PROC. ENTOMOL. SOC. WASH.
86(2), 1984, pp. 312–325

NATURAL HISTORY AND EVOLUTION OF *LYCOPERDINA FERRUGINEA* (COLEOPTERA: ENDOMYCHIDAE) WITH DESCRIPTIONS OF IMMATURE STAGES

JAMES PAKALUK

Department of Entomology, Cornell University, Ithaca, New York; Present address: Department of Entomology, University of Kansas, Lawrence, Kansas 66045.

Abstract.—Information on feeding biology, reproduction, host specificity, and the evolution of *Lycoperdina ferruginea* LeConte is presented. This species, which is primarily a gasteromycetophage, is widely distributed throughout North America. A description of the larva and pupa, including illustrations, is included. Known fungal host associations for species of *Lycoperdina* are summarized.

Lycoperdina ferruginea is the only Nearctic representative of a genus otherwise known from the Palaearctic and Ethiopian Regions (Strohecker, 1953). Although previous authors (Blatchley, 1910; Lawrence, 1977; Peterson, 1960) have noted the association between the puffball beetle *Lycoperdina ferruginea* and the fruiting bodies of the gasteromycete *Lycoperdon,* little is known about the biology of this beetle. Herein, I discuss various aspects of the natural history and evolution of this species. The larva and pupa are described in detail and illustrated.

Most North American endomychids have secretive habits; thus, they are rarely collected. *Lycoperdina ferruginea,* however, is commonly encountered, sometimes in large numbers. Adults (Fig. 2) are distinguished from all other North American beetles thus: often feeding upon spores of Lycoperdaceae; large size (6–8 mm); distinct pronotal foveae, pronotum with a well-developed stridulatory membrane; apparently contiguous procoxae. Most members of *Lycoperdina* are believed to be associated with puffballs. In addition to a discussion of host specificity in *Lycoperdina ferruginea,* I briefly review and summarize known host associations for other species of *Lycoperdina.*

METHODS

For examination, larvae were cleared in warm Nesbitt's solution and mounted directly into Hoyers medium. Selected structures (mouthparts and legs) were disarticulated to allow more accurate interpretation. Magnifications up to ×1000 were used for observation and illustration. All larval illustrations were prepared with an American Optical Microstar compound microscope equipped with a drawing tube. Pupal illustrations were made with a Wild M-5 dissecting microscope and a drawing attachment. The adult habitus was prepared by tracing the image projected from a 2 × 2 transparency.

I examined about 1000 adults and vouched each with labels dated "1982." Figure 15 is a summary of the known distribution of *Lycoperdina ferruginea.* Localities which could not be readily located on a standard reference map were omitted, and all unique state records without more specific locality information are represented by large dots at the geographic center of the state or province. Precise collecting data are on file at the Cornell University Insect Collection, Ithaca, New York. Dates of collections and habitat information are summarized under "Natural History." Acronyms in Table 1 designate insect depositories for particular specimens and follow those proposed by Arnett and Samuelson (1969).

NATURAL HISTORY

Lycoperdina ferruginea has been collected during all months of the year, and I have commonly taken it in central New York from the fruiting bodies of puffballs. Most collections were from forest litter situations (Fig. 16) or directly from the sporocarps of Lycoperdaceae (Figs. 17, 18). Collections from other fungi are considered either accidental host associations or direct feeding upon non-preferred alternate hosts.

It is not clear how many generations *Lycoperdina ferruginea* has per year since pupae have been collected in February, May, and June; early instar larvae have been collected in October and December; and teneral specimens have been recorded from each month March through September inclusive. From these data, I believe *Lycoperdina* does not have discrete breeding periods; reproduction and development are dictated primarily by host availability. Development of puffballs is variable, but most begin fruiting in the late summer or early fall and the gleba matures soon thereafter. This is an important aspect of larval development, since feeding upon host spores cannot begin until the gleba is fully mature. The larval mouthparts are highly adapted for sporophagy, and Lawrence (1977) has referred to the mandibular morphology of this animal as a "spore mill." The mola is greatly enlarged (with numerous tubercles), and the mandibular apices are reduced and truncate. These two modifications are particularly well suited for feeding upon spores in a spore-filled medium, such as the mature gleba of puffballs. In general, the larval mouthparts are similar to the feeding systems of microphagous larval forms outlined by Lawrence (1977) and Lawrence and Newton (1980).

Lycoperdina ferruginea and other species of *Lycoperdina* are probably not obligatorily gasteromycetophagous, although they do exhibit a strong preference for puffballs. Table 1 shows the known host associations for species of *Lycoperdina.* It is not clear whether reports from non-Lycoperdaceae are accidental occurrences or actual records of mycophagy upon alternate, non-preferred hosts, since direct feeding was not observed and gut contents were not examined. It is not uncommon to collect *Lycoperdina ferruginea* from forest litter or debris. Therefore, single or infrequent host associations are questionable, since this species inhabits a microhabitat that is especially rich in decaying organic matter that may potentially serve as a substrate for fungal growth. Obligate gasteromycetophagy for this group should not be discounted due to the occurrence of these beetles on other hosts since host specificity for a particular species may vary geographically, or seasonally, or both (Newton, In press). For mycophagous Coleoptera, the larval stages generally have a more restricted diet, so it is possible that the larvae are obligate gasteromycete feeders while the adults tolerate a greater diversity of fungal hosts.

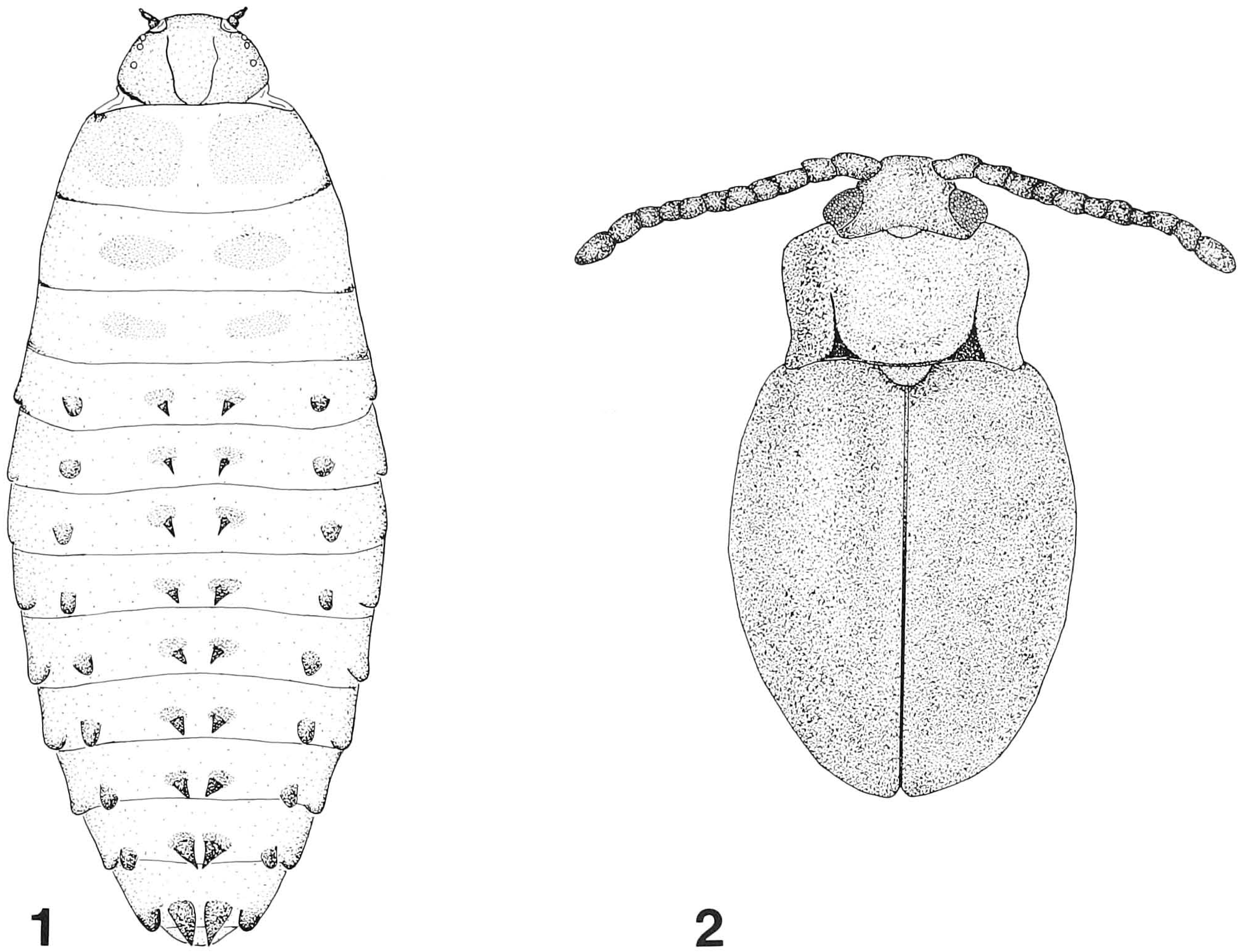
Table 1. Summary of known fungal associations for species of *Lycoperdina*.

Species	Fungus	Source
L. ferruginea LeConte	*Lycoperdon pyriforme*	Numerous sources
	L. perlatum	Pers. observ.[1]
	L. molle	Label data (LSUC)
	L. cf. *subvelatum*	Label data (LSUC)
	L. umbrinum	Pers. observ.[1]
	Peziza sp.	Label data (USNM)
	"Mushroom"	Label data (MCZC)
	Calvatia giganteum	Label data (FMNH)
	C. cyathiformis	Label data (LSUC)
L. penicillata Marseul	*Bovista plumbea*	Benick, 1952
	Lycoperdon gemmatum	Benick, 1952
L. succincta (Linnaeus)	*Lycoperdon gemmatum*	Benick, 1952
	Geastrum triplex	Sunhede, 1977
	Bovista nigrens	Horion, 1961
L. bovistae (Fabricius)	*Lycoperdon bovistae*	Benick, 1952
	L. excipuliforme	Rehfous, 1955
	L. caelatum	Benick, 1952
	L. gemmatum	Benick, 1952
	L. pyriforme	Benick, 1952
	Clitocybe splendens	Benick, 1952
	C. nebularis	Rehfous, 1955
	Bovista sp.	Ganglbauer, 1899
	Geaster fimbriatus	Rehfous, 1955
	G. rufescens	Rehfous, 1955
	Armillaria mellea	Rehfous, 1955
	Lactarius piperatus	Rehfous, 1955
	Russula delica	Rehfous, 1955
	Collybia fuscipes	Rehfous, 1955

[1] Host voucher specimens are deposited in the Herbarium of the Département de Botanique, Université de Liége, Liége, Belgium.

Acarid mites representing a new genus are commonly associated with this beetle and its fungal host. The deutonymph often occurs in large numbers inside the host fungus and is phoretic upon the adult and larva (Fig. 19). Reports of phoretic mites on beetle larvae are rare (Barry O'Connor, pers. comm.), and the significance of this behavior needs to be more fully examined. The adult mite is highly modified for life in a spore-filled puffball, since it "swims" through the ocean of spores with ease, but is incapable of walking outside the fruiting body (Barry O'Connor, pers. comm.). Deutonymphs of this mite species, or possibly a congener, were found on *Lycoperdina mandarinea* Gerstaecker from China (Barry O'Connor, in litt.). I have also collected acarid mites of yet another new genus from *Scleroderma citrinum* that was colonized by *Caenocara occulata* (Coleoptera: Anobiidae) in Tennessee.

The larvae of *Lycoperdina ferruginea* are relatively long-lived, and it is likely that most individuals overwinter as mid- to late-instar larvae. The fruiting bodies of most Lycoperdaceae are durable and often persist for a full year. Puffballs provide the larvae with a plentiful food source, as well as a stable habitat that

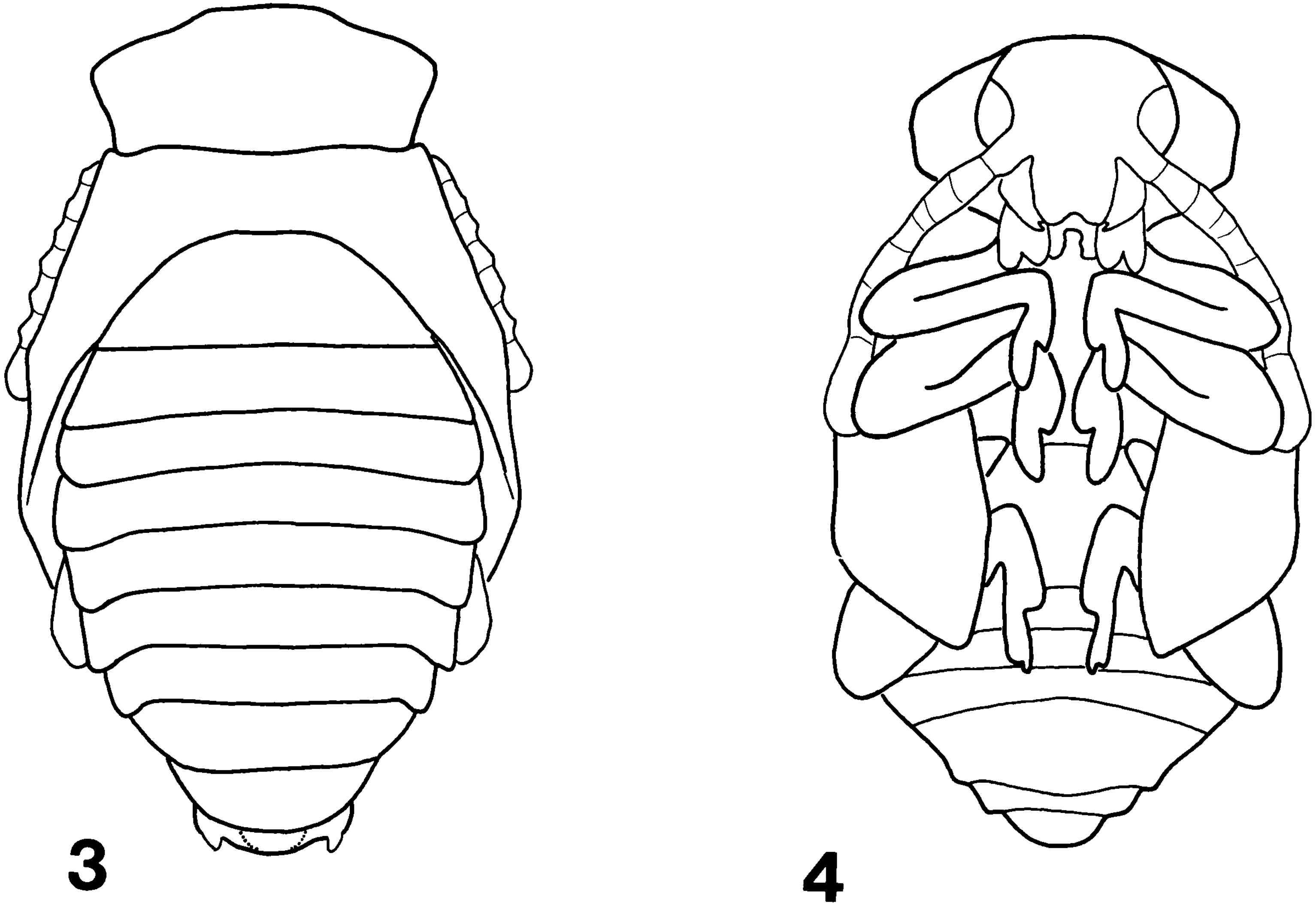


Figs. 1, 2. *Lycoperdina ferruginea.* 1, Larval habitus (dorsal). 2, Adult habitus (dorsal).

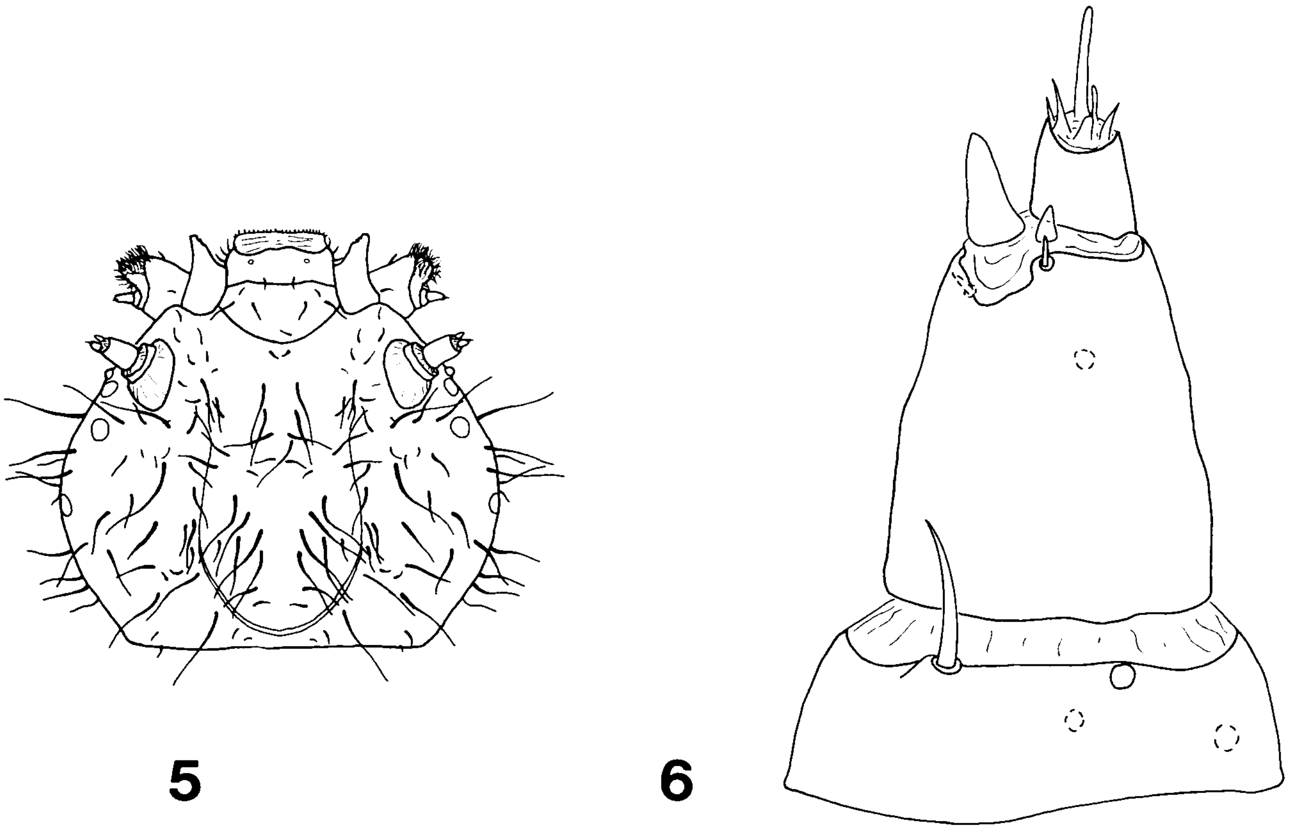
offers protection from predation and severe weather. The beetle pupates within the host fruiting body, and as many as eight pupae have been recorded in a single sporocarp, although the average is about three to four. The preferred location for pupation appears to be within the sterile base. Pupae are generally found within the spore mass only if available space within the sterile base has been utilized by other beetles which have burrowed into the spongy material.

Throughout their ontogeny, larvae frequently leave individual fruiting bodies and wander about, usually migrating to a different fruiting body. (Many species of *Lycoperdon* are gregarious and have large numbers of sporocarps in a small area (Fig. 18)). The larvae reenter a puffball to moult or feed. Their entrance into and their exit from the fruiting body is often via a hole that they have chewed through the peridium, although they also utilize the apical pore. Larval wandering behavior may contribute to spore dispersal in at least one of two ways. First, the larvae occassionally leave the external surface (peridium) of the puffball while wandering, so it is possible that their spore-covered bodies may brush spores onto an organic substrate, such as a rotting log. More important, however, is that the holes they chew in the peridium increase the likelihood of spore dispersal. Sunhede (1974, 1977) reports that similar gnaw-holes made by *Lycoperdina succincta* (Linnaeus) in *Geastrum triplex* enhance spore liberation.

The reasons for larval wandering in *Lycoperdina ferruginea* are unknown, but I will suggest three possible explanations for this behavior. 1) A small number of



Figs. 3, 4. *Lycoperdina ferruginea,* pupa. 3, Dorsal habitus. 4, Ventral habitus.



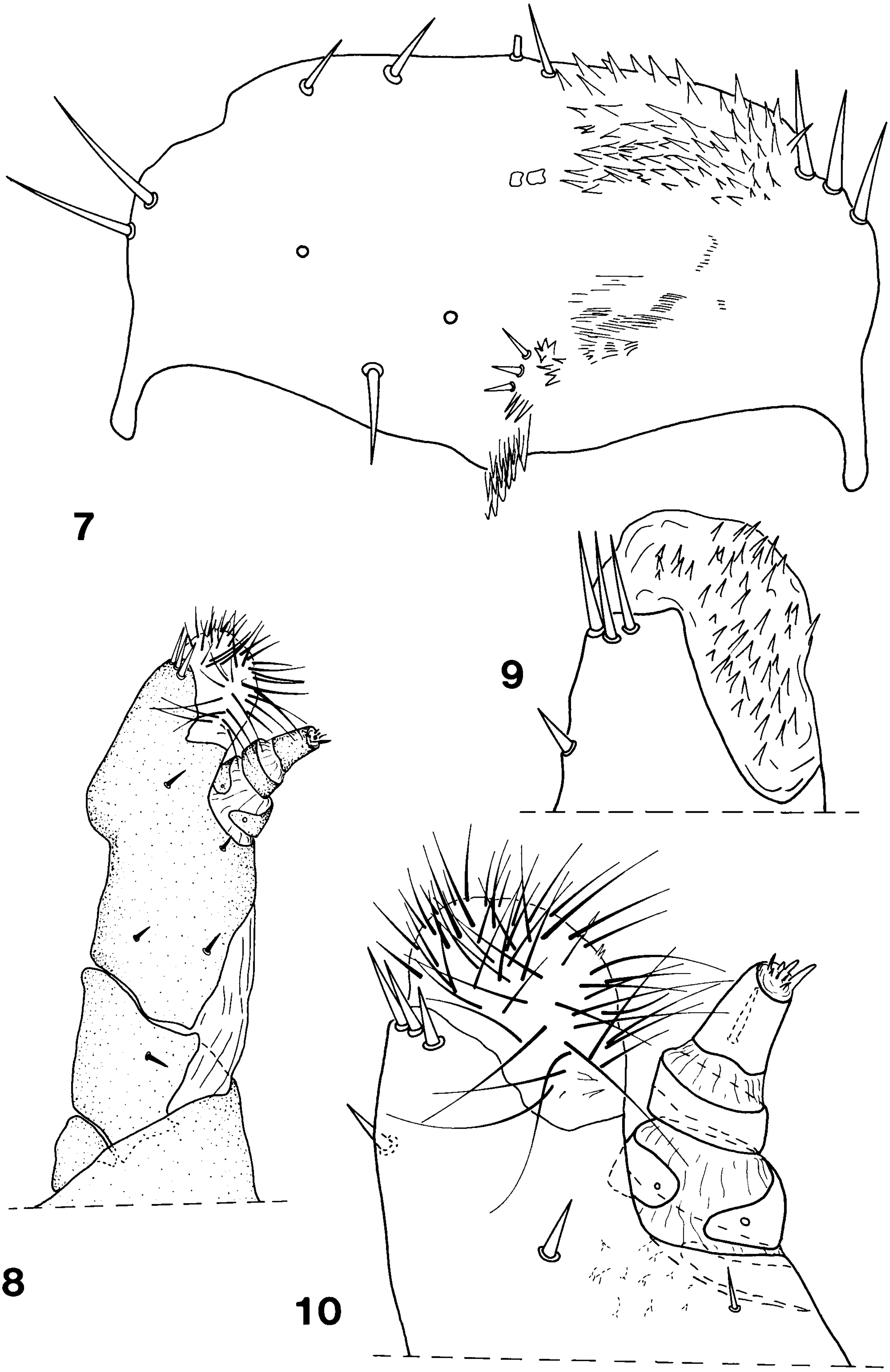
Figs. 5, 6. *Lycoperdina ferruginea,* larva. 5, Cranium (dorsal). 6, Antenna (ventral).

eggs are laid within a single fruiting body, but the food reserves within the puffball are insufficient for complete larval development. 2) Large numbers of eggs are deposited within each puffball, so the larvae must seek out nearby fruiting bodies for an additional, unexploited source of spores. 3) If a single female lays most or all of her eggs within a single fruiting body, and if food reserves within the puffball are sufficient for larval development, then wandering may be a device to prevent sib-matings. This presupposes that mating takes place, in at least some instances, before adults have left their puffball host following pupation.

The adults are predominantly brachypterous, although macropterous forms are present in low numbers. I selectively examined the wing condition of approximately 100 beetles from series that varied temporally and geographically. Both males and females were examined, and there was no genital variation among comparable forms. Only two macropterous individuals were recorded, one from Louisiana and the other from Michigan. From these data, I believe macroptery is maintained within the species at a low level. It should be emphasized, however, that fully winged forms are not necessarily capable of flight. Puffballs, or at least groups of puffballs, are somewhat isolated from each other, and their fruiting bodies are generally persistent for about a year. Thus, puffball feeders occupy stable habitats that are moderately isolated from each other. Both of these criteria are consistent with the conditions necessary to maintain a selective advantage for flight polymorphism within a species (see Harrison, 1980).

EVOLUTION

This section is based in part on the geological and climatological data for North America presented by Matthews (1979). Historical premises that I have accepted



Figs. 7–10. *Lycoperdina ferruginea*, larval mouthparts. 7, Epipharynx (left half) and labrum (right half). 8, Maxilla (ventral habitus). 9, Maxilla, mala (dorsal). 10, Maxilla, mala (ventral).

11

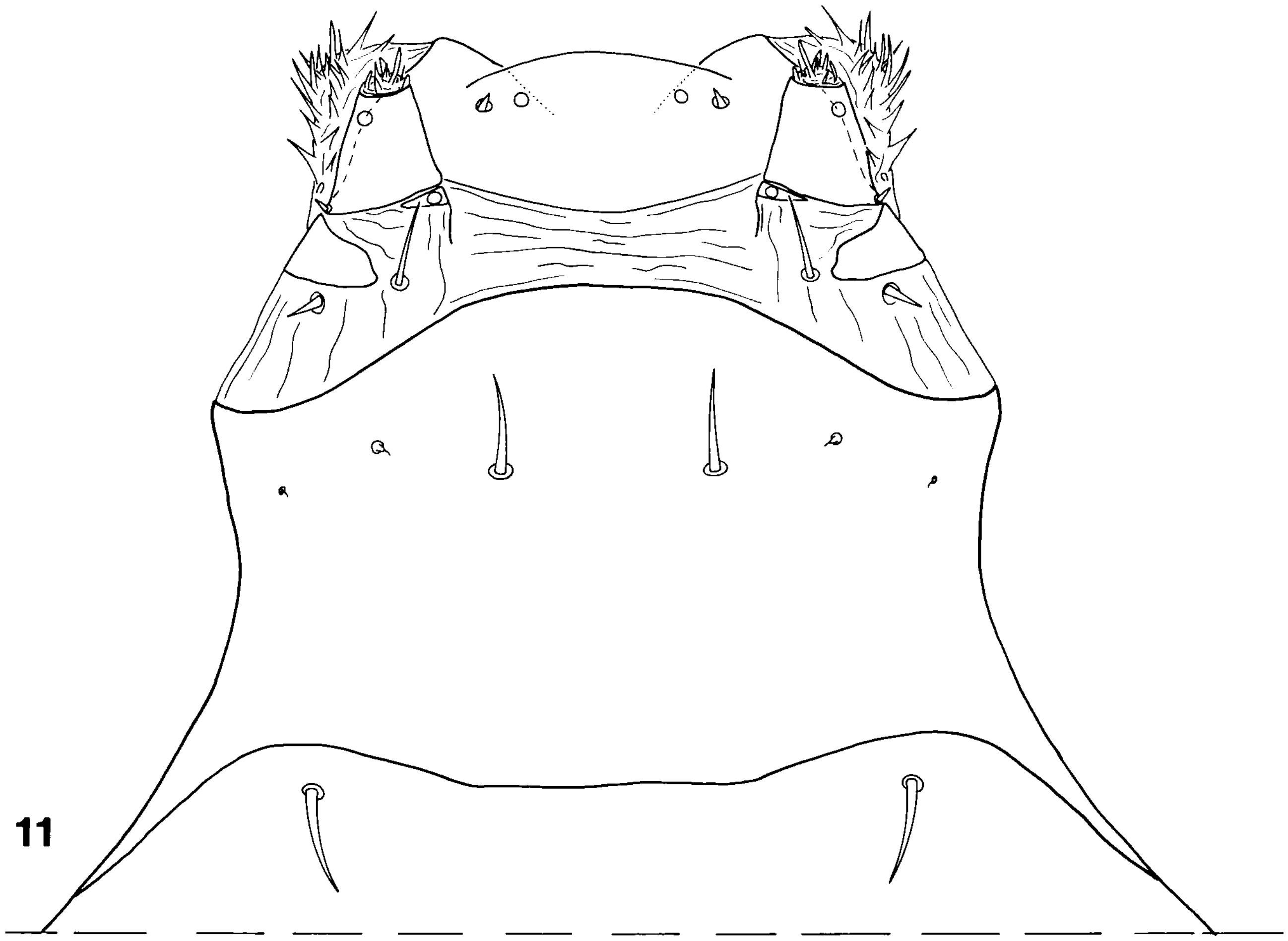
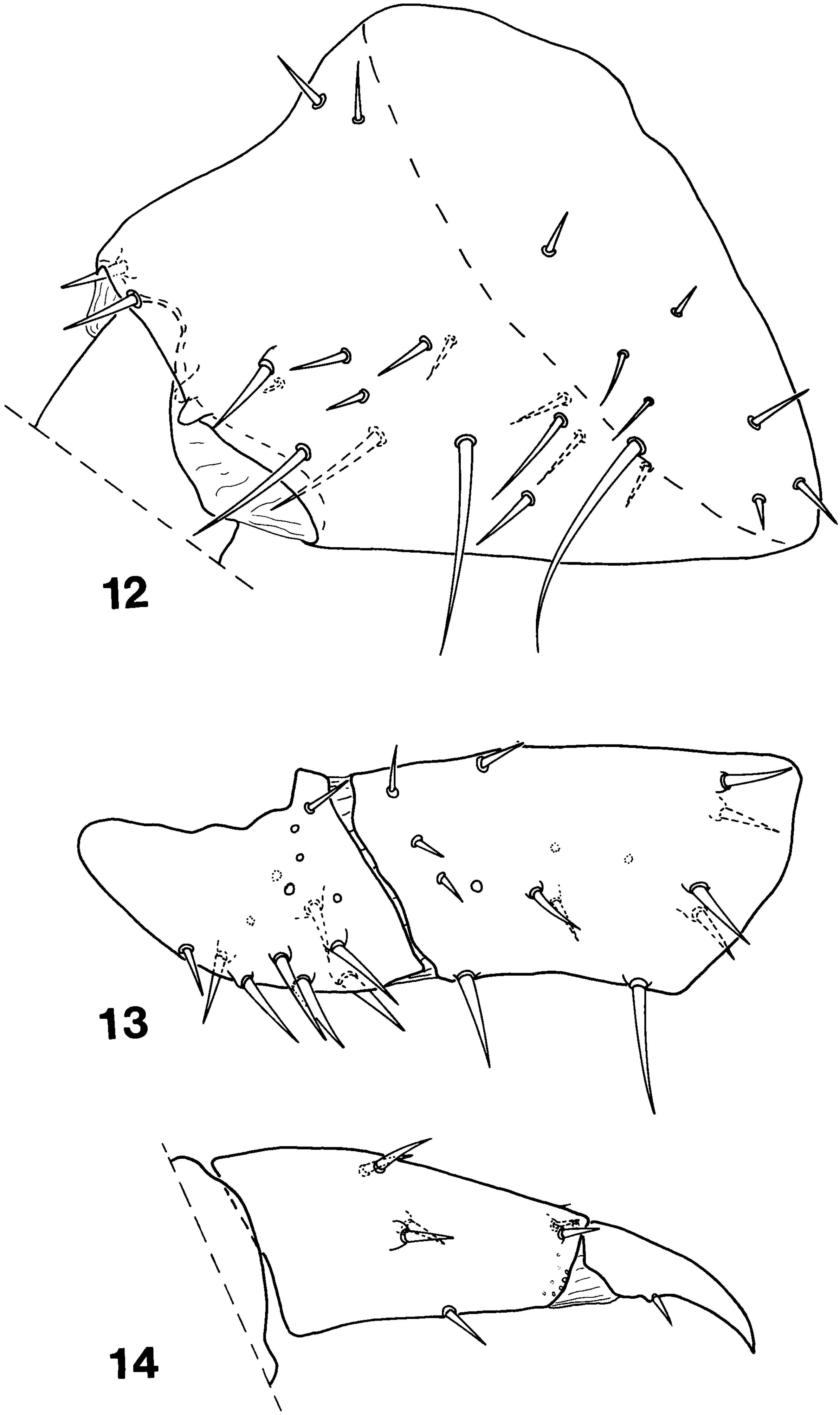


Fig. 11. *Lycoperdina ferruginea,* larval labium, distal portion of prementum (ventral).

which have influenced the following discussion and conclusions are: a redated Tertiary time scale placing the beginning of the Quaternary at about 1.6 million years ago, a recurring Beringian land bridge from the late Cretaceous until the late Pliocene, and a unique vegetational (and perhaps insect) character of each interglacial period, thus dismissing the concept of Geofloras.

Fossil *Lycoperdina* are known from the Oligocene (Strohecker, 1953), and this provides a minimum age for the genus. Given the relatively slow rate of evolution for *Lycoperdina* (see below), vicariance probably occurred between a widespread ancestral Beringian species about 3 million years ago. This event resulted in *Lycoperdina ferruginea* and its sister, probably the Siberian *L. koltzei* Reitter (see Strohecker, 1970). Puffballs were well established in North America at this time (Vincent Demoulin, in litt.), and they provided a widespread and abundant food source throughout the region east of the North American Cordillera and not much south of successive glacial advances. Genera preferring open grasslands and steppe, such as *Bovista* and *Calvatia,* may have been dominant in the north, while *Lycoperdon* was probably widespread and abundant in southern forested regions (Vincent Demoulin, in litt.). As the Wisconsin glaciation retreated about 10,000 years ago, *Lycoperdina ferruginea* began a northward migration extending to its present range.

Several speculations about *Lycoperdina ferruginea* and its relatives are: (1) Brachyptery is probably common throughout this group, but percentages of macropterous individuals may vary significantly both between species and between



Figs. 12–14. *Lycoperdina ferruginea*, larval leg. 12, Coxa. 13, Trochanter and femur. 14, Tibia and tarsungulus.

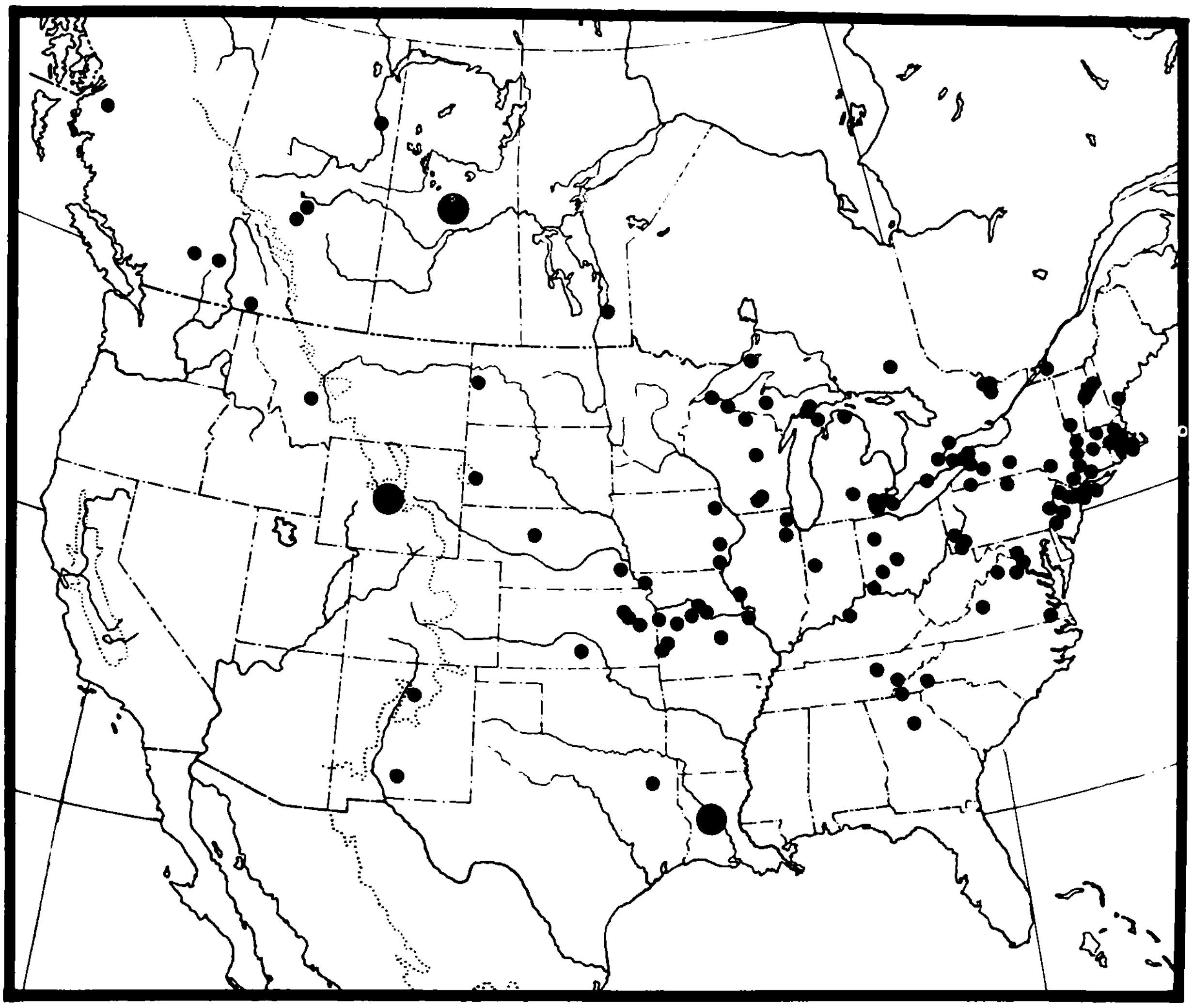


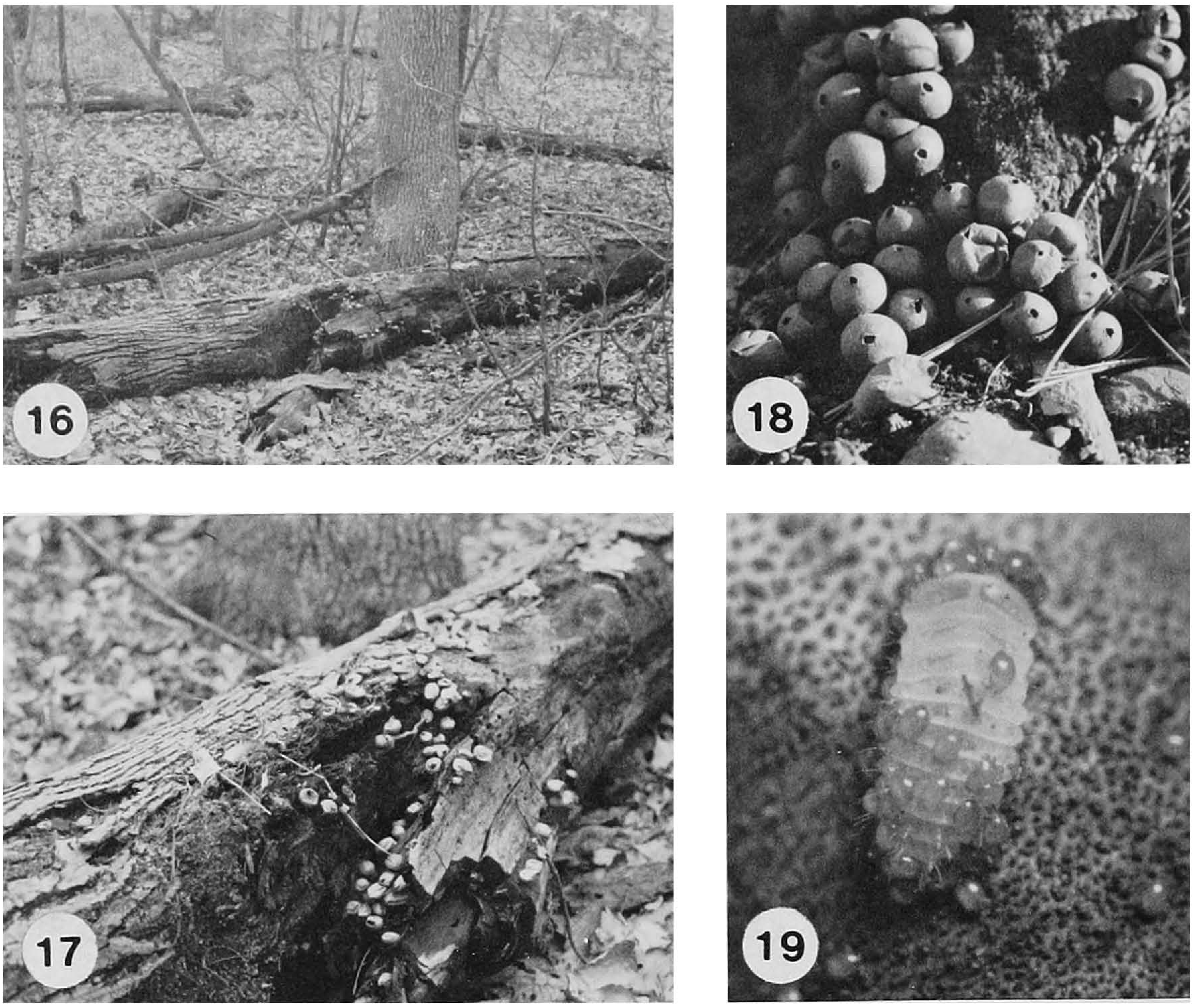
Fig. 15. Known distribution of *Lycoperdina ferruginea* in North America.

populations of a species.[1] (2) Based on out-group comparisons, brachyptery is an ancestral condition, thus consistent reduction of flight wings is a result of common ancestry rather than independent parallel loss. (3) Conditions selecting for brachyptery have probably changed in intensity through time, so Pleistocene *Lycoperdina* may have been almost entirely macropterous. Thus, they may have possessed strong and rapid dispersal capabilities.

Whitehead (1972) discussed two general patterns of speciation: islandic, which is relatively fast, and continental, which is relatively slow. Wheeler (1979) discussed gasteromycetophagy in relation to speciation patterns of *Creagrophorus* (Coleoptera: Leiodidae), and I concur that due to the widespread occurrence of puffballs (and possibly alternate, non-preferred hosts; see "Natural History") in suitable microhabitats, puffball feeders were probably unaffected by rapid climatic changes of the Pleistocene and thus demonstrate a continental pattern of speciation. Wheeler attributes the slow rate of speciation in *Creagrophorus* to the highly

---

[1] Dr. Strohecker has kindly examined the wing condition for 11 species of *Lycoperdina*, and he reports the occurrence of aptery or brachyptery for all 11 species. The species he examined are: *L. angusta* Arrow, *L. apicata* Fairmaire, *L. castaneipennis* Gorham, *L. koltzei* Reitter, *L. mandarinea* Gerstaecker, *L. morosa* (Arrow), *L. mus* Arrow, *L. pencillata* Marseul, *L. pulvinata* Reitter, *L. succincta* (Linnaeus), *L. validicornis* Gerstaecker. I have also examined brachypterous specimens of *L. bovistae*.



Figs. 16–19. *Lycoperdina ferruginea* habitats. 16, Hardwood forest in central New York. 17, *Lycoperdon pyriforme* sporocarps on prostrate log. 18, *Lycoperdon pyriforme* with well-developed apical pores. 19, *Lycoperdina ferruginea* larva, with phoretic acarid mites, wandering on peridium of *Lycoperdon pyriforme.*

vagile winged adults. How might brachyptery affect rates of speciation within *Lycoperdina,* and given the present predominantly flightless condition, how could *L. ferruginea* have dispersed so thoroughly throughout North America?

If a high level of brachyptery is a post-Pleistocene condition, there is little difficulty explaining *Lycoperdina*'s extensive North American distribution. If, however, *Lycoperdina ferruginea* has a long history of almost complete brachyptery, is a transcontinental distribution by natural dispersal mechanisms possible? I think this phenomenon can be easily explained: macropterous individuals, although rare, are sufficiently represented to maintain adequate interdemic gene flow. Ball and Negre (1972) discovered similar conditions in North American *Calathus* (Coleoptera: Carabidae), and I agree that in predominantly brachypterous species, macroptery may be sufficiently maintained to instill good dispersal power. I believe the widespread distribution of *Lycoperdina ferruginea,* without apparent geographical variation, are indicators of adequate dispersal and gene flow that have retarded reproductive segregation.

Description of Last Instar Larva

With characters of Endomychidae (Lawrence, 1982). Length at midline about 10 mm; body elongate (Fig. 1); widest at middle, gradually tapering anteriorly and posteriorly.

Cranium (Fig. 5) about as long as wide; 4 pairs of ocelli. Frontal suture U-shaped, almost reaching posterior margin of cranium; coronal suture absent. Antenna (Fig. 6) small, reduced. Sensory appendage triangular, anteroventrad and subequal in length to antennal segment III. Antennal segment I short, broad; 1 ventral and 2 dorsal pores; 1 large ventral seta as in Fig. 6. Segment II longest; subcylindrical, slightly tapering distally; 1 dorsal pore; 1 small dorsal seta and 1 small ventral seta, each near apex. Segment III small, about as long as sensory appendage; apex truncate, with 6 processes as in Fig. 6; longest apical process subequal in length to segment III. Labrum (Fig. 7, left half) transverse, about 2× as wide as long; with 2 sets of pores; 5 pairs of setae, with a single seta on midline. Epipharynx (Fig. 7, right half) with patch of short spines distad as figured; patch of spines and setae posteriorly along midline. Mandible (cf. Lawrence, 1977; Figs. 10–11) short, broad; apex truncate; molar enlarged, small teeth present; protheca membranous. Maxilla (Fig. 8–10) with small subtriangular juxtacardo. Cardo pentangular, with 1 seta. Stipes elongate; 2 setae proximad, 1 seta near base of palp, 1 seta centrally near base of mala, 6 anteroventral setae on mesal margin. Mala membranous, with dense fringe of hairs ventrally; many short spines dorsally. Palpifer small; palpus three-segmented. Palpal segment I an incomplete sclerotized ring with 2 ventral pores. Segment II narrower, about as long as segment I. Segment III elongate, subcylindrical; dorsal digitiform sensillum present; 8 apical sensory processes. Labium (Fig. 11) reduced; prementum short; postmentum large, well developed. Palp two-segmented, first segment a highly reduced mesal sclerite.

Prothorax about 2× as wide as long, broadest posteriorly; 2 large notal plates, each centrally depressed. Mesothorax and metathorax about 4× as wide as long; each with 2 small tergal plates subequal in size. Legs (Figs. 12–14) increasing in size posteriorly. Coxa (Fig. 12) subquadrate; 7 dorsal setae, 19 ventral setae. Trochanter (Fig. 13) subtriangular; 4 ventral pores, 2 dorsal pores; 6 ventral setae, 3 dorsal setae. Femur (Fig. 13) elongate, about 2× as long as wide; 1 pore ventrally, 2 pores dorsally; 3 setae on dorsum, 9 setae on venter. Tibia (Fig. 14) elongate, narrowing distally; 4 ventral setae, 3 dorsal setae; rows of micropores distally on both ventral and dorsal surface. Tarsungulus (Fig. 14) unisetose.

Abdominal terga I–IX with dorsolateral and lateral verrucae becoming approximate posteriorly. Paired dorsal spines along midline increasing in size caudally. Segments I–VIII about 4–5× as wide as long; segment III broadest; segment VIII about 3× as wide as long; segment IX about 2× as wide as long. Segment X reduced, posteroventrally positioned. Urogomphi absent.

Description of Pupa

As shown in Figs. 3–4. Partially enclosed by larval skin. Dorsum covered with fine pubescence; ventrites completely lacking setae. Head shape and dimensions similar to adult. Labrum elongate, extending to apex of mandibles, with emarginate apex. Mandibular apices bidentate, sclerotized. Abdominal spiracles I–V tuberulate, functional; tracheae well-developed. Spiracles VI–VII marked externally, not functional. Spiracle VIII barely visible externally, not functional.

Acknowledgments

The following institutions made material available for study. I thank the curators of these collections, without whose kind help this study would not have been possible: L. H. Herman, American Museum of Natural History; D. H. Kavanaugh, California Academy of Sciences; J. T. Doyen, University of California, Berkeley; J. M. Campbell, Canadian National Collection of Insects; Q. D. Wheeler, Cornell University Insect Collection; L. E. Watrous, Field Museum of Natural History; C. B. Barr, Louisiana State University; C. L. Hogue, Natural History Museum of Los Angeles County; A. F. Newton, Museum of Comparative Zoology; E. U. Balsbaugh, North Dakota State University; J. D. Lattin, Oregon State University; P. D. Ashlock, University of Kansas; G. E. Ball, University of Alberta; G. G. E. Scudder, University of British Columbia; C. L. Smith, University of Georgia; B. M. O'Connor, University of Michigan; E. G. Riley, University of Missouri; T. L. Erwin, National Museum of Natural History.

I thank Vincent Demoulin and Barry O'Connor who kindly made identifications and offered information about host Gasteromycetes and phoretic acarid mites respectively. John Rawlins prepared the photographs with mites phoretic upon *Lycoperdina* larvae, and E. Richard Hoebeke and Quentin Wheeler collected puffballs and contributed valuable field observations. Special thanks to George Byers, Barry O'Connor, Fred Strohecker, and Quentin Wheeler for critically reviewing this paper. This research was supported in part by grants from the Cornell University Chapter and the National Chapter of the Society of Sigma Xi, and Cornell University Hatch Project NYC139426 (Q. Wheeler, Project Director).

LITERATURE CITED

Arnett, R. H., Jr. and G. A. Samuelson. 1969. Directory of Coleoptera Collections of North America (Canada through Panama). Cushing-Malloy. Ann Arbor. 123 pp.

Ball, G. E. and J. Negre. 1972. The taxonomy of the Nearctic species of the genus *Calathus* Bonelli (Coleoptera: Carabidae: Agonini). Trans. Am. Entomol. Soc. 98: 412–533.

Benick, L. 1952. Pilzkäfer und Käferpilze. Acta Zool. Fenn. 70: 1–250.

Blatchley, W. S. 1910. An Illustrated Descriptive Catologue of the Coleoptera or Beetles known to Occur in Indiana. Indianapolis, Indiana. 1385 pp.

Ganglbauer, L. 1899. Die Käfer von Mitteleuropa. Dritter Band. Familienreiche Staphylinoidea. II. Theil. Druck und Verlag von Gerold's Sohn. Wien. 635 pp.

Harrison, R. G. 1980. Dispersal polymorphisms in insects. Ann. Rev. Ecol. Syst. 11: 95–118.

Horion, A. 1961. Faunistik der mitteleuropäischen Käfer. Band VIII: Clavicornia. 2. Teil (Thorictidae bis Cisidae) Teredilia Coccinellidae. Überlingen-Bodensee. 375 pp.

Lawrence, J. F. 1977. Extraordinary images show how beetles have adapted to live off plants and each other. Horticulture 55: 8–13.

———. 1982. Coleoptera, vol. 2, pp. 482–553. *In* S. P. Parker (ed.), Synopsis and Classification of Living Organisms. McGraw-Hill. New York.

Lawrence, J. F. and A. F. Newton. 1980. Coleoptera associated with the fruiting bodies of slime molds (Myxomycetes). Coleopt. Bull. 34(2): 129–143.

Matthews, J. V. 1979. Tertiary and Quaternary environments: Historical backgrounds for an analysis of the Candian insect fauna. *In* H. V. Danks (ed.), Canada and its insect fauna. Mem. Entomol. Soc. Can. 108: 31–86.

Newton, A. F. In press. Mycophagy in the Staphylinoidea. *In* Q. D. Wheeler and M. Blackwell (eds.), Fungus-Insect Relationships. Columbia University Press. New York.

Peterson, A. 1960. Larvae of insects. Part II, Coleoptera, Diptera, Neuroptera, Siphonaptera, Mecoptera, Trichoptera. Columbus, Ohio. 416 pp.

Rehfous, M. 1955. Contribution à l'étude des insectes des champignons. Mitt. Schweiz. entomol. Ges. 28: 1–106.

Strohecker, H. F. 1953. Genera Insectorum (Endomychidae). Fasc. 210. Desmet-Verteneuil. Bruxelles. 140 pp.

———. 1970. Ergebnisse der zoologischen Forschungen von Dr. Z. Kaszab in der Mongolei. 225. Endomychidae. Ann. Hist.-Nat. Musei Nat. Hung. 62: 245–7.

Sunhede, S. 1974. Studies in Gasteromycetes I. Notes on spore liberation and spore dispersal in Geastrum. Sven. Bot. Tidskr. 68: 329–343.

———. 1977. Morphology and intraspecific variation in *Geastrum triplex* Jungh. Bot. Not. 130: 403–416.

Wheeler, Q. D. 1979. Revision and cladistics of the Middle American genus *Creagrophorus* Matthews (Coleoptera: Leiodidae). Quaest. Entomol. 15: 447–479.

Whitehead, D. R. 1972. Classification, phylogeny, and zoogeography of *Schizogenius* Putzeys (Coleoptera: Carabidae: Scaratini). Quaest. Entomol. 8: 131–348.