Call Production by Myrmecophilous Riodinid and Lycaenid Butterfly Caterpillars (Lepidoptera): Morphological, Acoustical, Functional, and Evolutionary Patterns

P. J. DEVRIES[1]

ABSTRACT

One hundred thirty species of butterfly caterpillars in five families were surveyed for their ability to produce low-amplitude, substrate-borne calls. Among these, calling was found in 19 species of riodinids and 30 species of lycaenids. The trait occurs in taxa originating from South America, North America, Europe, Southeast Asia, and Australia, but is known only from species that form symbioses with ants. Descriptions and acoustic analyses of calls are provided for most of the taxa surveyed. New evidence indicates that vibratory papillae and epicranial granulations are components of riodinid stridulatory organs. Variation in the morphology of vibratory papillae and specialized epicranial granulations is described in the riodinid tribes Lemoniini and Nymphidiini, and is compared to that in members of the tribe Eurybiini. Morphological evidence indicates that the ability to call has evolved three times—twice in the riodinids, and at least once in the lycaenids. The calls of riodinid and lycaenid caterpillars and pupae are compared, and their function is discussed in the context of previous work. Evidence suggests that the ability to call may be important in other insect groups that form symbioses with ants.

INTRODUCTION

Among butterflies, only caterpillars in the families Riodinidae and Lycaenidae form symbiotic associations with ants. Myrmecophilous caterpillars in both groups may possess adaptations for forming such symbioses. These typically include organs that produce food secretions for ants, organs that produce semiochemicals that modify ant be-

[1] Visiting Research Scholar, Department of Zoology, University of Texas, Austin, TX 78712; Scientific Associate, Center for Conservation Biology, Stanford University, Stanford, CA 94305.

havior (Cottrell, 1984; DeVries, 1988; DeVries and Baker, 1989), and a thickened body cuticle (Malicky, 1970). The riodinids and lycaenids are separate monophyletic groups (Ehrlich 1958; Eliot, 1973; Kristensen, 1976; Harvey, 1987; Robbins, 1988) together forming what is often referred to as the lycaenoid butterflies. Differences of opinion exist as to whether riodinids and lycaenids should be considered separate families (sensu Eliot, 1973) or subfamilies within a single family (sensu Ehrlich 1958)—the phylogenetic relationships within and among these groups are unresolved. While the evolution of butterfly myrmecophily is most often treated as a single event (e.g., Hinton, 1951; Pierce, 1987), the nonhomologous nature of riodinid and lycaenid caterpillar organs indicates that myrmecophily has arisen at least twice (DeVries, 1991a). Tracing the phylogenetic relationships of the riodinids and lycaenids will necessitate a thorough cladistic analysis, a task well beyond the scope of this paper. However, because larval morphology indicates that myrmecophily evolved independently in the Riodinidae and Lycaenidae, I have considered them to be separate families.

During a study of symbioses between riodinid butterfly caterpillars and ants, I became interested in how three sets of myrmecophilous organs on *Thisbe irenea* (Stoll) caterpillars function to maintain the attention of ants (fig. 1). One set of myrmecophilous organs, termed vibratory papillae, were suggested to function as stridulatory organs (DeVries, 1988). That work led to the documentation of acoustical signals produced by both riodinid and lycaenid butterfly caterpillars that form symbioses with ants, and to the suggestion that caterpillar acoustical signals were an important part of the evolution of butterfly myrmecophily (DeVries, 1990).

This paper seeks to enhance our understanding of caterpillar signals in five ways: (1) furnishing basic caterpillar call descriptions and acoustic analyses for various riodinid and lycaenid species; (2) presenting and discussing new morphological and experimental evidence regarding how riodinid stridulatory mechanisms function; (3) providing a comparison of acoustic signals between riodinid and lycaenid caterpillars; (4) discussing the function and evolution of caterpillar and pupal signals in the context of forming symbioses with ants; and (5) presenting the caterpillar-ant system as a potential model that could be extended to other insect groups.

MATERIALS AND METHODS

Insect acoustical signals are often divided into two categories based on how their energy is transmitted. Although it is not always easy to separate the two types of signals (Gogala, 1985), those that are transmitted through air are called sound, and those that are substrate-borne are called vibrational signals. This paper is concerned with signals produced by riodinid and lycaenid butterfly caterpillars that are substrate-borne and are detectable only with sensitive instruments. These are technically considered vibrational signals. However, in choosing a term for such signals, I have considered two things: (1) unlike those found in lycaenid pupae (e.g., Downey and Allyn, 1978), the amplitude of caterpillar signals makes it unlikely that they function as defenses, and they are clearly not sexual in nature (DeVries, 1990, personal obs.), and (2) the experimental evidence suggests that ants detect and respond positively to caterpillars' signals (DeVries, 1990). Thus, the term "call" seems both appropriate and unambiguous for the signals produced by these caterpillars.

One hundred thirty species of live butterfly caterpillars in five families were surveyed for their ability to produce calls (tables 1–5). My caterpillar survey represents material from six biogeographic regions: South America, Central America, North America, Europe, Southeast Asia, and Australia. The material was either found during the course of my fieldwork or was provided by colleagues. Generally, late-instar caterpillars were examined, but whenever possible all instars of a taxon were surveyed. Calls were detected by a Bennett-Clark (1984) particle velocity microphone using the methods described in DeVries (1991b), and then recorded on a Marantz PMD 420 cassette tape recorder. Many of the calls were subsequently analyzed with a Kay DSP Model 5500 Sonagraph and a Data 6000 wave-form analyzer. The sonagrams and waveforms were made on a Kay
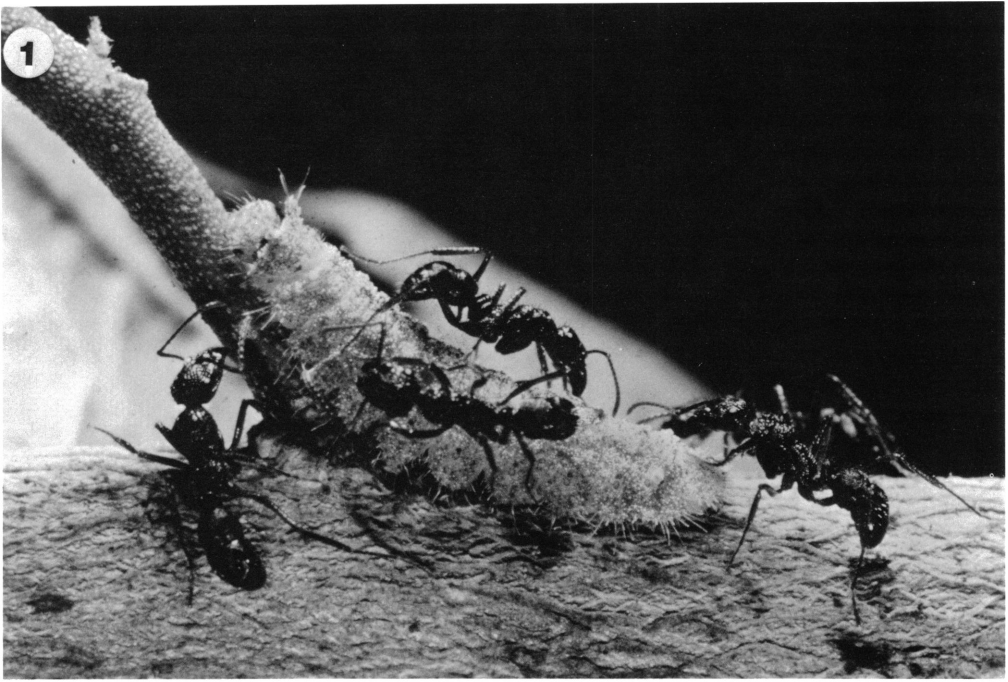
Fig. 1. Final instar of *Thisbe irenea* (Riodinidae: Lemoniini) from Panama producing a call while walking to a feeding area. An escort of *Ectatomma ruidum* (Ponerinae) ants, such as those illustrated, have been demonstrated to vigorously defend a caterpillar from predators.

Fig. 2. Mature instar of *Nymphidium* sp. (Riodinidae: Nymphidiini) from Ecuador being tended by a group of myrmecine ants. Unlike other congeners, this *Nymphidium* species produces a call.

TABLE 1
Caterpillar Species Tested that Did Not Produce Calls
(The groups represented are: Papilionidae-Papilioninae; Pieridae-Coliadinae, Pierinae; Nymphalidae-Charaxinae, Apaturinae, Nymphalinae, Heliconiinae, Melitaeinae, Ithomiinae, Danainae, Morphinae, Brassolinae, and Satyrinae.)

Taxon (number)	Origin
Papilionidae	
Papilio thoas nealces Rothschild & Jordan (3)	Panama
Papilio birchalli godmanii Rothschild & Jordan (2)	Costa Rica
Eurytides ilus (Fabricius) (1)	Panama
Parides nr *lycimenes* (1)	Panama
Pieridae	
Phoebis argante (Fabricius) (3)	Panama
Itaballiba demophile centralis Joicey & Talbot (1)	Panama
Nymphalidae	
Archaeoprepona demophoon gulina Fruhstorfer (5)	Panama
Siderone marthesia (Cramer) (1)	Panama
Hypna clytemnestra (Cramer) (4)	Panama
Memphis elara (Godman & Salvin) (1)	Costa Rica
Memphis oenomais (Boisduval) (4)	Panama, Costa Rica
Doxocopa clothilda (Felder) (1)	Costa Rica
Colobura dirce (Linnaeus) (2)	Panama
Historis odius (Fabricius) (1)	Costa Rica
Tigridia acesta (Linnaeus) (1)	Costa Rica
Ectima rectifascia Butler & Druce (2)	Panama
Hamadryas iptheme iptheme Bates (1)	Panama
Dynamine af *pierioides* (Butler) (1)	Panama
Eunica mira Godman & Salvin (2)	Panama
Eunica mygdonia Godart (1)	Panama
Temenis laothoe agatha (Fabricius) (3)	Panama
Diaethria sp. (4)	Ecuador
Callicore lyca aerias (Godman & Salvin) (3)	Costa Rica
Catonephele mexicana Jenkins (1)	Panama
Adelpha melanthe Bates (6)	Costa Rica
Adelpha leuceria (Druce) (5)	Costa Rica
Adelpha cocala lorzae Boisduval (1)	Panama
Adelpha lerna aeolia (Felder) (1)	Panama
Philaethria dido (Linnaeus) (1)	Panama
Heliconius pachinus Salvin (2)	Costa Rica
Heliconius cydno (various subspecies) (5)	Costa Rica, Colombia
Chlosyne narva (Fabricius) (1)	Costa Rica
Chlosyne lacinia (Geyer) (4)	Panama
Chlosyne janais (Drury) (4)	USA
Hyposcada virginiana evanides (Haensch) (3)	Costa Rica
Mechanitis menapis saturata Godman & Salvin (6)	Costa Rica
Mechanitis polymnia isthmia Bates (4)	Panama
Undetermined genus (1)	Costa Rica
Lycorea cleobaea atergatis Doubleday (1)	Costa Rica
Morpho theseus aquarius Butler (1)	Panama
Morpho peleides limpida Butler (2)	Panama, Costa Rica
Caligo memnon (Felder & Felder) (2)	Panama
Caligo sp. (1)	Panama
Eryphanis sp. (1)	Ecuador
Opsiphanes sp. (1)	Panama
Pierella helvetia incanescens Godman & Salvin (1)	Panama

TABLE 1 — (*Continued*)

Taxon (number)	Origin
Euptychia westwoodi Butler (>10)	Panama, Costa Rica
Cissia calixta (Butler) (5)	Costa Rica
Cissia hesione (Sulzer) (1)	Panama
Calisto confusa Lathy (1)	Dominican Republic

Sona-Graph 780 with 8 KHz input range, 300 Hz analysis filter, and no attenuation. Except where noted, dominant frequencies and pulse rates were estimated by inspection of sonagrams.

RIODINID AND LYCAENID CALLS

SURVEY OF THE RIODINIDAE

Of the 43 riodinid species surveyed, only myrmecophilous caterpillars produced calls (table 2, figs. 1–4)—except for some *Nymphidium* species (see below). Caterpillars of non-myrmecophilous species did not produce calls (table 3). In general, riodinid calls may be described as a series of rapid, high-pitched chirps, not unlike the scolding semiclick sound used for admonishing naughty children (usually accompanied by a wagging finger)—a rapid "tisch-tisch-tisch. . . ."

Following close observation of the caterpillars of *Thisbe irenea, Synargis mycone, Juditha molpe, Nymphidium mantus,* and *Theope* nr *matuta,* I determined that calling ability began after molting to third instar, a time corresponding to the development of other "ant organs" (DeVries, 1988, 1991a, 1991c). Repeated observations indicated that calling ability continues until immediately preceding pupation, and that caterpillars do not produce calls immediately prior to, during, or after a larval molt. Calls were typically produced when caterpillars were walking or when stressed (e.g., prodded by the observer); except for an occasional chirp, resting caterpillars never called. Caterpillars parasitized by tachinid fly maggots produced calls up to the exit of the parasite from the host's body.

Call signals were greatly reduced or undetectable when only the posterior segments of the caterpillar were allowed to touch the recording substrate. Despite the apparent monotony of riodinid calls (figs. 3, 4), the call rate varied slightly depending on the activity of an individual caterpillar. For example, walking caterpillars generally had a slower pulse rate than those that were stressed, and some variation was observed between individuals of the same instar (figs. 3A, D, F, I; 4A, D, F, I).

VIBRATORY PAPILLAE

A pair of mobile, rodlike appendages arising from the distal edge of segment T-1 was first noted for the myrmecophilous caterpil-

TABLE 2
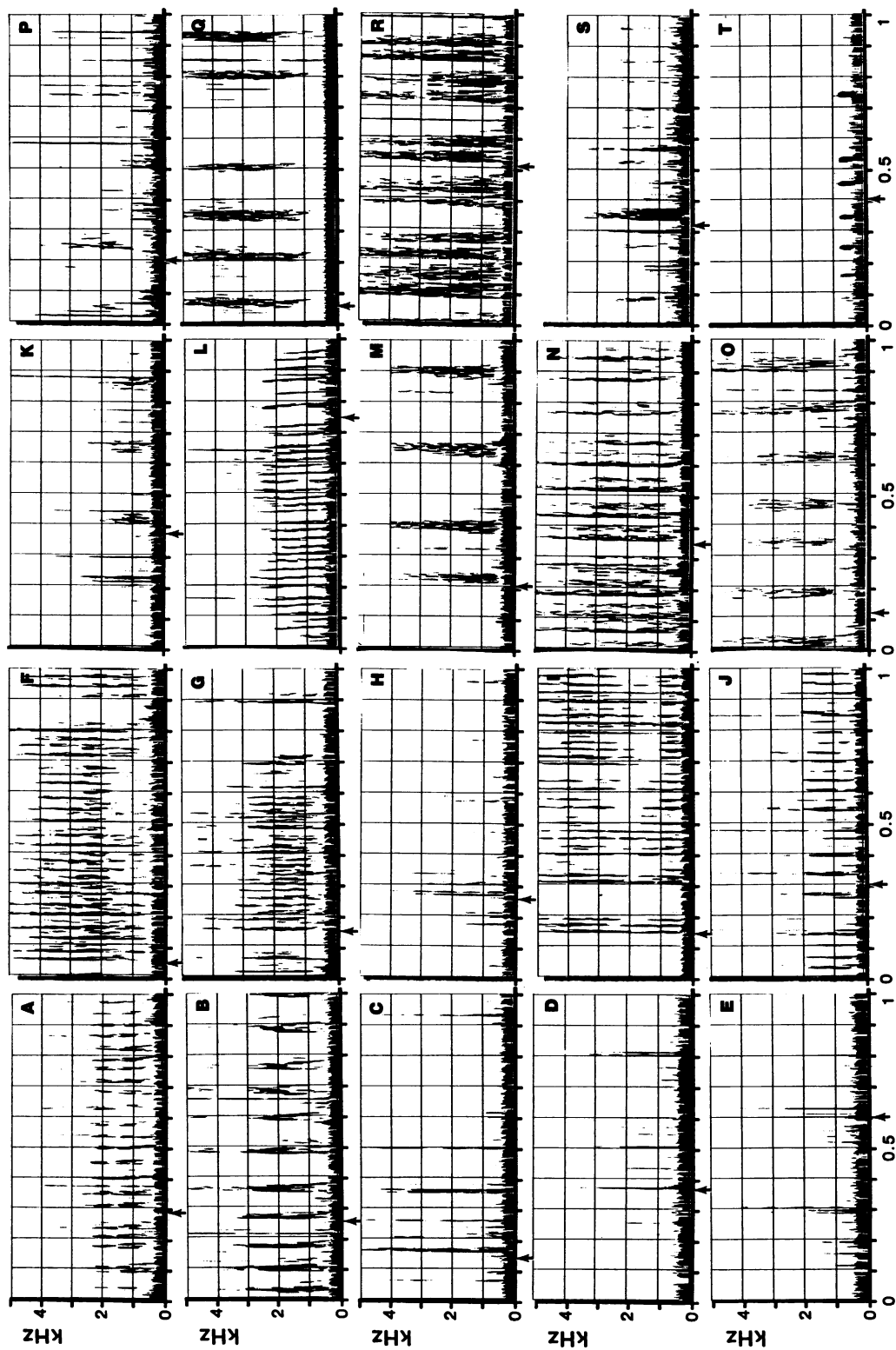**Species of Riodinid Caterpillars Tested that Produced Calls**
(All taxa are in the subfamily Riodininae, and they represent three tribes: Eurybiini, Lemoniini, and Nymphidiini. Classification follows Harvey (1987). An asterisk (*) immediately following a taxon indicates that the pupa was tested for sound production, and none produced sounds. All of the species listed here are typically myrmecophilous.)

Taxon (number)	Origin
Eurybiini	
Eurybia lycisca Westwood* (8)	Panama, Costa Rica
Eurybia patrona persona Staudinger (1)	Panama
Eurybia elvina Stichel (2)	Panama
Eurybia sp. (1)	Ecuador
Lemoniini	
Thisbe irenea (Stoll)* (>30)	Panama, Costa Rica, Belize
Synargis mycone (Hewitson)* (>10)	Panama, Costa Rica
Synargis gela (Hewitson)* (7)	Ecuador
Juditha molpe (Hübner)* (>10)	Panama, Costa Rica, Belize
Nymphidiini	
Menander menander (Cramer) (1)	Panama
Calospila cilissa (Hewitson)* (>10)	Costa Rica
Calospila emylius (Cramer)* (5)	Ecuador
Unknown genus (1)	Panama
Theope nr *thestias* Hewitson* (7)	Panama
Theope nr *matuta* Godman & Salvin* (6)	Panama
Theope virgilius (Fabricius)* (4)	Panama
Theope sp. (1)	Panama
Theope nr *decorata* Godman & Salvin* (>10)	Costa Rica
Nymphidium sp. (>10)	Ecuador
Nymphidium mantus (Cramer)* (>10)	Panama

lars of the genus *Audre* by Bruch (1926) and Borquin (1953). Later these appendages were described in greater detail for a species of *Lemonias* by Ross (1964), who termed them vibratory papillae. Further studies showed that other riodinid genera also have vibratory papillae (Schremmer, 1978; Callaghan, 1977, 1982, 1986). Along with other myrmecoph-

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Fig. 3.   Sound spectrograms of last instar caterpillar calls. All caterpillars are Neotropical riodinids unless noted otherwise. The arrow on the X-axis indicates the point of the signal where the wave form recording began (see fig. 4). Each vertical line represents $\frac{1}{10}$ of 1 sec. **A,** *Thisbe irenea,* voucher A-1, Panama, with two vibratory papillae; **B,** *Thisbe irenea,* voucher A-1, 15 min later with one vibratory papilla removed; **C,** *Thisbe irenea,* voucher A-1, 15 min later with both vibratory papillae removed. The spikes are from the tarsal claws popping off the substrate; **D,** *Thisbe irenea,* voucher mut-1, Panama, an individual found in nature with no vibratory papillae. The spikes are from the tarsal claws contacting the substrate; **E,** *Thisbe irenea,* voucher mut-2, Panama, an individual found in nature with no vibratory papillae. The spikes are from the tarsal claws popping off the substrate; **F,** *Juditha molpe,* voucher A-2, with two vibratory papillae; **G,** *Juditha molpe,* voucher A-2, 15 min later with one vibratory papilla removed; **H,** *Juditha molpe,* voucher A-2, 15 min later with both vibratory papillae removed. The spikes are from the tarsal claws popping off the substrate; **I,** *Juditha molpe,* voucher 22-88, Panama. Note the variance between this individual and that of individual A-2; **J,** *Theope virgilius,* Panama; **K,** *Theope* nr *thestias,* voucher 88-12, Panama; **L,** *Theope* nr *matuta,* voucher 88-21, Panama; **M,** *Synargis gela,* Ecuador; **N,** *Synargis mycone,* voucher 88-20, Panama; **O,** *Calospila emylius,* Ecuador; **P,** *Calospila cilissa,* Costa Rica; **Q,** *Nymphidium mantus,* voucher 88-12, Panama; **R,** *Nymphidium* sp., Ecuador; **S,** *Leptotes cassius* (Lycaenidae), Florida, USA; **T,** *Plebulina emigdionis* (Lycaenidae), California, USA.

Time in Seconds

TABLE 3
Species of Riodinid Caterpillars Tested that Did Not Produce Calls
(This sample represents two subfamilies, Euselasiinae and Riodininae, and eight tribes: Mesosemiini, incertae sedis, Riodinini, Symmachini, Charitini, Emesini, and Nymphidiini. Classification follows Harvey (1987). An asterisk (*) immediately following a taxon indicates the pupa was tested for sound production, and none produced sound. None of the taxa listed here, except the genus *Nymphidium* (see text), typically form symbiosis with ants.)

Taxon (number)	Origin
Euselasiinae	
Euselasia nr *leucorrhoa* Godman & Salvin* (1)	Panama
Riodininae	
Mesosemiini	
Leucochimona lagora Herrich-Schäffer* (5)	Panama, Costa Rica
Leucochimona sp. (2)	Panama
Leucochimona iphias Stichel (2)	Panama
Mesosemia telegone (Boisduval)* (1)	Panama
Mesosemia sp.* (1)	Ecuador
Insertae Sedis	
Cremna thasus subrutilia Stichel (3)	Panama
Napaea eucharilla rufolimbata Stichel* (1)	Panama
Riodinini	
Ancyluris inca (Saunders)* (>10)	Panama
Rhetus arcius (Linnaeus) (1)	Panama
Charis gynaea (Godart) (1)	Panama
Caria rhacotis (Godman & Salvin) (3)	Costa Rica
Melanis pixie (Boisduval) (3)	Costa Rica
Symmachiini	
Mesene sp. (1)	Panama
Mesenopsis bryaxis (Hewitson)* (2)	Panama
Esthemopsis sericina Bates* (1)	Panama
Symmachia tricolor Hewitson* (4)	Panama
Charitini	
Sarota gyas (Cramer) (1)	Panama
Anteros formosus micon Druce* (2)	Panama
Emesini	
Emesis tegula (Godman & Salvin) (2)	Costa Rica
Emesis lucinda (Cramer)* (>10)	Costa Rica
Nymphidiini	
Nymphidium haematostictum Godman & Salvin* (5)	Panama
Nymphidium azanoides occidentalis Callaghan* (>10)	Panama
Nymphidium cachrus (Fabricius)* (>10)	Costa Rica
Nymphidium chione onaeum Hewitson (>10)	Panama
Nymphidium caricae (Linnaeus) (>10)	Ecuador

ilous organs, the vibratory papillae are considered apomorphic traits for the tribes Lemoniini and Nymphidiini (Harvey, 1987). One reason call signals were reduced or undetectable when only the posterior segments were touching the recording substrate (except in the genus *Eurybia*; see below) is that call-producing structures are most likely located in the head region (DeVries, 1988).

Ross (1966) first suggested that the beating motion of *Lemonias* vibratory papillae might convey vibrations to ants. Later, DeVries (1988) used the morphology of the vibratory papillae, head movement, and the specialized

Fig. 4. Wave forms of riodinid and lycaenid caterpillar calls. The start of each wave form is marked with an arrow on the X-axis of sonagrams illustrated in fig. 3. Each wave form represents 0.214 sec, and distance between vertical lines represents 8.23 msec. **A,** *Thisbe irenea,* voucher A-1 with two vibratory papillae; **B,** *Thisbe irenea,* voucher A-1, 15 min later with one vibratory papilla removed; **C,** *Thisbe irenea,* voucher A-1, 15 min later with both vibratory papillae removed; **D,** *Thisbe irenea,* voucher mut-1, an individual found in nature with no vibratory papillae; **E,** *Thisbe irenea,* Panama, voucher mut 2, an individual found in nature with no vibratory papillae; **F,** *Juditha molpe,* voucher A-2 with two vibratory papillae; **G,** *Juditha molpe,* voucher A-2, 15 min later with one vibratory papilla removed; **H,** *Juditha molpe,* voucher A-2, 15 min later with both vibratory papillae removed; **I,** *Juditha molpe,* voucher 22–88; **J,** *Theope virgilius;* **K,** *Theope* nr *thestias;* **L,** *Theope* nr. *matuta;* **M,** *Synargis gela;* **N,** *Synargis mycone;* **O,** *Calospila emylius;* **P,** *Calospila cilissa;* **Q,** *Nymphidium mantus;* **R,** *Nymphidium* sp.; **S,** *Leptotes cassius;* **T,** *Plebulina emigdionis.*

epicranial granulations of *Thisbe irenea* caterpillars as a model of how vibratory papillae might act as components of a stridulatory organ. The model proposed that sound is produced when the head is oscillated, and the ringed shaft of each vibratory papilla grates on the specialized epicranial granulations. Support for this model comes from demonstration that calling ability is eliminated when the vibratory papillae are removed, but re-

turns when they are replaced at the next molt (DeVries, 1990).

Further support for the hypothesis that vibratory papillae are fundamental for call production in some riodinids is presented here. The sequential removal of single vibratory papillae (at 15 min intervals) of *Thisbe irenea* and *Juditha molpe* indicates the relationship between vibratory papillae and call production. Sonagrams (figs. 3A–C, F–H) and wave

forms (figs. 4A–C, F–H) display graphically that as the vibratory papillae are removed, the pulse train and wave form of the call decay sequentially until the only signal produced is that of the tarsal claws "popping" off the substrate while the caterpillars are walking. Two individual *T. irenea* caterpillars were found in nature without vibratory papillae (figs. 3D, E; 4D, E; 5E). Their signals mirror those of the individual caterpillar that had both its vibratory papillae removed experimentally (figs. 3C, H; 4C, H).

Previous studies (Bruch, 1926; Borquin, 1953; Ross, 1964; Schremmer, 1978; Callaghan, 1977, 1982, 1986; Harvey, 1987; DeVries 1988), together with the present one (figs. 5, 6), indicate that the usual complement of vibratory papillae is two per caterpillar. However, a large sample of Panamanian *Thisbe irenea* caterpillars (N > 200) yielded one individual with three vibratory papillae (two on one side and one on the other), and another two individuals without vibratory papillae (fig. 5E). Further, in the last three instars of four caterpillars (*Theope* nr. *matuta*) each individual had a total of six vibratory papillae—a pair with three shafts per attachment point (fig. 5M). Thus, exceptions to the standard complement can occur.

My taxonomic survey indicates that vibratory papillae divide roughly into two morphological types: (1) those that have annulations distributed evenly along the distal ⅔ of the shaft and with the cusp surfaces radiating out from the central axes; and (2) those with annulations of varying widths generally confined to the distal third and with the cusps directed in either an anterior or posterior direction. In the second type, the papillae are clubbed distally. The first type was found in species of *Thisbe, Juditha, Synargis, Calospila,* and *Menander* (fig. 5), while the second type was found in species of *Theope* and *Nymphidium* (figs. 5M, O, P; 6A–D). Other types of vibratory papillae may be found as more species of caterpillars become available for study.

EPICRANIAL GRANULATIONS

The epicranial surface where the vibratory papillae strike the head is covered with specialized granulations of differing types (figs.

5B–P; 6A–D). The granulations may consist of: (1) irregular rows of sharp, roughly conical granulations that project forward (*Thisbe, Synargis*), (2) longitudinally flattened disks that are directed slightly forward (*Calospila*), (3) sharp, erect wedges with the bases buttressed on two sides (*Menander*), (4) a raised, pointed edge with heavy buttressing at the posterior edge of the base (*Nymphidium mantus, Theope*), or (5) blunt hemispheres (*Nymphidium*). Only members of the Lemoniini and Nymphidiini had vibratory papillae and specialized epicranial granulations. All other riodinid genera surveyed (excepting *Eurybia*) had a smooth epicranium and no vibratory papillae (fig. 6G–L). Such species typically do not form symbioses with ants.

There are two exceptions to the association between having vibratory papillae and epicranial granulations, and producing calls. First, myrmecophilous caterpillars of the genus *Eurybia* produce distinct calls, yet do not possess vibratory papillae or granulations on the epicranium (fig. 6E, F). Second, five species of the genus *Nymphidium* were found to be unable to produce calls, even though they possess vibratory papillae and epicranial granulations (table 1; fig. 6A–D). Both of these genera are discussed below.

DESCRIPTIONS OF RIODINID CALLS

Eurybia: All four species produce a consistent pulse train of "eh-eh-eh-eh-eh. . ." with a short silence between pulses; mean pulse rate (N = 4) of 12–15 pulses/sec. No head oscillation was observed in any species, and none had vibratory papillae or specialized epicranial granulations (fig. 6E, F). Details of the calls will be reported elsewhere (DeVries, in prep.).

Thisbe irenea (figs. 1, 3A–E, 4A–E): A strong series of rapid, twittering chirps that inflect upward at the end of the pulse train; a mean pulse rate of (N = 30) 16.5 pulses/sec, mean dominant frequency ≈ 900 Hz [range ≈ 370–1500Hz].

Synargis mycone (figs. 3N, 4N): A strong series of fluttery, squeaky chirps; mean pulse rate of (N = 6) 34 pulses/sec; mean dominant frequency ≈ 1840 Hz [range ≈ 1120–3000 Hz].
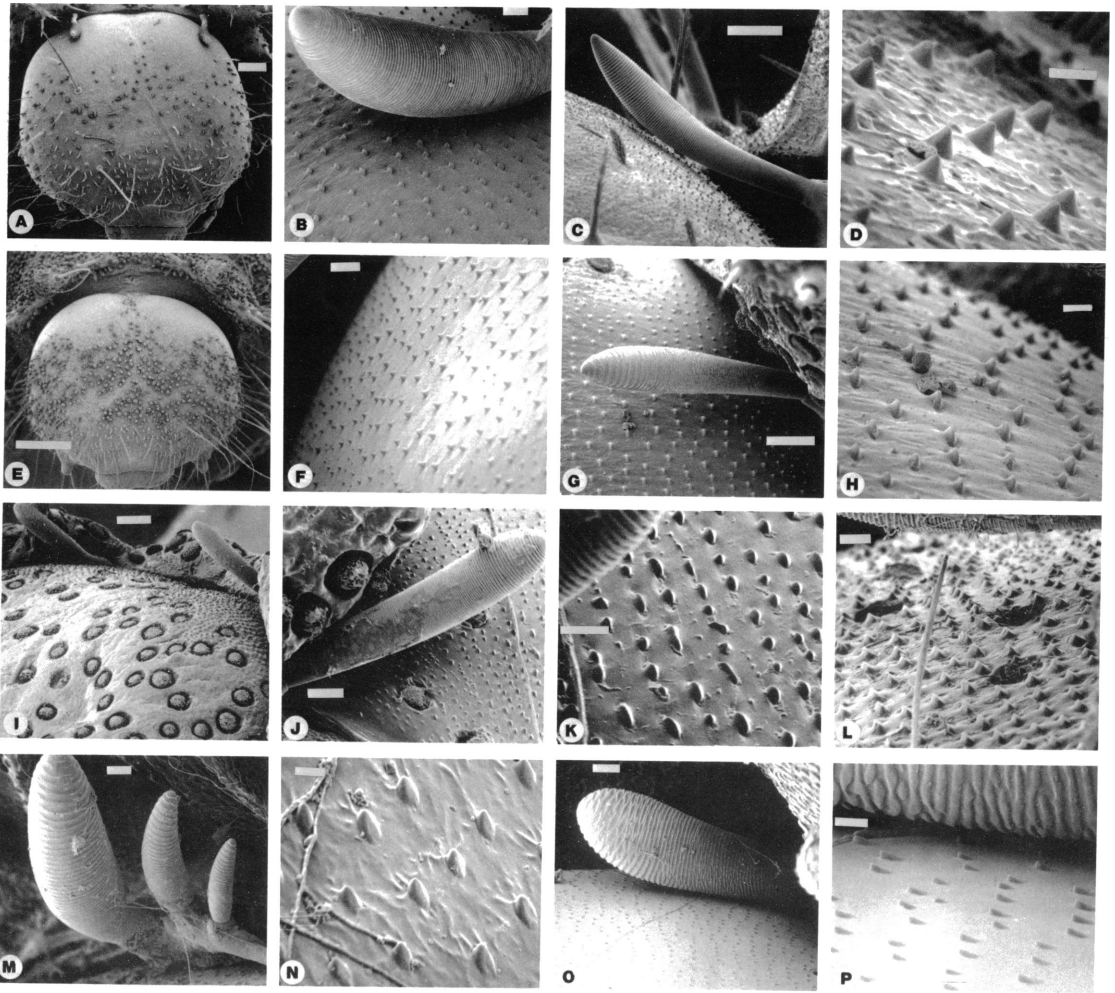
Fig. 5.   Scanning electron micrographs of riodinid caterpillars showing vibratory papillae and the epicranial surface where the vibratory papillae strike. **A,** Frontal view of *Synargis gela* head showing typical position of the vibratory papillae (scale bar = 200 μm). **B,** Detail of a *Synargis gela* vibratory papilla and epicranial granulations (scale bar = 20 μm). **C,** Lateral view of *Synargis mycone* epicranium showing a vibratory papilla and epicranial granulations (scale bar = 50 μm). **D,** *Synargis mycone* head granulations (scale bar = 5 μm). **E,** Frontal view of the head of an individual *Thisbe irenea* found in nature without vibratory papillae developed (scale bar = 500 μm). **F,** Epicranial granulations of *Thisbe irenea* (scale bar = 20 μm). Note annulations of the vibratory papilla in extreme upper left. **G,** A vibratory papilla of *Juditha molpe* and epicranial granulations (scale bar = 50 μm). **H,** *Juditha molpe* head granulations (scale bar = 10 μm). Note shaft of vibratory papilla in extreme upper right corner. **I,** Dorsal third of head of *Calospila emylius* showing both vibratory papillae. Note location of patch of epicranial granulations (scale bar = 50 μm). **J,** *Calospila cilissa* vibratory papilla and epicranial granulations (scale bar = 20 μm). **K,** Details of *Calospila cilissa* epicranial granulations (scale bar = 10 μm). **L,** *Menander menander* epicranial granulations. Note shaft of vibratory papilla at top of figure (scale bar = 20 μm). **M,** One set of *Theope* nr *matuta* vibratory papillae. Unlike all other known species, *T.* nr *matuta* has two sets of three. **N,** Details of *Theope* nr *matuta* head granulations (scale bar = 5 μm). **O,** *Theope* nr *thestias* vibratory papilla and epicranial granulations (scale bar = 20 μm). **P,** Detail of *Theope* nr *thestias* vibratory papilla and head granulations. Note cusps on vibratory papilla are directed posterior (scale bar = 5 μm).
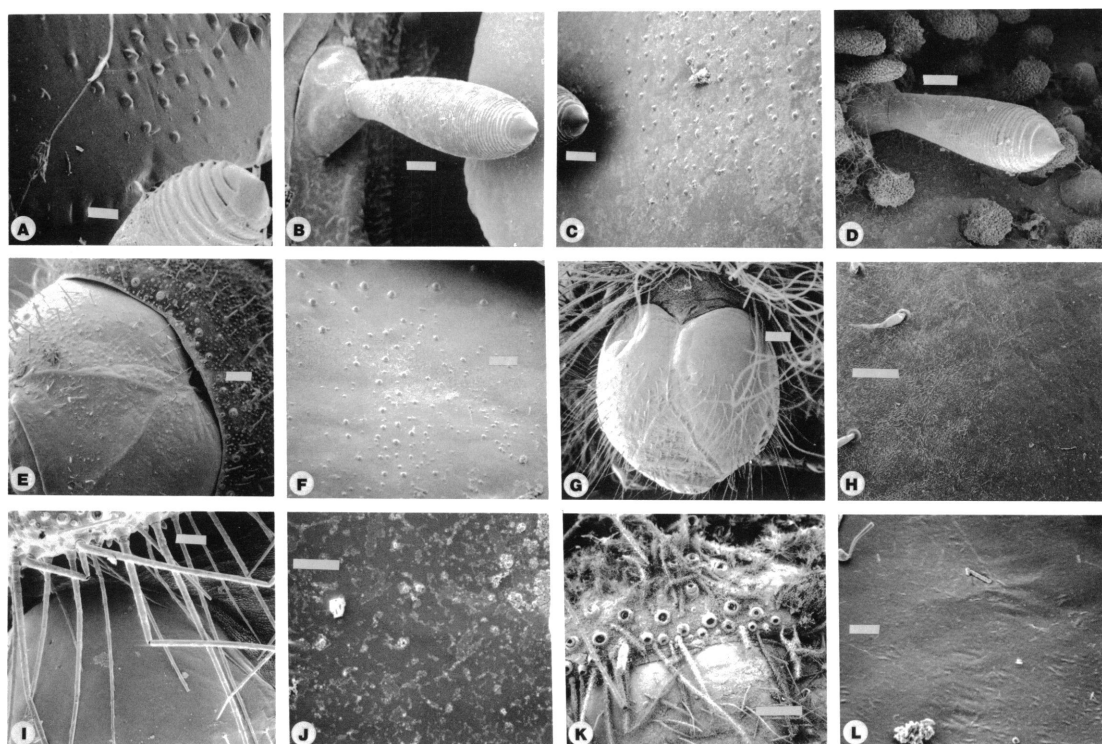
Fig. 6. Details of riodinid vibratory papillae and epicranium. **A,** Vibratory papilla of *Nymphidium mantus* and epicranial granulations (scale bar = 10 μm). **B,** Vibratory papilla of *Nymphidium haematostictum* (scale bar = 10 μm). Note that the head capsule is pulled away from the normal position. **C,** Detail of *Nymphidium haematostictum* epicranial granulations (scale bar = 10 μm). **D,** Vibratory papilla and epicranial granulations of *Nymphidium azanoides* (scale bar = 20 μm). Note that the area where vibratory papilla strikes is clogged with shrublike setae which presumably interfere with call production. **E,** An overview of the head of *Eurybia patrona*. Note absence of vibratory papillae (scale bar = 200 μm). **F,** Detail of *Eurybia patrona* epicranium showing a sparsely pebbled surface of hemispherical granulations (scale bar = 20 μm). **G,** Frontal view of *Cremna thasus* head. There are no vibratory papillae, only long setae (scale bar = 200 μm). **H,** Detail of the smooth epicranium of *Cremna thasus* (scale bar = 50 μm). **I,** Dorsal view of *Emesis lucinda* head. There are no vibratory papillae (scale bar = 100 μm). **J,** Detail of the smooth epicranium of *Emesis lucinda* (scale bar = 10 μm). **K,** Frontal view of *Ancyluris inca* head. There are no vibratory papillae, only long setae (scale bar = 200 μm). **L,** Detail of the smooth epicranium of *Ancyluris inca* (scale bar = 5 μm).

Synargis gela (figs. 3M, 4M): An irregular, short series of rasping chirps that inflect upward at the end of the pulse train; mean pulse rate of (N = 6) 15.2 pulses/sec; mean dominant frequency ≈ 1677 Hz [range ≈ 940–4000 Hz].

Juditha molpe (figs. 3F–I, 4F–I): A strong series of rapid, twittering chirps with a short silence between each pulse train; mean pulse rate of (N = 6) 15.2 pulses/sec; mean dominant frequency ≈ 2192 Hz [range ≈ 720–2020 Hz].

Menander menander: A strong series of

rasping chirps similar to those of *Synargis*. No detailed analyses were performed.

Calospila cilissa (figs. 3P, 4P): An infrequent series of chirps that sound like audible "kissing"; mean pulse rate of 6 pulses/sec; mean dominant frequency ≈ 1700 Hz [range ≈ 500–3500 Hz].

Calospila emylius (figs. 3O, 4O): An irregular series of "smooching" chirps that inflect upward at the end of the pulse train; mean pulse rate of (N = 6) 9.5 pulses/sec; mean dominant frequency of ≈ 2550 Hz [range ≈ 1980–4000 Hz].

TABLE 4

Species of Lycaenid Caterpillars Tested that Produced Calls

(This sample represents three subfamilies, Theclinae, Lycaeninae, and Polyommatinae, and five tribes: Eumaeini, Hypolycaenini, Zesiini, Lycaenini, and Polyommatini. Classification follows Eliot (1973). All of the species listed here are found in symbioses with ants.)

Taxon (number)	Origin
Theclinae	
Eumaeini	
Chlorostrymon simaethis (Drury) (>10)	Panama
Strymon yojoa Reakirt (3)	Panama, Costa Rica
Arawacus lincoides Draught (>10)	Panama, Costa Rica
Olynthus narbal (Stoll) (8)	Panama
Thereus pedusa (Hewitson) (>10)	Panama
Thereus nr *enenia* (Hewitson) (1)	Panama
Panthiades bitias (Cramer) (1)	Panama
Rekoa palegon (Cramer) (1)	Panama
Tmolus echion (Linnaeus) (6)	Costa Rica
Micandra platyptera (Felder & Felder) (2)	Costa Rica
Thecla legytha (Hewitson) (2)	Panama
Thecla sp. (1)	Costa Rica
Hypolycaenini	
Hypolycaena erylus (Godart) (1)	Thailand
Zesiini	
Jalmenus evagoras (Donovan) (4)	Australia
Lycaeninae	
Lycaena phaleas Linnaeus (6)	Germany
Lycaena hippothoe Linnaeus (4)	Germany
Polyommatinae	
Polyommatini	
Leptotes cassius (Cramer) (3)	USA
Cupido minimus Fuessly (7)	England, Germany
Maculinea arion Linnaeus (2)	Poland
Maculinea nausithaus Bergstrasser (2)	Germany
Maculinea teleius Bergstrasser (3)	Germany
Maculinea rebeli Hirschke (2)	France
Maculinea alcon Schiffermuller (2)	France
Plebulina emigdionis (Grinnell) (1)	USA
Lycaeides melissa samuelis Nabokov (1)	USA
Lysandra coridon caelestissima Verity (>10)	Spain
Lysandra hispana Herrich-Schaffer (5)	Spain, France
Lysandra bellargus Rottemburg (>10)	England, France
Polyommatus icarus Rottemburg (6)	England, Germany

Unknown genus (Nymphidiini) carnivorous on scale insects: A pulse series of fluttery, squeaky chirps, not unlike that of *Synargis mycone*; mean pulse rate of (N = 1) 16.6 pulses/sec; mean dominant frequency ≈ 2400 Hz [range ≈ 1940–3000 Hz].

Theope thestias (figs. 3K, 4K): A regular series of thin, watery sounding chirps; mean pulse rate of (N = 2) 7 pulses/sec; mean dom-

inant frequency ≈ 1875 Hz [range ≈ 1750–2000 Hz].

Theope nr *matuta* (figs. 3L, 4L): A series of guttural, grating chirps; a short silence between each pulse train; mean pulse rate of (N = 4) 48 pulses/sec; mean dominant frequency ≈ 2000 Hz [range ≈ 1400–2900 Hz].

Theope virgilius (figs. 3J; 4J): A fluttering series of oscillating, watery chirps; mean pulse

TABLE 5

Species of Lycaenid Caterpillars Tested that Did Not Produce Calls

All species are in the subfamily Theclinae, tribe Eumaeini. Classification follows Eliot (1973). None of the species listed here typically form symbioses with ants.

Taxon (number)	Origin
Theclinae	
Eumaeini	
Eumaeus godartii (Boisduval) (>20)	Panama, Costa Rica
Symbiopsis tanais (Godman & Salvin) (3)	Panama
Pseudolycaena damo (Druce) (2)	Panama
Thecla barajo (Reakirt) (1)	Costa Rica
Thecla nr *melma* Schaus (12)	Costa Rica
Thecla hisbon (Godman & Salvin (>10)	Panama

rate of (N = 3) 39 pulses/sec; mean dominant frequency ≈ 2000 Hz [range ≈ 1400–3000 Hz].

Theope sp.: A constant, fluttering series of watery chirps; mean pulse rate of (N = 1) 47 pulses/sec; mean dominant frequency ≈ 1650 Hz [range ≈ 1080–2220 Hz].

Theope nr *decorata*: A weak and infrequent chirping pulse of "chit-chit-chit" with silent sections between the pulse trains. Not analyzed in detail.

Nymphidium sp. (figs. 2, 3R, 4R): A strong, consistent series of grating chirps that sound as though someone were slowly bending a large section of sheet metal; mean pulse rate of (N = 5) 16 pulses/sec; mean dominant frequency ≈ 2000 Hz [range ≈ 1580–2600 Hz].

Nymphidium mantus (figs. 3Q; 4Q): A regular series of grating chirps that sound similar to the call of a scolding squirrel; mean pulse rate of (N = 2 in detail) 46 pulses/sec; mean dominant frequency ≈ 2000 Hz [range ≈ 940–3300 Hz].

SURVEY OF THE LYCAENIDAE

All but 6 of the 36 species of Lycaenidae surveyed (tables 4, 5) produced a call that was detectable when any part of a caterpillar was touching the recording substrate. The ability to produce calls probably has its onset at the instar when the other ant organs develop (usually the third). However, the possibility that earlier instars do call cannot be eliminated because only caterpillars of third or later instars were tested. Third and post-third instar caterpillars produced calls when moving or feeding (but not when resting). Caterpillars that were parasitized by tachinid maggots also produced calls. No call was detected immediately prior to or after a molt in any caterpillar. Depending on the recording circumstances and the physiological state of the individual caterpillars, call pulse rates varied both within and between individuals and taxa.

Unlike the relatively uniform sounds produced by lycaenid pupae (see Hinton, 1948;

→

Fig. 7. Sound spectrograms of caterpillar calls and pupal stridulations. All are from the family Lycaenidae. Each sonagram represents 1 sec of signal; vertical lines represent $\frac{1}{10}$ of 1 sec. The arrow on the X-axis indicates the point where the wave form recording began (see fig. 8). All caterpillar calls were recorded from last instar larvae unless noted otherwise. **A,** *Thereus pedusa* caterpillar, Panama; **B,** *Thereus pedusa* pupa, Panama; **C,** *Strymon simaethis* caterpillar, Panama; **D,** *Strymon simaethis* pupa, Panama; **E,** *Thereus* nr *enenia* caterpillar, Panama; **F,** *Arawacus lincoides* caterpillar, Costa Rica; **G,** *Olynthus narbal* caterpillar, Panama; **H,** *Strymon yojoa* caterpillar, Panama; **I,** *Panthiades bitias* caterpillar, Panama; **J,** *Polyommatus icarus* caterpillar, England; **K,** *Lysandra bellargus* caterpillar, southern France; **L,** *Lysandra hispana* caterpillar, Southern France; **M,** *Lysandra hispana* caterpillar, Spain, Barcelona; **N,** *Maculinea alcon* caterpillar, France; **O,** *Maculinea alcon* pupa, France; **P,** *Lysandra coridon caelestissima* caterpillar, Spain; **Q,** *Lycaena hippothoe* caterpillar, Westerwald, Germany; **R,** *Lycaena phaleas* caterpillar, Westerwald, Germany; **S,** *Jalmenus evagoras* caterpillar, Queensland, Australia; **T,** *Jalmenus evagoras* pupa, Queensland, Australia.
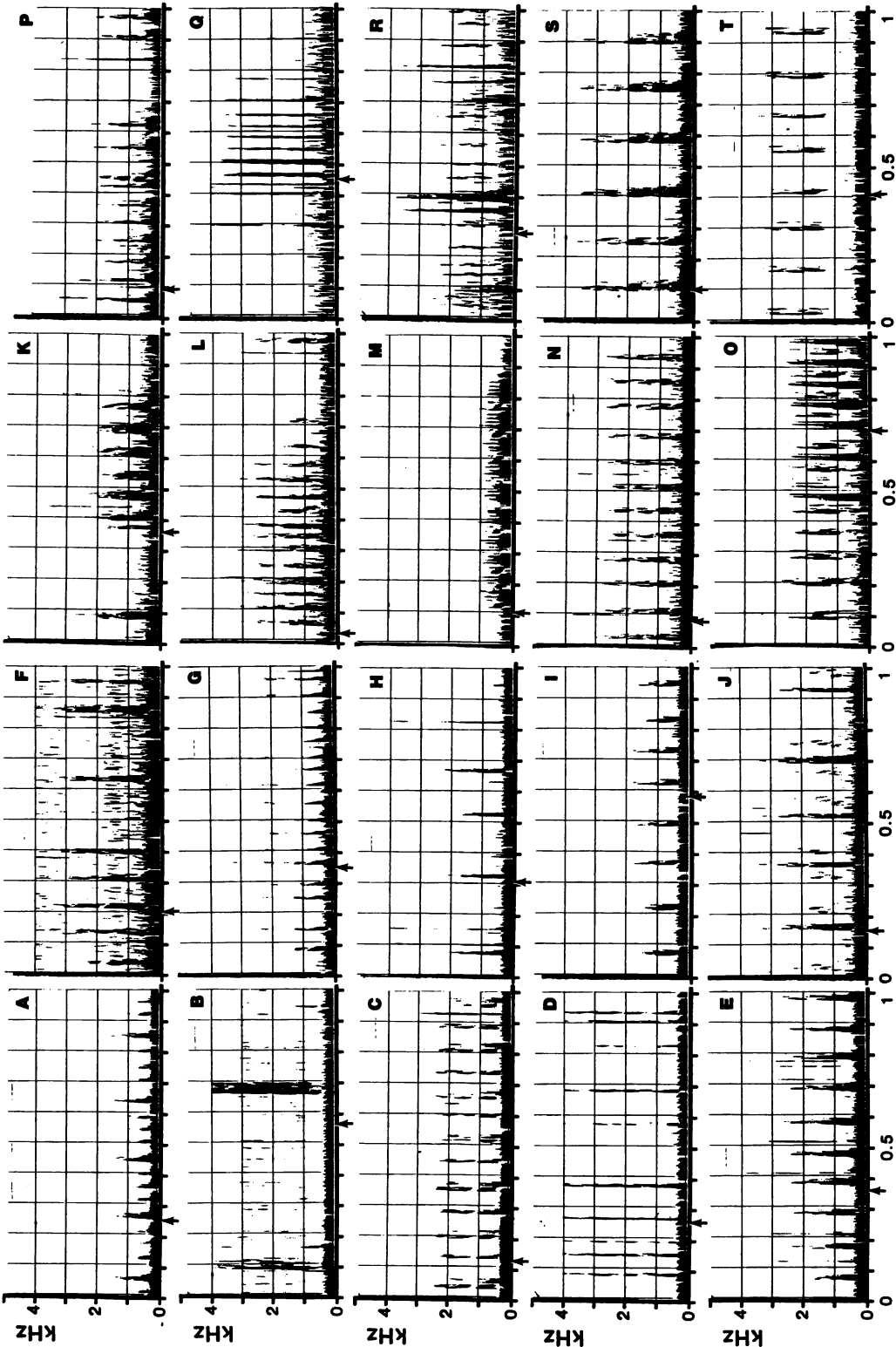
Time in Seconds

Fig. 8. Wave forms of caterpillar calls. The start of each wave form is marked with an arrow head on the X-axis of sonagrams illustrated in fig. 7. Each wave form represents 0.214 sec, and distance between vertical lines represents 8.23 μsec. **A,** *Thereus pedusa* caterpillar; **B,** *Thereus pedusa* pupa; **C,** *Strymon simaethis* caterpillar; **D,** *Strymon simaethis* pupa; **E,** *Thereus* nr *enenia*; **F,** *Arawacus lincoides*; **G,** *Olynthus narbal*; **H,** *Strymon yojoa*; **I,** *Panthiades bitias*; **J,** *Polyommatus icarus*; **K,** *Lysandra bellargus*; **L,** *Lysandra hispanus*; **M,** *Lysandra hispanus*; **N,** *Maculinea alcon* caterpillar; **O,** *Maculinea alcon* pupa; **P,** *Lysandra coridon*; **Q,** *Lycaena hippothoe*; **R,** *Lycaena phaleas*; **S,** *Jalmenus evagoras* larva; **T,** *Jalmenus evagoras* pupa.

Hoegh-Guldberg, 1972; Downey and Allyn 1973, 1979; Ellferich, 1988; figs. 7B, D, O, T; personal obs.), the sounds produced by lycaenid caterpillars are remarkably variable. For example, depending on the species, the calls may be described as: reminiscent of the throaty trills of chorusing toads (e.g., *Bufo*); a rhythmic "ah-ah-ah"; a grating crunch; or the whirring made by a small clockwork toy. Some species produced two distinct sounds simultaneously. Lycaenid caterpillars do not possess vibratory papillae (Cottrell, 1984; Harvey, 1987; Ballmer and Platt, 1988) or specialized epicranial structures, and they do not exhibit head oscillation behavior (personal obs.). They therefore must produce calls by different, as yet unknown means (see below).

DESCRIPTIONS OF LYCAENID CALLS

Chlorostrymon simaethis (figs. 7C, 8C): The caterpillar call has two components; a growling background with a wobbly, but consistent "beep-ahh-ahh-ahh, beep-ahh-ahh-ahh. . .";

mean pulse rate of (N = 4) 28 pulses/sec; mean dominant frequency ≈ 1500 Hz [range ≈ 1300–1700 Hz]. The pupa (figs. 7D, 8D) produces an irregular series of metallic clicks, with periods of silence between pulses; pulse rate (N = 1) 14 pulses/sec; mean dominant frequency ≈ 2290 Hz [range ≈ 1820–2760 Hz].

Strymon yojoa (figs. 7H, 8H): A constant pulse train that sounds like a metallic "fluttering of the tongue"; mean pulse rate of (N = 1) 15 pulses/sec; mean dominant frequency ≈ 700 Hz [range ≈ 540–830 Hz].

Arawacus lincoides (figs. 7F, 8H): A growling background with a pulse series of "bup-bup-bup. . ."; mean pulse rate of (N = 5) 13 pulses/sec; mean dominant frequency ≈ 700 Hz [range ≈ 300–1300 Hz].

Olynthus narbal (figs. 7G, 8G): A series of creaky, staccato trills of "duh-duh-duh-duh. . ."; mean pulse rate of (N = 3) 17 pulses/sec; mean dominant frequency ≈ 700 Hz [range ≈ 300–1500 Hz].

Thereus pedusa (figs. 7A; 8A): The caterpillar produces a vigorous and consistent growling background with a series of strong pulses, "bup-bup-bup. . ." that sound like a one-cylinder engine that fires only occasionally; mean pulse rate of (N = 4) 36 pulses/sec; mean dominant frequency ≈ 550 Hz [range ≈ 350–730 Hz]. The pupa (figs. 7B; 8B) produces two sounds—a consistent background whirring and occasional metallic chirps; pulse rate (N = 2) 19 pulses/sec; mean dominant frequency ≈ 1970 Hz [range ≈ 1400–2480 Hz]. *Note*: According to my fieldnotes, a mature caterpillar placed in a small, thin-walled plastic container produced a "faint, rhythmic bumping noise." This indicates that at least part of the call is airborne.

Thereus nr *enenia* (figs. 7E, 8E): A strong drumming series of "bup-bup-bup. . ." (like the calls of *Bufo marinus* toads); mean pulse rate (N = 1) 10 pulses/sec; mean dominant frequency ≈ 1600 Hz [range ≈ 900–2300 Hz].

Panthiades bitias (figs. 7I, 8I): A consistent series of evenly spaced drumming, "ooh-ooh-ooh-ooh. . ."; mean pulse rate (N = 2) 13 pulses/sec; mean dominant frequency ≈ 890 Hz [range ≈ 520–1250 Hz].

Thecla legytha: The call has two compo-

nents; a growling background and a series of barks that sound like bup-bup-bup. . ."; mean pulse rate (N = 1) 17 pulses/sec; mean dominant frequency ≈ 1600 Hz [range ≈ 960–2280 Hz].

Rekoa palegon: Call similar to *Thecla legytha*; man pulse rate (N = 3) 17 pulses/sec; mean dominant frequency ≈ 700 Hz [range ≈ 300–1500 Hz].

Tmolus echion: An infrequent series of "ah-ah, ah-ah. . ."; mean pulse rate (N = 6) 12 pulses/sec. Call not analyzed in detail.

Micandra platyptera: An infrequent "bup-bup-bup. . ." that is repeated sporadically; mean pulse rate (N = 2) 11 pulses/sec. Call not analyzed in detail.

Hypolycaena erylius: A constant nasal "yuh-yuh-yuh-yuh. . ."; termination of each individual pulse inflects upward; mean pulse rate (N = 1) 4 pulses/sec; mean dominant frequency ≈ 1400 Hz [range ≈ 300–2500 Hz].

Jalmenus evagoras (figs. 7S; 8S): The caterpillar call is a constant "khen-khen-khen-khen. . ."; pulse rate (N = 1) 7 pulses/sec; mean dominant frequency ≈ 1700 Hz [range ≈ 500–3000 Hz]. The pupa (figs. 7T; 8T) produces a series of metallic clicklike pulses, "kih-kih-kih-kih. . . ," with periods of silence between pulses; pulse rate (N = 1) 7.5 pulses/sec; mean dominant frequency ≈ 2300 Hz [range 1500–3100 Hz].

Lycaena phaleas (figs. 7R; 8R): The call has two components: a background that sounds like twisting a rubber balloon between one's hands, and a series of dominant "crunches" that appear at the end of each pulse train; pulse rate (N = 1) 20 pulses/sec; mean dominant frequency ≈ 1500 Hz [range ≈ 500–3600 Hz].

Lycaena hippothoe (figs. 7Q; 8Q): The call has two components; a ticking background, and a discrete, irregular series of dominant "bih-dup, bih-dup" pulses; pulse rate (N = 1) 8 pulses/sec; mean dominant frequency ≈ 1400 Hz [range ≈ 500–3500 Hz]. Calls much less frequently than does *L. phaleas*.

Leptotes cassius (figs. 3S; 4S): The call has two components; a ticking background and an irregular, galloping series of trills, "bih-dup bih-dup bih-dup. . . ," that gather momentum toward the end of the pulse train; pulse rate (N = 1) 5 pulses/sec; mean dom-

inant frequency ≈ 1500 Hz [range ≈ 500–3000 Hz].

Cupido minimus: The call is a constant series of repeated, stuttering "ah ah ah ah ah," a short interval of silence, then a repeated "ah ah ah ah ah"; pulse rate (N = 1) 8 pulses/sec; mean dominant frequency ≈ 1200 Hz [range ≈ 500–2000 Hz].

Maculinea alcon (figs. 7N; 8N): The caterpillar call has two components: a growling background, and a consistent, but wobbly series of "dik-a dik-a, dik-a, dik-a. . ."; pulse rate (N = 1) 12 pulses/sec; mean dominant frequency ≈ 350 Hz [range ≈ 100–2500 Hz]. The pupa produces a regular pulse train of "keh-keh-keh-keh. . ." terminating in a rattlelike pulse at the end of each series with a space between each pulse train (figs. 7O; 8O). A summary and analysis of *Maculinea* species and their attending ants will be presented elsewhere (DeVries et al., in prep.).

Plebulina emigdionis (figs. 3T; 4T): The call is an irregular, repeated series of "bi-da-da-da-dup. . ." with an upward inflection at the "dup," and a short silent interval between pulses; pulse rate (N = 1) 6 pulses/sec; mean dominant frequency ≈ 500 Hz [range ≈ 200–800 Hz].

Lycaeides melissa samuelis: An infrequent series of chirps; pulse rate (N = 1) 4 pulses/sec with long intervals (≈ 2 sec) between signals. The caterpillar calls infrequently. Not analyzed in detail.

Lysandra coridon (figs. 7P; 8P): A strong whimpering pulse train of "eh-eh-eh-eh. . ." (like a petulant child) that ascends in strength at the end of the pulse train (like toads trilling in the distance), and a short interval of silence between each pulse; pulse rate (N = 1) 13 pulses/sec; mean dominant frequency ≈ 1200 Hz [range ≈ 500–2000 Hz].

Lysandra hispana (figs. 7M, 8M): A caterpillar from Barcelona produced a consistent whimpering pulse, similar to that of *L. bellargus,* but ascending in strength at the end of each pulse train; pulse rate (N = 1) 15 pulses/sec; mean dominant frequency ≈ 1200 Hz [range ≈ 100–2000 Hz].

Lysandra hispana (figs. 7L, 8L): A caterpillar from France produced a strong, regular fluttering wheeze of pulses that "run out of air" at the end of each pulse train, and are separated by a short silence; pulse rate (N =

1) 15 pulses/sec; mean dominant frequency ≈ 1400 Hz [range ≈ 500–3000 Hz].

Lysandra bellargus (figs. 7K, 8K): A constant series of whimpering pulses "eh-eh-eh-eh. . ." (as a petulant child might make), with a short interval of silence between each pulse; each individual pulse sounds as though it has some reverberation in it (like toads trilling in the distance); pulse rate (N = 1) 10 pulses/sec; mean dominant frequency ≈ 500 Hz [range ≈ 300–700 Hz].

Polyommatus icarus (figs. 7J, 8J): A constant drumming series of "ba-da-da-dup, ba-da-da-dup. . ." that ends abruptly at an upward inflection point, and with a short silent interval between each trill; pulse rate (N = 1) 11 pulses/sec; mean dominant frequency ≈ 1500 Hz [range ≈ 300–3000 Hz].

SUMMARY OF RIODINID CALLS

Forty-four species of riodinid caterpillars from two subfamilies and nine tribes were surveyed for their ability to produce calls. Only 19 species from three tribes were shown to produce a call, and all 19 are myrmecophilous (tables 2–3). Removal of the vibratory papillae rendered caterpillars mute, and acoustic profiles for those are similar to caterpillars found in nature without vibratory papillae (figs. 3A–E). Thus, vibratory papillae are fundamental for call production (DeVries, 1988, 1990, figs. 3A–E, F–I; 4A–E, F–I).

Possession of vibratory papillae is considered a synapomorphy of the tribes Lemoniini and Nymphidiini (Harvey 1987). Thus, I expected that all caterpillars from these tribes would produce calls (DeVries, 1990). However, some caterpillars in the genus *Nymphidium* that possess vibratory papillae and epicranial granulae, and that exhibit head oscillation behavior, were found to be mute (table 3). This is probably because in these species, the epicranial granulations are reduced (fig. 6A–C), and there is a dense covering of mushroomlike setae on the epicranium (fig. 6D) that may prevent the vibratory papillae from contacting the epicranial granulations. Two species of *Nymphidium,* however, produced typical calls (table 2; figs. 3Q, R; 4Q, R). *Nymphidium* is apparently the only riodinid genus known where the possession

of vibratory papillae is not correlated with the ability to produce calls. Thus, it is important that we examine the caterpillars of other genera of the Nymphidiini (i.e., *Parnes, Periplacis, Zelotaea, Pandemos, Dysmathia, Hypophylla, Calliona, Rodinia, Adelotypa, Echenais, Calociasma, Setabis*) for the presence of mushroomlike setae on the epicranium, and for the ability to produce calls.

The caterpillars of all Eurybiini (*Eurybia, Alesa,* and *Mimocastnia*) are expected to possess myrmecophilous secretory organs, but not vibratory papillae (Harvey, 1987). In addition to lacking vibratory papillae, I found that *Eurybia* caterpillars do not have highly developed epicranial granulations (fig. 6E, F), and that they do not oscillate the head while calling. Since *Eurybia* caterpillars do call, this suggests that the ability to call has evolved at least twice within the Riodinidae. Two hypotheses might explain how calls are produced by *Eurybia* caterpillars: (1) the tiny bumps on the epicranium may grate on the distal edge of segment T-1 (although without obvious head movement this is unlikely), and (2) the call may be produced in a manner similar to the "shivering" in lycaenids (see below). A comparative study of the epicranial morphology, behavior, and calling ability in *Eurybia, Alesa,* and *Mimocastnia* may provide insight into the evolution of calling by riodinid caterpillars.

SUMMARY OF LYCAENID CALLS

Thirty species of lycaenid caterpillars, representing three subfamilies and five tribes, were found to produce calls, and all were species that associate with ants (table 4). Only six nonmyrmecophilous species (Theclinae, Eumaeini) were not observed to produce calls (table 5). The mechanism for lycaenid call production is unknown (see below), but riodinid and lycaenid myrmecophilous organs are not homologous (DeVries, 1988, 1991). This implies that calling ability in these butterfly groups is not homologous, but has evolved independently in these two families (DeVries, 1990, 1991a).

The only biogeographic area where calling by lycaenid caterpillars remains unknown is Africa (DeVries, 1990, tables 4–5). However, a posthumously published letter written in

Nigeria in 1917, suggests that C. O. Farquharson (1921: 376–377) was the first to detect lycaenid caterpillar calls. My annotations are in brackets:

> . . . in handling one of these [caterpillars], I suddenly was conscious of a curious sensation in my finger and thumb which is very difficult of description. As near as possible it reminded me of a very faint electric shock, not accompanied by prickly sensation but rather as if one were being tickled by a tiny brush of slightly strong bristles. [The species of this caterpillar was never identified. However, he then describes a different caterpillar, *Tanuetheria timon* Fabricius, as] I myself believe it to be electrical. I find it hard to say why, except it reminds me of nothing so much as the queer "internal" tickling that a faint discharge produces.

Eltingham (1921) found no electrical tissue in Farquharson's preserved caterpillars, but suggested that muscular contractions could have produced the "electrical sensation." Upon examining a live British lycaenid caterpillar [*Strymonidia pruni* Linnaeus] Eltringham commented (p. 485) that the caterpillar, ". . . did in fact shiver at short intervals. The movement was not sufficiently rapid to produce an electrical sensation, but it at least demonstrated that such muscular vibrations are possible." After listening to many calls, I find Eltringham's phrase "a shiver at short intervals" to be a useful description of the pulse trains produced by lycaenid caterpillars (figs. 3S, T; 5). Thus, on the strength of Farquharson's observations, Eltringham's description, and the taxonomic breadth of the survey here (table 4), I am confident that myrmecophilous African lycaenid caterpillars will be found to produce calls. In fact, this prediction was recently fortified when I found that the caterpillars of a lycaenid from Madagascar (tentatively identified as the genus *Hemiolaus*) produced calls.

I have observed the shivering behavior described by Eltringham (1921) in caterpillars of *Thereus pedusa, Arawacus lincoides, Jalmenus evagoras,* and *Lysandra bellargus.* Hence I believe that rapid muscular contractions are in some way fundamental to lycaenid caterpillar call production—even though my attempts to find sound-producing organs through dissection have failed. Answering two fundamental questions will provide a fuller understanding of the evolution of lycaenid calls, and will determine the course for future study: (1) What are the mecha-

nism(s) for production of caterpillars calls? and (2) Did the ability to produce caterpillar calls arise once or several times in the Lycaenidae?

COMPARISON OF LYCAENID AND RIODINID CALLS

To the human ear riodinid calls sound fast and "chirpy" while those of lycaenids sound like a slow "drumming." These differences are reflected in the verbal descriptions provided above. Overall, riodinid calls (14 species) show a mean dominant frequency of 1877.21 Hz (SE = 107.6; range 900–2550 Hz), and a mean pulse rate of 23.36 pulses/sec (SE = 4.21; range 6–48, while lycaenid calls (21 species) show a mean dominant frequency of 1085.24 Hz (SE = 96.42; range 500–1700 Hz) and a mean pulse rate of 13.76 pulses/sec (SE = 1.65; range 4–36). A comparison demonstrated that riodinid and lycaenid calls (one-way ANOVA) differ significantly both in mean dominant frequency (F[1] = 28.92, $p < .0001$) and in pulse rate (F[1] = 5.83, $p < .025$). Hence, riodinid calls sound "chirpy" simply because they tend to have a high dominant frequency and a fast pulse rate.

FUNCTION AND INFORMATION CONTENT OF CALLS

At least three lines of evidence suggest that caterpillar calls evolved in the context of ant symbioses. First, only myrmecophilous taxa are known to produce calls (tables 1–5). Second, the caterpillars that called also possessed secretory organs thought to be important in forming symbioses with ants (see Cottrell, 1984; Harvey, 1987; DeVries, 1988, 1991a; Ballmer and Platt, 1988). Finally, caterpillars gain protection against enemies by associating with ants (Pierce et al., 1987; DeVries, 1991c), and calling caterpillars can accrue and maintain the presence of more ants than those that are rendered mute (DeVries, 1990). Collectively these observations provide compelling support for the idea that caterpillar calls evolved only in the context of forming and maintaining symbioses with ants (figs. 1–2).

The range of frequencies found in caterpillar calls (300–3000 Hz) include frequencies that are known to travel considerable distances through appropriate substrate, and that are used by some insects in substrate-borne communication systems (Michelsen and Nocke, 1974; Gogala, 1985). In view of the fact that ants produce substrate-borne stridulations, and that co-workers respond positively to them (Markl and Hölldobler, 1978; Baroni-Urbani et al., 1988), it is likely that ants also respond to the calls of caterpillars (DeVries, 1990). Although the distance that caterpillar calls can travel through natural substrates is unknown, it may be a considerable distance; calls can travel the full length of a wooden meter stick (DeVries, unpubl.). Experiments designed to test the responses of ants to substrate-borne caterpillar calls are planned for the future, and will be reported elsewhere (DeVries, in prep.).

Insect calls have, in general, evolved to attract members of the same species (e.g., Alexander, 1962; Ewing, 1984; Dambach, 1989). It is therefore tempting to speculate that in the system described here, caterpillar calls may have evolved under selection for symbiosis to attract specific ant taxa. However, there is no evidence to suggest that such evolution has occurred. An analysis of the frequencies and pulse rates of *Maculinea* caterpillar calls showed little or no similarity to the stridulatory calls of the *Myrmica* ant species that tend them (DeVries et al., in prep.), even though *Maculinea* caterpillars are involved in obligate, species-specific associations with their host ants (Thomas et al., 1989). While some frequencies may eventually be found more attractive to ants than others, the most likely general hypothesis for the "information content" of caterpillar calls is simply that a constant, rhythmic call produces a positive, investigative response in ants. Once an ant has been attracted to a caterpillar, the secretory organs and specialized behaviors (Cottrell, 1984; DeVries, 1988; Fiedler and Maschwitz, 1988, 1989) in concert with calling may further induce the ant to maintain association with the caterpillar (DeVries, 1988, 1990).

SOUNDS PRODUCED BY PUPAE

Riodinid pupae are known to have intersegmental plates and files like those found in lycaenid pupae, and in both groups these are considered to act as a stridulatory mechanism

(Downey and Allyn 1973). Stridulation in lycaenid pupae is well documented (Hinton, 1948; Hoegh-Guldberg, 1972; Downey and Allyn, 1973, 1978; Elfferich, 1988; figs. 7B, D, O, T; 8B, D, O, T). Although it has been assumed that riodinid pupae produce sounds, there are no data to support this. Over a three-year period I surveyed the pupae of 26 riodinid species from two subfamilies and nine tribes for sound production (tables 2, 3). Surprisingly, I found no evidence that riodinid pupae produce sounds, even when I employed a particle velocity microphone. In view of these results, previous suggestions that pupal sound production is a universal trait among riodinids, and that it functions in myrmecophily or as a general defense (Ross, 1966; Downey and Allyn, 1973; Ellferich, 1988) need to be reevaluated.

FUTURE IMPLICATIONS

The observations described here provide a basis for predicting where to search for calling ability in butterfly caterpillars and other insects. In riodinids, only members of the tribes Eurybiini, Lemoniini and Nymphidiini produce calls (tables 2–3). Thus, it is likely that caterpillars of all non-myrmecophilous riodinid taxa will be found to be mute. For the Lycaenidae we have information for only five tribes and three subfamilies (tables 4, 5) of the eight subfamilies and 29 tribes proposed by Eliot (1973). Unfortunately, few data are available that address whether particular lycaenid taxa are typically myrmecophilous or not, especially among tropical groups. Hence, predicting which lycaenid taxa will produce calls is problematical. However, based on descriptions of Lipteninae and Poritiinae caterpillars (Clark and Dickson, 1971; Eliot, 1973; Cottrell, 1984), these are similar to nonmyrmecophilous riodinids (DeVries, 1991a), making it probable that their caterpillars are mute.

The ability to produce substrate-borne calls appears to be widespread among myrmecophilous butterfly caterpillars. With this system as a model, there is now a precedent to look for calling ability in other groups of insects that associate with ants. For example, given the propensity of Homoptera to produce calls (Ossiannilsson, 1949; Claridge

1985), and for some to form symbioses with ants (Way, 1963), the possibility exists that calls may be used to maintain ant association. In fact, some Neotropical Membracidae do appear to use vibrational communication when being tended by ants (DeVries, personal obs.). Thus, it seems appropriate to speculate that calling may be a trait of many myrmecophilous insects (e.g., Coleoptera, Orthoptera, Homoptera), and the techniques employed here might be utilized to investigate calling ability in all arthropod taxa that form symbiotic associations with ants (see Hölldobler and Wilson, 1990: 472–529, for a list).

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