infrequency of this observation was due in part to technical difficulties in the elimination of other possible stimuli as well as in detecting the noise proper.

Many times pupae would not respond to agitation of any sort. No doubt excessive application of unnatural stimuli failed to trigger the responses in certain individuals and particularly at certain times. For example, individuals of *henrici,* which overwinter as pupae, would tend to have normal stridulating responses both early and late in the pupal period. They stridulated only infrequently and unpredictably during the middle five months of their diapause. After accumulating some experience with each species, we were able to use sound as an index of pupal viability. Since individuals reacted differently to the same stimulation, and since this reaction also varied with the time of the pupal period, additional studies are warranted.

Origin of Organs.

It is thought that the origin of structures used in stridulation in the pupa is intimately associated with abdominal movements. This opinion rests primarily on the frequent existence and morphological similarity of a grainy reticular surface in Lepidoptera with highly flexible abdomens. The need for abdominal movement is apparent in certain moth groups; some species can only emerge from cocoons, or from rigid pupal cases, by vermian climbing or pushing from the container. Frequently nearly the entire pupa pushes through the cocoon prior to adult eclosion. Since these groups exhibit a number of other features considered to be primitive, abdominal flexion may be ancestral in the order (for a discussion see Tutt, 1900, and Mosher, 1916). Obtect butterfly pupae have become relatively more rigid and have lost all motion of abdominal segments except in membranes 4, 5, and 6. The Lycaenidae are considered to have very advanced forms of obtect pupae supposedly because of even greater loss of motion. However, not all motion is lost in these seemingly rigid pupae, and retention of some flexibility, at least in the dorsal part of membrane 5, is a reflection of functional need. That need in this family may also be, as in the primitive moths, for physical adjustments necessary for adult eclosion. This may still be the main physiological explanation for the retention, irrespective of the fact that the movement is small and that any sound produced may have proved advantageous to the species.

Butterflies and moths with obtect pupae almost invariably have some sort of partially sclerotized flexible surface on any movable abdominal segment. This surface is usually located between the more rigid sclerite and the infolded membranous cuticle. These areas have surfaces which are plastic enough to flex but still retain almost the same degree of sclerotization as the rigid part of the segment and hence have the same degree of protection which their external exposure might require. This surface is beautifully illustrated in the grainy reticular posterior margins of abdominal segments 4, 5, and 6, and to a lesser extent 7, in the moth *Callosamia promethea* Drury. Pupae of the butterfly *Junonia evarete* (Cram.) also have granular flexible areas between a few of the abdominal segments. In such species as *Citheronia regalis* Fabr., the flexible part of the segment has fine transverse striae, rather than a granular network. The anterior margin of individual segments in many species likewise becomes variously ridged, grooved, tuberculate, or dentate and may become rather flexible, though this is not as marked as in the posterior margin. Both margins usually appear slightly less sclerotized than the middle of the segment. It would seem that when abdominal movement is extensive in a pupa, some sort of flexible strip of granular texture occurs between the rigid annulations and the flexible conjunctivae on each movable segment.

It can thus be theorized that as pupae of the ancestral proto-lycaenid became more rigid, need for any flexible granular margins on abdominal segments was also reduced, and these structures gradually disappeared. Probably they were first lost between those segments which became completely fused (7 and 8, then 4 and 5). In partially fused segments, a protective advantage would be retained longer, thus the flexible granular surfaces would persist near their juncture with the rigid part of the segment. Intersegmental movement appears to be lost first ventrally, so that between partially fused segments, the flexible surface might have been retained only in the dorsal regions. It is thought that the stridulating organs, particularly the very similar plate, are remnants of this flexible sclerotized band. They are still retained dorsally in most lycaenids in the most flexible intersegmental area. In groups such as the riodinidae with longer and more flexible abdomens, the stridulating organs encircled the body and are still preserved on other movable intersegmental areas.

Taxonomic Considerations.

Although it has been indicated that stridulatory structures have possible taxonomic use, it is not the purpose of this paper to discuss higher taxa within the Lycaenidae. Rather, it is intended to point out that, in addition to their use in identifying species, the structures seem to have a value in reflecting group relationships. One example might suffice. Ehrlich (1957, 1958) lowered the Riodinidae to subfamilial rank within the Lycaenidae on the basis of adult morphology. Not all authors agree with this assignment (see Garth and Tilden, 1963). We have been unable to locate stridulating devices in the pupae of several Nearctic species of Papilionidae, Pieridae, and Nymphalidae examined. The riodinids, however, not only have the structures, but they are definitely of similar type to those found in other lycaenids. We think these organs reflect common origin and can be used to strengthen the taxonomic relationships proposed by Ehrlich.

It may be noted in Table I that stridulation has been reported in species from all six major biogeographical regions. Summarized by number of species reported as sound producers, these are: Nearctic 41, Neotropical 3, Australian 10, Oriental 10, Palearctic 12, Ethiopian 5. The worldwide distribution of this behavior, as well as the taxonomic diversity of the species involved, suggests that the Lycaenidae have been capable of sound production for a long time.

FUNCTION OF SOUND

The major emphasis in this study has been morphological, with relatively little effort directed toward the difficult task of discovering the possible function of sound. Nonetheless, knowledge of the biology of the lycaenids involved, together with some generalizations on the morphological aspects, permit some implications to be drawn. It should be understood, however, that the function of the sounds is not known, and the following explanations are speculative.

Prell (1913) suggested two possible functions for sound in pupae; for defense and to congregate larvae. The same author (1913: 500) noted that the "weakness" of the sound might negate the former function. Since gregarious associations of prepupal larvae or pupae are relatively rare in the family and since sound receptors have never been detected in the larvae, it seems that the concept of a "congregating" function to pupal sound is not as tenable.

Hinton (1948) presents an excellent discussion of possible functions of pupal sound and states that it is primarily defensive. He arrived at this conclusion by eliminating sound as being involved with social or sexual behavior, with emergence of the adult, or with slight adjustments to temperature or humidity that a small proportion of sound-producing pupae may be able to make. Hinton notes that the defensive function, though unsupported by direct evidence, is strengthened by the fact that the pupae, as a rule, only stridulate when they are disturbed.

Haskell (1961) and Wynter-Blyth (1957) also believe that the defensive function is the most plausible of those suggested. Further corroborating the defensive function, Carter (1952) reported that stridulation in *Strymonidia w-album* Knoch is loud enough to deter a predacious bird. However, in a paper by Cole (1959) devoted exclusively to the defensive mechanisms of lepidopterous pupae against Ichneumonidae, sound was not mentioned.

An added complication in considering the defensive function is the fact that the larval stage is subject to more parasitism and predation than the pupal stage. Not only are more parasite species involved with larval stages, but most of the parasites, such as Tachinidae, Ichneumonidae, and Braconidae which emerge from the pupa, result from early stages in the butterfly larvae. Should sound production be an excellent defensive mechanism, one would be hard pressed to explain its almost universal occurrence in lycaenid pupae and its almost universal absence in larvae. Perhaps the increased parasitism is only an aftermath of the greater availability of larvae or a physiological necessity of the parasite; I seriously doubt that the compartively low rate of pupal parasitism is due solely to protection afforded by sound. In this connection, however, it should be mentioned that Dodd (1916) reported that large lycaenid larvae in Australia *were* capable of sound production when "bunched up for moulting." We have thus far been unable to detect noise in Nearctic larvae nor have we located any structures which could produce such noise.

It may be a mistake to look for single over-riding functional reasons for sound production. Consequently, other possible functions not discussed by earlier writers should be suggested as an aid and guideline for future research in this area. Contrary to Hinton's opinion that the noise does not play a part in sexual behavior, it may be that pupal sound attracts adult insects to the vicinity of pupal niches so that mating can occur immediately after emergence of the adult. In many species females mate soon after emergence. This function need not be universal, so that we might not expect such a function in pupae which are deep within the ground where sound could not reach the surface. The point to be made here is that we cannot completely dismiss the "adult-attracting" function even though it is weakened by the following facts: the slightness of sounds produced, lack of knowledge of adult sound receptors, equality of sound in both sexes, sound production both early and late in the pupal period, and optical rather than acoustical stimuli seeming to be the key release mechanism in initiating mating responses.

Another possibility is that stridulation is only secondary to the movements responsible for it, and the movements themselves may be a metabolic necessity. Certainly the external contact of parts of an insect's body when it is moving, depending on the degree of friction, can produce some sound. So little is known of the physiological activity during the pupal stages, however, that further discussion on metabolic need for movement is fruitless. We have earlier mentioned that physical need for movement during eclosion is apparent in certain nonlycanenid species.

Implied above in the suggestion that sound might be only an aftermath of movement, is the fact that there need not be a function. That is to say, the sound may be only incidentally and accidentally produced. Of course very little is known about ultrasonics, and only those sounds are studied which fall within the human auditory range, and only those which are sufficiently loud to attract attention. It is of interest that almost every insect which is studied for possible sound is found to produce noise. Perhaps there are many other sounds produced which we do not hear. As techniques and equipment for recording and measuring ultrasonic sounds becomes perfected, no doubt explanations of function of sound will also increase. However, we cannot dismiss the fact that there may be no direct function. The occurrence of sound in such divergent taxonomic groups, however, together with the definitive organs involved, weakens the explanation based on accident.

Another suggested explanation for the function of pupal sound in the Lycaenidae is involved with their symbiotic relationship with ants. Larvae of most Lycaenidae are tended by ants for the secretions from exudate glands of the larvae. These glands, particularly those on the seventh abdominal segment, may remain functional in the pupa, which may likewise be tended by ants. The evolution of this association between ants and the immature stages of lycaenids is reviewed in part by Balduf (1938, 1939) and Hinton (1951) and has been noted by me in several western Nearctic species. It will be worthwhile to consider briefly some aspects of this relationship.

Immature individuals of the lycaenids are thought to derive some benefits from the ants. These benefits are easily observed in some species, somewhat more subtle in others, and unknown for certain species. Among the most obvious advantages to certain butterfly immatures include: protection from predators and parasites, a means of transportation for food (from plant-to-plant) or shelter (plant-to-ant nest or to special resting chambers), and internidal development and care (feeding by regurgitation). The divergence of behavioral patterns, the great number of ant and lycaenid species involved, and the wide geographical occurrence of the relationship, suggest that the two types of insects have been associated for a long time.

The function of the exudate gland would seem to be obvious in the myrmecophily, but many species which possess the glands have never been reported with ants. Other species are known where the glands are restricted to positions other than abdominal segment seven, or, as in the genus *Lycaena,* they may be scattered over the body. In some species the glands are not evident, but the larvae are still attended by ants. All of these conditions have been explained on a presumed phylogenetic basis. That is, occurrence of the gland and the myrmecophilous relation is thought to be ancestral. Loss of the gland in certain genera, or extremes in the relationship with ants (from complete internidal development to no association) are considered to have been independently acquired.

The development of zoophagous feeding habits is thought to have been intimately associated both with the propensity for lycaenid species to be cannibalistic, and their intimate relations with ants. In fact, several species which are phytophagous during their early instars become predacious during their last larval stage, feeding on ant young. The adult ants transport the mature lycaenid larvae to the nest and not only tolerate zoophagy by their guests, but actually may feed their own young to the butterfly larvae. It is only a short evolutionary step from this intermediate feeding habit to the completely predacious existence. It should be noted that the zoophagous feeders in this family are either on ants, aphids, scales, jassids, or membracids with which ants are intimately associated.

Let us now consider a few additional observations on sound which may be pertinent. Bethune-Baker (1905) was informed by Dodd that three species of the Australian genus *Ogyris* would emit sounds in the pupal state only in the presence of ants. If the ants were taken away, the pupae remained silent. Dodd also stated that if the pupae were not attended by ants, it was an almost certain indication that they were dead. Wheeler (1913: 512) says that *ants also stridulate*. Sound-making ability has been noted in many ant subfamilies and has been known since 1878 (Swinton, 1878–1879). Wheeler (1913: 513) notes that stridulation is an important means of communication among ants. More recent studies on ant communication have not verified the importance of sound but have disclosed the widespread use of chemical communication by means of pheromones (see Wilson, 1963). While not wanting to deemphasize the implications of the chemical vocabulary in ants presently being analyzed, it seems likely that other sensory mechanisms are also concurrently involved. These include visual, tactile, and auditory signals, and the latter warrant attention here.

It is possible that noises produced by lycaenid pupae advertise their presence to ants. Originally this ability may have developed in the pupa together with a functional exudate gland, in which case noise may not only have helped attract ants, but served to excite them into feeding activity. Lycaenid larvae are also equipped with eversible tentacles whose function has been debated (see Downey, 1962) but which may be to attract and excite ants by production of pheromones. Since these tentacles are not functional in the pupal stages, even when exudate glands are present, it is possible that stridulating devices assume attractant function in the pupa. It should not be difficult to design an experiment to show whether audible and ultarsonic sounds produced by the pupa attract and stimulate or repel the ants. A comparison of sounds produced by ant and pupa would likewise prove interesting, particularly where the associations are rather specific.

Moreover, we can conceive that, much like the exudate gland and the myrmecophilous condition in general, ability to stridulate has been retained in pupae of many different taxonomic groups within the family. Perhaps its retention in some groups has been on the basis of a secondarily derived benefit, particularly in those species which no longer have exudate glands, or like *tarquinius*, are not tolerated by ants. This advantage could be protection afforded the pupa by stridulation, which character would perhaps have been reinforced as ancestral pupal types lost the protection afforded them by ants. Thus, the presumed defensive function of pupal sound need not be discarded, but can be strengthened.

Some information on function may be obtained from the species which appear to lack stridulatory devices. One such species, *Glaucopsyche lygdamus* (Dbldy.), is strongly myrmecophilous; the larvae are tended by at least three species of ants (Downey, 1965), and it is the only Nearctic species reported with an internidal pupal stage (Tilden, 1947) and with functional pupal exudate glands (Downey, 1965). One would assume that if stridulation was involved in the symbiotic relationship of pupa and ants, *lygdamus* would have a superior noise apparatus. Instead, it is one of the very few which lack these devices. Conversely, the carnivorous *Feniseca tarquinius*, whose larvae prey on aphids and are subject to attacks by aphid-tending ants, retains stridulatory organs in the pupa. Also as indicated above, there is evidence that the ant-feeding *Liphyra brassolis* Westw., which is viciously attacked by the tree ants in whose nest it lives, also has noise making devices in the pupa, even though Dodd (1916) claimed this species did not make sounds. Dodd has been the only author to express the opinion that pupal movements and sounds were necessary in the symbiotic relationship of ants and larvae.

If one assumes an "ant-attracting" function for the organs, at least in origin, some attempt should be made to explain retention of stridulation in species which ants do not tolerate. Most lycaenids of this type are internidal, and thus not exposed to regular predators and parasites. In this case even a protective function to the noise is not tenable since it does not deter the ants, nor is it necessary for other animals in this niche. The stridulatory structures may have been retained here due to pleiotropy; a genetic tie with other needed characters.

In analyzing the function of sound and its origin in this family I speculate as follows: stridulatory organs and associated structures, such as muscles involved in moving the devices, are considered ancestral characters present in the protolycaenid stock. They developed from structures originally involved in abdominal flexion and adult eclosion. The noise produced then became increasingly more functional and advantageous to the pupa either in a myrmecophilous relationship, or in protection from parasites or predators, or both. These assumptions are presently being tested.

SUMMARY

1. Pupae of 81 species (38 genera) of the family Lycaenidae (*sensu lato*, including Riodinidae *auct.*) have the ability to make noise: six species "hammer" their bodies against the substrate; 75 possess stridulatory organs.

2. Pupae of three species (two genera) of the family lack the stridulatory organs and presumably are unable to make noise.

3. Pupae of certain moths and some butterflies belonging to other families, including the common Monarch, are capable of sound production, so that this feature is not unique to the Lycaenidae.

4. The stridulatory organs in various lycaenid pupae are located on the same structures, and have a basic morphological similarity, which suggests common origin.

5. Three main parts of the sound-producing structure include a stridulating plate, a membranous region, and a file. The latter bears teeth and other protuberances which rasp against the anterior plate. Three types of surfaces are recognized on the plate: tuberculate, reticular, and ridged.

6. There is some question as to the physiological stage of the life cycle here involved. The "pupa" might be considered a pharate adult. However, the muscles and sensory apparatus involved in sound production are still present in an emerged adult, while the stridulating devices proper seem limited to the pupal integument. Sound also seems to be limited to this particular stage of development regardless of name.

7. The organs may have originated from grainy reticular surfaces associated with flexible abdominal segments. As obtect pupae lost their motility, these surfaces were retained only in the movable segments. In the rigid pupa of many Lycaenidae, some flexion has persisted in certain abdominal segments, perhaps retained only because of its necessity in sound production.

8. Of the many possible functions of sound in the Lycaenidae, two seem most plausible: a defensive mechanism and an auditory signal for associated symbiotic ants.

9. The stridulatory organs have many characters of possible taxonomic use. The worldwide distribution of the characters, as well as the taxonomic diversity of the adults involved, suggests that sound production is both universal and ancestral in the family. Species which have lost the structures, retain modified structures, or have lost the presumed basic functions, have acquired these traits secondarily.

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NOTES ON W. H. EDWARDS SPECIMENS IN TWO MIDWESTERN COLLECTIONS

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INTRODUCTION

Early in 1947, while studying some butterflies received from my friend Murray O. Glenn, of Henry, Illinois, my attention was attracted to a specimen of *Phyciodes texana* (Edw.) which bore a label reading "E. cincta ♂/bred Oct. 78." Recalling Holland's discussion of the name *cincta* (1931), I wrote Dr. W. R. Sweadner of the Carnegie Museum regarding this specimen, and although I had no reason to suppose there was anything unusual about the label other than the name in question, I sent it to Sweadner. He replied stating that he had compared it with holograph labels of W. H. Edwards in that institution, and that he believed it to be in the handwriting of Edwards. He suggested that I publish a note regarding the discovery of the specimen, tracing its history if possible. This, however, I did not do, although I found among the butterflies received from Glenn a considerable number of others bearing labels in the same handwriting.

In the spring of 1963 I again became interested in the Edwards specimens as a result of learning of F. Martin Brown's studies of the type material of Edwards, and I resolved to carry out the late Dr. Sweadner's suggestion, which had been so long deferred. I forwarded all of the Edwards specimens in my possession to the Carnegie Museum, where Brown examined them and pronounced them genuine. He reiterated the opinion that an account of their discovery was worthy of publication. Thus encouraged, I proceeded to attempt to trace the steps whereby these specimens had reached the collection of Glenn. Meanwhile, further examination of the latter's collection resulted in the finding of still more Edwards specimens, which Glenn, with his characteristic generosity, turned over to me in view of my interest in their historical importance. These subsequent specimens were also examined by Brown.

It is the purpose of this paper, not to advance any opinion upon possible taxonomic significance of these specimens, but merely to call attention to their existence and present location; and incidentally to present an interesting bit of entomological history, as well as brief and previously unpublished biographical sketches of two Illinois amateur collectors of an earlier day.