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SYSTEMATICS, EVOLUTION, AND ZOOGEOGRAPHY OF THE CAVERNICOLOUS CAMPODEIDS OF THE GENUS LITOCAMPA (DIPLURA: CAMPODEIDAE) IN THE UNITED STATES

Virginia Polytechnic Institute and State University PH.D. 1981

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SYSTEMATICS, EVOLUTION, AND ZOOGEOGRAPHY OF THE CAVERNICOLOUS CAMPODEIDS OF THE GENUS <u>LITOCAMPA</u> (DIPLURA: CAMPODEIDAE) IN THE UNITED STATES

by

Lynn Milton Ferguson

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Zoology

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF ILLUSTRATIONS

How much do we know about life on this little-known planet beneath our feet, the planet earth? We have not even approached the end of cataloguing the creatures that share the earth with us: and this should be the very first step in our knowledge.

—Howard Ensign Evans, Life on a Little-known Planet

To do science is to search for repeated patterns, not simply to accumulate facts; and to do the science of geographical ecology is to search for patterns of plant and animal life that can be put on a map.

—Robert H. MacArthur, Geographical Ecology

INTRODUCTION

Diplurans are slender, white, eyeless, and wingless hexapods (Fig. 1) which live under rocks, in the soil, and in caves. Among the apterygotes the Campodeidae is the group which, along with the Collembola, contains the majority of the cavernicolous forms (Vandel, 1965). Only eight species of cavernicolous campodeids have been described from the United States, all belonging to the genus *Litocampa* (formerly *Plusiocampa*, in part). Four of these species occur in caves of southwestern Virginia: *L. cookei* plus three new species (Ferguson, 1980; in press). *Litocampa cookei* is also found in central Kentucky caves including Mammoth Cave, its type locality (Packard, 1871), although there is some dispute over its status (Silvestri, 1934b; Condé, personal communication with T. C. Barr, Jr.; Barr, 1967). *Litocampa jonesi* was described from a cave in north central Tennessee, *L. valentinei* and *L. henroti* from caves in Madison County, Alabama, and *L. fieldingi* from a cave in Greenbrier County, West Virginia (Condé, 1949b). Descriptions of the last four species are limited to adult females in three cases and an immature male in the other. Only one other species of *Litocampa* has been described from North America, a cavernicole from Mexico (Wygodzinsky, 1944b). Several taxonomic papers have been written on epigean campodeids in the United States (Gardner, 1914; Hilton, 1932, 1936; Silvestri, 1933e; Condé and Thomas, 1957; Bareth and Condé, 1958;

FIGURE 1.--Litocampa barringerorum, new species, a cavernicolous campodeid dipluran from the type locality, Fallen Rock Cave, Tazewell Co., Virginia. (Photograph by the author)

Condé and Geeraert, 1962); however, a member of the genus Litocampa has never been reported although epigean species do exist in other parts of the world (Condé, 1956a).

The present study was originally intended to be a treatise on the cavernicolous campodeids of the United States. However, due to the wealth of material finally gathered, the study has been restricted to an investigation of the species of the genus Litocampa. Cavernicolous species belonging to other genera, Haplocampa and Metriocampa (Ferguson, 1975) and Eumesocampa (Ferguson, 1978), have already been treated elsewhere. These taxa as well as other genera and species known from caves in the United States are listed in Appendix I and indicated on Map IA.

The general objective of this research is to shed some light on the evolutionary relationships and zoogeography of the cavernicolous Litocampa in the United States. The primary objective is the discovery and description of new species, redescription of earlier described species based on new material, and resolution of the taxonomic problem involving Litocampa cookei. Secondary objectives are to determine the geographic distribution of these species and how it relates to the dispersal of the group, and to collect supplementary information on the life history, parasites, food preference, and ecology of the group.

The current investigation has revealed twelve new species of Litocampa. A cladistic analysis of their characters, combined with zoogeographical data, suggests that the American Litocampa have radiated from the Southern Appalachian highlands. The overall primitiveness of this group of arthropods and the distribution of the *Litocampa* and the closely related *Plusiocampa* strongly suggest an ancient equatorial distribution that has been disrupted by plate tectonics.

MATERIALS AND METHODS

In addition to obtaining specimens for study from the individuals and institutions listed under Acknowledgements, I visited caves in Virginia, West Virginia, Pennsylvania, Massachusetts, Tennessee, Alabama, Kentucky, Indiana, South Dakota, Idaho, Washington, and Oregon in search of cave diplurans. Several undescribed species of invertebrates other than diplurans were collected on these trips. These have been sent to other systematists for study. I also visited the National Museum of Natural History (Smithsonian Institution), the Museum of Comparative Zoology (Harvard University), and the Peabody Museum (Yale University), where I examined additional material, including the type specimen of Litocampa cookei (Packard) at Harvard University.

In caves, campodeids were generally found by searching along clay and silt banks of subterranean streams, by looking under stones, and by examining, in particular, any organic matter that was present. The chances of finding campodeids were greatly enhanced by the use of some type of bait. Roquefort cheese and blue cheese worked quite well. Once found, the campodeids were collected with an aspirator or, preferably, with a small camel's hair brush dipped in the preservative (70 - 75% ethyl alcohol). Campodeids should be swiped from the side with the moistened brush since this is much less likely to damage them or cause the loss of antennae and cerci.

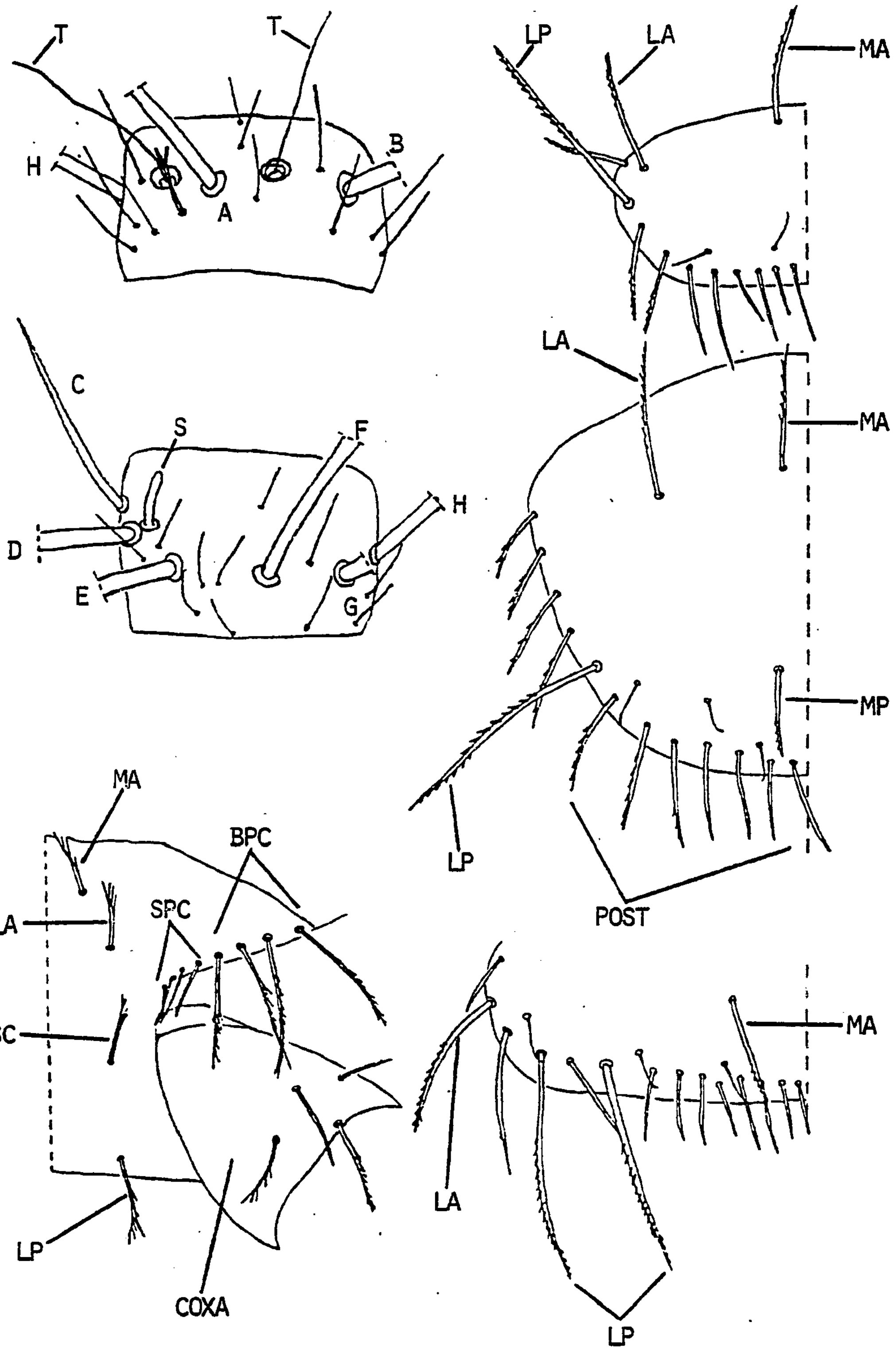
Data for each collection were entered serially in a log book, the number assigned to it being my catalogue number. All collection data, which sometimes included ecological and other notes as well as location, collection date, and collector, were also recorded on index cards and arranged alphabetically according to state, county, and cave.

For a systematic study, various legs and any loose antennae and cerci were mounted on glass slides. A whole mount was then made of the campodeid's body (ventral side up) and remaining appendages. The specimens were mounted in Hoyer's medium, either as prepared according to Baker and Wharton (1952) or as purchased from Carolina Biological Supply Company. All slides were covered with #1 glass cover slips and placed on a warming tray at 50° C. for a week. At first, I ringed the coverslips two or three times with clear fingernail polish. Then, due to a breakdown of the polish allowing air bubbles to form under the cover slips, many slides were remounted and ringed with three coats of varnish. Recently I have used Glyptol 1201 red enamel insulating paint (made by General Electric Company) to ring slides. One coat of Glyptol is applied around the edge of the cover slip. Then the slide is heated for at least one day at 50° C. A second coat is applied and heated before the slides are considered sealed. Mounted specimens were examined and measured with a Leitz model SM-Lux microscope equipped with an ocular micrometer. Drawings were made with the aid of a Leitz drawing tube.

During the course of this study one or more specimens (usually all) were mounted and identified from 372 dipluran collections from 268 caves in twenty-two states. Two hundred sixty-eight of these collections contained specimens belonging to the genus Litocampa, from 174 caves east of the Mississippi River, from 17 caves of the Ozark Plateau of Missouri and Arkansas, and from one cave in New Mexico. Nearly every specimen from these collections was mounted on slides as described above (the exceptions are specimens from large collections from Mammoth Cave, from two caves in Virginia, and the most recently received material). In all, I prepared and examined 1598 microscopic slides. Additional information on most of the caves and cave areas referred to in this work can be obtained from the following cave surveys and reports: Barr (1961) and Matthews (1971) for Tennessee; Holler (1975, 1979) for North Carolina; Weaver and Johnson (1980) and Bretz (1956) for Missouri; Powell (1961) for Indiana; Douglas (1964) and Holsinger (1975) for Virginia; Davies (1965) and Hempel (1975) for West Virginia; Jones and Varnedoe (1968) and Varnedoe (1973, 1975) for Alabama; and Mylroie (1978, 1979), Bishop (1973), Sperka (1973), and George (1973) for Kentucky.

For this study I utilized more taxonomic characters than in an earlier study (Ferguson, 1974). Most of the new characters concern additional measurements of various macrochaetae, antennal trichobothria, parts of the metathoracic legs, and styli. The phaneres (ectodermal derivatives such as macrochaetae, setae, etc.) of the antennal segments were examined more closely. For the third antennal segment the letters a, b .... h refer to the long phaneres; a is located dorsally between the two trichobothria, b is situated laterally from a, and the remaining phaneres are labeled consecutively, ending with h (see Figure 2). New

FIGURE 2.--Morphological details of campodeid diplurans. A, dorsal view of right third antennal segment showing trichobothria (_t_) and labeled phaneres (see text); B, ventral view of right third antennal segment showing labeled phaneres and sensillum (_s_); C, pronotum, mesonotum, and abdominal tergite showing location of medial anterior macrochaetae (_ma_); lateral anterior macrochaetae (_la_), lateral posterior macrochaetae (_lp_), medial posterior macrochaetae (_mp_), and posterior marginal setae (_post._); D, ventral view of mesosternite indicating the location of important phaneres; barbed precoxal macrochaetae (_bpc_), smooth precoxal setae (_spc_), subcoxal macrochaeta (_sc_), and other macrochaetae (abbreviations same as above).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taxonomic characters used in the following descriptions include the chaetotaxy of the thoracic sternites. The names applied to these phaneres are indicated in Figure 2. For a discussion of the taxonomic characters and morphology of the campodeidae, one should consult B. Condé's 1956 monograph.

The standard abbreviations used in the following descriptions are: ma for medial anterior macrochaetae; mp for medial posterior macrochaetae; la for lateral anterior macrochaetae; and lp for lateral posterior macrochaetae (see Figure 2). Various ratios of these macrochaetae are presented, such as lp_I/lp_{II}, which is the ratio expressing the quantitative relationship between the lengths of the prothoracic and mesothoracic lp's; ma/D_I is the ratio of the length of the medial anterior macrochaeta to the distance from its base, or insertion, to the bases of the posterior marginal setae of the same abdominal tergite, the first in this case; ma/Sep ma-ma is the length of the medial anterior macrochaetae relative to the distance separating the two medial anterior macrochaetae on a given tergite. It is standard procedure not to give means for the various ratios and measurements since campodeids continue to grow and molt throughout their lives and such measurements are, therefore, meaningless for identification purposes (Mayr, 1969); the ranges are more important. However, since different species with quite different macrochaetal lengths can have the same ratios, there is considerable merit in reporting the actual lengths of the macrochaetae. All measurements are in microns unless stated otherwise. The number of macrochaetae, sensilla, and various setae on the left and right halves of a tergite or sternite is indicated by notations such as 3 + 3.

SYSTEMATICS

The Order Diplura

Small to large, elongate, parallel-sided hexapods. Chewing mouth-parts enclosed within the head capsule (entognathus); mandible often with a movable prostheca. Antennae long, many-segmented, moniliform. Compound eyes and ocelli absent. Legs five-segmented with a single, undivided tarsus. Abdomen with 10 distinct segments and rudimentary structures of a possible eleventh; lateral styli and eversible vesicles on most of the first seven urosternites; gonopore between segments VIII and IX. Cerci present, long and filamentous, short and annulated, or short and forceps-like; sometimes containing the duct of a silk gland. Median caudal filament absent. Tracheae relatively well developed, with two to four pairs of spiracles on thoracic pleura and none or seven on abdominal pleura. Body covered with setae or, rarely, with scales. Larval development epimorphic.

REMARKS.--The diplurans (entotrophi) are an order of entognathus apterygote hexapods which are considered as a separate class by some zoologists and as an order of the Class Insecta by others (Mackerras, 1970). Of the entognathus hexapods, which also includes the Protura and Collembola, the Diplura are most like true insects, particularly the Thysanura with which they were once included.

The following key to the families of Diplura is basically that of Pagés (1959), and incorporates the modifications by Smith (1960) and Gonzalez (1964).

Key to the Suborders, Superfamilies, and Families of Diplura

1. Cerci one segmented, forcipiform; mandible without lacinia mobilis mobilis (prostheca); with or without trichobothria on antennae; if present, on antennal segments IV to VI or IV to XIII; two or four pairs of thoracic spiracles; abdominal spiracles present; styli without several distinctly developed setae; anal valvules not well developed.. ....Suborder DICELLURATA, Superfamily JAPYGOIDEA...2

1'. Cerci multisegmented, filiform; mandible with lacinia mobilis (prostheca); trichobothria present, beginning on antennal segments III, IV, or V; two or three pairs of thoracic spiracles present or absent; styli with several very distinctly developed setae; anal valvules well developed.................Suborder RHABDURA...4

2. Labial palps present; four pairs of thoracic spiracles.............. ....Family JAPYGIDAE Lubbock

2'. Labial palps absent; two pairs of thoracic spiracles...............3

3. Antennae without trichobothria; lateral subcoxal appendages present on both sexes; pretarsus with empodium bent backwards dorsally, forming a median unpaired claw (unguiculus); forceps with glandular orifice on proximal tergal surface; small sized forms.........

..................................Family PARAJAPYGIDAE Pagés

3'. Trichobothria present on at least segments IV and XV; pretarsal empodium rounded off, without projections; females without lateral subcoxal appendages; forceps without glandular orifice; gigantic forms......................Family DINJAPYGIDAE Gonzalez

4. Trichobothria beginning on antennal segment III; maxilla without palpus, lacinia without pectens; urosternite I without styli, with one pair of subcoxal appendages; styli present on urosternites II-VII; abdominal spiracles absent; cerci long or short, without inner canal, closed at apex..........Superfamily CAMPODEOIDEA...6

4'. Trichobothria beginning on antennal segments IV or V; palpus on maxilla, pectens on lacinia; urosternite I with one pair of lateral posterior styli and one pair of sublateral posterior subcoxal appendages; styli present on urosternites I-VII; seven pairs of abdominal spiracles present; cerci short, with inner canal, opening apically.......................Superfamily PROJAPYGOIDEA...5

5. Epicranial suture complete; trichobothria on antennal segments IV to XXII, terminal segment with one anterior and one posterior sensory pit; lacinia of maxilla simple; labial palpi well developed and subcylindrical; three pairs of thoracic spiracles; all thoracic sternal apodemes well developed, Y-shaped; subcoxal appendages of urosternite I cylindrical, pilose, with terminal glandular setae; eversible vesicles absent on urosternites; Malpighian tubules absent; genital papilla of male of <u>Projapyx</u> type; genital papilla of female very reduced.....................

....Family PROJAPYGIDAE Cook

5'. Epicranial suture incomplete, reduced to its posterior branch (coronal suture); trichobothria on antennal segments V to X, and on even numbered segments thereafter in some species; large placoid sensilla at apex of terminal segment of antenna; lacinia of maxilla bifid; labial palpi very reduced; two pairs of thoracic spiracles; prothoracic sternal apodeme apparently reduced to posterior branch; subcoxal appendages of urosternite I pyriform, only slightly pilose, without glandular setae; urosternites II-VII with eversible vesicles; 16 Malpighian tubules present; genital papilla of male similar to Campodea type; genital papilla of female not reduced..................Family ANAJAPYGIDAE Paclt

6. Epicranial suture incomplete, reduced to proximal portion of posterior branch (coronal suture); trichobothria on antennal segments III to VII; terminal segment of antennae without cupuliform structure; labial palpi absent; two pairs (intermediate absent) of thoracic spiracles; urosternite I with one pair of very small subcoxal appendages; cerci short.................................
.................................Family PROCAMPODEIDAE Silvestri

6'. Epicranial suture complete, beaded on entire extent; trichobothria on antennal segments III to VI; terminal segment of antennae with cupuliform structure at its apex; labium with palpi in form of flattened protuberances with setigerous plates, and with one pair of internal palpiform processes (labial palpi of some authors); three pairs of thoracic spiracles; urosternite I with one pair of well developed subcoxal appendages; cerci long..Family CAMPODEIDAE Lubbock

Family Campodeidae

Campodeidae Lubbock, 1873:211.

DIAGNOSIS.--By the combined characters given in the key.

REMARKS.--Condé (1956a) subdivided the family Campodeidae into three subfamilies: Hemicampinae, Lepidocampinae, and Campodeinae. Paclt (1957) divided it into five subfamilies, adding the Syncampinae and Plusiocampinae to those already erected. As explained further below, the last two subfamilies do not appear to be natural phyletic groupings, and they are not recognized here.

Key to the Subfamilies of the Campodeidae

1. Body with scales. Lateral pretarsal claws simple, anterior claw similar to posterior, pretarsus with or without small median claw (unguiculus); lateral pretarsal appendices always present. Posterior marginal setae of urosternite VIII may show sexual dimorphism 2

1'. Body without scales. Lateral pretarsal claws simple or with laterotergal crests, anterior claw similar to posterior or smaller; pretarsus with (*Eutrichocampa hispanica* only) or without small median claw (unguiculus); lateral pretarsal appendices absent, rudimentary, or well developed, subcylindrical or flattened, smooth or pubescent. Posterior marginal setae of urosternite VIII similar on both sexes........................Campodeinae

2. Scales on entire trunk. Pretarsus with (Lepidocampa) or without (Syncampa) small median claw (unguiculus); lateral pretarsal appendices flattened, with long pubescence. Posterior marginal setae of urosternite VIII show sexual dimorphism (larger setae with numerous barbs on males.....................Lepidocampinae

2'. Scales on metathorax and abdomen (Tritocampa) or on abdomen only (Hemicampa). Pretarsus without small median claw (unguiculus); lateral pretarsal appendices subcylindrical, smooth. Posterior marginal setae of urosternite VIII not showing any sexual dimorphism..Hemicampinae

Subfamily Lepidocampinae

Lepidocampinae Condé, 1956a:93.

Syncampinae Paclt, 1957:49. NEW SYNONYMY.

REMARKS.--This subfamily contains 2 genera, Lepidocampa Oudemans, 1890, and Syncampa Silvestri, 1931b. Heterocampodea Hilton (1938) of Cuba, is considered a synonym of Lepidocampa. Syncampa is represented by a single species, S. smithi, from southern China. Species of Lepidocampa are found throughout the tropics and subtropics, and also at very high altitudes in the Andes Mountains of Bolivia (2500 to 4200 m) and in the Himalayas (4800 m) (Condé, 1960; Condé and Nguyen Duy, 1968). All species are endogeans.

In 1957, Paclt created a new subfamily (Syncampinae) for Syncampa which differs solely from the genus Lepidocampa by the presence of a small unpaired median pretarsal claw (unguiculus). Considering the possible modifications of the pretarsus as observed in the genera Eumesocampa and Metriocampa, I feel that the presence of an unguiculus is not sufficient justification for the formation of a new subfamily. This conclusion is further supported by the discovery of an unguiculus on the claws of Eutrichocampa hispanica, (Condé and Barbier, 1965) of the subfamily Campodeinae.

Subfamily Hemicampinae

Hemicampinae Condé, 1956a:93

REMARKS.--This subfamily contains two genera, Hemicampa Silvestri, 1912a, of Mexico, Texas, and Louisiana, and Tritocampa Silvestri, 1933d, of Guyana (British Guiana). All species are endogeans.

Subfamily Campodeinae

Campodeinae Condé, 1956a:94.

Plusiocampinae Paclt, 1957:42. NEW SYNONYMY.

REMARKS.--There is difficulty in the recognition of the subfamily Plusiocampinae as proposed by Paclt (1957). The erection of this subfamily separates the genera Plusiocampa and Litocampa which are similar enough morphologically to have been considered congeneric at one time (Silvestri, 1933d). There is also geographical data to support a close relationship between the two. On the contrary, the elevation of Lito-campa by Paclt (1957) to generic rank seems quite justified, indeed Wygodzinsky (1944a) proposed such an action. Paclt (1957) also included in his new subfamily the species Paratachycampa boneti Wygodzinsky, a Mexican troglobite which does not meet the criteria established for the subfamily (Condé, 1959).

The final objection to this subfamily is the presence of a newly discovered species in the southeastern United States, which is intermediate in morphology to Plusiocampa and Litocampa. Based on Paclt's diagnoses and keys, this species would have to be placed in the subfamily Plusiocampinae, whose species are otherwise concentrated in the Mediterranean region of Europe and Asia (see Figure 42). But the species also displays some equally important characters that show affinity to the Litocampa of the Campodeinae, such as 1 + 1 macrochaetae on urosternite VIII. There are other morphological, as well as geographical, reasons to indicate that this new species arose from a primitive stock of Litocampa in the United States. Rather than trying to justify what appears to me to be an artificial category, and based on new information, I propose the placing of the subfamily Plusiocampinae in synonymy with the subfamily Campodeinae, the latter having priority.

As recognized here, the subfamily consists of 31 to 34 genera. This variation in number is the result of the elevation of certain subgenera to generic status by some authors, and not by others. Endogeans and cavernicoles (troglophiles and troglobites) are present. The key that follows is an attempt to present a key to all genera which might be confused with or related to the Litocampa and Plusiocampa.

Key to the Genera of the Campodeinae with Latero-tergal Crests or More Than 3 + 3 Pronotal Macrochaetae

1. Without lateral pretarsal appendices................................2

1'. With lateral pretarsal appendices...................................3

2. Pronotum with 3 + 3 or 4 + 4 M; pretarsal claws with well developed latero-tergal crests; endogeans and cavernicoles of western United States and Canada...............Haplocampa Silvestri 1912a

2'. Pronotum with 7 + 7 M; pretarsal claws without latero-tergal crests; endogeans of South Africa..............Silvestricampa Condé 1950b

3. Lateral pretarsal appendices flat...................................4

3'. Lateral pretarsal appendices subcylindrical........................8

4. Mesonotum with 1 + 1 M; metanotum without macrochaetae.............5

4'. Mesonotum with 6 + 6 or 7 + 7 M; metanotum with 5 + 5 or 6 + 6 M...6

5. Pronotum with 3 + 3 M; mesonotum with 1 + 1 medial anterior M; urosternite I with 14 + 14 or 15 + 15 M; urosternites II-VII with 7-9 + 7-9 M; urosternite VIII with at least 2 + 2 M; pretarsal claws not pilose; lateral pretarsal appendices flat, covered with fine pubescence, and enlarged apically; cavernicole of Guerrero, Mexico.............................Juxtlacampa Wygodzinsky 1944b

5'. Pronotum with 4 + 4 M; mesonotum with 1 + 1 lateral posterior M; urosternite I with 9-12 + 9-12 M; urosternites II-VII with 5 + 5 very distinctive M; urosternite VIII with 1 + 1 M; base of pretarsal claws covered by long simple hairs, sometimes bifurcated, which extend onto part of lateral crests; lateral pretarsal appendices flat, bearing long hairs; proximal part of appendices with simple slender hairs covering its ventral surface; distal part of appendices with highly modified hairs on its margins, hairs enlarged into stalked palettes with 2 to 6 apical branches; cavernicole of Pendjab, India........................Simlacampa Condé 1957

6. Femur III without dorsal macrochaetae; tibia III without ventral macrochaetae; lateral pretarsal appendices flat, expanded into subtriangular palette in middle region, covered by long, dense pubescence; apical region of appendices subcylindrical, tapering, smooth; urosternites I, II-VII, and VIII with 15 + 15, 7-8 + 7-8, and 3 + 3 M, respectively; cavernicole of Sardinia................ ....Patrizicampa Condé 1956c

6'. Femur III with one dorsal macrochaeta; tibia III with ventral macrochaetae; lateral pretarsal appendices flat, pubescent, but not expanded into subtriangular palette in middle region; urosternites I, II-VII, and VIII with 7 + 7 or 8 + 8, 5 + 5 or 6 + 6, and 2 + 2 M, respectively...7

7. Pronotum with 6 + 6 M; tibia III with two or three ventral macrochaetae; lateral pretarsal appendices gradually tapering upwards apex, with long, dense ventral pubescence; urosternite I with 8 + 8 M; urosternites II-VII with 6 + 6 M; cavernicole of Lebanon........ ....Vandelicampa Condé 1955a

7'. Pronotum with 7 + 7 M; tibia III with one or two ventral macrochaetae; lateral pretarsal appendices not tapering towards apex; urosternite

I with 7 + 7 M; urosternites II-VII with 5 + 5 M; cavernicoles of Italy..................................Cestocampa Condé 1956a

8. Lateral pretarsal appendices pubescent on their proximal half, two-thirds, or more...13

8'. Lateral pretarsal appendices smooth, or with only 3-4 small barbules 9

9. Pronotum, mesonotum, and metanotum without macrochaetae; urosternite VIII with 1 + 1 M; endogean of Guinea..Spaniocampa Silvestri 1933f

9'. Pronotum with macrochaetae; urosternite VIII with 1 + 1 or more M.. 10

10. Pronotum with 2 + 2 M; mesonotum without macrochaetae; urosternite VIII with 1 + 1 M; cavernicole of Morocco....................... ....Tachycampa Silvestri 1936

10'. Pronotum with more than 2 + 2 M; mesonotum with macrochaetae; urosternite VIII with 1 + 1 or more M............................11

11. Pronotum with 3 + 3 M; urosternite VIII with 2 + 2 M.............12

11'. Not as above..14

12. Mesonotum with 4 + 4 M (ma, la, 2 lp); metanotum with 2 + 2 lateral posterior M; femur III with two dorsal macrochaetae; endogean of South Africa................Anisocampa purcelli Silvestri 1932[1]

12'. Mesonotum with 3 + 3 M (ma, 2 la); metanotum with 1 + 1 medial anterior M; femur III with one dorsal macrochaeta; cavernicole of Nuevo León, Mexico............Paratachycampa Wygodzinsky 1944b

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[1]Only species of this genus having latero-tergal crests.

13. Femur III with five dorsal macrochaetae; tibia III with two dorsal macrochaetae; urosternite VIII with 2 + 2 M; cavernicole of Jura Mountains, France and Switzerland.......Hystrichocampa Condé 1948c

13'.Femur III with one dorsal macrochaeta; tibia III without dorsal macrochaetae; urosternite VIII with 1 + 1 M; cavernicole of Nevada, U.S.A...Undescribed Genus A

14. Pronotum with 3 + 3 or more M (if more than 3 + 3 M, abdominal tergites with medial anterior M); abdominal tergites with or without medial anterior M; urosternite I with 5 + 5, 6 + 6, or 7 + 7 M; urosternites II-VII with 4 + 4 or 5 + 5 distinctive M; urosternite VIII with 1 + 1 M; femur III with or without one dorsal macrochaeta...15

14'.Pronotum with more than 3 + 3 M; abdominal tergites without medial anterior M; urosternite I usually with 7 + 7 M, occasionally more; urosternites II-VII with 5 + 5, or more, distinctive M; urosternite VIII with 2 + 2 or more M, rarely 1 + 1, femur III without or with one or two dorsal macrochaetae.........Plusiocampa Silvestri 1912b

15. Pronotum with 4 + 4 M (ma, $la_{1,2}$, lp); abdominal tergites with medial anterior M; urosternite I with 6 + 6 M; apical tarsal setae bifurcated..Undescribed Genus B

15'.Pronotum with 3 + 3 M (ma, la, lp); abdominal tergites with or without medial anterior M; urosternite I with 5 + 5, 6 + 6, or 7 + 7 M; apical tarsal setae not bifurcated..........................16

16. Femur III without dorsal macrochaetae; tibia III with one ventral macrochaeta; latero-tergal crests of pretarsal claws very reduced

in size, no heel or proximal flange present; abdominal tergites without medial anterior macrochaetae; tergites I-VII without macrochaetae; tergite VIII with 2 + 2 lateral posterior M; abdominal segment IX with 4 + 4 M (total)...Cocytocampa (Paclt 1957)

16'.Femur III with or without dorsal macrochaetae; tibia III with one or more ventral macrochaetae; latero-tergal crests of pretarsal claws very reduced in size or well developed, sometimes possessing a heel, or proximal flange, which covers apical tip of tarsus; abdominal tergites with or without medial anterior macrochaetae; macrochaetae on at least some of abdominal tergites I-VII; tergite VIII with 3 + 3 or more lateral posterior M; abdominal segment IX with 5 + 5 or more M (total)...........Litocampa (Silvestri 1933d)

Genus *Plusiocampa*

Plusiocampa Silvestri, 1912b:141.

Troglocampa Denis, 1930:34.

TYPE OF THE GENUS.--*P. corcyraea* Silvestri (type by original designation).

DIAGNOSIS.--By the combined characters given in the key.

REMARKS.--In 1912, Silvestri founded the genus *Plusiocampa* to receive three concurrently described species from the Mediterranean basin: *P. corcyraea* (type species) from Corfu Island, Greece, and *P. notabilis* and *P. italica* from Calabria, Italy. *P. italica* differed from the other species remarkably by the form of its lateral pretarsal appendices which were flat and pubescent while those of the other species were subcylindrical and smooth. Later, Condé (1956a) proposed the genus *Cestocampa* to receive this divergent species.

Species of the presently recognized genus *Litocampa* were formerly included with the *Plusiocampa* as a subgenus (Silvestri, 1933d) due to their morphological similarity. If this similarity reveals true affinity of the two genera, then it may be of value to look at the *Plusiocampa* species and their distribution.

Key to the Subgenera of *Plusiocampa*

1. Femur III without dorsal macrochaetae....*Stygiocampa* Silvestri 1934a

1'. Femur III with dorsal macrochaetae...............................2

2. Femur III with two dorsal macrochaetae......Didymocampa Paclt 1957

2'. Femur III with one dorsal macrochaeta..........Plusiocampa s. str.

Subgenus Plusiocampa s. str.

Plusiocampa Silvestri (and above).

TYPE OF THE SUBGENUS.--P. corcyraea Silvestri

INCLUDED SPECIES.--Twenty-seven species and eight subspecies are known world-wide. See Figure 42 and Appendix II for a listing of these species and their locations.

DIAGNOSIS.--Pronotum with more than 3 + 3 macrochaetae; femur III with one dorsal macrochaeta; tibia III with two or three ventral macrochaetae, rarely lacking (P. dargilani); abdominal tergites without medial anterior macrochaetae; urosternite VIII with 2 + 2 macrochaetae, rarely 3 + 3 (P. dargilani).

REMARKS.--The subgenus is composed of troglobitic and endogean species found on the European periphery of the Mediterranean Sea, and its islands. These species are known from the Aegean area westward; the endogeans are not known west of Corsica, whereas the troglobites reach the eastern border of the Pyrenees (Condé, 1959).

Except for P. dargilani (discussed below and under the subgenus Stygiocampa), only three species deviate from the normal pattern of 7 + 7 macrochaetae on the urosternite I, 5 + 5 macrochaetae on urosternites II-VII, and 2 + 2 macrochaetae on urosternite VIII. P.

dargilani has 11 + 11, 11 + 11, and 3 + 3 macrochaetae on the urosternites, I, II-VII, and VIII, respectively. P. fagei Condé, 1954c, has 6 + 6 or 8 + 8 macrochaetae on urosternite I; P. breuili Condé, 1954c, has 8 + 8 macrochaetae on urosternite I. Lastly, P. balsani Condé, 1947c, has 6 + 6 macrochaeta on urosternites II-VII. In other respects these three species are similar to the other species of the subgenus. P. fagei and P. breuili are cavernicoles on the Balearic Islands (Islands of Ibiza and Mallorca, respectively) and may represent a small species group or lineage.

P. balsani is a cavernicole known from caves in the Department of Aveyron and Herault, France. It is geographically near P. dargilani and apparently shows some affinities with this species (Condé, 1947c, 1948a). P. pouadensis Denis, 1930, and P. provincialis Condé, 1949a, are believed to belong to the same lineage as the above two species (Condé, 1956a). All four species are located on the periphery of the Mediterranean, from Catalonia, Spain, to Provence, France. In addition to the above two lineages several others apparently exist. For the species included in this subgenus, as presently defined, Condé earlier (1956a) recognized two major species groups, four subgroups, and several unassigned species.

Subgenus Stygiocampa

Stygiocampa Silvestri, 1933: 180. (1934a).

TYPE OF THE SUBGENUS.--P. nivea (Joseph) (type by original designation).

INCLUDED SPECIES.--P. bureschi Silvestri, 1931a; P. dalmatica Condé, 1959; (?) P. denisi Condé, 1947b; P. nivea (Joseph, 1882); P. remyi Condé, 1947b; P. rauseri Rusek, 1965.

DIAGNOSIS.--Pronotum with more than 3 + 3 macrochaetae; femur III without dorsal macrochaetae; tibia III without macrochaetae or with two ventral macrochaetae; tarsal claws with well developed latero-tergal crests, embellished with fine stria; abdominal tergites without medial anterior macrochaetae; urosternite I with 7 + 7, 15 + 15, or more, macrochaetae; urosternites II-VII with 5 + 5, 11 + 10, or more, macrochaetae; urosternite VIII with 2 + 2, 3 + 3, or 6 + 6 macrochaetae; field of glandular hairs present on urosternite I of males of at least two species (P. remyi and P. denisi). Cavernicoles of Yugoslavia and Bulgaria.

REMARKS.--The subgenus Stygiocampa undoubtedly represents a natural grouping, being composed of highly evolved troglobites in the Dinaric region of Yugoslavia. The exact subgeneric status of two or three included species is still uncertain however.

Three Yugoslavian species are outstanding due to the excessive number of macrochaetae on their urosternites I-VII. P. nivea (Joseph, 1882), P. remyi Condé, 1947b, and P. dalmatica Condé, 1959, have from 15 + 15 to to 23 + 23 macrochaetae on urosternite I and 11 + 10 to 19 + 19 (14 + 14 most often) macrochaetae on urosternites II-VII. Urosternite VIII has 3 + 3 or 6 + 6 macrochaetae in P. remyi, 2 + 2 or 3 + 3 macrochaetae in P. nivea, and 2 + 2 macrochaetae in P. dalmatica. Trending northwest to southeast along the Adriatic Sea, these three species are geographically close to one another in Yugoslavia, starting at the northwest corner of Yugoslavia (near Trieste) with P. nivea, then P. dalmatica near

Šibenik, and farther south (near Dubrovnik and Titograd), P. *remyi*. All three species lack dorsal macrochaetae on femur III and ventral macrochaetae on tibia III. This rather anomalous occurence of macrochaetae on the legs is also present on P. *bureschi* Silvestri, 1931a, and P. *rauseri* Rusek, 1965, troglobites from adjoining Bulgaria. P. *bureschi* and P. *rauseri* have, however, the more normal chaetotaxy on the urosternites: 7 + 7 macrochaetae on urosternite I, 5 + 5 on II-VII, and 2 + 2 on VIII.

If P. *bureschi* and P. *rauseri* are included in the subgenus *Stygiocampa* (Condé, 1956a, 1959), then it is easier to make a similar case for P. *denisi* Condé, 1947b. P. *denisi* also has the normal chaetotaxy on the urosternites and is geographically much nearer the first three species, being known from a cave near Novi Pazar, Yugoslavia. It lacks the dorsal macrochaeta on the metathoracic femur like all of the above species, but it does have two ventral macrochaetae on the metathoracic tibia. From my own observations of other campodeids, I have found this character to be much more variable than the others under consideration. P. *denisi* also has fewer macrochaetae (5 + 5) on the pronotum than the other species (7 + 7 or 9 + 9).

One other species should be considered in light of the above characters found in the subgenus *Stygiocampa*. P. *dargilani* (Moniez, 1893) is another highly evolved troglobite which is known from the Grotte de Dargilan in the Department of Lozère, in southcentral France. This remarkable species has many morphological similarities with P. *nivea*, indicated by Denis (1923), such as an excessive number of macrochaetae on the urosternites and the morphology of clothing setae, abdominal styli, and claws. Condé's redescription (1946) indicates that there are 11 + 11 macrochaetae on the urosternites I-VII and 3 + 3 macrochaetae on urosternite VIII. The abdominal sternal chaetotaxy is very much like that of P. nivea, P. dalmatica, and P. remyi; its tergal chaetotaxy is very similar to that of P. dalmatica.

Like the above three species, it also lacks any trace of a ventral macrochaeta on tibia III, but it does have one dorsal macrochaeta on femur III (see Appendix II). Due to this last character, Paclt (1957) places P. dargilani in the subgenus Plusiocampa s. str. This is probably a correct assignment regardless of the great similarity in the sternal chaetotaxy and other characters that it shares with members of the subgenus Stygiocampa. This similarity is most likely due to convergent evolution between this species and several of those belonging to the Stygiocampa, all of which are the most specialized cavernicoles known among the genus Plusiocampa. There are a number of minor morphological differences between P. dargilani and P. nivea, indicated by Denis (1923), and there are undoubtedly more. Nevertheless, a reexamination and comparison of P. dargilani and the species belonging to the subgenus Stygiocampa is certainly warranted. The discovery of some geographically intermediate forms could help solve the taxonomic placement of P. dargilani, as well.

In addition to the six species presently assigned to the Stygiocampa, Paclt (1957) included Paratachycampa boneti Wygodzinsky, a troglobite of Mexico. Although Paratachycampa boneti shows some morphological similarities with the Plusiocampa, it clearly does not belong in the subgenus Stygiocampa as Condé (1959) pointed out. Paratachycampa has only 3 + 3 macrochaetae on the pronotum (Wygodzinsky, 1944b).

Subgenus Didymocampa

Didymocampa Paclt, 1957: 43, 46.

TYPE OF SUBGENUS.--P. sinensis Silvestri (type by original designation).

INCLUDED SPECIES.--P. evallonychia Silvestri, 1949; P. sinensis Silvestri, 1931b.

DIAGNOSIS.--Pronotum with more than 3 + 3 macrochaetae; femur III with two dorsal macrochaetae; tibia III with one or two macrochaetae; abdominal tergites without medial anterior macrochaetae; urosternite VIII with 1 + 1 or 2 + 2 macrochaetae. Males unknown.

REMARKS.--Paclt (1957) erected this subgenus to contain the two above species, based on their having two dorsal macrochaetae on the femur of the metathoracic leg. P. sinensis, an endogean species from southern China, has 1 + 1 macrochaetae on the urosternite VIII, while P. evallonychia is a troglobite from the Crimea, north of the Black Sea, and has the usual 2 + 2 macrochaetae on urosternite VIII found on Plusiocampa species, which also have more than 3 + 3 macrochaetae on the pronotum. Therefore, it is not certain whether P. sinensis should be included in the genus Litocampa, which has only 1 + 1 macrochaetae on urosternite VIII. For the present, the simultaneous occurence of a complex pronotal chaetotaxy and, especially, of the anomalous two dorsal macrochaetae on the femur in these two species probably justifies their being grouped together. *P. evallonychia* is also the closest *Plusiocampa* geographically to *P. sinensis*.

Genus *Cocytocampa* NEW STATUS

Plusiocampa (*Microcampa*) Silvestri, 1934c:519 (subgenus of *Plusiocampa*; name preoccupied: *Microcampa* Kawada 1930, Lepidoptera).

Litocampa (*Cocytocampa*) Paclt, 1957:27 (replacement name for *Microcampa*).

TYPE OF THE GENUS.--*Plusiocampa* (*Microcampa*) *perkinsi* Silvestri (type by original designation).

INCLUDED SPECIES.--*C*. *perkinsi* (Silvestri, 1934c): *C*. *solomonis* (Bareth and Condé, 1972).

DIAGNOSIS.--The original diagnosis given by Silvestri (1934c) was: "This subgenus differs from subgenus *Litocampa* Silv. by the shorter posterior macrochaetae of the meso- and metanotum; by legs lacking macrochaetae on the dorsal part of femur; by tergites of abdomen lacking macrochaetae from the first to the seventh." To this can be added: body size small, length 3.3 mm or less; antennae short, 16-18 segments; abdominal tergite VIII with 2 + 2 lateral posterior macrochaetae; abdominal segment IX with 4 + 4 macrochaetae (total); tibia III with one ventral macrochaeta; latero-tergal crests only slightly developed; urosternite I with 5 + 5 or 6 + 6 macrochaetae; vesiculose hairs present or absent on urosternites II-VII except in larva I; urosternite VIII with 1 + 1 macrochaetae; endogeans of Pacific islands (Hawaiian and Solomon Islands).

REMARKS.--In 1957, Paclt raised the subgenus *Litocampa* Silvestri to generic status and placed in it the former Plusiocampa subgenus Microcampa Silvestri. He indicated that the name was preoccupied (Microcampa Kawada, 1930, for a lepidopteran) and proposed the replacement name Cocytocampa for the subgenus. All former species of Plusiocampa with 3 + 3 pronotal macrochaetae (i.e., Litocampa) and lacking a dorsal macrochaeta on the metathoracic femur (Appendix II) were included in this subgenus. This produced an unquestionably heterogeneous mixture of species.

Except for the claws, Cocytocampa perkinsi differs considerably from all species of Litocampa observed by the writer, and from all other species whose descriptions have been studied. For morphological and biogeographical reasons, the species did not seem to belong in the same category with the Litocampa species. The discovery and description by Bareth and Condé (1972) of a second species closely related to C. perkinsi provides much additional information regarding the taxonomic position of these forms. They possess characters completely unique to the two species (vesiculose hairs on urosternites II-VII in C. solomonis) plus characters in common with the genus Indocampa, which is found in the Oriental regions, Australia, and Malagasy. I concur with Bareth and Condé (1972) in the restriction of the taxon Cocytocampa to the two presently known Pacific forms. Furthermore, in an attempt to arrive at a more natural classification, I am recommending its removal from the Litocampa and elevation to generic rank.

Genus *Litocampa*

Plusiocampa (*Litocampa*) Silvestri, 1933d:177.

Litocampa s. str. (Silvestri), Paclt, 1957:26.

Litocampa (*Cocytocampa*) Paclt, 1957:26 (in part).

Litocampa (*Tychocampa*) Paclt, 1957:26.

TYPE OF THE GENUS.--*Plusiocampa* (*Litocampa*) *neotropica* Silvestri (type of the subgenus by original designation).

INCLUDED SPECIES.--Thirty-two species are known world-wide, including the twelve newly described species herein. See Appendix II for a listing of these species and their locations.

DIAGNOSIS.--Body without scales. Pronotum with 3 + 3 (*ma*, *la*, *lp*) macrochaetae; posterior marginal setae long and slender. Meso- and metanotum generally with 3 + 3 (*ma*, *la*, *lp*) and 2 + 2 (*ma*, *lp*) macrochaetae; rarely with more, 4 + 4 (*ma*, *mp*, *la*, *lp*) and 3 + 3 (*ma*, *mp*, *lp*); or less, 2 + 2 (*ma*, *lp*) and 1 + 1 (*ma*) or 0. Femur III with or without a dorsal macrochaeta; tibia III with 1 or 2 ventral macrochaetae. Pretarsal claws unequal in size, enlarged at their base and bent; with or without well-developed laterotergal crests, always larger on posterior claw. Pretarsal appendix smooth and setiform. Abdominal tergites with or without medial anterior macrochaetae; tergite VIII with 3 + 3 or more lateral posterior macrochaetae; abdominal segment IX with 5 + 5 or more macrochaetae (total). Urosternite I of males with or without glandular setae, and with 6 + 6 or 7 + 7 macrochaetae. Urosternites II-VII with 4 + 4 or 5 + 5 well-differentiated macrochaetae. Urosternite VIII with 1 + 1 macrochaetae. Apical and subapical setae of the styli not densely barbed. Cerci with long macrochaetae.

REMARKS.--According to the classification of Paclt (1957), the genus Litocampa is subdivided into three subgenera: Litocampa s. str., Cocytocampa, and Tychocampa. As presented above, the type species of the subgenus Cocytocampa appears to be quite removed morphologically and geographically from the other species of the genus Litocampa. In an attempt to form a more natural classification, it was recommended that the type species of the subgenus Cocytocampa and one other species, L. (C.) solomonis, be included in this taxon and raised to generic rank. The remaining species of Cocytocampa are incorporated back into the Litocampa s. str. by me at this time. Until further analysis of those species without dorsal macrochaetae on the femurs (the only apparent criterion for the erection of the subgenus) can be shown to have other important characters in common, this seems to be the logical choice.

The subgenus Tychocampa has a sole member, L. henroti. The morphological basis for this subgenus is the presence of medial posterior macrochaetae on the meso- and metanota. In light of the discovery of a new (believed related) species which lacks the extra thoracic macrochaetae (as well as a possible intermediate form between the two), I hesitate to recognize the subgenus. To do so, as presently defined, would separate two species which I feel are closely related. Indeed, I think it is premature to erect formal subgenera for the Litocampa considering our present state of knowledge. Accordingly, I have only proposed species groups.

Species Groups of Litocampa

REMARKS.--Condé (1956a) subdivided the former genus *Plusiocampa* (and *Litocampa*) into two sections: those species with a complex thoracic chaetotaxy and those species with the typical thoracic chaetotaxy. The first section is represented today by the subfamilies *Stygiocampa*, *Didymocampa*, and *Plusiocampa* s. str. He stated that this division showed apparent close affinity. The second division is more heterogeneous and wide spread geographically. He further subdivided the two divisions into five and six species groups, respectively. The species groups of the second division (*Litocampa*) are of interest to us. He placed the five species known from the United States, at that time, in one group.

In my opinion, the differences in important morphological characters displayed by *L. cookei*, *L. henroti*, and *L. fieldingi* are considerable, and warrant further subdivision and comparison. Since the number of species of *Litocampa* in the United States now constitutes sixty-three percent of the known world fauna of that genus, I felt that it might be more productive to group the American species into new species groups, rather than trying to incorporate them into Condé's groups. It was hoped that these groups would facilitate an analysis of their evolution and dispersal. Eight such groups, with their included species, are presented below.

If one compares the new groups to Condé's (1956a), several interesting discoveries are made. In 1953, Condé stated that the American species were most like L. drescoi, L. coiffaiti, and L. espanoli found in caves of the central and western Pyrenees of France and Spain. L. drescoi and L. coiffaiti (Condé's Group IV) are possibly more like the species of the American keithi or virginiana groups, while L. espanoli (Group V) is more like L. jonesi of the following cookei group. The new bifurcata group (representatives of which Condé did not have) seem to resemble his Group III, which is represented by L. vandeli of, again, the central Pyrenees. Finally, he includes L. atoyacensis (Wygodzinsky) of Mexico in his Group II which contains another central Pyreneean species and L. humilis, which has a wide and discontinuous distribution in France. He gives no explanation for the great separation of species in this group.

Key to Species Groups of Litocampa in the United States

1. Abdominal tergites without medial anterior macrochaetae............ ....cookei group

1'. Some abdominal tergites with medial anterior macrochaetae..........2

2. Femur III without dorsal macrochaeta................bifurcata group

2'. Femur III with dorsal macrochaeta.................................3

3. Medial anterior macrochaetae on abdominal tergites I-II only........ ....hawksleyi group

3'. Medial anterior macrochaetae on more than abdominal tergites I-II...

....4

4. Urosternite I with 6 + 6 macrochaetae.............fieldingi group

4'. Urosternite I with 7 + 7 macrochaetae.............................5

5. Metanotum without lateral posterior macrochaetae...valentinei group

5'. Metanotum with lateral posterior macrochaetae....................6

6. Medial anterior macrochaetae on abdominal tergites I-IX...........

....keithi group

6'. Medial anterior macrochaetae on abdominal tergites I-VII..........7

7. Abdominal tergite IV with 1 + 1 ma, 1 + 1 la, and 2 + 2 lp macrochaetae...virginiana group

7'. Abdominal tergite IV with 1 + 1 ma and 1 + 1 lp macrochaetae.......

....henroti group

The *Cookei* Group

DIAGNOSIS.--Antennal segment III with phanere *e*, metanotum with or without lateral posterior macrochaetae, femur III with dorsal macrochaeta, pretarsal claws with or without large latero-tergal crests, abdominal tergites VI-VII with 2 + 2 posterior macrochaetae, abdominal tergites without medial anterior macrochaetae, urosternite I with 7 + 7 macrochaetae, and posterior margin of urosternite I of males with or without glandular setae.

REMARKS.--Four species are presently included in the *cookei* group. *Litocampa jonesi* (Condé) is rather distinct, but the other three species are morphologically quite similar. Three of the species have small, practically insular ranges, but *L. cookei* has the largest range of any presently known cavernicolous campodeid in the United States, being found in caves from central Kentucky to southeastern Tennessee and into southwestern Virginia. The possibility definitely exists that this "species" (*L. cookei*) represents a complex of sibling species, but so far, only certain populations in eastern Kentucky can be satisfactorily shown to be morphologically distinct.

Key to the Species of the *Cookei* Group

1. Pretarsal claws without well-developed latero-tergal crests; 1 + 1

lateral anterior and 2 + 2 lateral posterior macrochaetae on abdominal tergites IV...*L. jonesi*

1'. Pretarsal claws with well-developed latero-tergal crests; 1 + 1, 2 + 2, or 0 posterior macrochaetae on abdominal tergite IV........2

2. Abdominal tergite I without macrochaetae; tergites II-III with 1 + 1 posterior macrochaetae; tergite IV with 2 + 2 posterior macrochaetae...*L. holsingeri*

2'. Abdominal tergites I-III without macrochaetae; tergite IV with 1 + 1 or 0 posterior macrochaetae...3

3. Meso- and metasternites with 4 + 4 barbed precoxal macrochaetae..*L. cookei*

3'. Meso- and metasternites with 5 + 5 barbed precoxal macrochaetae..*L. sperkai*, new species

Litocampa cookei (Packard)

Campodea cookei Packard, 1871:747. [Mammoth Cave, Kentucky; Mus. Comp. Zool., Harvard]; Cope, 1872:409; Packard, 1873:46; Hubbard, 1880:34, 79, fig. 8; Packard, 1886:383; 1888:67, plate 17, figs. I, Ia-Ii; MacGillivray, 1891:269; Blatchley, 1897:171, 200; Call, 1897:379; 1912:107, 109; Banta, 1907:86; Denis, 1930:20; Giovannoli, 1933:615-616; Silvestri, 1933e:156; 1934b:379-380; Dearolf, 1941:172; 1942:49, 51, 52; 1948:20; Condé, 1949b:125; 1956a:22, 169; Barr, 1955: 282; Paclt, 1957:26; Holsinger, 1961a:4-5; 1976:78.

Campodea staphylinus var. cookei: Viré, 1897:89, 93, 94-95, fig. 2; Wolf, 1937-38: vol. 2.

Plusiocampa (Litocampa) nearctica Silvestri, 1934b:380-383, figs. I, II. [Mammoth Cave, Kentucky; repository unknown]; Condé, 1949b:125-127, fig. 1; 1956:124, 132, 169, 178, 187; Nicholas, 1960:140.

Litocampa (Litocampa) nearctica (Silvestri), Paclt, 1957:26.

Plusiocampa cookei (Packard), Chandler, 1956:113; Barr, 1967b:152, 167-168, 192, 193, 202, fig. 17 (plate 53); 1968:53, 56, fig. 11; Ferguson, 1973:19.

MATERIAL EXAMINED.--KENTUCKY: Barren Co.: Edmonds Cave, 2 ♂, 7 ♀, 19 Feb. 1965, T. C. Barr, Jr., R. M. Norton, and T. G. Marsh, (LMF 285);

Hansons Cave, SE of Cave City, 1♀, 17 July 1973, S. B. Peck, (LMF 361); Walnut Hill Cave, 37°04'02", 86°03'14", Park City Quadrangle, 1♀, 14 July 1971, R. Sperka, (LMF 379); Edmonson Co.: Dixon Cave, 3♂, 4♀, 18 July 1929, L. Giovannoli, (LMF 38); Great Onyx Cave, 37°13'09", 86°04'41", Mammoth Cave Quadrangle, 1 immature, 2 Aug. 1970, R. Sperka, (LMF 373); 1♀, 3 June 1971, R. Sperka, (LMF 376); 1♀, 3 June 1971, W. Alexander, (LMF 377); Long's Cave, Cave City, 1♂, 2♀, 22 Aug. 1935, K. Dearolf, (LMF 55); Mammoth Cave, near Dead Sea and Poulson's sediment plots and at Great Relief Hall, 1♀, 1 immature, 14 Apr. 1973, L. M. and B. L. Ferguson, et al., (LMF 445); at end of Audubon Ave., 4♂, 3♀, 1 immature, 14 Apr. 1973, L. M. and B. L. Ferguson, et al., (LMF 444); passage off Marion Ave. near elevator, 3♂, 3♀, 14 Apr. 1973, L. M. and B. L. Ferguson, R. M. Norton, and T. C. Barr, Jr., (LMF 486); Marion Ave., 14♂, 11♀, 45 unmounted, molasses trap, removed 14 Apr. 1973, R. M. Norton, (LMF 364); Rafinesque Hall off Audubon Ave., 13♂, 12♀, 1 immature, 15-16 Mar. 1975, L. M. and B. L. Ferguson, (LMF 456); Running Branch Cave, Mammoth Cave National Park, 1♀, 25 June 1973, S. B. Peck, (LMF 356); Sanders Spring Cave, Cave City, 1♂, 27 June 1937, K. Dearolf, (LMF 56); Whites Cave, Mammoth Cave National Park, 1♂, 3♀, 16 Aug. 1929, L. Giovannoli, (LMF 131); 2♂, 3♀, 27 May 1972, S. B. and J. Peck, (LMF 332); 1♂, 2♀, 14 Apr. 1973, L. M. and B. L. Ferguson, R. M. Norton, T. G. Marsh, et al., (LMF 443); Green Co.: Tater Cave, 1.3 mi. SW of Bloyds Crossing, 2♀, 2 Apr. 1966, T. C. Barr, Jr., (LMF 252); Whitlock Cave, 3♀, 16 Apr. 1961, T. C. Barr, Jr., (LMF 266); Wisdom Cave, 2 mi. S. of Pierce, 3♀, 28 Aug., 1 Sept., 1967, S. B. Peck and A. Fiske, (LMF 235); 1 ♀, 26 June - 17 July 1973, S. B. Peck and C. Laing, (LMF 360); <u>Hart Co.</u>: Bald Knob Cave, 3♀, 11 Sept. 1965, R. M. Norton, (LMF 260); Barnes Smith Cave, 3.5 mi. WNW of Linwood, 7 ♂, 10 ♀, 2 immatures, 28 Aug. 1967, S. B. Peck and A. Fiske, (LMF 281); Copelin Cave, 1 ♀, 3, 8 Sept. 1972, S. B. and J. Peck (LMF 339); Crump Spring Cave, Horse Cave Quadrangle, 1 ♂, 20 Jan. 1973, J. Saunders, (LMF 380); Mammoth Onyx Cave, Cave City, 1♀, 29 June 1937, K. Dearolf, (LMF 52); Ronalds Cave, 2 mi. N. of Cave City, 4 ♀, 28 June 1973, S. B. Peck, R. M. Norton, and C. Laing, (LMF 344); <u>Pulaski Co.</u>: Richardson Cave, ♂♂♀♀, 22 July 1978, T. C. Barr, Jr., (LMF 584); <u>Trigg Co.</u>: Cool Spring Cave, SE of Cadiz, 2 ♀, 28 June 1965, S. B. and J. Peck, (LMF 189); <u>Warren Co.</u>: Bypass Cave, Bowling Green, 2♀, 31 Aug. 1967, S. B. Peck and A. Fiske, (LMF 240); Friendship Cave, 1 ♀, 13 Oct. 1979, T. C. Barr, Jr., (LMF 588); Horseshoe Cave, Bowling Green, 4 ♂, 5 ♀, 18-27 June 1973, S. B. Peck, (LMF 346); Pruett Saltpeter Cave, 1 mi. S. of Anna, 2 ♂, 4 ♀, 31 Aug.-4 Sept. 1967, S. B. Peck and A. Fiske, (LMF 271); <u>Wayne Co.</u>: Big Spring Cave, 2.3 mi. S. of Hardwick, ♂♂♀♀, 23 July 1979, T. C. Barr, Jr., and T. C. Barr III, (LMF 585); Cooper Cave, ♂♂♀♀, 23 July 1979, T. C. Barr, Jr., (LMF 586); Tom Jones Cave, 1♂, 2♀, 1 immature, 25 July 1979, T. C. Barr, Jr., (LMF 587).

TENNESSEE: <u>Anderson Co.</u>: Flowstone Cave, Anderson Co. Park, 2 sex ?, 10 July 1965, R. M. Norton (LMF 259); Hatmaker Cave, 1♂, 18 Aug. 1937, A. R. Cahn, (LMF 124); Turtle Graveyard Cave, 2♂, 26 Dec. 1966, R. M. Norton, (LMF 282); <u>Bledsoe Co.</u>: Lowe Gap Cave, 3 ♀, 24 July 1972, L. M. and B. L. Ferguson (LMF 212); 7 ♂, 2 ♀, 27 July 1972, L. M. and B. L.

Ferguson (LMF 217); Campbell Co.: Meredith Cave, 6 mi. SE of LaFollete, 1 ♂, 5 ♀, 21 Aug. 1972, J. R. Holsinger and D. C. Culver, (LMF 226); 5 ♂, 13 ♀, 18 July 1960, collector ?, (LMF 257); ♂♂♀♀, 29 Sept. 1979, T. C. Barr, Jr., (LMF 592); Norris Dam Cave, 2.5 mi. NW of Norris, 2 ♀, 28 Sept. 1979, T. C. Barr, Jr., (LMF 593); Cannon Co.: Cave, 3.5 mi. SSW of Bradyville, 3 ♂, 1 ♀, 1 sex ?, 21 Aug. 1967, S. B. Peck and A. Fiske, (LMF 242); Fisher Cave, 1 ♀, 1 July 1973, S. B. Peck, (LMF 359); Henpeck Mill Cave, 1.7 mi. NE of Woodbury, 1 ♀, 9 Aug. 1967, S. B. Peck and A. Fiske, (LMF 246); 2 ♂, 22 Aug. 1967, S. B. Peck and A. Fiske, (LMF 274); John Hollis Cave, 7 mi. NNE of Woodbury, 2 ♂, 3 ♀, 9 Aug. 1967, S. B. Peck and A. Fiske, (LMF 267); Reed Cave, 2.5 mi. N. of Hollow Springs, 1 ♀, 8 Aug. 1967, S. B. Peck and A. Fiske, (LMF 275); Tenpenny Cave, 2 mi. NW of Woodbury, 1 ♀, 9 Aug. 1967, S. B. Peck and A. Fiske, (LMF 284); Claiborne Co.: Tazewell Saltpeter Cave, 1.5 mi. E. of Tazewell, 1 immature, 19 Aug. 1972, J. R. Holsinger and D. C. Culver, (LMF 225); Clay Co.: Sheals Cave, 0.5 mi. E. of Celina, 1 very young ♂, 28 July 1972, L. M. and B. L. Ferguson, (LMF 218); Coffee Co.: Burk Cave, 2.5 mi. NE of Gossburg and 5 mi. NE of Beechgrove, 1♂, 1♀, 21 Aug. 1967, S. B. Peck and A. Fiske, (LMF 268); 2♂, 7♀, 12-24 May 1972, S. B. and J. Peck, (LMF 338); 1♂, 16 July 1972, T. C. Barr, Jr., (LMF 591); Cumberland Co.: Grassy Cove Saltpeter Cave, ca. 1 mi. from entrance, 1♂, 12 Aug. 1965, C. E. DePoe, (LMF 264); Grainger Co.: Indian Cave, N. of Jefferson City, 5300 ft. from entrance, 1♂, 1♀ ?, with letter of 4 Feb. 1933, J. D. Ives, (LMF 49); 3 sex ?, 5 or 6 ft. from mound of bat castings 1 mi. from entrance, in absolute darkness, with letter of 4 Feb. 1933, J. D. Ives, (LMF 51); Hancock Co.: Panther Creek Cave, 6 mi. NE of Sneedville, 1 ♀, 20 Nov. 1972, J. R. Holsinger, (LMF 594); Suber's Cave, 5 mi. SSE of Ewing, Va., 1 ♂, 25 Aug. 1972, J. R. Holsinger and D. C. Culver, (LMF 227); Marion Co.: Nickajack Cave, 0.5 mi. S. of Shellmound, 1 ♀, 11 Nov. 1967, J. E. and M. R. Cooper, (LMF 200); 1 ♂, 2 ♀, 11 Nov. 1967, J. R. Holsinger and M. Richmond, (LMF 201); 1 ♂, 2 ♀, 8 Apr. 1967, S. B. Peck, (LMF 234); 2 ♂, 8 ♀, 29 July 1967, S. B. Peck, A. Fiske, and J. E. Cooper, (LMF 237); Cave in Tennesse (Nickajack ?), 1 ♀, from flat rock about 3 miles from entrance of cave, letter - no date, J. D. Ives, (LMF 101); Rutherford Co.: Burk Spring Cave, at Burk Cave, 6 ♀, 15 July 1973, S. B. Peck, (LMF 357); Taylor Herring Cave, near Lascassas, 1 ♂, 1 ♀, 23 July 1972, L. M. and B. L. Ferguson, (LMF 211); 4 ♂, 2 ♀, 1 immature, 26 July 1972, L. M. and B. L. Ferguson, (LMF 214); 5 ♀, 5 Jan. 1966, T. C. Barr, Jr. and T. G. Marsh, (LMF 270). VIRGINIA: Lee Co.: Gallohan Cave No. 1, 1 ♀, 19 Mar. 1966, J. R. Holsinger and D. Finley, (LMF 10); 6 ♀, 1 young sex ?, 3 Aug. 1975, T. C. Kane, (LMF 545); Molly Wagle Cave, 1 ♂, 18 Aug. 1965, J. R. Holsinger, (LMF 185); 2 ♀, 2 Aug. 1975, T. C. Kane, (LMF 543); Sweet Potato Cave, 2 ♀, 1 immature, 1 young sex ?, 2 Aug. 1975, T. C. Kane, (LMF 544); Young-Fugate Cave, 1 ♂, 15 Aug. 1965, J. R. Holsinger, (LMF 184); Scott Co.: Spurlock Cave, 1 ♀, 25 Nov. 1966, J. R. Holsinger, (LMF 2); Wise Co.: Little Kennedy Cave, 2 ♂, 1 ♀, 26 Nov. 1970, J. R. Holsinger, R. A. Baroody, and R. M. Norton, (LMF 162); Parsons Cave, 1 ♀, 19 Nov. 1966, J. R. Holsinger, (LMF 14); Rocky Hollow Cave, 1 ♀, 26 Nov. 1966, J. R. Holsinger, (LMF 6).

Material to be deposited in the American Museum of Natural History, the National Museum of Natural History (Smithsonian Institute), and the author's collection.

DIAGNOSIS.--Distinguished from other species of Litocampa in the United States by presence of 3 + 3 and 2 + 2 macrochaetae on meso- and metanota, one dorsal macrochaeta on femur III, tibia III with 1 ventral macrochaeta, claws with well-developed latero-tergal crests, medial anterior macrochaetae absent on abdominal tergites I-IX, 1 + 1 (sometimes 0) posterior macrochaetae on tergite IV, 1 + 1 lateral anterior and 2 + 2 (sometimes 1 + 1) posterior macrochaetae on tergite V, 1 + 1 lateral anterior and 2 + 2 posterior macrochaetae on tergites VI-VII, 7 + 7 macrochaetae on urosternite I, 4 + 4 well differentiated macrochaetae on urosternites II-VII, and 4 + 4 barbed precoxal macrochaetae on the meso- and metasternites.

DESCRIPTION.--Corresponding to the descriptions of Plusiocampa nearctica by Silvestri (1934b) and Condé (1949b), with the following additions.
Size: Males: body length, 3.8-8.4 mm.; head width, 0.58-1.02 mm; pronotal width, 0.35-0.71 mm. Females: body length, 4.3-8.5 mm.; head width, 0.63-1.10 mm.; pronotal width, 0.38-0.81 mm. Immatures: body length, 3.2-3.7 mm.; head width, 0.53-0.58 mm.; pronotal width, 0.31-0.38 mm.
Head: Disregarding 2 antennae of 32 segments and another of 22 segments which had long apical segments and were obviously regenerating (they were also paired with antennae of 37 and 34 segments, respectively), the

the number of segments on 72 complete antennae of 3 immature and 42 mature specimens from Mammoth Cave are as follows:

No. segments:		33	34	35	36	37	38	39	40	41
Frequency:	♂	0	0	1	6	12	7	5	2	1
	♀	1	2	3	12	7	5	3	0	1
	immature	0	1	0	3	0	0	0	0	0

Length of longest antenna 9.85 mm., or about 1.28 times body length. Antennal segment III with ventral bacilliform sensillum, inserted between phaneres d and e: Ma, Mb, seta c, Md (long with 2 distal rows of barbules), sen. (long, exceeding distal border of segment), Me (smooth or with 1 barb), Mf, Mg, Mh; length of d about 1.85 times c; a with 1 distal barbule, other long macrochaetae smooth. Length of latero-dorsal trichobothrium of segment V up to 373 microns, about 34 percent of head width. Segment X length 1.6-2.2 times width. Cupuliform organ of apical segment with 11 sensilla.

Frons with 3 macrochaetae on rostrum; anterior macrochaeta 1.6 times length of posterior pair. Macrochaetae bordering line of insertion of antennae 3 + 3; anterior macrochaeta approximately two-thirds as long as intermediate; anterior and posterior macrochaetae subequal, anterior slightly shorter than posterior; all three macrochaetae barbed on distal half. No macrochaetae anterior to arms of epicranial suture, near sagittal plane. Occipital setae barbed on distal half; length about 58 percent that of pronotal lp. Latero-anterior sensillum of labial palp subcylindrical, sickle-shaped.

Posterior mental setae smooth; lateral submental macrochaetae smooth. Thorax: Clothing setae smooth; notal chaetotaxy 3 + 3, 3 + 3, 2 + 2. Lengths and ratios of macrochaetae of mature specimens from Mammoth Cave, as follows:

	ma	la	lp	ma/la	lp/ma
Th. I	81-194	81-227	167-346	0.85-1.09	1.64-2.07
Th. II	97-232	119-275	211-367	0.80-0.91	1.45-2.22
Th. III	81-227	--	119-362	--	1.47-2.11

Mesonotum: ma/Sep ma-ma, 1.14-1.64; ma/Sep ma-la, 0.91-1.13; la/Sep ma-la, 1.10-1.42; lp_I/lp_{II}, 0.79-1.02; lp_{II}/lp_{III}, 1.00-1.77. Pronotum with 3 + 3 to 8 + 8 barbed lateral posterior marginal setae and 4 to 6 smooth medial posterior marginal setae; mesonotum with 3 + 5 to 7 + 7 lateral, 4 medial posterior marginal setae; metanotum with 2 + 2 to 5 + 5 lateral, 6 medial posterior marginal setae.

Presternite of prosternum with 2 + 2 M; prosternite with 4 + 4 barbed precoxal M; 3 + 3 to 5 + 5 smooth precoxal setae; 1 + 1 subcoxal M; 2 + 2 lp. Mesosternite with 4 + 4 barbed precoxal M; 4 + 4 to 6 + 6 smooth precoxal setae; 1 + 1 ma; 1 + 1 la; 1 + 1 subcoxal M; 2 + 2 lp. Metasternite with 4 + 4 barbed precoxal M; 4 + 4 to 6 + 6 smooth precoxal setae; 1 + 1 ma; 1 + 1 la; 1 + 1 subcoxal M; 1 + 1 lp (Fig. 3A).

Length of leg III about 45 percent of body length, reaching abdominal segment IX. Femur I without dorsal macrochaetae; femurs II and III with one dorsal macrochaeta. Dorsal macrochaeta inserted on distal half of femur III, 1.4-1.6 times width of femur at point of insertion;

barbed on its distal 0.6. Femur III with 4 anterior marginal macrochaetae; 2 most ventral barbed on distal 60 percent; distal pair barbed on distal 50 percent. Tibia III length 7.6-10.1 times width, with one bifurcated ventral macrochaeta with 0 to 5 small barbs proximal to bifurcation; tibial spurs with 2 rows of long barbs. Tarsus III with 20 ventral setae in anterior row. Posterior claw longer than anterior; latero-tergal crests well developed; flange on posterior claw. Pretarsal appendices long, slender, and smooth; length exceeding tip of claws. Abdomen: Distribution of tergal macrochaetae:

	la	post
Ab. I-III	0	0
Ab. IV	0	1 + 1 (0)
Ab. V	1 + 1	2 + 2 (1 + 1)
Ab. VI-VII	1 + 1	2 + 2
Ab. VIII	0	3 + 3
Ab. IX	0	5 + 5 (total)

Lateral anterior macrochaetae of Ab. V-VII about 0.6 to 0.7 length of posterior macrochaetae. Posterior macrochaetae long and robust, similar to thoracic lp; barbed on distal half to two-thirds. Lengths and ratios of certain tergal macrochaetae, as follows:

	la	$post_1$	$post_2$	$post_1$/Sep $post_1$-$post_1$
Ab. V	76-216	162-346	113-319	0.64-0.73
Ab. VII	103-265	194-367	173-367	0.61-0.82

Abdominal tergite IV with up to 15 posterior marginal setae separating sublateral posterior macrochaetae nearest sagittal plane; tergite V with up to 12 such setae; VI with 14; VII with 15; VIII with 13; IX with 15. Supra-anal valvule with 1 smooth subapical seta, 1 medial setiform sensillum, 2 + 2 to 4 + 4 barbed lateral setae.

Urosternite (coxosternite) I with 7 + 7 differentiated macrochaetae, 4 + 4 on middle portion; 1 + 1 submacrochaetae at latero-posterior angle of urosternite of some specimens. Posterior margin without glandular setae on males and females. Lateral subcoxal appendages subcylindrical among females; broader on males; asymmetrical on largest males, being greatly expanded on the external side. Females with up to 30 glandular-like setae on each appendage near internal point of attachment to urosternite; numerous glandular setae on appendages of males.

Urosternites II-VII with 4 + 4 well differentiated macrochaetae, with branches and barbs; 2 + 2 weakly differentiated macrochaetae inserted on both sides of styli. Apical seta of styli with 1 distal barbule and 2 short basal branches, proximal branch about one-half length of distal; subapical seta smooth; medial ventral seta forked, with barbule proximal to bifurcation; clothing setae smooth. Stylus VII of largest male length 4.7 times width; apical seta about 35 percent as long as stylus. Urosternite VIII with 1 + 1 macrochaetae. Genital papilla of males with 15-19 short setae encircling gonopore.

Length of longest cercus about 1.90 times body length, composed of a base, subdivided into 4 secondary segments, and 17 primary segments. Segmental lengths (in mm): base = 0.18, 0.18, 0.22, 0.31; primary segments = 0.36, 0.41, 0.43, 0.52, 0.55, 0.55, 0.62, 0.71, 0.78, 0.97, 1.05, 1.19, 1.24, 1.34, 1.36, 1.43, 1.43. Covering of base and proximal segments composed of long macrochaetae, length of macrochaetae about 2.8 times width of segments, long barbs on distal half. Proximal primary segments with whorls of 7 barbed macrochaetae, long smooth setae, and 10 short subapical setae. Penultimate segment length 37.7 times width, with 8 whorls of macrochaetae, alternating with whorls of long and short smooth setae; macrochaetae with 5-8 distal barbs; 7 short subapical setae. Macrochaetae of apical segment arranged in 9 whorls, length of macrochaetae about 4.3 times width of segment, alternating with whorls of long and short smooth setae; all macrochaetae smooth except some of proximal 3 whorls, with 3 small distal barbules.

Variation: Except for the variation mentioned above in the diagnosis and description, little variation exists between populations of *Litocampa cookei*. Considering the extensive range and apparent disjunct nature of the distribution of this species, the lack of appreciable variation is remarkable. Only some of the campodeids inhabiting caves in Cannon County, Tenn., show any major divergences. The variation consists of the addition of 1 + 1 or 1 + 0 posterior macrochaetae on abdominal tergites II and/or III. However, the normal *cookei* chaetotaxy exists in specimens from these caves, as well as all gradations in-between.

REMARKS.--Due to the similarity of some Mammoth Cave specimens and specimens from caves in eastern Kentucky, I indicated that two species of campodeids might be inhabiting Mammoth Cave (Ferguson, 1974). Additional study of all _cookei_-like specimens has revealed that most eastern Kentucky specimens from Pulaski and Rockcastle counties represent an undescribed species which is morphologically distinct from all Mammoth Cave specimens. Also, there is a complete gradation of the abdominal chaetotaxal variation seen in the Mammoth Cave specimens. Therefore, there is no evidence at present to indicate more than one species of campodeid dipluran in Mammoth Cave.

My examination of the type specimen of _Campodea cookei_ Packard at the Museum of Comparative Zoology of Harvard University confirmed that this species belongs to the genus _Litocampa_ and conforms to the description presented above. Therefore, Silvestri (1934b) and Paclt (1957) were in error in treating _Campodea cookei_ as a _nomen dubium_. This makes _Plusiocampa nearctica_ Silvestri a junior synonym of _Litocampa cookei_ (Packard). In fact, _Plusiocampa nearctica_ Silvestri (1934b) may be a manuscript name or _nomen nudum_ (see Silvestri, 1933e).

TYPE LOCALITY.--Mammoth Cave of the Flint-Mammoth Cave System, in Mammoth Cave National Park located in Edmonson, Barren, and Hart counties, Kentucky. With 212 miles of surveyed passages, and 16 entrances (Coons and Engler, 1980), the Flint-Mammoth Cave System is the longest known cave system in the world. The caves are formed in the Middle Mississippian aged Ste. Genevieve and Girkin limestones (Davidson and Bishop, 1971).

DISTRIBUTION AND ECOLOGY.--_Litocampa cookei_ is known from other caves in the Mammoth Cave Plateau and the adjacent Pennyroyal Plateau of Kentucky. Members of this species also occur in central, southeastern, and northeastern Tennessee, southeastern Kentucky, and southwestern Virginia. As presently known, the species appears to have a very large disjunct distribution with about five major clusters of populations (Fig. 43), in the areas just mentioned.

In Mammoth Cave I have twice collected _L. cookei_ from Rafinesque Hall off Audubon Avenue. The passage ends in a slope of rocks, silt, and clay, known as a terminal breakdown (White, 1976), where the passage approaches the surface. Using bait, specimens were found farther down the slope in early March, 1975, than previously in April, 1973. Cold surface water seeps down the slope in winter. At the time I thought that the campodeids had moved further into the cave because of the lower temperature at the top of the slope (many specimens were found at the base of the breakdown slope). However, the increased water flow in winter may have just saturated the sediment of the slope, driving out the campodeids, similar to what occurs to earthworms following heavy rains.

A specimen of _L. cookei_ from Little Kennedy Cave, Wise Co., Virginia, had a partly digested mite in its gut, along with spiral fungal spores (_Helicomyces_ type). The mite has been tentatively identified as an acarid hypopus (a phoretic deutonymph) probably of the family Histiostomidae (W. C. Welbourn, in litt.).

Litocampa sperkai, new species

(Figs. 3-4)

MATERIAL EXAMINED.--KENTUCKY: *Pulaski Co.*: Sloans Valley Cave (NSS#KYPU0019), 36°56'13", 84°32'39", 1♀ (holotype), 22 Mar. 1970, D. P. Beiter, (LMF 370); paratypes: 1♀, 1 Feb. 1970, R. Sperka, (LMF 368); 1♂, 19 Mar. 1970, R. Sperka, (LMF 369); 1♀, 12 Apr. 1970, R. Sperka, (LMF 371); 1♂, 2♀, 1 May 1970, D. P. Beiter, (LMF 372); 1 young ♂, 24 Jan. 1971, D. P. Beiter, (LMF 375); Stab Cave, 1♀, A. Newsome, (LMF 547); *Rockcastle Co.*: Climax Cave, 3♂, 5♀, 12 Dec. 1967, T. C. Barr, Jr., (LMF 188); 3♀, Sept. 1972, T. Seibert, (LMF 317); 2♂, 12 Jan. 1973, T. Seibert, (LMF 319); Goochland Cave, 3♂, 1♀, 27 Jan. 1973, T. Seibert, (LMF 321); Green Hill Cave, 2♂, 14 Jan. 1967, J. Reddell, T. C. Barr, Jr., (LMF 255); Millers Cave No. 2, 1 young ♀, Sept. 1972, T. Seibert, (LMF 318); Mullins Spring Cave, 1♂, 1♀, Nov. 1972, T. Seibert, (LMF 320); 1♂, 10 Feb. 1973, T. Seibert, (LMF 322); 2♂, 3♀, 23 Mar. 1973, T. Seibert, (LMF 447); Pine Hill Cave, 1♀, 4 Mar. 1967, J. Reddell, (LMF 229); Teamers Cave (NSS#KYRP-0006), 37°21'04", 84°12'22", 1♀, 10 Oct. 1970, R. Sperka, (LMF 374); 2♂, 1 immature, 8 July 1971, R. Sperka, (LMF 378); Tedmens Cave, 1♀, 20 Nov. 1972, T. Seibert, (LMF 323); Up and Down Cave, 1♀, 23 Mar. 1973, T. Seibert, (LMF 448).

Holotype (LMF 370-1) and paratypes to be deposited in the American Museum of Natural History and the author's collection.

DIAGNOSIS.--Very similar to L. cookei from which it can be distinguished by the presence of 5 + 5 barbed precoxal macrochaetae on the meso- and metasternites (instead of 4 + 4 on L. cookei). Some specimens of L. sperkai lack the metanotal lp, which is always present on L. cookei. Abdominal tergites I-IV without macrochaetae, and tergite V with 1 + 1 lateral anterior and 1 + 1 posterior macrochaetae (L. cookei usually with 1 + 1 posterior macrochaetae on tergite IV and with 1 + 1 lateral anterior and 2 + 2 posterior macrochaetae on tergite V). Abdomen X usually without lateral anterior macrochaetae (generally present on L. cookei).

DESCRIPTION.--Size: Males: body length, 4.3-5.4 mm; head width, 0.62-0.75 mm; pronotal width, 0.39-0.52 mm. Females: body length, 5.8-6.9 mm; head width, 0.82-0.90 mm; pronotal width, 0.55-0.62 mm. Head: Disregarding antennae of 20, 21, 25, and 31 segments, which were obviously regenerating, the number of segments on 37 complete antennae are as follows:

No. segments:		29	30	31	32	33	34	35	36
Frequency:	♂	0	1	1	1	1	1	5	0
	♀	1	3	4	2	7	4	5	1

Length of longest antenna 7.38 mm, or about 1.07 times body length. Antennal segment III with ventral bacilliform sensillum, inserted between phaneres d and e: Ma, Mb, seta c, Md (long, smooth), sen. (long, exceeding distal border of segment), seta e (smooth or with 1 barb), Mf, Mg, Mh; length of d about 1.58 times c; all macrochaetae smooth. Length of latero-dorsal trichobothrium of segment V up to 295 microns, about 36 percent of head width. Segment X length 1.4-1.9 times width. Cupuliform organ of apical segment with 12 sensilla.

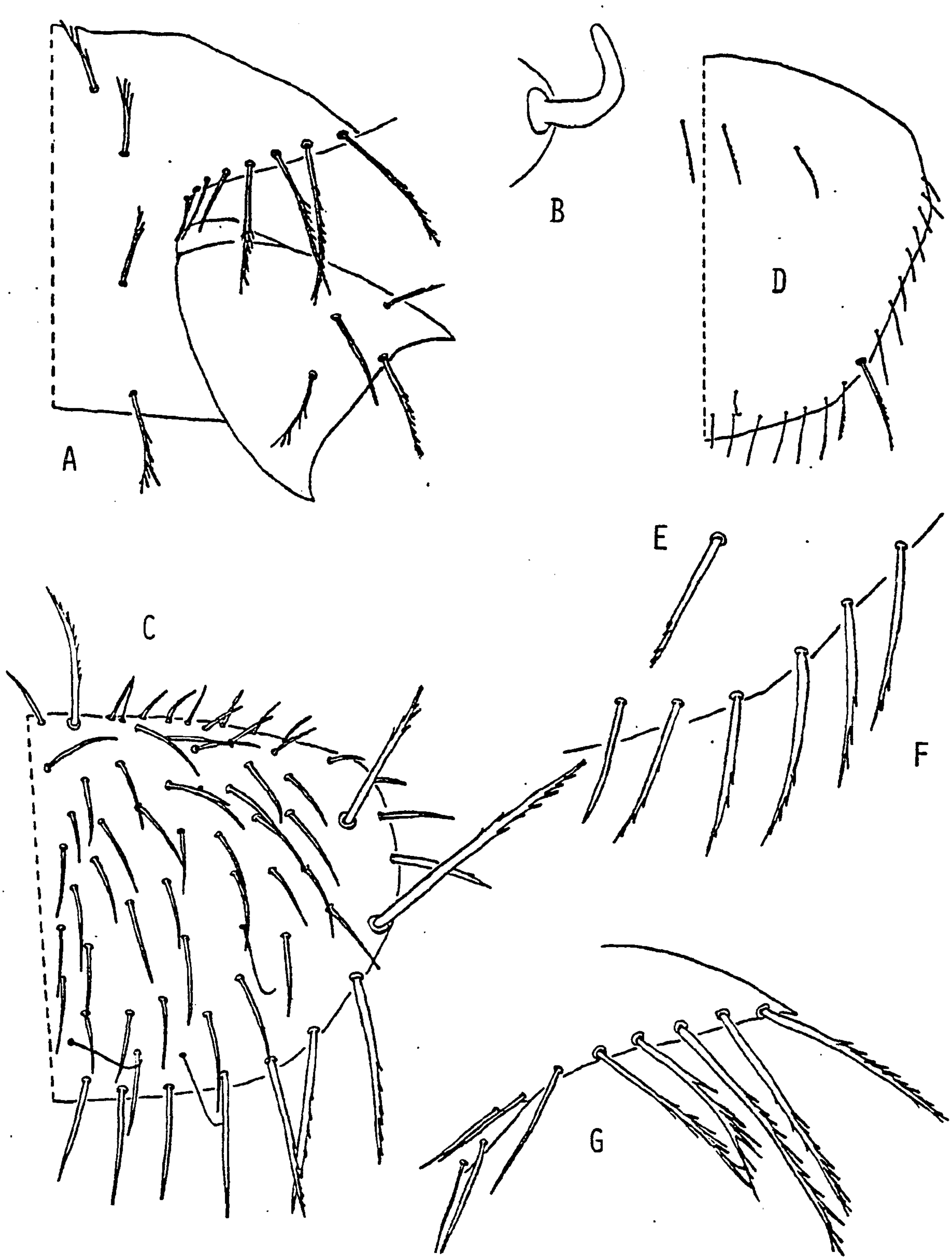
Frons with 3 macrochaetae on rostrum; anterior macrochaeta 1.5 times length of posterior pair. Macrochaetae bordering line of insertion of antennae 3 + 3; anterior macrochaeta approximately 0.8 as long as intermediate; anterior and posterior macrochaetae subequal, anterior slightly shorter than posterior; all three macrochaetae barbed on distal two-thirds. No macrochaetae anterior to arms of epicranial suture, near sagittal plane. Occipital setae barbed on distal half; length about 70 percent that of pronotal lp. Latero-anterior sensillum of labial palp subcylindrical, sickle-shaped (Fig. 3B). Posterior mental setae smooth; lateral submental macrochaetae smooth.

Thorax: Clothing setae smooth; notal chaetotaxy 3 + 3, 3 + 3, 2 + 2 or 1 + 1 (ma) (Fig. 3C-F). Lengths and ratios of macrochaetae of mature specimens from Sloans Valley Cave, as follows:

	ma	la	lp	ma/la	lp/ma
Th. I	92-119	97-146	151-216	0.81-0.94	1.65-1.82
Th. II	97-157	113-140	151-227	0.86-1.12	1.45-1.56
Th. III	81-108	--	135 (0)	--	1.25 (0)

Mesonotum: ma/Sep ma-ma, 1.29-1.32; ma/Sep ma-la, 0.95-1.07; la/Sep ma-la, 0.96-1.11; lp_{I}/lp_{II}, 0.95-1.00; lp_{II}/lp_{III}, 1.68 (-). Pronotum

FIGURE 3.--*Litocampa cookei* (Packard). A, left half of metasternite and coxa III (clothing setae not shown). *Litocampa sperkai*, new species. B, latero-anterior sensillum of left labial palp; C, pronotum; D, mesonotum; E, *ma* of metanotum; F, latero-posterior border of metanotum; G, precoxal macrochaetae of metasternite. A, female (8.3 mm; head width, 1.10 mm), Mammoth Cave, Kentucky. B-G, female (6.9 mm; head width, 0.89 mm), Sloan's Valley Cave, Kentucky.


A
B
C
D
E
F
G

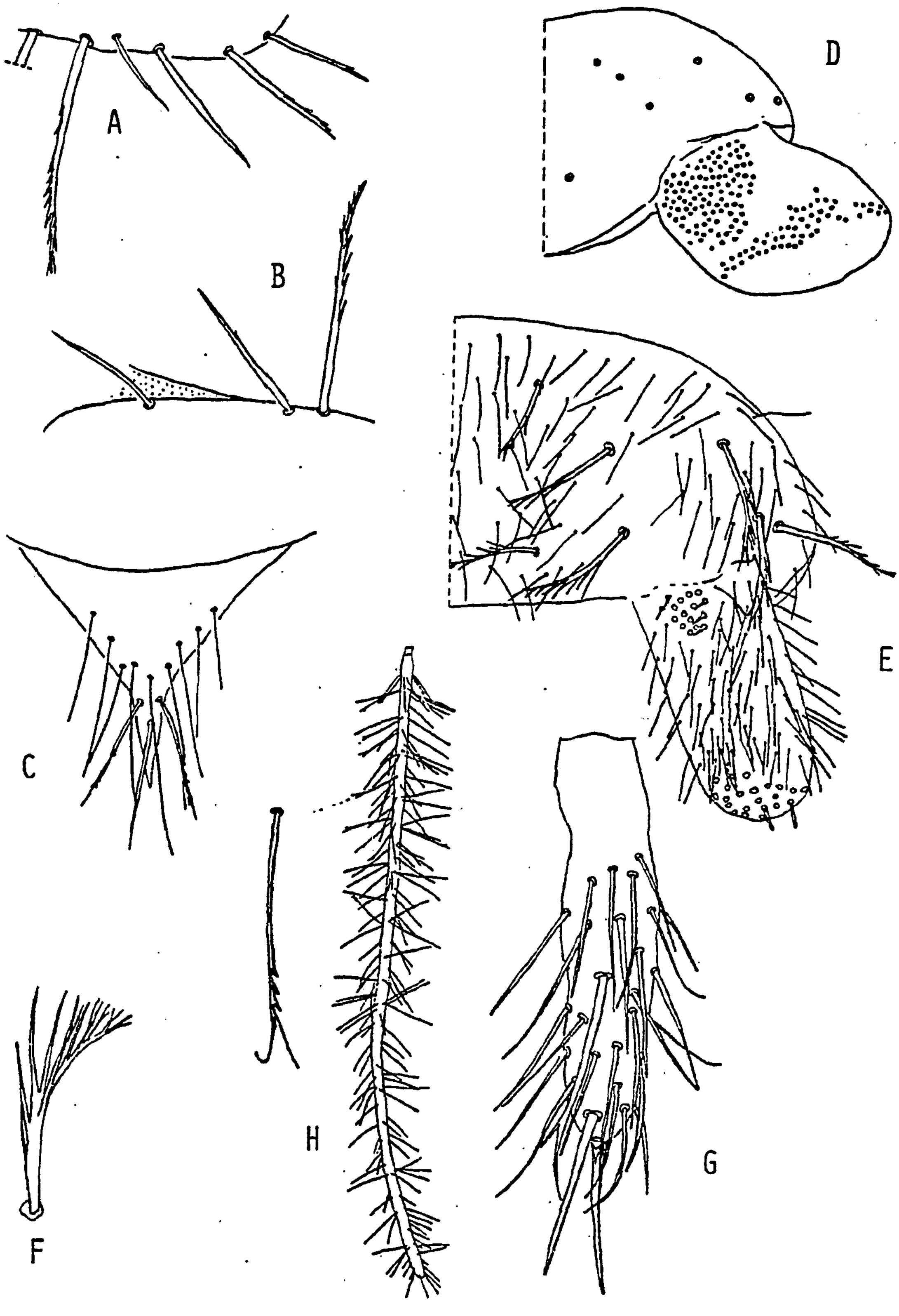
with 1 + 2 to 2 + 2 densely barbed lateral posterior marginal setae and 9 medial posterior marginal setae; mesonotum with 1 + 1 to 2 + 3 lateral, 9 to 10 medial posterior marginal setae; metanotum with 1 + 1 to 3 + 3 lateral, 9 to 10 medial posterior marginal setae.

Presternite of prosternum with 2 + 2 M; prosternite with 4 + 4 barbed precoxal M; 3 + 3 to 4 + 4 smooth precoxal setae; 1 + 1 subcoxal M; 2 + 2 lp. Meso- and metasternite with 5 + 5 barbed precoxal M; 3 + 4 to 4 + 4 smooth precoxal setae (3 + 3 to 5 + 5 on metasternite); 1 + 1 ma; 1 + 1 la; 1 + 1 subcoxal M; 2 + 2 and 1 + 1 lp on meso- and metasternite, respectively (Fig. 3G).

Length of leg III about 45 percent of body length, reaching abdominal segment IX. Femur I without dorsal macrochaetae; femurs II and III with 1 dorsal macrochaeta. Dorsal macrochaeta inserted in middle of femur III, 1.00-1.03 times width of femur at point of insertion; barbed on its distal 0.6. Femur III with 4 anterior marginal macrochaetae; 2 most ventral barbed on distal 60 percent; proximal macrochaeta of distal pair smooth; distal macrochaeta with few barbs on distal 0.33 (Fig. 4A,B). Tibia III length 7.1-10.6 times width, with one bifurcated ventral macrochaeta with 0 to 2 small barbs proximal to bifurcation; tibial spurs with 2 rows of long barbs and 1 intermediate row of short barbs. Tarsus III with 19 ventral setae in anterior row. Posterior claw longer than anterior; latero-tergal crests well developed; flange on posterior claw. Pretarsal appendices long, slender, and smooth; apex reaching tip of claws.

Abdomen: Distribution of tergal macrochaetae:

FIGURE 4.--*Litocampa sperkai*, new species. A, anterior distal margin of femur III; B, posterior distal margin of femur III; C, supra-anal valvule; D, urosternite I of male (macrochaetae represented by their bases, a field of short glandular-like setae located near internal point of attachment of lateral subcoxal appendages represented by their bases, only some of the glandular setae on the tip of the lateral appendage represented by their bases, regular clothing setae not shown); E, urosternite I of female (clothing setae diagrammatic; only some of glandular and glandular-like setae shown, others represented only by their bases); F, macrochaeta at base of eversible vesicle of urosternite VII; G, left stylus of urosternite VII; H, apical segment of cercus and macrochaeta (enlarged). D, male (6.8 mm; head width, 0.87 mm), Mullins Spring Cave, Kentucky. G-H, female (6.9 mm; head width, 0.90 mm); others, female (6.9 mm; head width, 0.89 mm), Sloan's Valley Cave, Kentucky.


II
A
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H

	la	post
Ab. I-IV	0	0
Ab. V	1 + 1 (0)	1 + 1 (0)
Ab. VI-VII	1 + 1	2 + 2
Ab. VIII	0	3 + 3
Ab. IX	0	5 + 5 (total)

Lateral anterior macrochaetae of Ab. VI-VII about 0.5 to 0.6 length of posterior macrochaetae. Posterior macrochaetae long and robust, similar to thoracic lp; barbed on distal half to two-thirds. Lengths and ratios of certain tergal macrochaetae, as follows:

	la	$post_1$	$post_2$	$post_1$/Sep $post_1$-$post_1$
Ab. VI	119-162	205-302	194-319	0.71-0.73
Ab. VII	119-189	227-324	205-329	0.71-0.75

Abdominal tergite VI with up to 14 posterior marginal setae separating sublateral posterior macrochaetae nearest sagittal plane; tergite VII with up to 14 such setae; VIII with 9; IX with 12. Tergite X generally without lateral anterior macrochaetae. Supra-anal valvule with 2 smooth medial setae, up to 4 + 5 barbed or smooth lateral setae, and 1 barbed subapical seta (Fig. 4C).

Urosternite (coxosternite) I with 7 + 7 differentiated macrochaetae, 4 + 4 on middle portion. Posterior margin without glandular setae on males and females. Lateral subcoxal appendages subcylindrical among females; broader on males; asymmetrical on largest males, being expanded on external side (Fig. 4D,E). Females with up to 16 glandular setae on each appendage near internal point of attachment to urosternite; numerous glandular setae on appendages of males.

Urosternites II-VII with 4 + 4 well differentiated macrochaetae, with branches and barbs (Fig. 4F); 2 + 2 weakly differentiated macrochaetae inserted internally and externally at base of each stylus. Apical seta of styli smooth and with 2 short basal branches, proximal branch about one-half length of distal; subapical seta smooth; medial ventral seta bifurcated; clothing setae smooth (Fig. 4G). Stylus VII length 4.6-6.1 times width; apical seta about 33 percent as long as stylus. Urosternite VIII with 1 + 1 macrochaetae. Genital papilla of males with 14-19 short setae encircling gonopore.

Length of longest cercus about 1.47 times body length, composed of a base, subdivided into 4 secondary segments, and 7 primary segments. Segmental lengths (in mm): base = 0.18, 0.19, 0.25, 0.40; primary segments = 0.49, 0.75, 0.94, 1.29, 1.52, 1.91, 2.24. Covering of base and proximal segments composed of long macrochaetae, length of macrochaetae about 3.3 times width of segments, long barbs on their distal 0.6. Proximal primary segments with whorls of 7 barbed macrochaetae, long smooth setae, and 7-9 short subapical setae. Penultimate segment length 39 times width, with 11 whorls of macrochaetae, alternating with whorls of long smooth setae; macrochaetae with several barbules; 9 short subapical setae. Macrochaetae of apical segment arranged in 14 whorls, length of macrochaetae about 5.1 times width of segment, alternating with whorls of long and short smooth setae (Fig. 4H); macrochaetae smooth except some of proximal 9 whorls, with large subapical barbule and several barbules proximal to subapical.

Variation: The most notable variation is that of the lateral posterior macrochaetae of the metanotum and the chaetotaxy of abdominal tergite V. The metanotal *lp* is shortened on some individuals of nearly every cave population of *Litocampa sperkai*, and is completely lacking on most specimens from the Sloan's Valley Cave System. The chaetotaxy of abdominal tergite V is quite variable in all populations, and lacks macrochaetae entirely on the Sloan's Valley Cave specimens.

TYPE LOCALITY.--Sloan's Valley Cave System, located at the community of Sloan's Valley in Pulaski County, Ky. This cave is the second longest cave system known in Kentucky, with 24.2 miles of surveyed passages and 16 entrances. The cave is developed in the Upper Mississippian-aged Newman limestone (Schuchert, 1943). The lower levels of the cave system have been flooded by the impounded waters of Lake Cumberland (Simpson, 1981).

DISTRIBUTION AND ECOLOGY.--Known from 11 caves of the Highland Rim in Pulaski and Rockcastle counties of eastern Kentucky. Except for Sloan's Valley Cave, all of the caves are located north of the Cumberland River. *Litocampa sperkai* probably has a range similar to that of the cave beetle, *Darlingtonia kentuckensis*, and the cave cricket, *Hadenoecus cumberlandicus* (Hubbell and Norton, 1978), and will likely be found in caves farther to the northeast in Kentucky.

ETYMOLOGY.--It is a pleasure to name this species after one of its discoverers, Roger J. Sperka. Roger collected campodeids from several Kentucky caves, and he compiled other campodeid collections and made them available for study.

Litocampa jonesi (Condé)

(Figs. 5-6)

Plusiocampa jonesi Condé, 1949b: 135-137, fig. 6. [Dunbar Cave, Montgomery Co., Tennessee; repository unknown]; 1956: 131, fig. 31C, 132, 170, 178, 187; Nicholas, 1960: 140; Barr, 1961:39.

Litocampa (Litocampa) jonesi (Condé), Paclt, 1957: 26; Ferguson, (in press).

MATERIAL EXAMINED.--Kentucky: Christian Co.: Glover's Cave (erroneously labeled Todd Co.), 1 ♂, 18 April 1964, S. B. Peck, (LMF 250).

Specimen (LMF 250-1) is on loan to the author from the American Museum of Natural History.

DIAGNOSIS.--Distinguished from other species of Litocampa in the United States by presence of 3 + 3 and 2 + 2 macrochaetae on meso- and metanota, one dorsal macrochaeta on femur III, tibia III with 1 ventral macrochaeta, claws without well-developed latero-tergal crests, medial anterior macrochaetae lacking on abdominal tergites, 1 + 1 lateral anterior and 2 + 2 lateral posterior macrochaetae on tergites IV - VII, 7 +7 macrochaetae on urosternite I, and 4 + 4 well differentiated macrochaetae on urosternites II - VII.

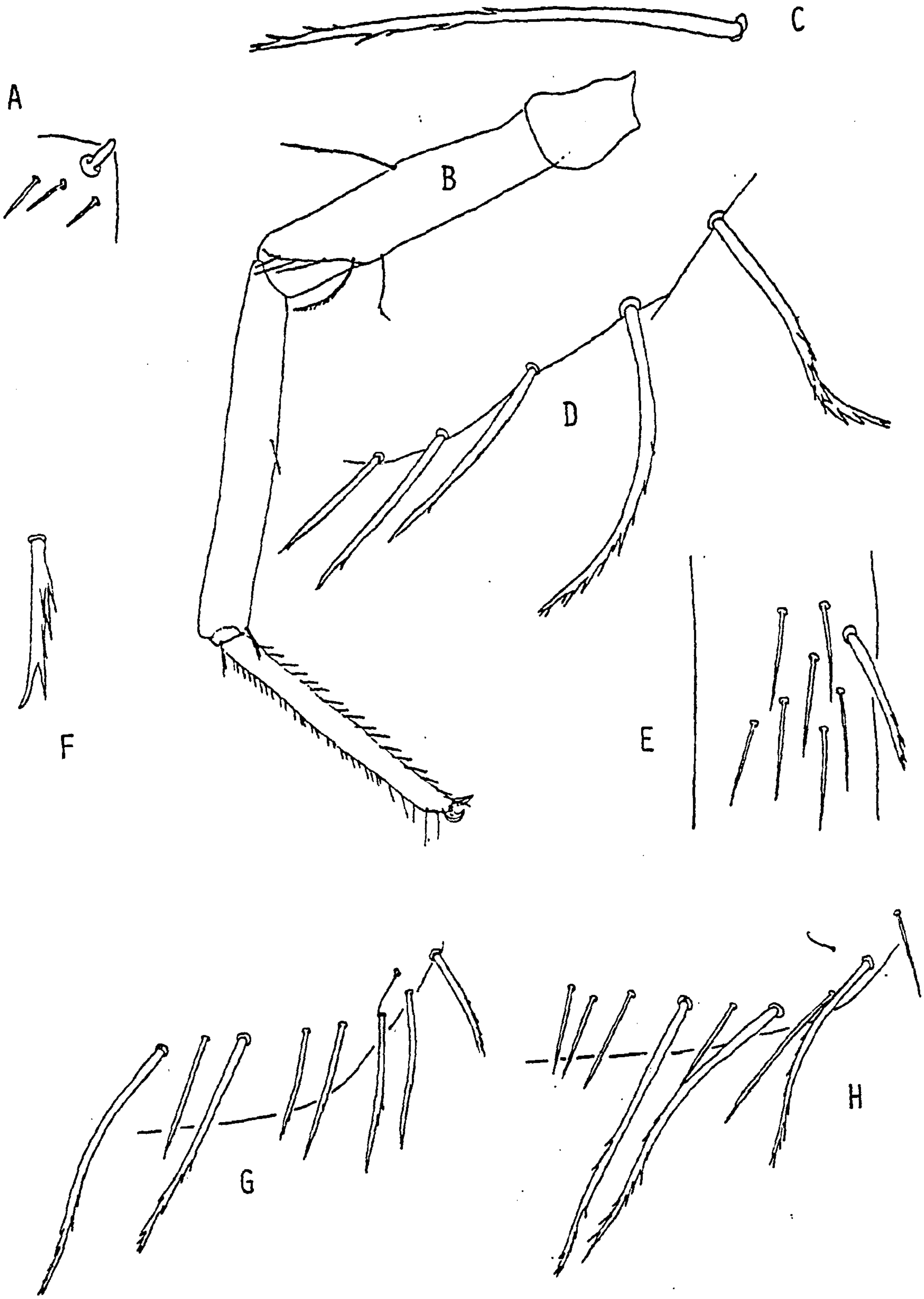
DESCRIPTION.--Corresponding to the description by Condé (1949b) for a single female specimen from Dunbar Cave, Tennessee. Additions and description of the male follows.

Size: Male: body length, 6.0 mm; head width, 0.72 mm; pronotal width 0.49 mm.

Head: Antennal segments 28 on only complete antenna; 25 and 26 segments on type specimen. Length of antenna 4.13 mm, or about 68 percent of body length, reaching middle of abdominal segment V. Antennal segment III with ventral bacilliform sensillum, inserted between phaneres d and e: Ma, Mb, seta c, Md (short with 2 distal barbs), sen. (exceeds distal border of segment), seta e (with 2 barbs), Mf, Mg, Mh; length of d slightly less than c; b with 2 minute distal barbs, other long macrochaetae smooth. Length of latero-dorsal trichobothrium of segment V up to 305 microns, about 42 percent of head width. Segment X length 1.7 times width. Cupuliform organ of apical segment with 8 sensilla.

Frons with 3 macrochaetae on rostrum, barbed on their distal half; anterior macrochaeta 1.6 times length of posterior pair. Macrochaetae bordering line of insertion of antennae 3 + 3; anterior macrochaeta approximately one-half as long as intermediate; anterior and posterior macrochaetae subequal, anterior slightly shorter than posterior; all three macrochaetae barbed on distal half. No macrochaetae anterior to arms of epicranial suture, near sagittal plane. Occipital setae with numerons barbs on their distal half or two-thirds; length about 45 percent as long as pronotal 1p. Latero-anterior sensillum of labial palp subcylindrical, straight, somewhat swollen in middle region (Fig. 5A). Posterior mental setae smooth; lateral submental macrochaetae smooth.

FIGURE 5.--Litocampa jonesi (Condé). A, latero-anterior sensillum of left labial palp; B, metathoracic leg; C, dorsal macrochaeta of femur III; D, anterior distal margin of femur III; E, ventral macrochaeta of tibia III; F, tibial spur of leg III; G, lateral posterior margin of tergite IV; H, lateral posterior margin of tergite VII. Male (6.0 mm; head width, 0.72 mm), Glover's Cave, Kentucky.


C
A
B
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H

Thorax: Clothing setae smooth; notal chaetotaxy 3 + 3, 3 + 3, 2 + 2. Pronotal ma barbed on distal 58 percent, la on distal 62 percent, lp on distal 55 percent; mesonotal ma barbed on distal 55 percent, la on distal 62 percent, lp on distal 56 percent; metanotal ma barbed on distal 58 percent, lp on distal 51 percent. Lengths and ratios of macrochaetae of only specimen from Glover's Cave:

	ma	la	lp	ma/la	lp/ma
Th. I	151	162	270	0.93	1.79
Th. II	151	211	281	0.72	1.86
Th. III	151	--	259	--	1.71

Mesonotum: ma/Sep ma-ma, 1.36; ma/Sep ma-la, 0.95; la/Sep ma-la, 1.30; lp_I/lp_{II}, 0.96; lp_{II}/lp_{III}, 1.08. Pronotum with 3 + 4 barbed posterior marginal setae and 8 smooth (or with small barbules) medial posterior marginal setae; mesonotum with 2 + 2 barbed, 10 smooth posterior marginal setae; metanotum with 1 + 1 barbed, 10 smooth posterior marginal setae.

Presternite of prosternum with 2 + 2 M; prosternite with 4 + 4 barbed precoxal M; 5 + 5 smooth precoxal setae; 1 + 1 subcoxal M: 2 + 2 lp. Mesosternite with 4 + 4 barbed precoxal M; 6 + 6 smooth precoxal setae; 1 + 1 ma; 1 + 1 la; 1 + 1 subcoxal M; 2 + 2 lp. Metasternite with 4 + 4 barbed precoxal M; 5 + 5 smooth precoxal setae; 1 + 1 ma; 1 + 1 la; 1 + 1 subcoxal M; 2 + 2 lp.

Length of leg III about 36 percent of body length, reaching abdominal segment VII. Femur I without dorsal macrochaetae; femurs II and III with one dorsal macrochaeta. Dorsal macrochaeta inserted on distal half of femur III, 1.6 times width of femur at point of insertion; barbed on its distal half (Fig. 5B,C). Femur III with 5 anterior marginal macrochaetae; 2 most ventral barbed on their distal half; others usually with 1 distal barbule (Fig. 5D). Tibia III length 8 times width, with one bifurcated ventral macrochaeta with 2-3 small barbs proximal to bifurcation (Fig. 5E); tibial spurs with 2 rows of long barbs (Fig. 5F). Tarsus III with 16 ventral setae in anterior row. Posterior claw only slightly longer than anterior; laterotergal crests very reduced; no flange on posterior claw. Pretarsal appendices long, slender, and smooth; length exceeding tip of claws.

Abdomen: Distribution of tergal macrochaetae (Fig. 5G,H):

	la	lp
Ab. I-III	0	0
Ab. IV-VII	1 + 1	2 + 2
Ab. VIII	0	3 + 3
Ab. IX	0	5 + 5 (total)

Lateral anterior macrochaetae fairly short on Ab. IV, two times longer on Ab. VII. Lateral posterior macrochaetae long and robust, similar to thoracic lp; barbed on distal half. Lengths and ratios of certain tergal macrochaetae, as follows:

	la	lp_1	lp_2	lp_1/Sep lp_1-lp_1
Ab. IV	86.4	238	189	0.88
Ab. VII	184	248	259	0.66

Abdominal tergite IV with 14 posterior marginal setae separating sublateral posterior macrochaetae nearest sagittal plane; tergite V with 14 such setae; VI with 13; VII with 15; VIII with 12; IX with 12. Supra-anal valvule with 3 smooth setae forming a triangle; subapical median seta thicker than others.

Urosternite (coxosternite) I with 7 + 7 very differentiated macrochaetae, 4 + 4 on middle portion. Posterior margin with glandular setae on males; approximately 5 rows of glandular setae on middle portion, larger concentration laterad. Lateral subcoxal appendages suboval in shape on mature male. Approximately 100 glandular setae on tip of appendages of male (Fig. 6A).

Urosternites II-VII with 4 + 4 well differentiated macrochaetae, with branches and barbs (Fig. 6B); 2 + 2 weakly differentiated macrochaetae inserted on either side of styli. Apical seta of styli with 2 distal barbules and 2 short basal branches, proximal branch about one-half length of distal; subapical seta with 1 barb on proximal half; medial ventral seta forked; clothing setae smooth (Fig. 6C). Stylus VII length 6.5 times width; apical seta about 45 percent as long as stylus; with 10 clothing setae and setiform sensilla. Urosternite VIII with 1 + 1 macrochaetae. Genital papilla of male distorted, but covered with clothing setae.

Cerci missing.

Variation: The male specimen from Glover's Cave agrees very closely with the species description of Condé (1949b). The male appears, however, to have somewhat longer legs than the female that Condé described. Also, the long notal and tergal macrochaetae are barbed

FIGURE 6.--Litocampa jonesi (Condé). A, urosternite I (many glandular setae represented only by their bases); B, medial posterior macrochaeta and macrochaeta at base of eversible vesicle of urosternite VI; C, left stylus of urosternite VI. Male (6.0 mm; head width, 0.72 mm), Glover's Cave, Kentucky.


A
B
C

on slightly more than their distal one-half, whereas Condé reports barbules on their distal two-thirds.

TYPE LOCALITY.--Dunbar Cave, 2 miles northeast of Clarksville, Montgomery Co., Tennessee. The cave contains a large, deep stream which emerges to become a tributary of Red River. The cave is over a mile in length and is developed in the Mississippian aged St. Louis limestone (Barr, 1961).

DISTRIBUTION AND ECOLOGY.--Known only from the type locality and Glover's Cave, 4 miles southwest of Trenton, in the eastern edge of Christian Co., Kentucky. Glover's Cave is reported to be 2.25 miles in length (over 8000 feet have been surveyed), with numerous damp silt banks (Barr, 1959a; Mylroie, 1978). Both caves lie in a southern portion of the Pennyroyal Plateau.

The cave beetle, *Pseudanophthalmus ciliaris ciliaria* Valentine, has been found in both caves, as well as in Bell Witch Cave and Buzzard Cave in northwest Robertson Co., Tennessee, which is east and adjacent to Montogomery Co.. *P. ciliaris* is restricted to caves of the Red River drainage, but is part of the *pubescens* group of *Pseudanophthalmus* which is also found in caves of the Green and Barren drainages of south-central Kentucky. Other beetles not found to the south in the Red River drainage are *Neaphaenops* and the *menetriesi* group of *Pseudanophthalmus*. This represents an abrupt change in the beetle fauna between these two areas according to Barr (1959 a,b). At present it is not clear what the barriers to dispersal are that restrict the beetle

P. *c*. *ciliaris* and the campodeid *Litocampa jonesi* to this small portion of the Pennyroyal Plateau, while excluding other beetles and campodeids, such as the wide ranging *L*. *cookei*.

The campodeid specimen from Glover's Cave had, in its foregut and midgut, approximately 16 separate legs plus portions of two bodies with legs attached belonging to mites (unidentified at present).

REMARKS.--Male campodeids from the type locality are needed in order to ascertain whether or not the Glover's Cave population represents a distinct subspecies.

Litocampa holsingeri Ferguson

(Figs. 7-8)

Plusiocampa n. sp., Ferguson, 1971a: 34; 1979: 178, 182.

Litocampa (*Litocampa*) *holsingeri* Ferguson, (in press); figs. 1, 2.

MATERIAL EXAMINED.--VIRGINIA: *Scott Co.*: Queens Cave, 3.3 mi. west of Dungannon, 1 ♂, 17 Nov. 1979, J. R. Holsinger and R. Powers, (LMF 595). KENTUCKY: *Letcher Co.*: Angel Cave, near Cumberland, 1 ♂, 1 ♀, 21 Oct. 1979, T. C. Barr, Jr., (LMF 589); plus the material reported earlier (Ferguson, in press).

DIAGNOSIS.--Distinguished from other species of *Litocampa* in the United States by presence of 3 + 3 and 2 + 2 macrochaetae on meso- and metanota, with 1 dorsal macrochaeta on femur III, tibia III with 1 ventral macrochaeta, claws with well-developed latero-tergal crests, medial anterior macrochaetae absent on abdominal tergites, 1 + 1 posterior macrochaetae on tergites II-III, 2 + 2 posterior macrochaetae on tergite IV, 1 + 1 lateral anterior and 2 + 2 posterior macrochaetae on tergites V-VII, 7 + 7 macrochaetae on urosternite I, and 4 + 4 well differentiated macrochaetae on urosternites II-VII.

DESCRIPTION.--Corresponding to the earlier description (Ferguson, in press), with the following additions.

Head: Antennal segment III with ventral bacilliform sensillum, inserted between phaneres d and e: Ma, Mb, seta c, Md, sen. (apex exceeding distal border of segment), Me (short, with subapical barb), Mf, Mg, Mh; length of d about 2 times c; d with several barbules on distal half; g with subapical barb; other long macrochaetae smooth. Length of latero-dorsal trichobothrium of segment V up to 312 microns, about 32 percent of head width. Segment X length 1.6 times width. Cupuliform organ of apical segment with 13 sensilla.

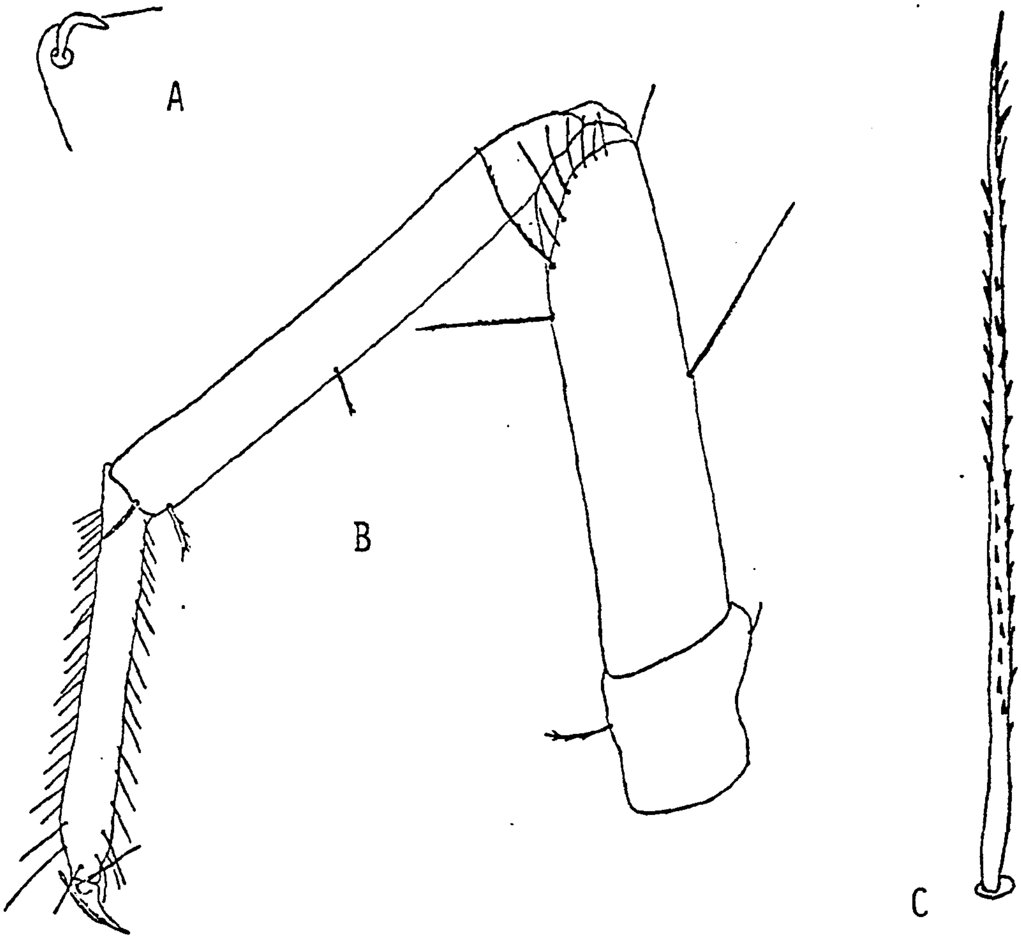
Occipital setae with numerous barbs on their distal eight-tenths; length about 78 percent as long as pronotal lp. Latero-anterior sensillum of labial palp long, subcylindrical, sickle shaped (Fig. 7A).

Thorax: Additional macrochaetal ratios for specimens of the type series from McDavids Cave, as follows: mesonotum: ma/Sep ma-ma, 2.62-2.90; ma/Sep ma-la, 1.32-1.79; la/Sep ma-la, 1.52-2.05.

Presternite of prosternum with 2 + 2 M; prosternite with 4 + 4 barbed precoxal M; 3 + 3 to 5 + 4 smooth precoxal setae; 1 + 1 subcoxal M; 2 + 2 lp. Mesosternite with 4 + 4 barbed precoxal M; 4 + 4 to 4 + 5 smooth precoxal setae; 1 + 1 ma; 1 + 1 la; 1 + 1 subcoxal M; 2 + 2 lp. Metasternite with 4 + 4 barbed precoxal M; 4 + 3 to 4 + 4 smooth precoxal setae; 1 + 1 ma; 1 + 1 la; 1 + 1 subcoxal M; 1 + 1 lp.

Leg III with dorsal macrochaeta inserted on proximal half of femur; length of macrochaeta 1.7-1.8 times width of femur at point of insertion; small barbs on its distal eight-tenths (Fig. 7B,C). Tibia III length 5.6-8.3 times width, with one bifurcated ventral macrochaeta. Tarsus III with 12-16 ventral setae in anterior row.

FIGURE 7.--*Litocampa holsingeri* Ferguson. A, latero-anterior sensillum of right labial palp; B, metathoracic leg; C, dorsal macrochaeta of femur III. A, female (7.0 mm; head width, 0.99 mm); B, C, female (6.2 mm; head width, 1.04 mm), McDavids Cave, Virginia


A
B
C

Abdomen: Additional ratios for certain tergal macrochaetae, as follows: $post_1$/Sep $post_1$-$post_1$, 1.16-2.25 on Ab. II, 1.43-2.44 on Ab. IV, 0.91-2.08 on Ab. VII. Abdominal tergite II with up to 7 posterior marginal setae separating pair of submedial-sublateral posterior macrochaetae nearest sagittal plane; tergite III with up to 8 such setae; IV with 7; V with 8; VI with 10; VII with 11; VIII with 6; IX with 8.

Urosternite (coxosternite) I with subcylindrical lateral subcoxal appendages on females, broader appendages on males (Fig. 8A,B). Largest male with about 140 short glandular-like setae on each subcoxal appendage near their internal point of attachment to urosternite; 6 such setae on each appendage of largest female.

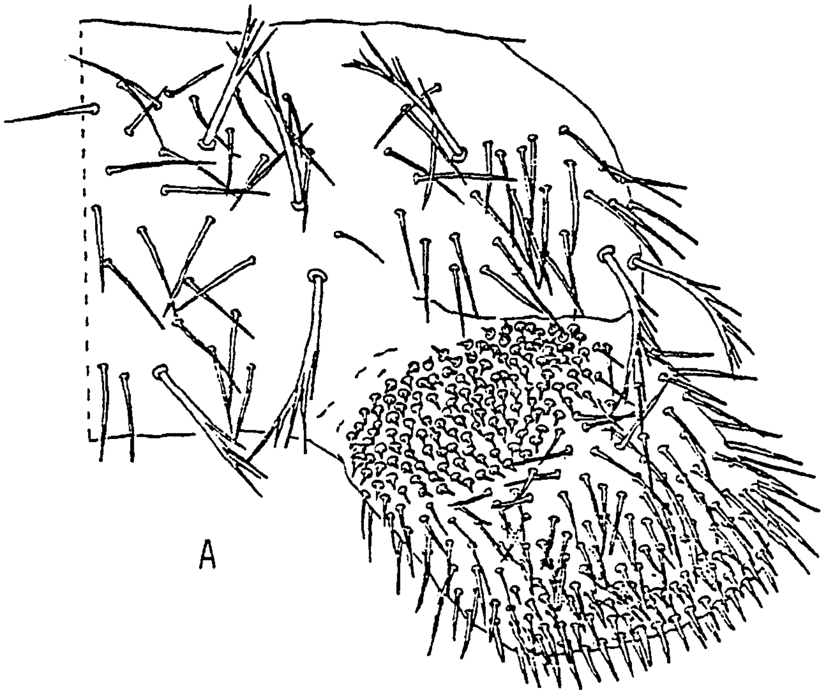
Stylus VII length 4.0-4.1 times width; apical seta about 40-45 percent as long as stylus; with up to 28 clothing setae and setiform sensilla.

Proximal primary segments of cerci with whorls of 7 barbed macrochaetae, long smooth setae, and 10-18 small subapical setae. Penultimate segment length 19.6 times width, with 5-7 whorls of macrochaetae, alternating with whorls of long and shorter smooth setae; 11 small subapical setae.

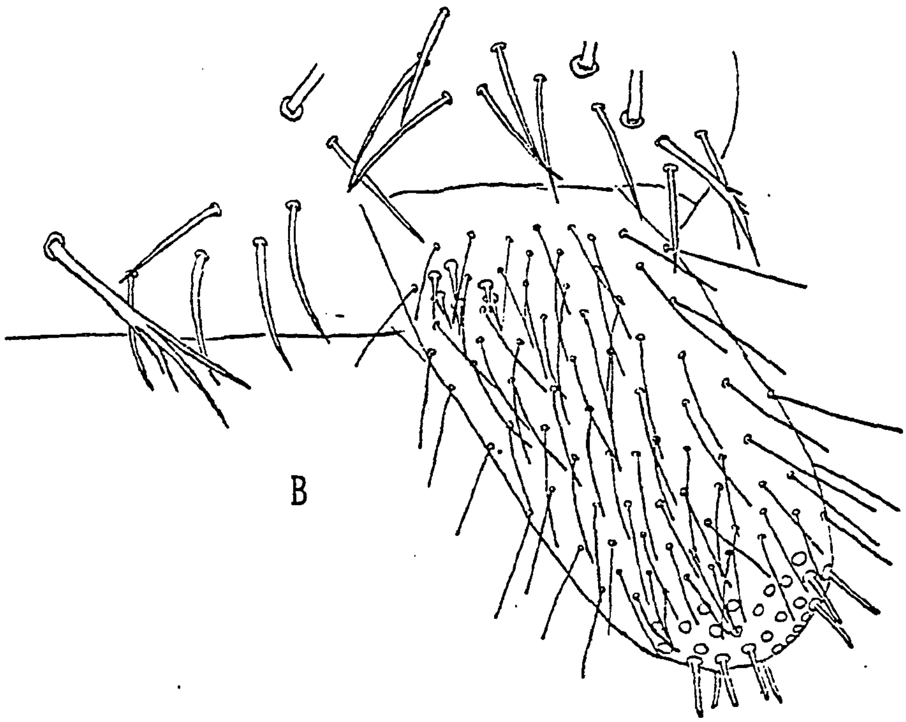
TYPE LOCALITY.--McDavids Cave, 2 miles east of Natural Tunnel, in Scott Co., Virginia. The cave is developed in the Middle Ordovician aged Rye Cove Limestone, and has 5000 feet of passages (Holsinger, 1975).

DISTRIBUTION AND ECOLOGY.--*Litocampa holsingeri* is now known from four caves, three in the Rye Cove area of Scott Co., Virginia, and

FIGURE 8.--*Litocampa holsingeri* Ferguson. A, urosternite I of male; B, lateral posterior part of urosternite I of female (some glandular setae represented by their bases; simple clothing setae of subcoxal appendage diagrammatic). A, male (5.1 mm; head width, 0.89 mm); B, female (6.2 mm; head width, 1.04 mm), McDavids Cave, Virginia.



A



B

one in Letcher Co., Kentucky. Although the Kentucky specimens appear to belong to this species, whether or not this represents true affinity or convergent evolution must await further study.

The *Bifurcata* Group

DIAGNOSIS.--Antennal segment III without phanere *e*, metanotum with lateral posterior macrochaetae, pretarsal claws with or without large latero-tergal crests, abdominal tergites V-VII with 1 + 1 or 2 + 2 lateral posterior macrochaetae, medial anterior macrochaetae on abdominal tergites I-VIII (IX), urosternite I with 6 + 6 macrochaetae, and posterior margin of urosternite I of males with or without glandular setae.

REMARKS.--Three species displaying a combination of characters particular to this group are known from caves in the Blue Ridge Province of Tennessee and North Carolina, and in the adjacent Valley and Ridge Province of southwestern Virginia.

Key to the Species of the *Bifurcata* Group

1. Abdominal tergites IV-VII with 2 + 2 lateral posterior macrochaetae ....*L. barryi*, new species

1'. Abdominal tergites IV-VII with 1 + 1 lateral posterior macrochaetae 2

2. Pretarsal claws without large latero-tergal crests; medial anterior macrochaetae on abdominal tergites I-IX...............*L. bifurcata*

2'. Pretarsal claws with large latero-tergal crests; medial anterior macrochaetae on abdominal tergites I-VIII.....*L. holleri*, new species

Litocampa bifurcata Ferguson

(Fig. 9)

Plusiocampa n. sp., Ferguson, 1971a: 34; 1979: 181-182.

Litocampa (*Litocampa*) *bifurcata* Ferguson, (in press): figs. 5, 6.

MATERIAL EXAMINED.--VIRGINIA: *Pulaski Co.*: Fifty-Foot Hell Cave, 3 mi. NE of Dublin, 4 ♀, 5 Oct. 1979, J. R. Holsinger, V. Tipton, and D. Derowitsch, (LMF 596); Sam Bells Cave, 0.8 mi NNW of Dublin, ♂♂♀♀, 5 Oct. 1979, J. R. Holsinger, V. Tipton, and D. Derowitsch, (LMF 597); *Washington Co.*: Brass Kettle Hole, 4 mi. NW of Damascus, 3 ♀, 13 July 1979, J. R. Holsinger and D. C. Culver, (LMF 567); plus the material reported in earlier (Ferguson, in press).

DIAGNOSIS.--Distinguished from other species of *Litocampa* in the United States by presence of 3 + 3 and 2 + 2 macrochaetae on meso and metanota, without dorsal macrochaetae on femur III, tibia III with 1 ventral macrochaeta, claws without well-developed latero-tergal crests, medial anterior macrochaetae present on abdominal tergites I-IX, 1 + 1 lateral anterior and 1 + 1 lateral posterior macrochaetae on tergites IV-VII, 6 + 6 macrochaetae on urosternite I, and 4 + 4 well differentiated macrochaetae on urosternites II-VII.

DESCRIPTION.--Corresponding to the earlier description (Ferguson, in press), with the following additions.

<u>Head</u>: Antennal segment III with ventral bacilliform sensillum, inserted between phaneres <u>d</u> and <u>f</u>: <u>Ma</u>, <u>Mb</u>, seta <u>c</u>, <u>Md</u>, sen. (apex exceeding distal border of segment), <u>Mf</u>, <u>Mg</u>, <u>Mh</u> (short, with subapical barb); length of <u>d</u> greater than <u>c</u>; long macrochaetae smooth. Length of latero-dorsal trichobothrium of segment V up to 221 microns, about 35 percent of head width. Segment X length 1.5 times width. Cupuliform organ of apical segment with 8 sensilla.

Occipital setae with numerous barbs on their distal six-tenths; length about 58 percent as long as pronotal <u>lp</u>.

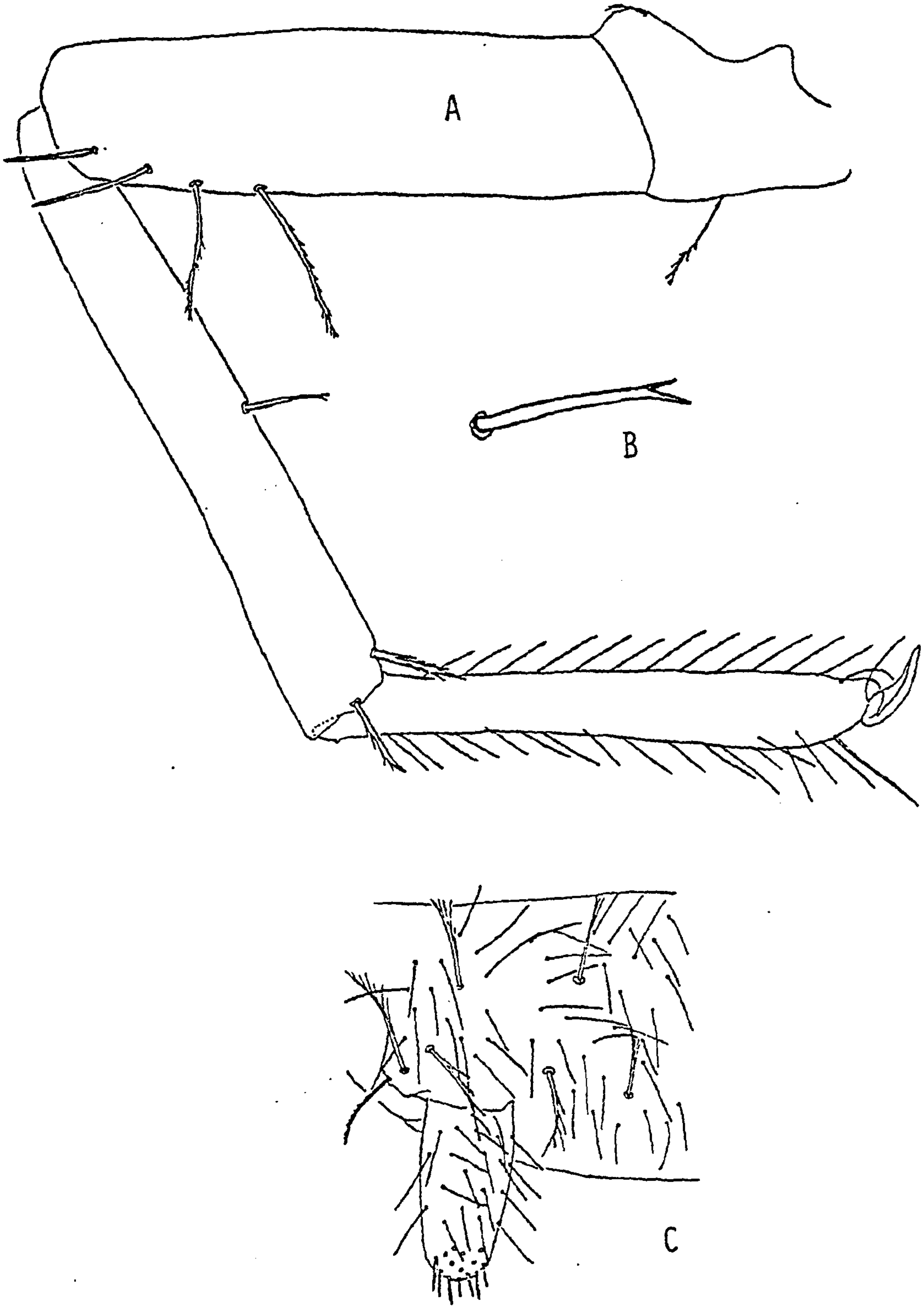
<u>Thorax</u>: Additional macrochaetal ratios for specimens of the type series from Speedwell Cave No. 1, as follows: mesonotum: <u>ma</u>/Sep <u>ma</u>-<u>ma</u>, 1.15-1.42; <u>ma</u>/Sep <u>ma</u>-<u>la</u>, 0.85-0.88; <u>la</u>/Sep <u>ma</u>-<u>la</u>, 0.93-1.18.

Presternite of prosternum with 2 + 2 M; prosternite with 4 + 4 barbed precoxal M; 4 + 4 smooth precoxal setae; 1 + 1 subcoxal M; 2 + 2 <u>lp</u>. Meso- and metasternite with 4 + 4 barbed precoxal M; 4 + 4 smooth precoxal setae; 1 + 1 <u>ma</u>; 1 + 1 <u>la</u>; 1 + 1 subcoxal M; 2 + 2 <u>lp</u>.

Tibia III length 6.2-7.0 times width, with one bifurcated ventral macrochaeta (Fig. 9A,B). Tarsus III with 13-14 ventral setae in anterior row.

<u>Abdomen</u>: Additonal ratios for certain tergal macrochaetae, as follows: <u>ma</u>/Sep <u>ma</u>-<u>ma</u>, 0.74-0.76 on Ab. I, 0.55 on Ab. IV, 0.50-0.64 on Ab. VII. Abdominal tergite IV with up to 16 posterior marginal setae separating sublateral posterior macrochaetae nearest sagittal plane; tergite V with up to 18 such setae; VI with 18; VII with 15; VIII with 11; IX with 11.

FIGURE 9.--*Litocampa bifurcata* Ferguson. A, metathoracic leg; B, ventral macrochaeta of tibia III; C, urosternite I of female (only bases of some glandular setae represented; smooth clothing setae diagrammatic). Female (5.1 mm; head width, 0.63 mm), Speedwell Cave No. 1, Virginia.


A
B
C

Urosternite (coxosternite) I of female with subcylindrical lateral subcoxal appendages (Fig. 9 C).

Stylus VII length 3.5-4.1 times width; apical seta about 55-60 percent as long as stylus; with up to 8 clothing setae and setiform sensilla.

Proximal primary segments of cerci with whorls of 7 barbed macrochaetae, long smooth setae, and 7 short subapical setae. Penultimate segment length 8.75 times width, with 2 whorls of macrochaetae, alternating with whorls of long and shorter smooth setae; 6 short subapical setae.

TYPE LOCALITY.--Speedwell Cave No. 1, south of Speedwell, Wythe Co., Virginia. The cave is located in Cave Hill in the Cambrian aged Rome Formation, and has about 750 feet of passages (Douglas, 1964; Holsinger, 1975).

DISTRIBUTION.--*L. bifurcata* is now known from 7 locations, all in southwestern Virginia. The species is known from caves southeast of Walker Mountain and northwest of Iron Mountain and other western foothills of the Blue Ridge Mountains to the North. The caves are located in the drainage basins of the Middle and South Forks of the Holston River and New River. One collection is known from a cave northeast of New River in Montgomery County. Although New River appears to be a barrier to dispersal for *L. virginiana*, the occurence of *L. bifurcata* northeast of New River may indicate that the ancestral range of the latter species encompassed the southern Virginia portion of the Blue

Ridge Mountains, stradling, as it were, New River. Like *L. virginiana* this species has not been found in caves in adjacent Tennessee.

Litocampa barryi, new species

(Figs. 10-11)

MATERIAL EXAMINED.--TENNESSEE: Unicoi Co.: Blankenship Cave, 6 ♂, 5 ♀, 1 immature (holotype and paratypes), 8 July 1972, L. M. and B. L. Ferguson, (LMF 204); Carter Co.: Carter Saltpeter Cave, 2 ♀(paratypes), 7 July 1972, L. M. and B. L. Ferguson, (LMF 203).

Holotype (LMF 204-1) and several paratypes deposited in American Museum of Natural History; remaining paratypes deposited in B. Condé's collection, Université de Nancy, Nancy, France, and the author's collection.

DIAGNOSIS.--Distinguished from other species of Litocampa in the United States by presence of 3 + 3 and 2 + 2 macrochaetae on meso- and metanota, femur III without dorsal macrochaeta, tibia III with one ventral macrochaeta, pretarsal claws with slightly developed latero-tergal crests, 1 + 1 medial anterior macrochaetae on abdominal tergites I-IX, 2 + 2 lateral posterior macrochaetae on tergites IV-VII, 6 + 6 macrochaetae on urosternite I, and 4 + 4 well differentiated macrochaetae on urosternites II-VII.

DESCRIPTION.--Size: Males: body length, 3.7-4.9 mm; head width, 0.50-0.62 mm; pronotal width, 0.35-0.43 mm. Females: body length, 4.2-7.1 mm; head width, 0.53-0.85 mm; pronotal width, 0.35-0.63 mm. Immature:

body length, 3.3 mm; head width, 0.48 mm; pronotal width, 0.33 mm. Head: Antennal segments, 23-27. Disregarding 4 antennae of 17, 18, 19 (paired with antenna of 26 segments), and 24 segments (paired with antenna of 27 segments) which had very large, long apical segments and were obviously regenerating, number of segments of 11 complete antennae as follows:

		23	24	25	26	27
No. segments:		23	24	25	26	27
Frequency:	♂	1	0	0	1	2
	♀	3	2	0	1	0
	immature	0	0	0	1	0

Length of longest antenna 2.92 mm, or about 60 percent of body length, reaching abdominal segment IV. Antennal segment III with ventral bacilliform sensillum, inserted between phaneres d and f: Ma, Mb, seta c, Md (short with 3-4 distal barbs), sen. (long, exceeding distal border of segment), Mf, Mg, Mh; length of d and c subequal; b with 1 small barbule, h with long subapical barb, other long macrochaetae smooth. Length of latero-dorsal trichobothrium of segment V up to 289 microns, about 34 percent of head width. Segment X length 1.3-1.7 times width. Cupuliform organ of apical segment with 8 sensilla.

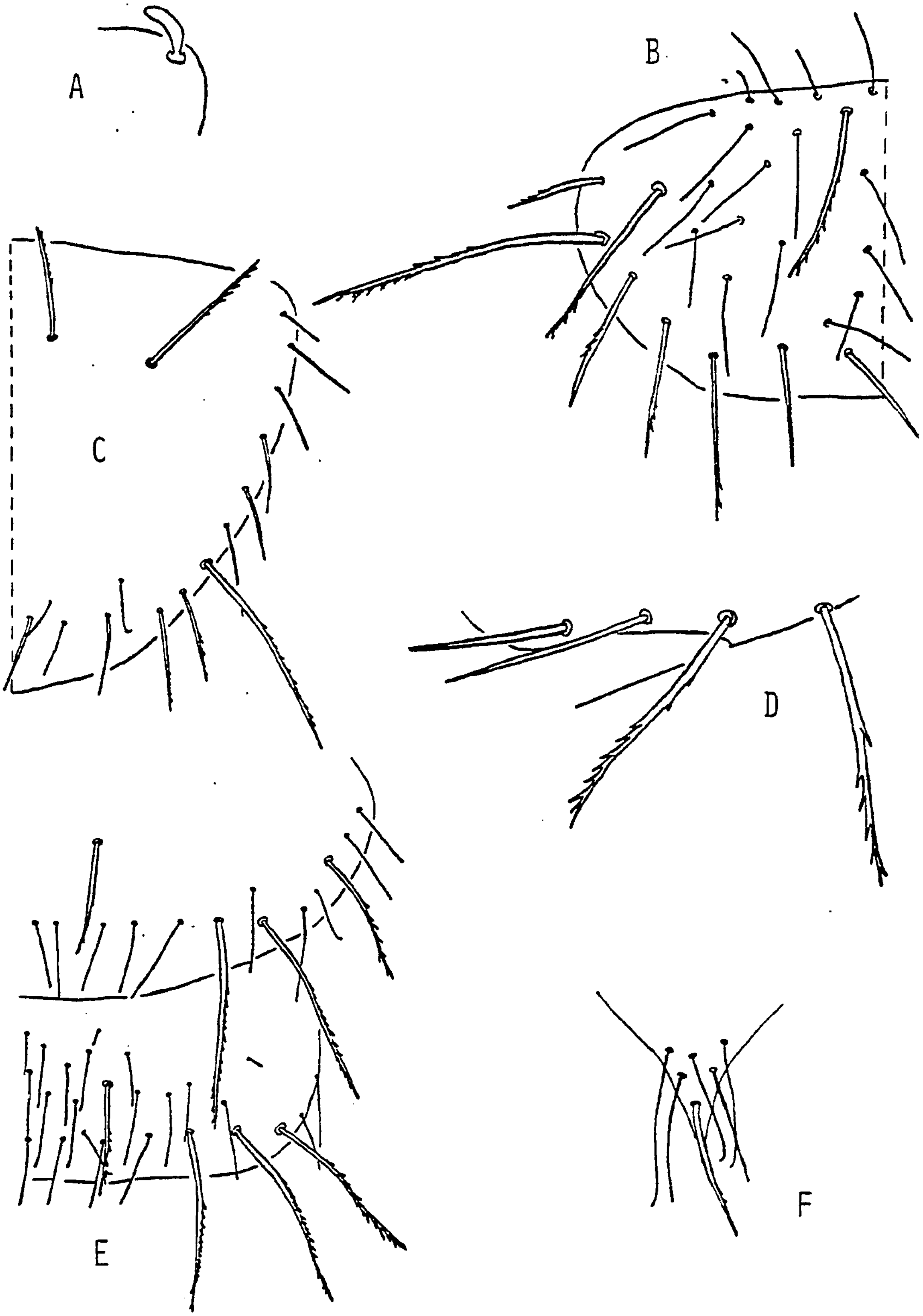
Frons with 3 macrochaetae on rostrum; anterior macrochaeta 1.1 times length of posterior pair. Macrochaetae bordering line of insertion of antennae 3 + 3; anterior macrochaeta 0.56 length of intermediate; anterior 0.75 length of posterior; all three macrochaetae barbed on distal half. No macrochaetae anterior to arms of epicranial suture, near sagittal plane. Occipital setae with barbs on distal two-thirds; length about 55 percent that of pronotal lp. Latero-anterior sensillum of labial palp subcylindrical, curved towards sagittal plane, swollen in middle region (Fig. 10A). Posterior mental setae smooth; lateral submental macrochaetae smooth. Thorax: Clothing setae smooth; notal chaetotaxy 3 + 3, 3 + 3, 2 + 2 (Fig. 10B-C). Lengths and ratios of macrochaetae of specimens from Murray Spring Cave, as follows:

	ma	la	lp	ma/la	lp/ma
Th. I	97-194	108-200	173-302	0.90-0.97	1.56-1.78
Th. II	108-238	157-286	216-346	0.69-0.83	1.45-2.00
Th. III	113-248	--	189-346	--	1.39-1.67

Mesonotum: ma/Sep ma-ma, 2.22-2.44; ma/Sep ma-la, 0.95-1.13; la/Sep ma-la, 1.36-1.38; lp_{I}/lp_{II}, 0.80-0.88; lp_{II}/lp_{III}, 1.00-1.14. Pronotum with 2 + 2 to 3 + 3 barbed lateral posterior marginal setae and 6 smooth medial posterior marginal setae; mesonotum with 2 + 2 to 2 + 4 lateral, 6 to 9 medial posterior marginal setae; metanotum with 2 + 1 lateral, 6 to 8 medial posterior marginal setae.

Presternite of prosternum with 2 + 2 M; prosternite with 4 + 4 barbed precoxal M; 3 + 3 to 4 + 4 smooth precoxal setae; 1 + 1 subcoxal M; 2 + 2 lp. Meso- and metasternite with 4 + 4 barbed precoxal M; 3 + 3 to 4 + 4 smooth precoxal setae; 1 + 1 ma; 1 + 1 la; 1 + 1 subcoxal M; 2 + 2 lp.

FIGURE 10.--Litocampa barryi, new species. A, latero-anterior sensillum of left labial palp; B, pronotum; C, mesonotum (clothing setae omitted); D, anterior distal marginal macrochaetae of femur III; E, abdominal tergites VII-VIII (clothing setae not shown on VII); F, supra-anal valvule. D, F, male (4.9 mm; head width, 0.56 mm); others, male (4.5 mm; head width, 0.59 mm), Blankenship Cave, Tennessee.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Length of leg III about 35 percent of body length, reaching abdominal segment VII. Femurs I, II, and III without dorsal macrochaetae. Femur III with 4 anterior marginal macrochaetae; 2 most ventral barbed on distal two-thirds; distal pair smooth (Fig. 10D). Tibia III length 5.4-6.7 times width, with one bifurcated ventral macrochaeta with 2-4 small barbs proximal to bifurcation; tibial spurs with 2 rows of long barbs. Tarsus III with 13 ventral setae in anterior row. Posterior claw slightly longer than anterior; laterotergal crests moderately developed; flange on posterior claw. Pretarsal appendixes long, slender, and smooth; flattened at the tip; length exceeding tip of claws.

Abdomen: Distribution of tergal macrochaetae (Fig. 10E):

	ma	la	lp
Ab. I-III	1 + 1	0	0
Ab. IV-VII	1 + 1	1 + 1	2 + 2
Ab. VIII	1 + 1	0	3 + 3
Ab. IX	1 + 1	0	5 + 5 (total)

Medial anterior macrochaetae long, robust, with 5-6 barbs on distal third; very slight increase in length posteriorly to Ab. VII; decrease in length on Ab. VIII and IX; apex exceeds bases of posterior marginal setae on all tergites. Lateral anterior macrochaetae moderately short on Ab. IV, shorter than ma; increases in length by one-third on Ab. VII. Laterial posterior macrochaetae long and robust, similar to thoracic lp; barbed on distal three-fourths. Lengths and ratios of certain tergal macrochaetae, as follows:

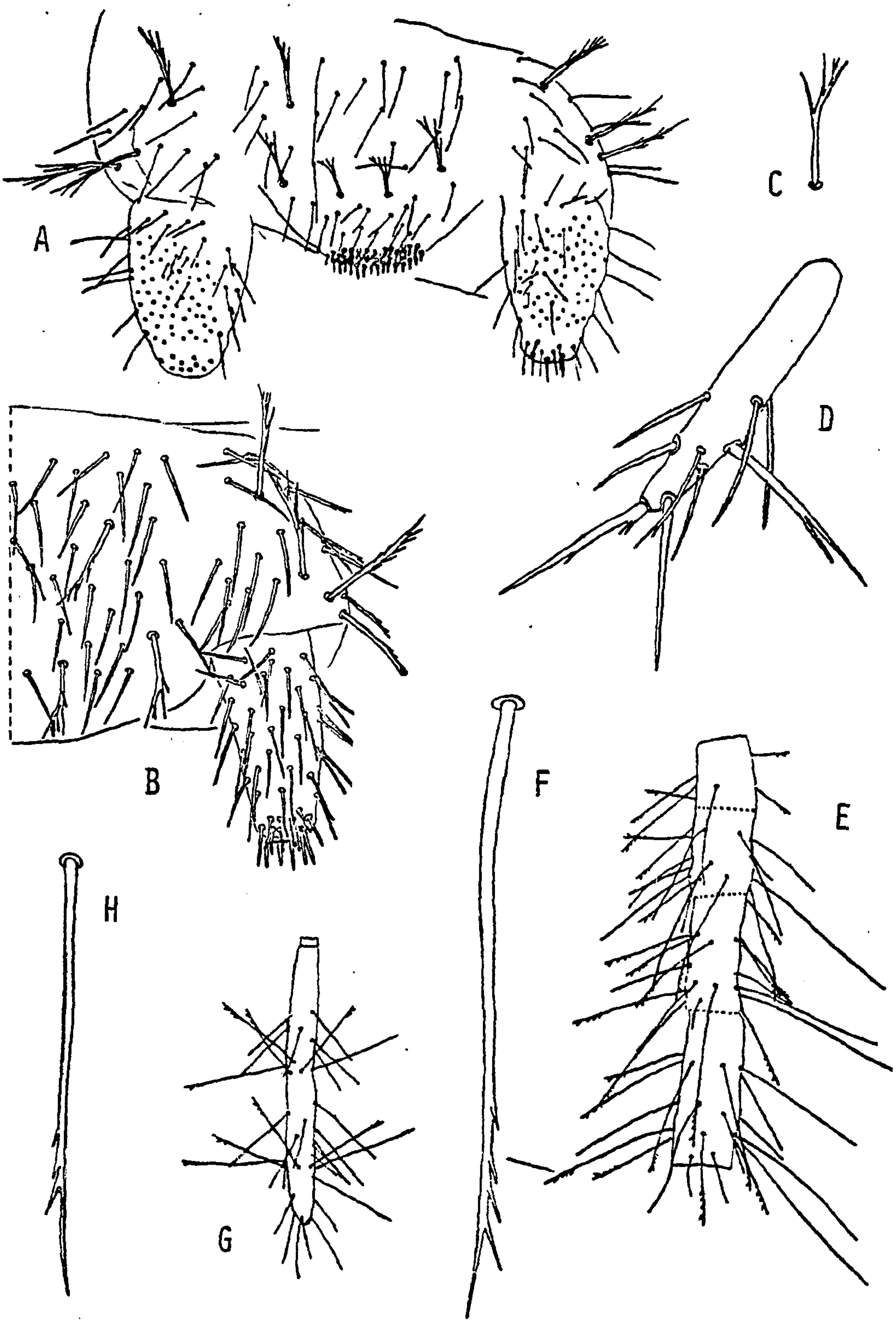
	ma	la	lp_1	lp_2	ma/D	ma/Sep ma-ma
Ab. I	97-227	--	--	--	1.06-1.35	1.29-1.45
Ab. IV	103-238	97-173	173-324	130-302	1.12-1.33	0.86-1.13
Ab. VII	119-248	130-227	205-335	184-324	1.38-1.44	1.00-1.21

Abdominal tergite IV with up to 10 posterior marginal setae separating sublateral posterior macrochaetae nearest sagittal plane; tergite V with up to 12 such setae; VI with 12; VII with 12; VIII with 8; IX with 9. Supra-anal valvule with 2 + 2 smooth or barbed lateral setae; 1 slender, smooth medial seta; subapical seta thicker, barbed (Fig. 10F).

Urosternite (coxosternite) I with 6 + 6 differentiated macrochaetae, 3 + 3 on middle portion; 1 + 1 submacrochaetae at latero-posterior angle of urosternite of female. Posterior margin with glandular setae on males, in middle region; lacking on females. Lateral subcoxal appendages subcylindrical among females; broader, sublanceolate on males (Fig.11A, B). Females without glandular-like setae on each appendage near internal point of attachment to urosternite; numerous glandular-like setae on appendages of males.

Urosternites II-VII with 4 + 4 well differentiated macrochaetae, with branches and barbs (Fig.11C); 2 + 2 weakly differentiated macrochaetae inserted internally and externally at base of each stylus. Apical seta of styli smooth, or with 1 distal barbule, and

FIGURE 11.--Litocampa barryi, new species. A, urosternite I of male; B, urosternite I of female; C, macrochaeta at base of eversible vesicle of urosternite III; D, left stylus of urosternite VI; E, base of cercus; F, macrochaeta from base of cercus; G, apical segment of cercus; H, macrochaeta from apical segment of cercus. A, male (4.9 mm; head width, 0.56 mm); B-C, female (6.1 mm; head width, 0.78 mm); D-H, male (4.5 mm; head width, 0.59 mm), Blankenship Cave, Tennessee.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2 short basal branches, proximal branch about one-half length of distal; subapical seta smooth; medial ventral seta forked, with 1 long barb proximal to bifurcation; clothing setae smooth (Fig.11D). Stylus VII length 3.7-4.2 times width; apical seta about 45 percent as long as stylus. Urosternite VIII with 1 + 1 macrochaetae. Genital papilla of male with up to 16 short setae encircling gonopore.

Length of longest cercus about 0.99 times body length, composed of a base, subdivided into 4 secondary segments, and 10 primary segments. Segmental lengths (in mm): base = 0.17, 0.23, 0.25, 0.32; primary segments = 0.36, 0.41, 0.44, 0.49, 0.52, 0.59, 0.66, 0.70, 0.70, 0.70. Covering of base (Fig.11E,F) and proximal segments composed of long macrochaetae, length of macrochaetae about 1.9 times width of segments, 3-4 small barbs and 1 long subapical barb on distal half. Proximal primary segments with whorls of 7 barbed macrochaetae, long smooth setae, and 8-9 short subapical setae. Penultimate segment length 13 times width, with 2 whorls of macrochaetae, alternating with whorls of long smooth setae; macrochaetae with long subapical barb and 1-5 barbules below subapical; 5 short subapical setae. Macrochaetae of apical segment arranged in 2 whorls, length of macrochaetae about 4.2 times width of segment, alternating with whorls of long and short smooth setae (Fig. 11G,H); all macrochaetae with 1 subapical barb and 1-3 barbules.

TYPE LOCALITY.--Blankenship Cave, 2 miles NE of Erwin, Unicoi Co., Tennessee. This is a small cave which is developed along the axis of an anticline in the Lower Cambrian Shady dolomite or Rome formation (Barr, 1961).

DISTRIBUTION AND ECOLOGY.--Also known by 2 specimens from Carters Saltpeter Cave, Carter Co., Tenn., located approximately 9 mi. SW of the type locality. Carter Saltpeter Cave has mainly a single large passage which trends SE for 1550 feet (Barr, 1961). Each specimen was taken at bait.

ETYMOLOGY.--It is indeed a pleasure to name this species in honor of my brother, Barry L. Ferguson, who assisted with the collection of this species and many others.

Litocampa holleri, new species

(Figs. 12-13)

MATERIAL EXAMINED.--NORTH CAROLINA: *Swain Co.*: Flowstone Cave (NC 0026SW), 6 ♀ (holotype and paratypes), 22 Mar. 1975, C. O. Holler, Jr. and J. Warren, (LMF 454).

Holotype (LMF 454-4) and paratypes to be deposited in American Museum of Natural History.

DIAGNOSIS.--Can be distinguished from other species of *Litocampa* in the United States by presence of 3 + 3 and 2 + 2 macrochaetae on meso- and metanota, without macrochaetae on femur III, tibia III with 2 ventral macrochaetae, claws with well-developed latero-tergal crests, medial anterior macrochaetae present on abdominal tergites I-VIII, 1 + 1 lateral anterior and 1 + 1 lateral posterior macrochaetae on tergites IV-VII, 6 + 6 macrochaetae on urosternite I, and 4 + 4 well differentiated macrochaetae on urosternites II-VII.

DESCRIPTION.--*Size*: Females: body length, 4.1-7.4 mm; head width, 0.57-0.86 mm; pronotal width, 0.39-0.61 mm.

Head: Antennal segments, 34-37. Number of segments of 5 complete antennae, as follows:

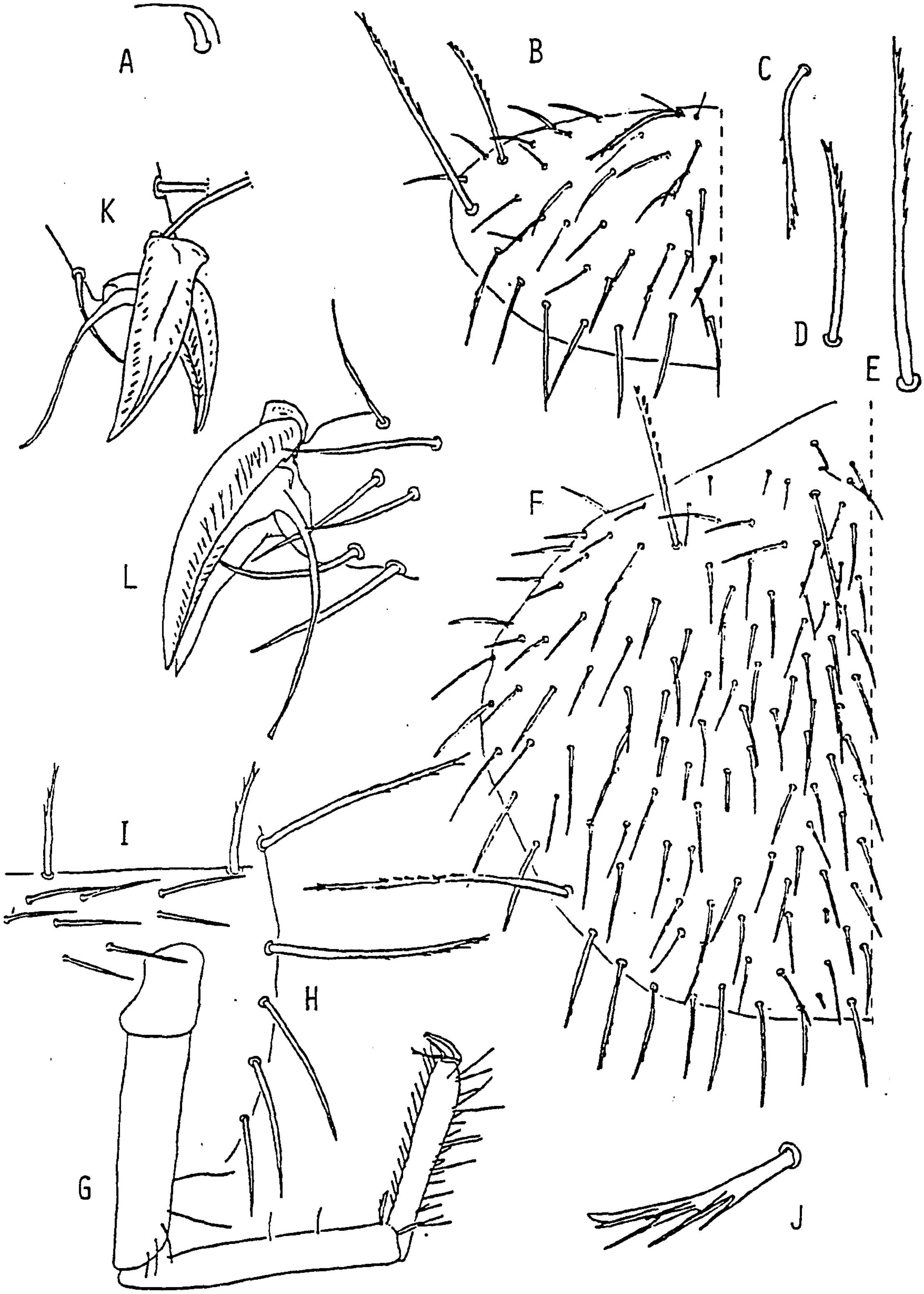
No. segments:	34	35	36	37
Frequency: ♀	2	1	1	1

Length of longest antenna 4.93 mm, or about 81 percent of body length, reaching abdominal segment VII. Antennal segment III with ventral bacilliform sensillum, inserted between phaneres d and f: Ma, Mb, seta c, Md, sen. (not reaching distal border of segment), Mf, Mg, Mh; length of d 1.3 times c; d long, smooth or with 2-3 distal barbs, other long macrochaetae smooth. Length of latero-dorsal trichobothrium of segment V up to 279 microns, about 33 percent of head width. Segment X length 1.7-1.9 times width. Cupuliform organ of apical segment with 8 sensilla.

Frons with 3 macrochaetae on rostrum; posterior macrochaetae smooth or with 1 small barbule; anterior macrochaeta smooth, 1.6 times length of posterior pair. Macrochaetae bordering line of insertion of antennae 3 + 3; anterior macrochaeta approximately eight-tenths as long as intermediate; anterior and posterior macrochaetae subequal, anterior slightly shorter than posterior; all three macrochaetae barbed on distal half. No macrochaetae anterior to arms of epicranial suture, near sagittal plane. Occipital setae barbed on their distal two-thirds; length about 70 percent as long as pronotal lp. Latero-anterior sensillum of labial palp cone-shaped, slightly curved (Fig. 12A). Posterior mental setae smooth; lateral submental macrochaetae with long branches.

Thorax: Clothing setae smooth; notal chaetotaxy 3 + 3, 3 + 3, 2 + 2 (Fig. 12B-F). Largest specimen with pronotal ma barbed on distal 78 percent, la on distal 64 percent, lp on distal 69 percent; mesonotal ma

FIGURE 12.--Litocampa holleri, new species. A, latero-anterior sensillum of labial palp; B, pronotum; C, pronotal ma; D, pronotal la; E, pronotal lp; F, mesonotum; G, metathoracic leg; H, anterior distal margin of femur III; I, ventral macrochaetae of tibia III; J, tibial spur; K, posterior view of pretarsus of leg III; L, anterior view of distal portion of tarsus and pretarsus of leg III. A-F, K, female (4.8 mm; head width, 0.65 mm); G-J, L, female (6.1 mm; head width, 0.86 mm), Flowstone Cave, North Carolina.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barbed on distal 60 percent, la on distal 51 percent, lp on distal 62 percent; metanotal ma on distal 41 percent, lp on distal 72 percent. Lengths and ratios of macrochaetae of specimens from Flowstone Cave, as follows:

	ma	la	lp	ma/la	lp/ma
Th. I	76-140	86-151	162-248	0.88-0.93	1.74-2.14
Th. II	97-140	108-184	184-243	0.76-0.90	1.69-2.10
Th. III	86-119	--	162-238	--	1.88-2.38

Mesonotum: ma/Sep ma-ma, 0.98-1.18; ma/Sep ma-la, 0.87-1.01; la/Sep ma-la, 0.97-1.21; lp_I/lp_{II}, 0.88-1.02; lp_{II}/lp_{III}, 1.02-1.16. Pronotum with 3 + 3 to 3 + 4 barbed lateral posterior marginal setae and 6 to 7 medial posterior marginal setae with 1-2 barbules or smooth; mesonotum with 3 + 4 to 4 + 4 lateral, 6 to 11 medial posterior marginal setae; metanotum with 2 + 2 to 3 + 3 lateral, 8 medial posterior marginal setae.

Presternite of prosternum with 2 + 2 M; prosternite with 4 + 4 barbed precoxal M; 4 + 5 to 5 + 6 smooth precoxal setae; 1 + 1 subcoxal M; 2 + 2 lp. Mesosternite with 4 + 4 barbed precoxal M; 4 + 4 to 5 + 5 smooth precoxal setae; 1 + 1 ma; 1 + 1 la; 1 + 1 subcoxal M; 2 + 2 lp. Metasternite with 4 + 4 barbed precoxal M; 3 + 3 to 5 + 5 smooth precoxal setae; 1 + 1 ma; 1 + 1 la; 1 + 1 subcoxal M; 1 + 1 lp.

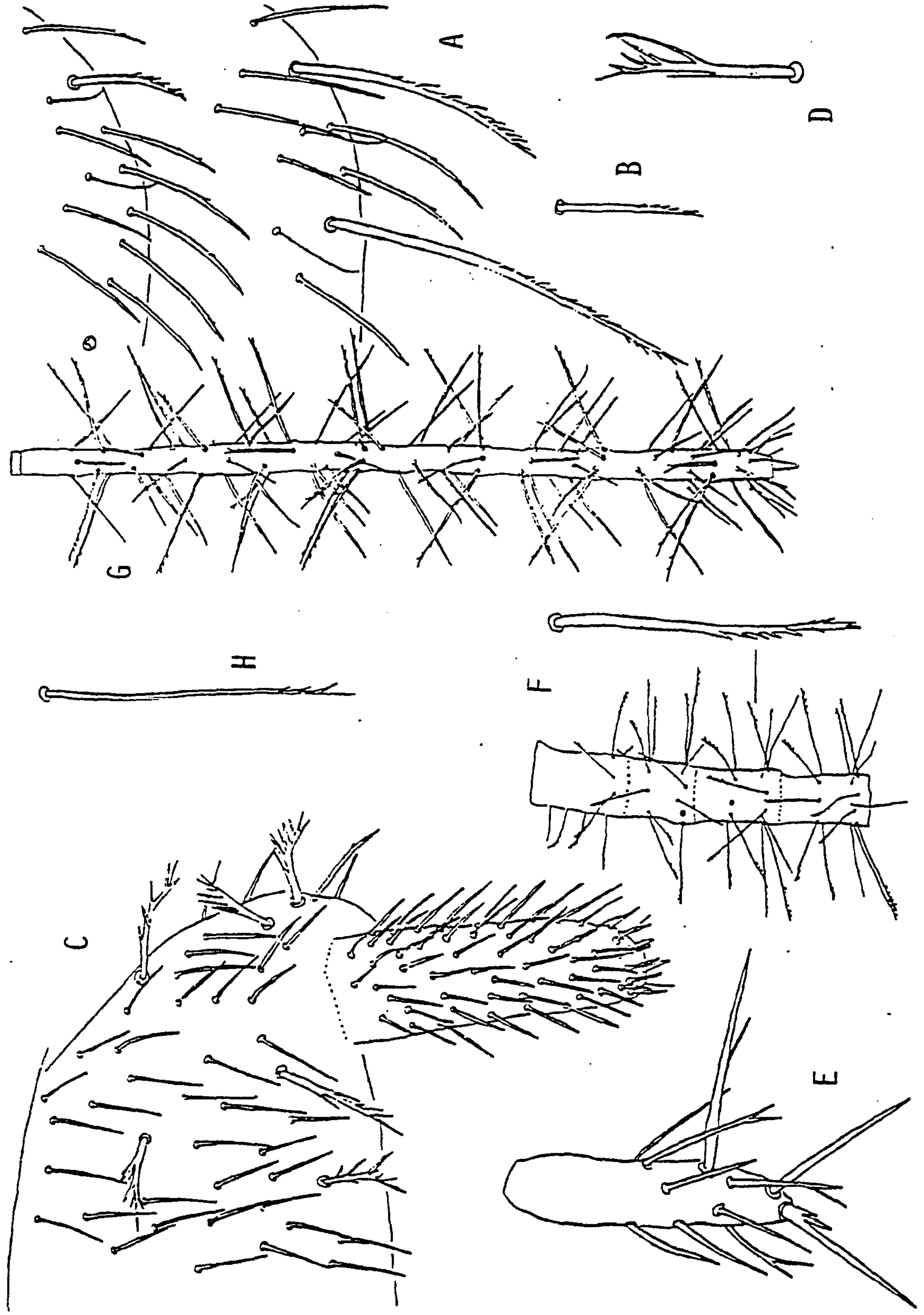
Length of leg III about 33-38 percent of body length, reaching abdominal segment VI. Femur I, II, and III without dorsal macrochaetae (Fig. 12G). Femur III with 4 anterior marginal macrochaetae; 2 most ventral barbed on their distal two-thirds; distal pair smooth (Fig. 12H). Tibia III length 6.3-7.1 times width, with 2 ventral macrochaetaes inserted on distal half; macrochaetae bifurcated with 2 barbs proximal to bifurcation (Fig. 12I); tibial spurs with 2 rows of long barbs (Fig. 12J). Tarsus III with 13-16 ventral setae in anterior row; 6 or more very long smooth setae on dorsal surface; length of long dorsal setae 2.0-2.4 times length of clothing setae. Tarsus slightly swollen on distal half. Posterior claw longer than anterior; latero-tergal crests very well-developed; large flange on posterior claw covering apex of tarsus. Pretarsal appendices long, slender, and smooth, enlarged at apex; length easily exceeding tip of claws (Fig. 12K,L).

Abdomen: Distribution of tergal macrochaetae (Fig. 13A,B):

	ma	la	lp
Ab. I-III	1 + 1	0	0
Ab. IV-VII	1 + 1	1 + 1	1 + 1
Ab. VIII	1 + 1	0	3 + 3
Ab. IX	0	0	5 + 5 (total)

Medial anterior macrochaetae slender, with numerous barbs on distal half; length increases 1.2-1.4 times by Ab. VII; apex reaches bases of posterior marginal setae on Ab. VIII only. Lateral anterior macrochaetae moderately long on Ab. IV, slightly longer than ma; increases in length by one-half on Ab. V, by three-fourths on Ab. VI, sometimes doubles in length by Ab. VII. Lateral posterior macrochaetae long and

FIGURE 13.--*Litocampa holleri*, new species. A, lateral posterior margins of abdominal tergites IV and VII with base of *lp* only shown on IV; B, *ma* of tergite VII; C, urosternite I of female; D, macrochaeta at base of eversible vesicle of urosternite VI; E, left stylus of urosternite IV; F, base of cercus (one macrochaeta enlarged); G, most distal (apical?) segment of cercus; H, macrochaeta of most distal segment. C, female (5.9 mm; head width, 0.73 mm); others, female (4.8 mm; head width, 0.65 mm), Flowstone Cave, North Carolina.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robust, similar to thoracic lp; barbed on distal half to two-thirds. Lengths and ratios of certain tergal macrochaetae, as follows:

	ma	la	lp	ma/D	ma/Sep ma-ma
Ab. I	65-92	--	--	0.39-0.67	0.47-0.57
Ab. IV	76-97	81-108	151-227	0.53-0.88	0.41-0.61
Ab. VII	76-130	119-216	205-292	0.67-0.93	0.51-0.61

Abdominal tergite IV with up to 18 posterior marginal setae separating sublateral posterior macrochaetae nearest sagittal plane; tergite V with up to 20 such setae; VI with 19; VII with 20; VIII with 14; IX with 12. Supra-anal valvule with 6-8 setae; subapical seta thicker, barbed; others smooth.

Urosternite (coxosternite) I with 6 + 6 differentiated macrochaetae, 3 + 3 on middle portion; 1 + 1 submacrochaetae at latero-posterior angle of urosternite of female. Posterior margin without glandular setae; lateral subcoxal appendages subcylindrical, long, on older females (Fig. 13C). Females with up to approximately 12 glandular setae on tip of appendages.

Urosternites II-VII with 4 + 4 well differentiated macrochaetae, with branches and barbs (Fig. 13D); 2 + 2 weakly differentiated macrochaetae inserted on either side of styli, external macrochaetae fairly large. Apical seta of styli smooth, with basal branches; distal branch about 2.7 times length of proximal, sometimes longer; subapical seta smooth; medial ventral seta forked; clothing setae smooth or bifurcated (Fig. 13E). Stylus VII length 4.0-4.2 times width; apical seta 44 to 53 percent as long as stylus; with 13 clothing setae and setiform sensilla. Urosternite VIII with 1 + 1 macrochaetae.

Length of longest incomplete cercus 6.22 mm, composed of a base, subdivided into 5 secondary segments, and 9 primary segments. Segmental lengths (in mm): base = 0.15, 0.13, 0.15, 0.16, 0.18; primary segments = 0.26, 0.29, 0.35, 0.41, 0.57, 0.78, 0.85, 0.94, 1.00. Covering of base (Fig. 13F) and proximal segments composed of long smooth setae and macrochaetae; length of macrochaetae about 1.9 times width of segments, long barbs on their distal half. Proximal primary segments with whorls of 7 barbed macrochaetae, long smooth setae, and 8 short subapical setae. Most distal segment available (apical segment missing) with length 26 times width, with 7 whorls of macrochaetae, alternating with whorls of long smooth setae; macrochaetae with long subapical barb and 2 or more barbules below subapical; length of macrochaeae about 4.1 times width of segment; 8 short subapical setae (Fig. 13G,H).

Variation: Largest female has one anomalous sublateral posterior macrochaeta on the right side of abdominal tergite III. Another specimen has one ventral macrochaeta on one tibia III, the usual two on the other.

TYPE LOCALITY.--Flowstone Cave, approximately 14 miles southwest of Bryson City, in the Hewitt Community, Swain Co., North Carolina. The cave is located just west of Talc Mountain and on the north side of the Nantahala River, at an elevation of 2000 feet. The cave is developed in the Lower Cambrian-aged Murphy marble and has approximately 300 feet of traversable passages (Holler, 1975, and personal communication).

DISTRIBUTION AND ECOLOGY.--Diplurans have been reported from all of the Nantahala Gorge area caves, as well as a questionable sighting in Hibriten Mountain Cave, Caldwell Co., North Carolina (Holler, 1975; 1979). Unprepared specimens from two other caves in Swain Co. will probably belong to *L. holleri*. Several other troglobites have been found in the vicinity, notably a new species of flatworm of the genus *Phagocata* and an aquatic isopod.

ETYMOLOGY.--It is a pleasure to name this species after its discoverer and caving enthusiast, Dr. Cato O. Holler, Jr.

The *Fieldingi* Group

DIAGNOSIS.--Antennal segment III without phanere *e*, metanotum with 1 + 1 lateral posterior macrochaetae, femur III with dorsal macrochaeta, pretarsal claws with large latero-tergal crests, abdominal tergites V-VII with 2 + 2 lateral posterior macrochaetae, medial anterior macrochaetae on abdominal tergites I-VIII (medial posterior macrochaetae on IX), urosternite I with 6 + 6 macrochaetae, and posterior margin of urosternite I of males with glandular setae.

REMARKS.--This group is composed of a single species that occupies caves in the New - Greenbrier River drainage basin of southeastern West Virginia. It has several peculiar characteristics in common with members of the *bifurcata* group, yet it differs significantly from members of that group by other characters included in the diagnosis.

Litocampa fieldingi (Condé)

(Fig. 14)

Plusiocampa fieldingi Condé, 1949:132-135, figs. 4-5. [McClungs Cave, Greenbrier Co., West Virginia; repository unknown]; 1956:51, 62, fig. 15A, 131, fig. 31A-B, 132, 170, 171, 187; Nicholas, 1960:140; Holsinger et al., 1976:6, 32, 55, 58, 78; Ferguson, 1979: 179-181.

Litocampa (Litocampa) fieldingi (Condé), Paclt, 1957:26; Ferguson, (in press).

MATERIAL EXAMINED.--WEST VIRGINIA: Greenbrier Co.: Arbuckle Cave, 1 mi. E. of Maxwelton 2 ♂, 1 immature, summer 1973, D. C. Culver, (LMF 362); Benedicts Cave, near Maxwelton and Greenbrier Valley Airport, 1 ♂, 5 Mar. 1966, J. Gravenmeir, (LMF 19); 2 ♀, 1 Dec. 1979, W. and P. Douty, and L. M. Ferguson, (LMF 582); 2 ♀, 8 Dec. 1979, W. Douty, T. Brecht, and L. M. Ferguson, (LMF 583); Buckeye Creek Cave, 2 ♀, 18 July 1976, L. M. and L. L. Ferguson and members of Blue Ridge Grotto, (LMF 487); Ludington Cave, 1 ♀, 13 Nov. 1965, J. Rutherford, (LMF 18); McClungs Cave, 3 ♀, 1 sex ? or immature, 1 immature, 28 Mar. 1970, L. M. and B. L. Ferguson, (LMF 34); 1 ♀, 4 Apr. 1970, L. M. and B. L. Ferguson, (LMF 35); The Hole (Boggs Entrance section), near Frankford, 1 ♂, 1 ♀, 28 Aug. 1967, J. R. Holsinger, (LMF 16); Wades Cave, between McClungs Cave and Lewisburg on E. side of route 219, 1 sex ?, 14 May 1966, J. Rutherford, (LMF 21); Monroe Co.: Hunt Cave, near Sinks Grove, 2 ♀, 5 Apr. 1971, J. R. Holsinger, D. C. Culver, and R. A. Baroody, (LMF 228); Steeles Cave, 3 ♀, 8 Aug. 1957, C. Krekeler and J. Rittmann, (LMF 182); 2 ♂, 29 July 1970, L. M. and B. L. Ferguson, (LMF 154); 6 ♂, 7 ♀, 2 immature , Oct. 1975, L. M. Ferguson and B. Balascio, (LMF 469); Union Cave, 1 ♀, 8 Aug. 1957, C. Krekeler and J. Rittmann, (LMF 183); Pocahontas Co.: Bolling Cave, 1 ♂, 1 July 1972, D. C. Culver and R. A. Baroody, (LMF 219); Clyde Cochrane Sinks Cave No. 3, 1 ♀, 25 July 1957, C. Krekeler and J. Rittmann, (LMF 180); 1 ♂, 12 Aug. 1966, J. R. Holsinger and W. Biggers, (LMF 15); Tub Cave, 1 ♀, 24 July 1957, C. Krekeler and J. Rittmann, (LMF 181); 3 ♂, 1 ♀, 21 July 1973, L. M., L. L., and B. L. Ferguson, (LMF 441).

Material will be deposited in the American Museum of Natural History, National Museum of Natural History (Smithsonian Institution), and the author's collection.

DIAGNOSIS.--Distinguished from other species of *Litocampa* in the United States by presence of 3 + 3 and 2 + 2 macrochaetae on meso- and metanota, one dorsal macrochaeta on femur III, tibia III with 1 ventral macrochaeta, claws with well-developed latero-tergal crests, medial anterior macrochaetae present on abdominal tergites I-VIII, 1 + 1 lateral anterior and 2 + 2 lateral posterior macrochaetae on tergites IV-VII, 1 + 1 medial posterior and 5 + 5 lateral posterior macrochaetae on segment IX, 6 + 6 macrochaetae on urosternite I, and 4 + 4 well differentiated macrochaetae on urosternites II-VII.

DESCRIPTION.--Corresponding to the description of *Plusiocampa fieldingi* by Condé (1949b), with the following additions.

Size: Males: body length, 3.7-7.2 mm; head width, 0.58-0.85 mm; pronotal width, 0.41-0.58 mm. Females: body length, 3.7-7.7 mm; head width, 0.57-0.95 mm; pronotal width, 0.39-0.70 mm. Immatures: body length, 3.6-3.7 mm; head width, 0.49-0.55 mm; pronotal width, 0.33-0.35 mm.

Head: Disregarding several antennae of 26-28 segments which were obviously regenerating and usually paired with longer antennae, the number of segments of 47 complete antennae are as follows:

		28	29	30	31	32
No. segments:		28	29	30	31	32
Frequency:	♂	0	3	9	3	0
	♀	3	8	6	9	2
	immature	0	0	0	0	4

Length of longest antenna 5.34 mm, or about 78 percent of body length, reaching abdominal segment VII. Antennal segment III with ventral bacilliform sensillum, inserted between phaneres d and f: Ma, Mb, seta c, Md (short, smooth or with distal barbules), sen. (long, but not exceeding distal border of segment), phanere e absent, Mf, Mg, Mh; length of d about 1.3 times c; b with several distal barbules, h with 2 distal barbules; other long macrochaetae smooth. Length of latero-dorsal trichobothrium of segment V up to 310 microns, about 34 percent of head width. Segment X length 1.5 times width. Cupuliform organ of apical segment with 15 sensilla.

Frons with 3 macrochaetae on rostrum; anterior macrochaeta 1.3 times length of posterior pair. Macrochaetae bordering line of insertion of antennae 3 + 3; anterior macrochaeta approximately two-thirds as long as intermediate; anterior and posterior macrochaetae subequal, anterior 0.9 length of posterior; all three macrochaetae barbed on distal half. Macrochaetae anterior to arms of epicranial suture, near sagittal plane, 1 + 1; longer than macrochaetae at posterior border of antennal insertion; barbed on distal half.

Occipital setae barbed on distal half; length about 45 percent that of pronotal lp. Latero-anterior sensillum of labial palp subcylindrical, curved towards the sagittal plane, swollen in middle region (Fig. 14A). Posterior mental setae smooth; lateral submental macrochaetae smooth. Thorax: Clothing setae smooth; notal chaetotaxy 3 + 3, 3 + 3, 2 + 2. Lengths and ratios of macrochaetae of mature specimens, as follows:

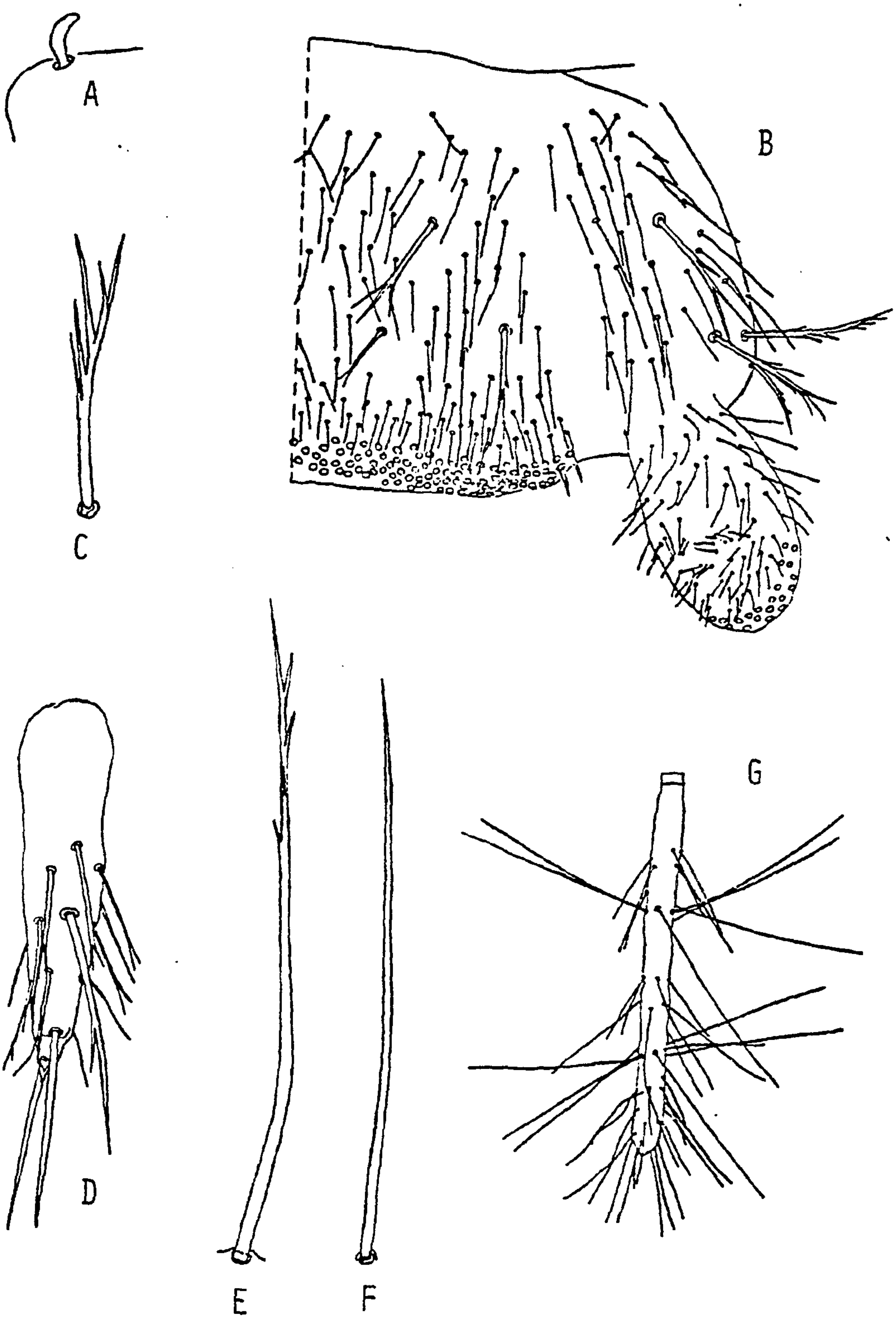
	ma	la	lp	ma/la	lp/ma
Th. I	130-275	130-248	227-400	1.00-1.11	1.45-1.75
Th. II	151-313	200-367	248-405	0.76-0.85	1.29-1.64
Th. III	157-346	--	248-405	--	1.17-1.59

Mesonotum: ma/Sep ma-ma, 2.00-2.35; ma/Sep ma-la, 1.40-1.45; la/Sep ma-la, 1.70-1.85; lp_{I}/lp_{II}, 0.91-0.99; lp_{II}/lp_{III}, 1.00. Pronotum with 3 + 3 to 4 + 4 barbed lateral posterior marginal setae and 6 to 7 smooth medial posterior marginal setae; mesonotum with 2 + 2 to 2 + 3 lateral, 9 to 14 medial posterior marginal setae; metanotum with 1 + 2 to 2 + 2 lateral, 9 to 15 medial posterior marginal setae.

Presternite of prosternum with 2 + 2 M; prosternite with 4 + 4 barbed precoxal M; 4 + 4 to 5 + 5 smooth precoxal setae; 1 + 1 subcoxal M; 1 + 1 lp or 1 + 1 lp and 1 + 1 slp. Meso-and meta-sternite with 4 + 4 barbed precoxal M; 4 + 4 to 5 + 5 smooth precoxal setae; 1 + 1 ma; 1 + 1 la; 1 + 1 subcoxal M; 1 + 1 lp.

Length of leg III about 40 percent of body length, reaching abdominal segment VII. Femur I without dorsal macrochaetae; femurs II and III with one dorsal macrochaeta. Dorsal macrochaeta inserted

FIGURE 14.--Litocampa fieldingi (Condé). A, latero-anterior sensillum of right labial palp; B, urosternite I of largest male (glandular setae represented by their bases; clothing setae diagrammatic); C, macrochaeta at base of left eversible vesicle of urosternite VII; D, left stylus of urosternite II; E, macrochaeta from base of cercus; F, macrochaeta from penultimate segment of cercus; G, apical segment of cercus. A-B, male (7.2 mm; head width, 0.85 mm), Tub Cave, W. Va. D, female (7.0 mm; head width, 0.92 mm), Buckeye Creek Cave, W. Va. Others, female (7.7 mm; head width, 0.95 mm), Steeles Cave, W. Va.


A
B
C
D
E
F
G

in middle of femur III, 1.5 times width of femur at point of insertion; barbed on its distal three-fourths. Femur III with 4 anterior marginal macrochaetae; 2 most ventral barbed on distal 65 percent; distal pair smooth. Tibia III length 7.0–9.1 times width, with one bifurcated ventral macrochaeta sometimes with 1 small barbule proximal to bifurcation; tibial spurs with 2 rows of long barbs. Tarsus III with 14 ventral setae in anterior row. Posterior claw longer than anterior; latero-tergal crests well developed; flange on posterior claw. Pretarsal appendices long, slender, and smooth; flattened at the tip; length exceeding tip of claws.

Abdomen: Distribution of tergal macrochaetae:

	ma	mp	la	lp	
Ab. I-III	1 + 1	0	0	0	
Ab. IV-VII	1 + 1	0	1 + 1	2 + 2	
Ab. VIII	1 + 1	0	0	3 + 3	
Ab. IX	0	1 + 1	0	5 + 5	(total)

Medial anterior macrochaetae long, robust, with numerous barbs on distal two-thirds; very slight increase in length posteriorly to Ab. VII; apex exceeds bases of posterior marginal setae on all tergites. Lateral anterior macrochaetae of Ab. IV shorter than ma; increases in length posteriorly, usually longer than ma on Ab. VII. Lateral posterior macrochaetae long and robust, similar to thoracic lp; barbed on distal three-fourths. Lengths and ratios of certain tergal macrochaetae, as follows:

	ma	la	lp_1	lp_2	ma/D	ma/Sep ma-ma
Ab. I	113-292	--	--	--	1.50-1.74	1.17-1.64
Ab. IV	184-281	65-238	162-308	130-319	2.17-3.40	0.85-1.21
Ab. VII	189-270	151-335	216-410	216-400	2.08-3.89	0.79-1.35

Abdominal tergite IV with up to 21 posterior marginal setae separating sublateral posterior macrochaetae nearest sagittal plane: tergite V with up to 22 such setae; VI with 20; VII with 18; VIII with 15; IX with 8 marginal setae separating medial posterior macrochaetae. Supra-anal valvule with 2 smooth medial setae and up to 2 + 2 smooth lateral setae or setiform sensilla.

Urosternite (coxosternite) I with 6 + 6 differentiated macrochaetae, 3 + 3 on middle portion; 1 + 1 submacrochaetae at latero-posterior angle of urosternite of male and female. Posterior margin with up to 3-4 rows of glandular setae on males; glandular setae more numerous laterally. Lateral subcoxal appendages subcylindrical, short, among males and females (Fig. 14B).

Urosternites II-VII with 4 + 4 well differentiated macrochaetae, with branches and barbs (Fig. 14C); 1 + 1 weakly differentiated macrochaetae inserted externally at base of each stylus. Apical seta of styli smooth and with 2 short basal branches, proximal branch about one-half length of distal; subapical seta smooth; medial ventral seta forked; most clothing setae smooth, some bifurcated (Fig. 14D). Stylus VII length 4.6-4.9 times width; apical seta about 50 percent as long as stylus. Urosternite VIII with 1 + 1 macrochaetae. Genital papilla of male with up to 18 short setae encircling gonopore.

Length of longest cercus about 0.87 times body length, composed of a base, subdivided into 4 secondary segments, and 11 primary segments. Segmental lengths (in mm): base = 0.18, 0.16, 0.21, 0.29; primary segments = 0.33, 0.39, 0.43, 0.46, 0.48, 0.51, 0.54, 0.60, 0.68, 0.72, 0.76. Covering of base (Fig. 14E) and proximal segments composed of long macrochaetae, length of macrochaetae about 2.7 times width of segments, 5-8 barbs and barbules on distal half. Proximal primary segments with whorls of 7 barbed macrochaetae, long smooth setae, and 8 short subapical setae. Penultimate segment length 12 times width, with 2 whorls of macrochaetae, alternating with whorls of long smooth setae; macrochaetae smooth (Fig. 14F); 8 short subapical setae. Macrochaetae of apical segment arragned in 2 whorls, length of macrochaetae about 7.6 times width of segment, alternating with whorls of long and short smooth setae (Fig. 14G); all macrochaetae smooth.

TYPE LOCALITY.--McClung Cave, 1.5 miles northeast of Maxwelton, in Greenbrier Co., West Virginia. The cave is the fifth longest in West Virginia, with 14.9 miles of surveyed passages (Looney and Looney, 1980), and is developed in the Upper Mississippian-aged Hillsdale Limestone, Greenbrier Series (Davies, 1965).

DISTRIBUTION AND ECOLOGY.--_Litocampa fieldingi_ is known from 13 caves formed in the massive limestones of the Mississippian-aged Greenbrier

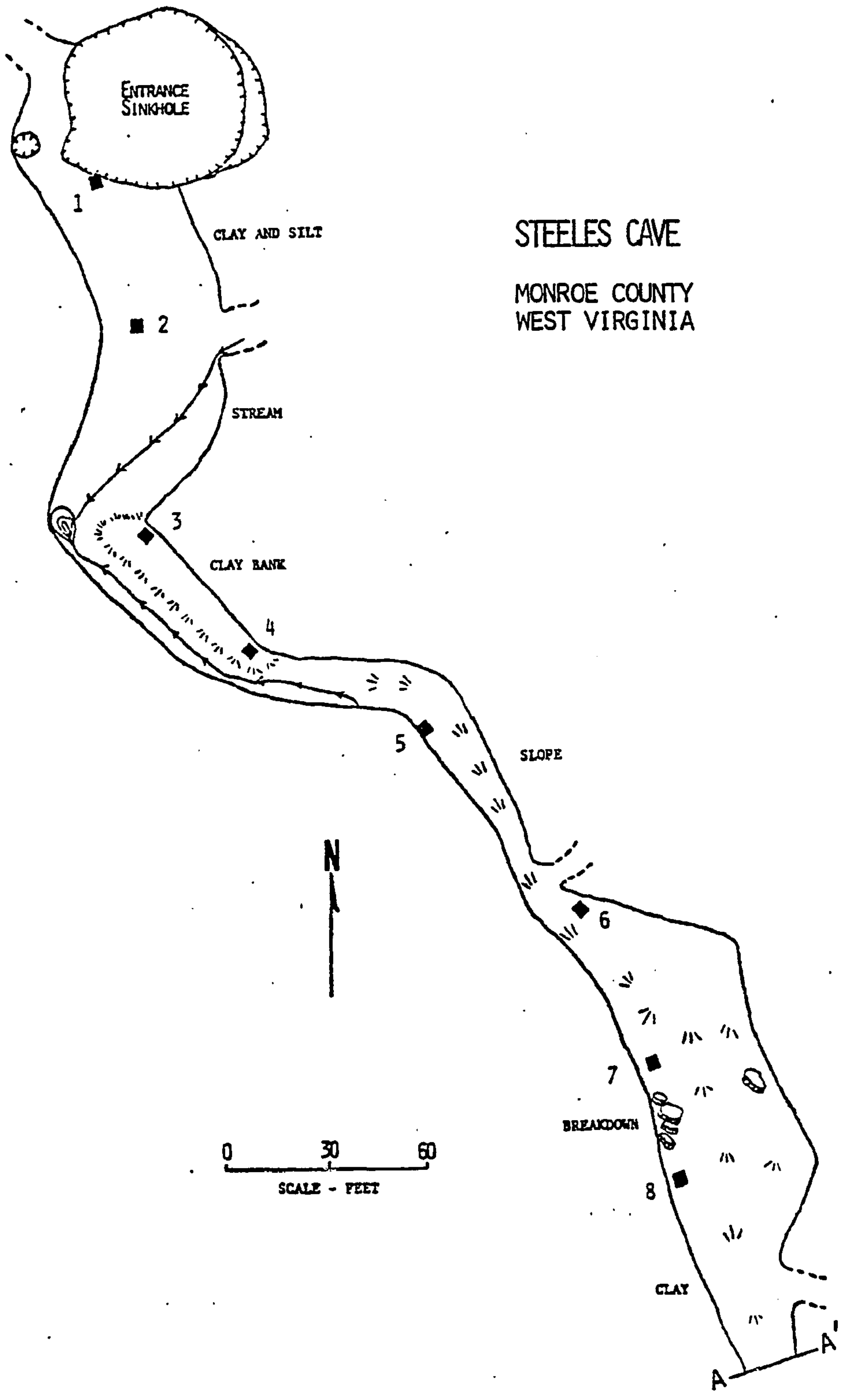
Series. The majority of these caves are located along the Greenbrier River valley, north of Lewisburg in Greenbrier Co., West Virginia. The species extends north into Pocahontas County, and a specimen seen in Cass Cave, which probably belongs to this species, would represent the northernmost locality known.

Several locations are known south of Lewisburg in Monroe County. All localities, however, are north of New River. One of these localities, Steeles Cave, is of considerable interest since it is one of only two caves presently known in the United States to contain two different species of campodeid diplurans. The other species belongs to another genus, *Eumesocampa*.

In an attempt to collect more specimens and to gather possible information on the spatial relationship for the two species, blue cheese and raw liver was used as bait at stations approximately 50 feet apart throughout the cave. In September, 1980, temperatures and relative humidities were taken at the bait stations, and this procedure was repeated on the consecutive weekend. The same was done on two trips in November. See Figure 15 for location of the stations in the cave and Figs. 16-18 for the findings.

Mid-passage air temperature and the relative humidity were determined by means of a sling psychrometer. The surface temperature of the substrate was determined by a dial thermometer. Part of the difference between the substrate temperature and that of the passage air (Fig. 18) may be due to a difference in calibration of the two instruments used. No statistical tests have been done to determine

FIGURE 15.--Map of Steeles Cave, Monroe County, West Virginia. Solid squares indicate bait stations where temperature and humidity readings were made.


STEELES CAVE
MONROE COUNTY
WEST VIRGINIA
ENTRANCE
SINKHOLE
CLAY AND SILT
STREAM
CLAY BANK
SLOPE
BREAKDOWN
CLAY
N
0
30
60
SCALE - FEET
1
2
3
4
5
6
7
8
A
A'

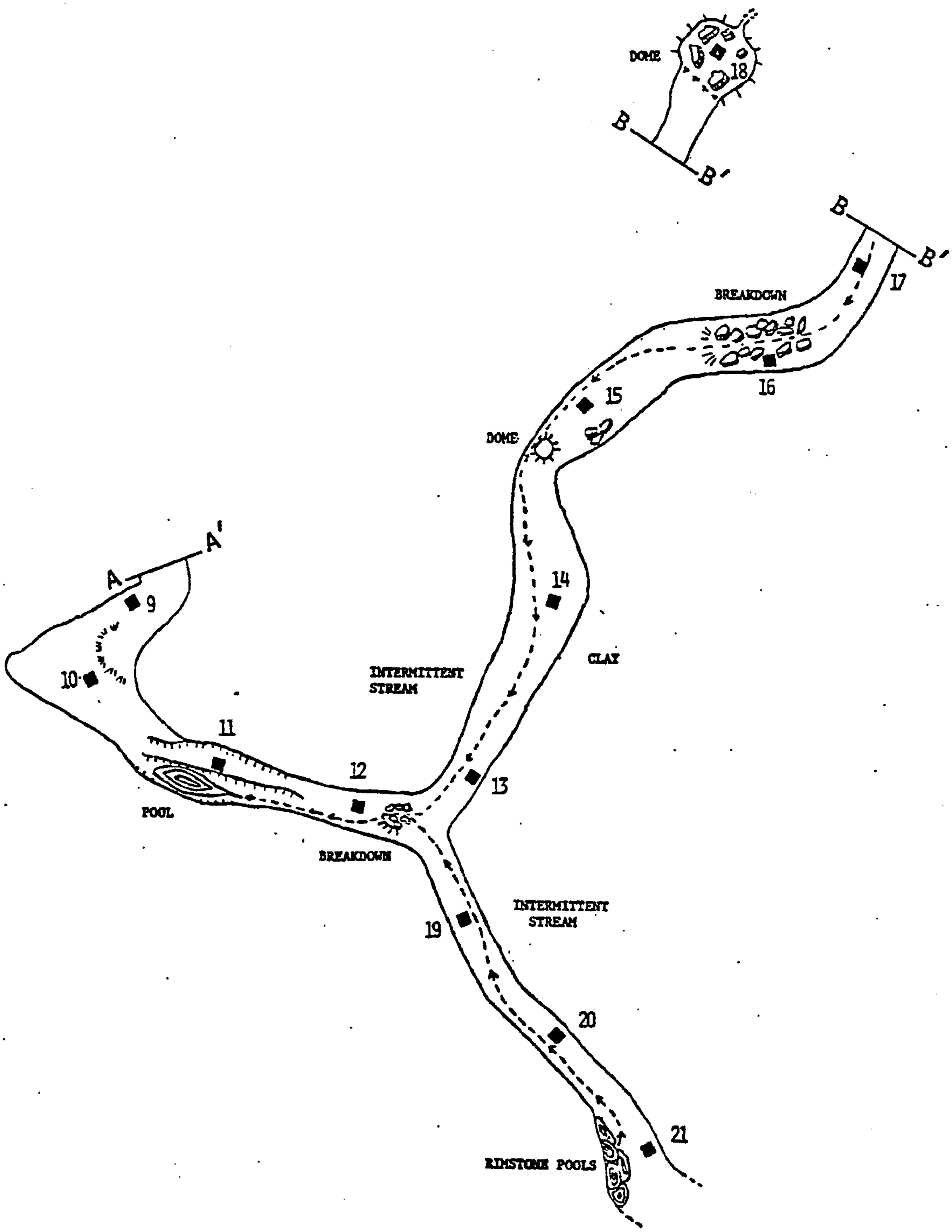

DOME
18
B
B'
B
B'
BREAKDOWN
17
16
15
DOME
A
A'
9
10
14
CLAY
INTERMITTENT
STREAM
11
12
13
POOL
BREAKDOWN
INTERMITTENT
STREAM
19
20
21
RIMSTONE POOLS

FIGURE 16.--Average mid-passage relative humidities at each station in Steeles Cave. The solid line represents the average for September and the dashed line the average for November. Station -1 is outside of the sinkhold, station 0 is in the center of the sinkhold, and station 1 is at the entrance to the cave proper.

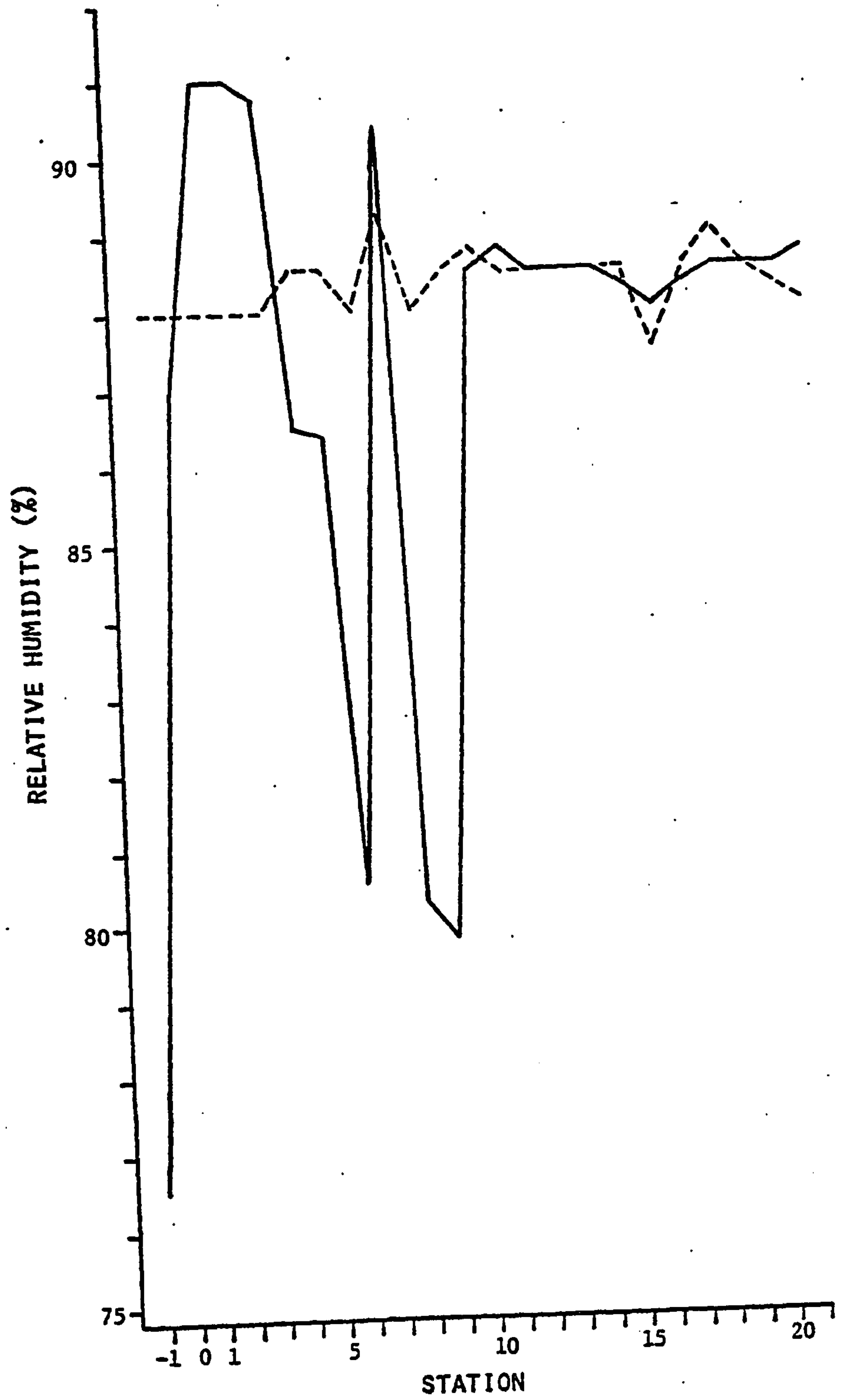

90
85
80
75
RELATIVE HUMIDITY (%)
-1 0 1
5
10
15
20
STATION

FIGURE 17.--Average mid-passage air temperatures at each station in Steeles Cave. The solid line represents the average for September and the dashed line the average for November. Station -1 is outside of the sinkhole, station 0 is in the center of the sinkhole, and station 1 is at the entrance to the cave proper.

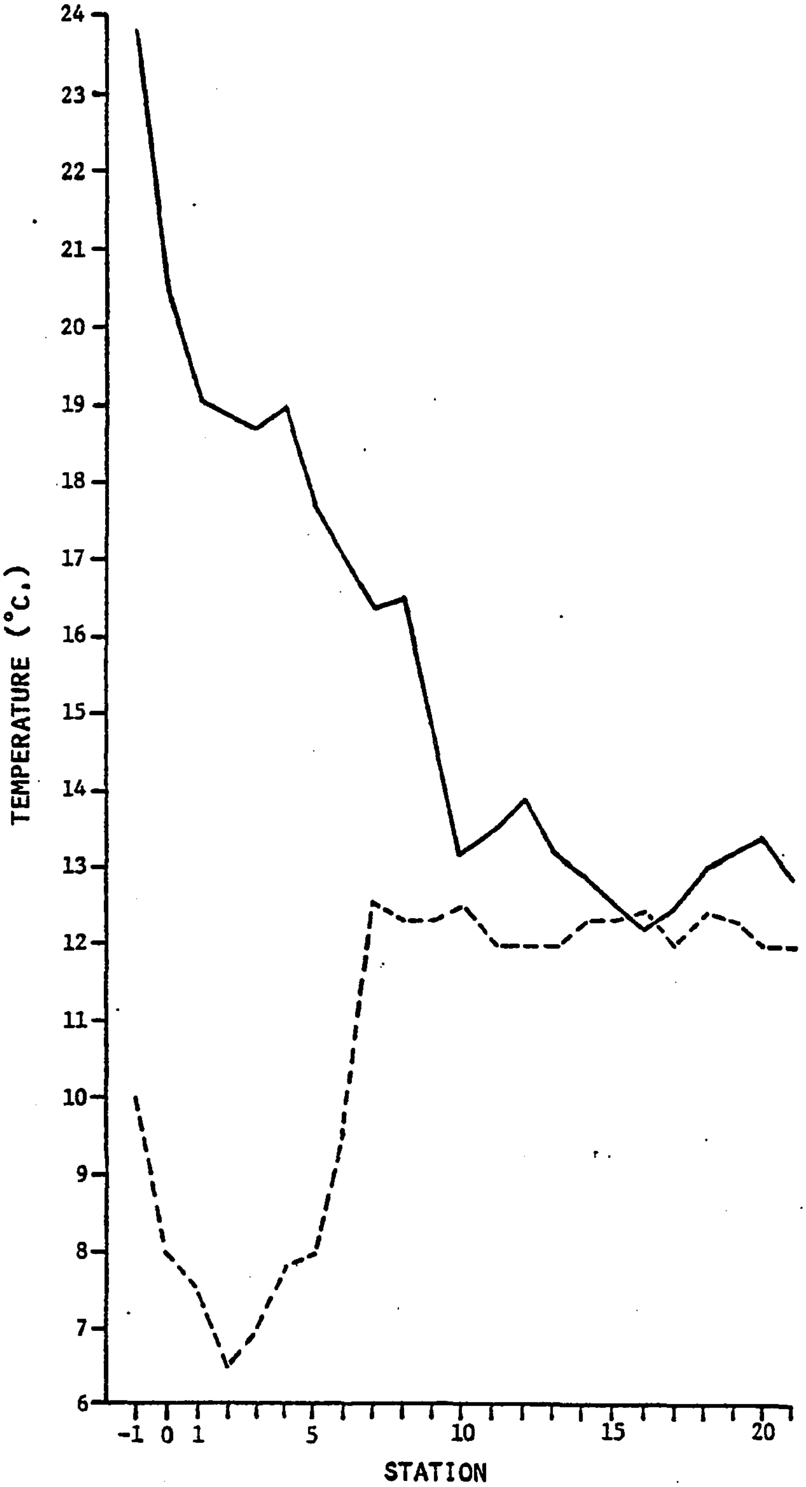
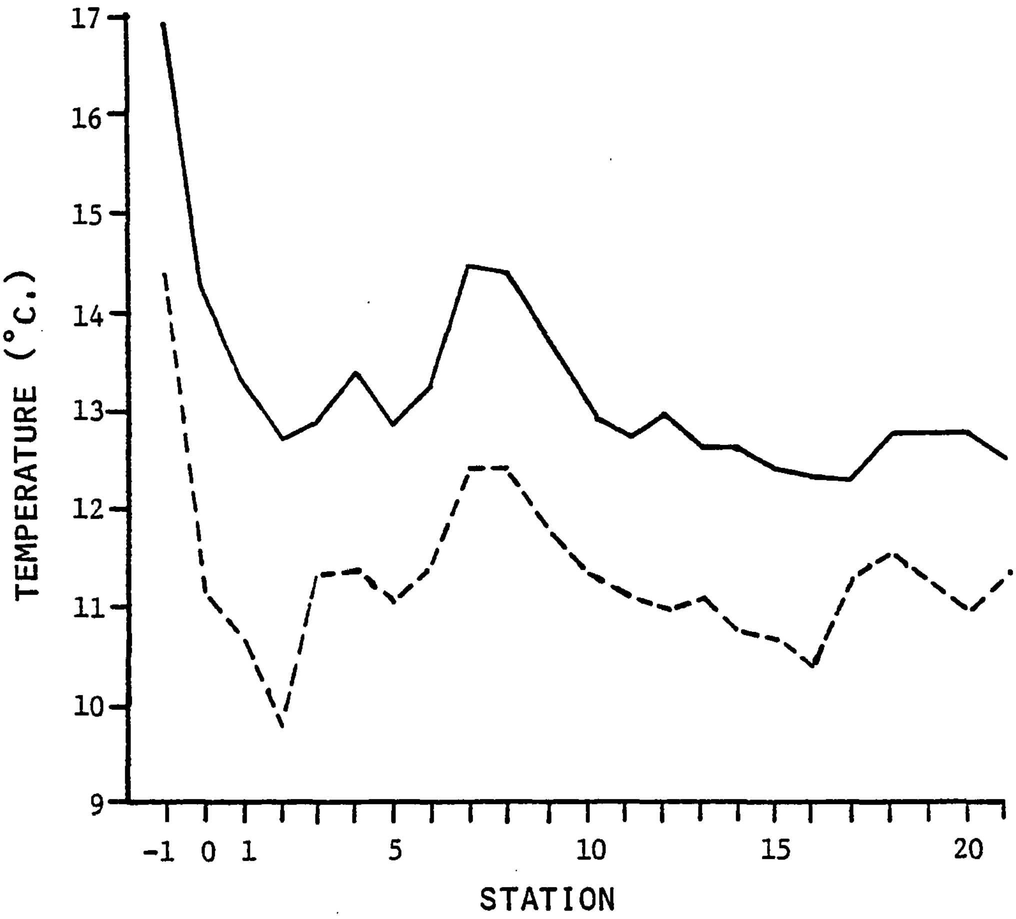

24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
9
8
7
6
TEMPERATURE (°C.)
-1
0
1
5
10
15
20
STATION

FIGURE 18.--Average temperatures in Steeles Cave by station. The solid line represents mid-passage air temperature, the dashed line substrate temperature. Station -1 is outside of the sinkhole, station 0 is in the center of the sinkhole, and station 1 is at the entrance to the cave proper.


17
16
15
14
13
12
11
10
9
TEMPERATURE (°C.)
-1 0 1
5
10
15
20
STATION

the significance of the differences shown in the graphs, since such a study of the abiotic conditions of a cave was not the aim of this thesis. However, Keith (1976) has done such a study of a cave in Indiana, and he found significant monthly variations in temperatures and relative humidities.

The Steeles Cave data indicate that the variable temperature and humidity zone of the cave extend from the entrance to about station 10. Part of the tremendous variation observed within this zone is due to the presence of the cave stream, which goes underground (sinks) only a few hundreds of feet from its appearance in the cave. An ample supply of leaves, sticks, and other debris is brought into the cave by this stream as well. Many crayfish, salamanders, and several medium-sized fish were seen in the stream. The water temperature was 15.5° C. in September and 4° C. in November. The temperature of the water in the rimstone pools near station 21 was, respectively, 10.6° and 10.4° C. for the same dates. I have collected many specimens of _L. fieldingi_ on the west clay near these pools.

John R. Holsinger, who collected the _Eumesocampa_ specimens (♂, ♀, and immature) in August, 1967, reports that they were taken near the cave stream (personal communication). A previous baiting attempt in the month of October with cheese only and the more recent September baitings attracted campodeid diplurans at station 10 and at other stations farther into the cave. In November, campodeids were found beginning at station 9. All specimens were _Litocampa fieldingi_. This restriction of _L. fieldingi_ to the remote sections of the cave is taken to indicate the true cavernicolous (troglobitic) status of this species. Another Eumesocampa species is known from caves in Missouri and Illinois, but most species are from epigean habitats in Colorado, New York, and Pennsylvania (Condé and Geeraert, 1962; Ferguson, 1978). The species found in Steeles Cave is probably a troglophile, since an immature form was found in the cave along with the sexually mature forms.

The *Keithi* Group

DIAGNOSIS.--Antennal segment III with phanere *e*, metanotum with 1 + 1 lateral posterior macrochaetae, femur III with dorsal macrochaeta, pretarsal claws without large latero-tergal crests, abdominal tergites V-VII with 1 + 1 or 2 + 2 lateral posterior macrochaetae, medial anterior macrochaetae on abdominal tergites I-IX, urosternite I with 7 + 7 macrochaetae, and posterior margin of urosternite I of males without glandular setae.

REMARKS.--Only three widely separated locations are known for the three species placed in this group: one each in southern Indiana, central New Mexico, and northeastern Tennessee. Morphologically the species in this group are somewhat intermediate between the members of the *bifurcata* group and those of the *virginiana* group.

Key to the Species of the *Keithi* Group

1. Abdominal tergites IV-VII with 1 + 1 lateral posterior macrochaetae ....*L. welbourni*, new species

1'. Abdominal tergites IV-VII with 2 + 2 lateral posterior macrochaetae 2

2. Meso- and metasternites with 4 + 4 barbed precoxal macrochaetae; urosternites II-VII with 4 + 4 well differentiated macrochaetae...

..................................*L. inexspectata*, new species

2'. Meso- and metasternites with 5 + 5 barbed precoxal macrochaetae; urosternites II-VII with 5 + 5 well differentiated macrochaetae.. ....*L. keithi*, new species

Litocampa keithi, new species

(Figs. 19-21)

MATERIAL EXAMINED.--INDIANA: *Orange Co.*: Murray Spring Cave, 1 ♂, 4 ♀ (holotype and paratypes), 20 Aug. 1973, J. H. Keith, (LMF 442).

Holotype (LMF 442-2) and paratypes to be deposited in American Museum of Natural History.

DIAGNOSIS.--Can be distinguished from other species of *Litocampa* in the United States by presence of 3 + 3 and 2 + 2 macrochaetae on meso- and metanota, one dorsal macrochaeta on femur III, tibia III with 1 ventral macrochaeta, claws without well-developed latero-tergal crests, medial anterior macrochaetae present on abdominal tergites I-IX, 1 + 1 lateral anterior and 2 + 2 lateral posterior macrochaetae on tergites IV-VII, 7 + 7 macrochaetae on urosternite I, and 5 + 5 well differentiated macrochaetae on urosternites II-VII.

DESCRIPTION.--*Size*: Male: body length, ?; head width, 0.63mm; pronotal width, ?. Females: body length, 4.4-5.3mm; head width, 0.62-0.67mm; pronotal width, 0.38-0.45mm.

Head: Only unbroken antenna with 27 segments; apical segment long, antenna probably regenerating. Length of antenna 3.27mm, or about 62 percent of body length, reaching abdominal segment IV. Antennal segment III with ventral bacilliform sensillum, inserted between phaneres *d* and *e*: *Ma*, *Mb*, seta *c*, *Md* (short with 4 distal barbs), sen. (long, but not exceeding distal border of segment), seta e (smooth or with 1 barb), Mf, Mg, Mh; length of d slightly more than c; b with 3 distal barbs, other long macrochaetae smooth. Length of latero-dorsal trichobothrium of segment V up to 233 microns, about 35 percent of head width. Segment X length 1.5-1.7 times width. Cupuliform organ of apical segment with 11 sensilla.

Frons with 3 macrochaetae on rostrum, barbed on their distal half; anterior macrochaeta 1.3 times length of posterior pair. Macrochaetae bordering line of insertion of antennae 3 + 3; anterior macrochaeta approximately two-thirds as long as intermediate; anterior and posterior macrochaetae subequal, anterior slightly shorter than posterior; all three macrochaetae barbed on distal half. Macrochaetae anterior to arms of epicranial suture, near sagittal plane, 1 + 1; shorter than macrochaetae at posterior border of antennal insertion; smooth. Occipital setae with few barbs on their distal half; length about 55 percent as long as pronotal lp. Latero-anterior sensillum of labial palp subcylindrical, weakly curved, slightly swollen in middle region (Fig. 20A). Posterior mental setae smooth; lateral submental macrochaetae smooth.

Thorax: Clothing setae smooth; notal chaetotaxy 3 + 3, 3 + 3, 2 + 2 (Fig. 19A-H). Pronotal ma barbed on distal 61 percent, la on distal 71 percent, lp on distal 69 percent; mesonotal ma barbed on distal 55 percent, la on distal 58 percent, lp on distal 68 percent; metanotal ma with 4 long barbs on distal 53 percent, lp with approximately 12 long barbs on distal 67 percent.

FIGURE 19.--*Litocampa keithi*, new species. A, pronotum and mesonotum; B, lateral posterior marginal seta of pronotum; C-E, *ma*, *la*, and *lp* of pronotum; F-H, *ma*, *la*, and *lp* of mesonotum. Female (5.3 mm; head width, 0.67 mm), Murray Spring Cave, Indiana.

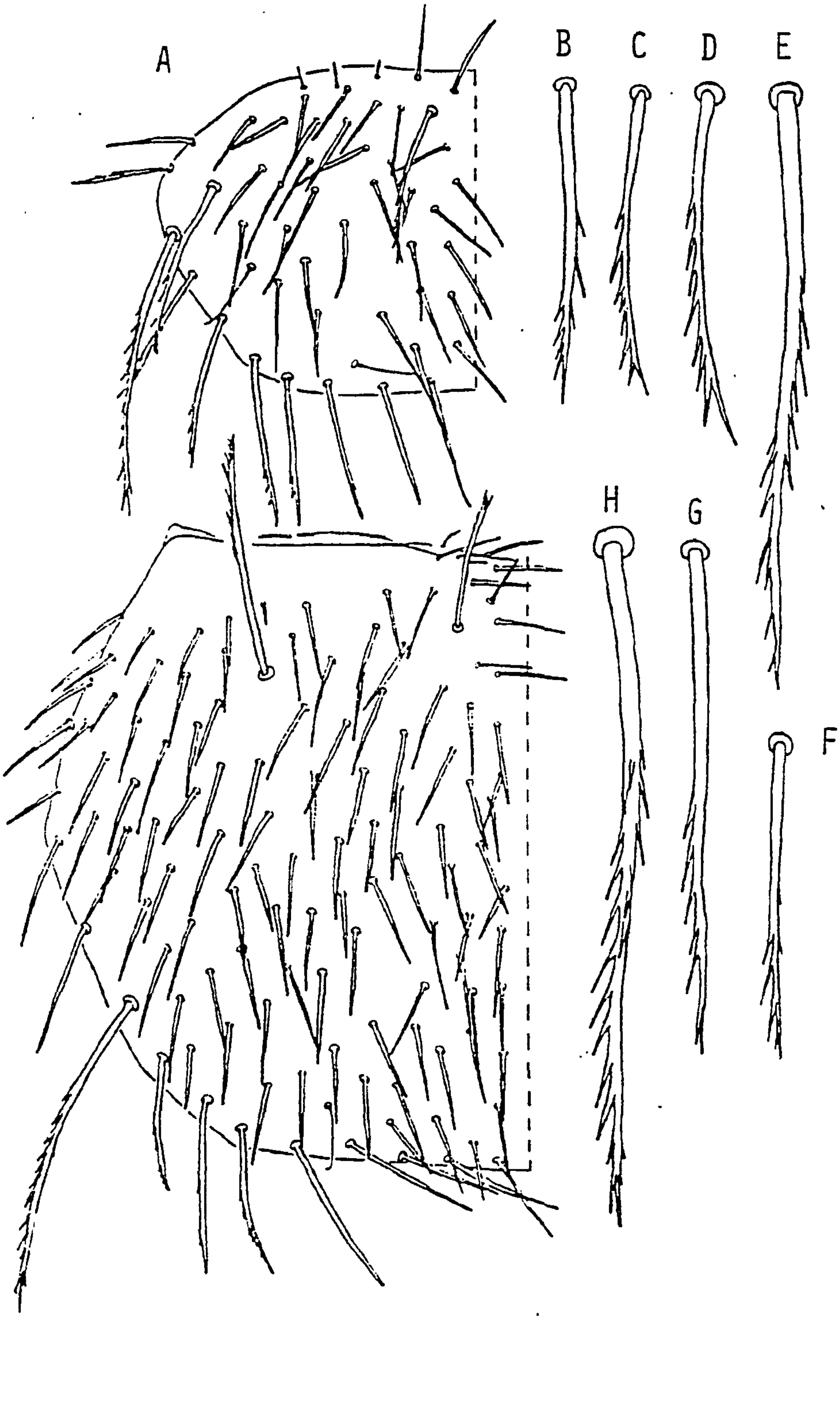
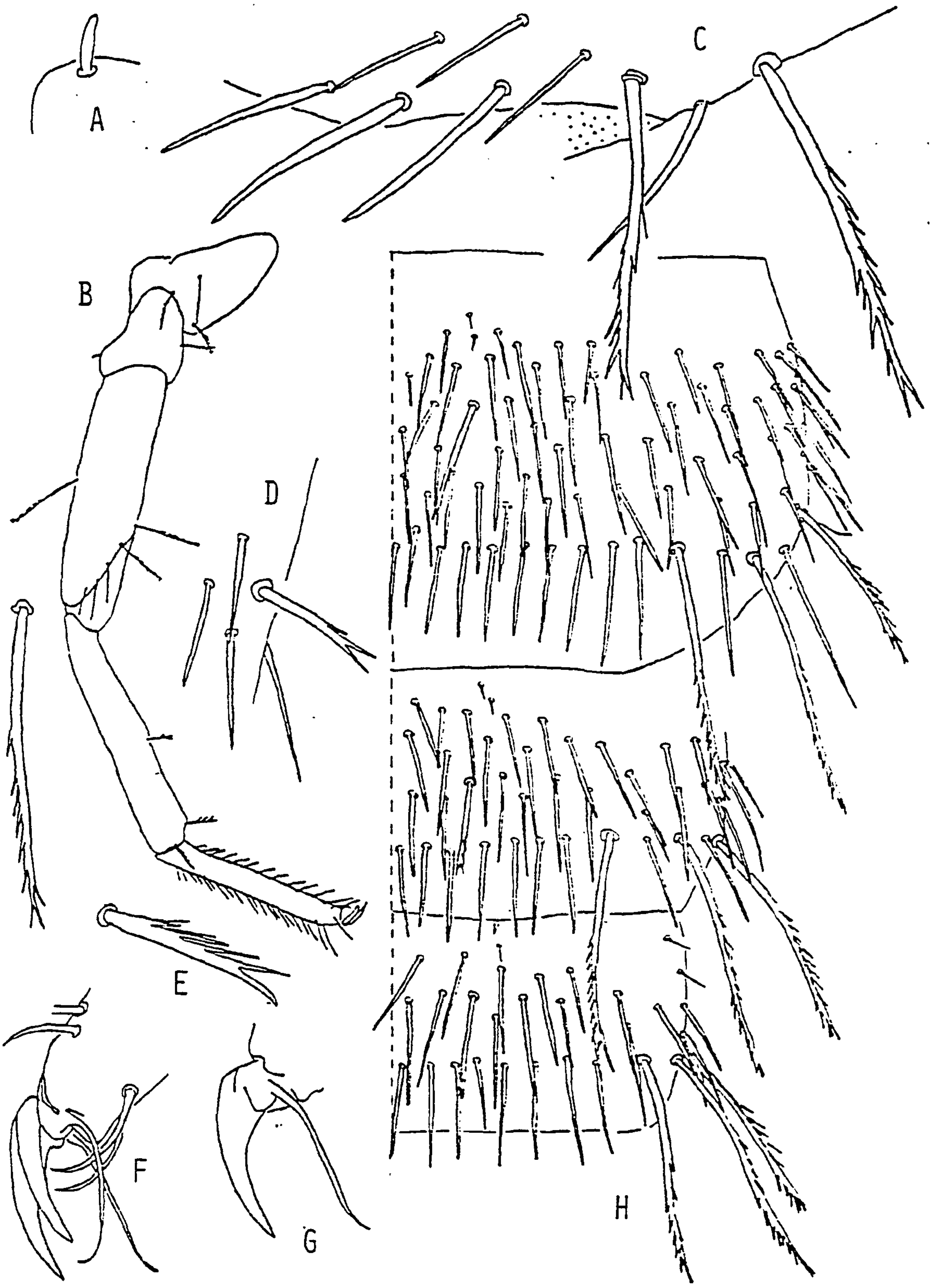

A
B
C
D
E
H
G
F

FIGURE 20.--Litocampa keithi, new species. A, latero-anterior sensillum of right labial palp; B, metathoracic leg (dorsal macrochaeta of femur enlarged); C, anterior distal margin of femur III; D, ventral macrochaeta of tibia III; E, posterior tibial spur of leg III; F, anterior view of pretarsal claws of leg III; G, posterior view of posterior claw of leg III; H, abdominal tergites VII-IX. Female (5.3 mm; head width, 0.67 mm), Murray Spring Cave, Indiana.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Lengths and ratios of macrochaetae of specimens from Murray Spring Cave, as follows:

	ma	la	lp	ma/la	lp/ma
Th. I	92-113	103-130	184-211	0.85-0.89	1.86-2.00
Th. II	92-108	140-173	184-238	0.63-0.65	1.89-2.29
Th. III	97-108	--	189-232	--	1.94-2.15

Mesonotum: ma/Sep ma-ma, 1.22; ma/Sep ma-la, 0.67-0.75; la/Sep ma-la, 1.17-1.24; lp_I/lp_{II}, 0.87-1.00; lp_{II}/lp_{III}, 0.97-1.02. Pronotum with 2 + 4 to 3 + 3 barbed posterior marginal setae and 6 to 8 smooth medial posterior marginal setae; mesonotum with 2 + 3 to 3 + 1 barbed, 11 to 12 smooth posterior marginal setae; metanotum with 1 + 1 barbed, 11 smooth posterior marginal setae.

Presternite of prosternum with 2 + 2 M; prosternite with 4 + 4 barbed precoxal M; 5 + 5 smooth precoxal setae; 1 + 1 subcoxal M; 2 + 2 lp. Meso- and metasternite with 5 + 5 barbed precoxal M; 5 + 5 smooth precoxal setae; 1 + 1 ma; 1 + 1 la; 1 + 1 subcoxal M; 2 + 2 lp.

Length of leg III about 50 percent of body length, reaching abdominal segment VI. Femur I without dorsal macrochaetae; femurs II and III with one dorsal macrochaeta. Dorsal macrochaeta inserted on distal half of femur III, 1.1-1.3 times width of femur at point of insertion; barbed on its distal six-tenths (Fig. 20B). Femur III with 4 anterior marginal macrochaetae; 2 most ventral barbed on their distal 60 to 70 percent; distal pair smooth (Fig. 20C). Tibia III length 6.2-6.4 times width, with one bifurcated ventral macrochaeta with 1 small barb proximal to bifurcation (Fig. 20D); tibial spurs with 2 rows of long barbs (Fig. 20E). Tarsus III with 13 ventral setae in anterior row. Posterior claw only slightly longer than anterior; latero-tergal crests very reduced; no flange on posterior claw. Pretarsal appendices long, slender, and smooth; length exceeding tip of claws (Fig. 20F,G).

Abdomen: Distribution of tergal macrochaetae (Fig. 20H):

	ma	la	lp	
Ab. I-III	1 + 1	0	0	
Ab. IV-VII	1 + 1	1 + 1	2 + 2	
Ab. VIII	1 + 1	0	3 + 3	
Ab. IX	1 + 1	0	5 + 5	(total)

Medial anterior macrochaetae slender, with 3 or 4 barbs on distal half; slight increase in length posteriorly to Ab. VII; apex not reaching bases of posterior marginal setae. Decrease in length of ma on Ab. VIII; slight increase in length on Ab. IX, but less than on Ab. VII; apex exceeds bases of posterior marginal setae on Ab. VIII-IX. Lateral anterior macrochaetae moderately short on Ab. IV, slightly longer than ma; increases in length by one-half on Ab. VII. Lateral posterior macrochaetae long and robust, similar to thoracic lp; barbed on distal half to two-thirds. Lengths and ratios of certain tergal macrochaetae, as follows:

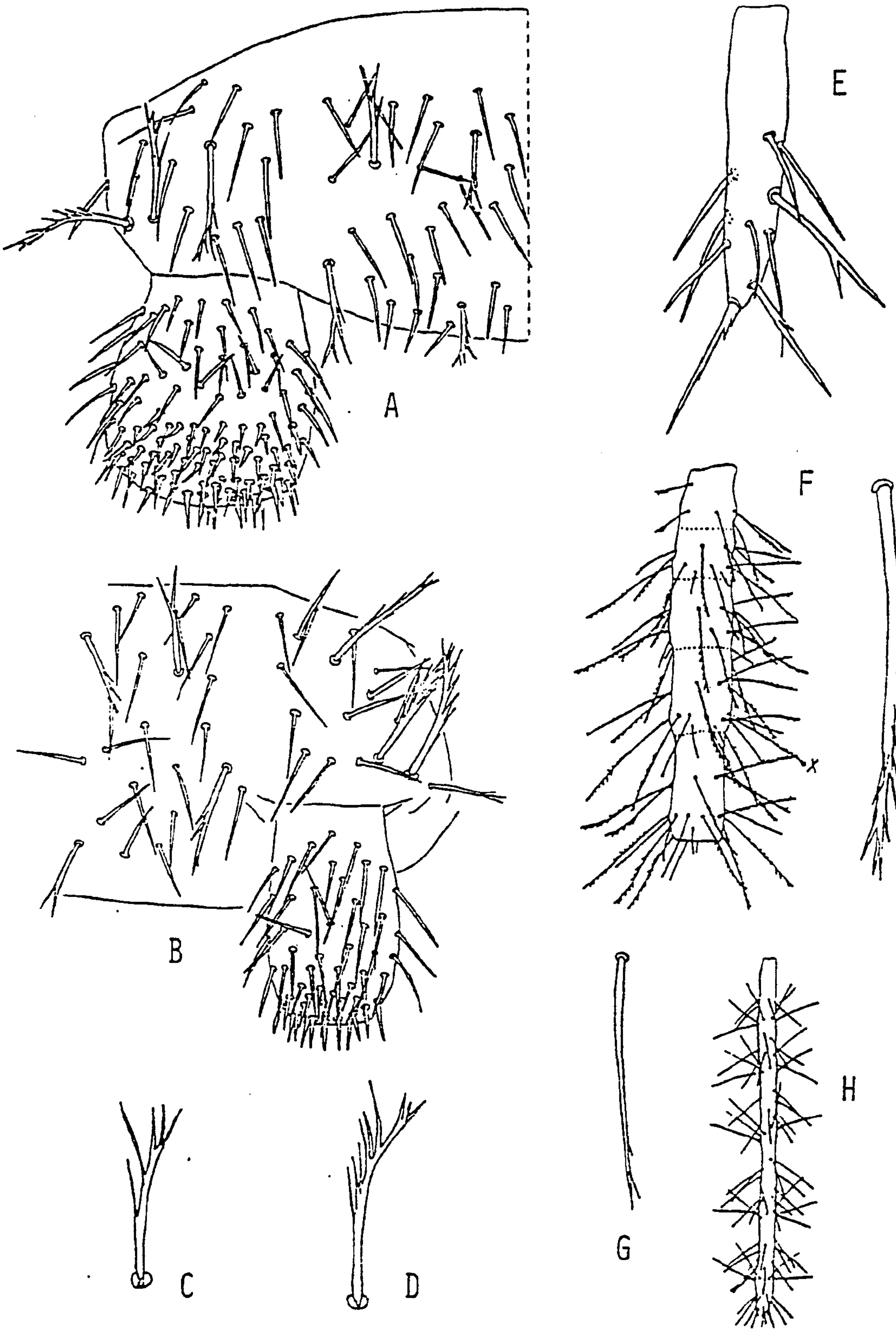
	ma	la	lp_1	lp_2	ma/D	ma/Sep	ma-ma
Ab. I	70-76	--	--	--	0.70-0.81	0.62-0.67	
Ab. IV	81-92	86-103	189-205	167-184	0.65-0.68	0.61-0.63	
Ab. VII	86-108	146-151	200-216	211-227	0.80-0.91	0.62-0.63	

Abdominal tergite IV with up to 14 posterior marginal setae separating sublateral posterior macrochaetae nearest sagittal plane; tergite V with up to 16 such setae; VI with 16; VII with 15; VIII with 13; IX with 13. Supra-anal valvule with 2 smooth medial setae; subapical seta thicker.

Urosternite (coxosternite) I with 7 + 7 differentiated macrochaetae, 4 + 4 on middle portion; 1 + 1 submacrochaetae at latero-posterior angle of urosternite of female. Posterior margin without glandular setae on males and females. Lateral subcoxal appendages subcylindrical, short, among females; subcylindrical, 1.5 times broader on mature male (Fig. 21A,B). Females with up to 25 glandular setae on tip of appendages; approximately 75 glandular setae on tip of appendages of male.

Urosternites II-VII with 5 + 5 well differentiated macrochaetae, with branches and barbs (Fig. 21C,D);1 + 1 weakly differentiated macrochaetae inserted at internal border of each stylus. Apical seta of styli with 1 distal barbule and 2 short basal branches, proximal branch about one-half length of distal; subapical seta with 1 long barb on proximal half; medial ventral seta forked; clothing setae smooth (Fig. 21E). Stylus VII length 3.7-4.4 times width; apical seta about

FIGURE 21.--Litocampa keithi, new species. A-B, urosternite I of male and female; C-D, medial posterior macrochaeta and macrochaeta at base of eversible vesicle of urosternite III; E, left stylus of urosternite VI; F, base of cercus (one macrochaeta enlarged); G, macrochaeta from proximal half of penultimate segment of cercus; H, apical segment of cercus. A, male (head width, 0.63 mm); E, female (4.4 mm; head width, 0.62 mm); others, female (5.3 mm; head width, 0.67 mm), Murray Spring Cave, Indiana.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50 percent as long as stylus; with 9 clothing setae and setiform sensilla. Urosternite VIII with 1 + 1 macrochaetae. Genital papilla of male with 14 short setae encircling gonopore.

Length of longest cercus about 1.14 times body length, composed of a base, subdivided into 6 secondary segments, and 10 primary segments. Segmental lengths (in mm): base = 0.10, 0.10, 0.14, 0.17, 0.20, 0.24; primary segments = 0.27, 0.30, 0.35, 0.42, 0.49, 0.54, 0.61, 0.67, 0.72, 0.71. Covering of base (Fig. 21F) and proximal segments composed of long macrochaetae, length of macrochaetae about 2.5 times width of segments, long barbs on their distal two-thirds. Proximal primary segments with whorls of 7 barbed macrochaetae, long smooth setae, and 9-10 short subapical setae. Penultimate segment length 18 times width, with 5 whorls of macrochaetae, alternating with whorls of long smooth setae; macrochaetae with long subapical barb and 1 or 2 barbules below subapical (Fig. 21G); 10 short subapical setae. Macrochaetae of apical segment arranged in 5 whorls, length of macrochaeae about 3.5 times width of segment, alternating with whorls of long and short smooth setae (Fig. 21H); all macrochaetae smooth except 2 of proximal whorl, one with 1 and one with 2 small subapical barbules.

TYPE LOCALITY.--Murray Spring Cave, about 0.5 mile east of Paoli, Orange Co., Indiana. The cave is developed in the Mississippian aged Ste. Genevieve limestone and contains about 1600 feet of stream passage. The cave is located on the eastern edge of the Crawford Upland (Powell, 1961; Keith, 1976).

DISTRIBUTION AND ECOLOGY.--*L. keithi* is known only from the type locality. However, due to the nature of the flat-lying limestone strata and the extensive cave systems of that state (Powell, 1961; Palmer and Powell, 1973), it would not be surprising to find it in other caves throughout the Mitchell Plain and Crawford Upland regions, south of the glacial moraines (Figs. 43, 49). Cope (1872) reports "*Campodea cookei*" from Wyandotte Cave located 24 miles southeast of Murray Spring Cave, in Crawford County, Indiana. There is also a questionable sighting for Buckner Cave, Monroe County. Baiting with blue cheese in the portion of the cave where the campodeid was supposedly seen, as well as in other likely spots, failed to produce any specimens.

One ecological note of interest is the observation of a specimen of *L. keithi* being seized and eated by the troglobitic carabid beetle, *Pseudanophthalmus tenuis* (J. H. Keith, 1976, and personal communication).

ETYMOLOGY.--It is a pleasure to name this species in honor of the collector, Dr. James H. Keith, a biospeleologist from Indiana.

Litocampa inexspectata, new species

(Figs. 22-23)

MATERIAL EXAMINED.--TENNESSEE: Hancock Co.: Panther Creek Cave, 1♀ (holotype), 20 Nov. 1979, J. R. Holsinger, (LMF 594-1).

Holotype to be deposited in American Museum of Natural History.

DIAGNOSIS.--Similar to Litocampa keithi, from which it can be distinguished by the presence of 4 + 4 barbed precoxal macrochaetae on the meso- and metasternite (in place of 5 + 5 barbed precoxal macrochaetae on L. keithi) and 4 + 4 well differentiated macrochaetae on urosternites II-VII (instead of 5 + 5 on L. keithi).

DESCRIPTION.--Size: Female: body length, 3.7 mm; head width, 0.56 mm; pronotal width, 0.37 mm.

Head: Both antennae broken, with 14 and 21 segments remaining. Length of longest broken antenna 1.98 mm, or about 54 percent of body length, reaching abdominal segment III. Antennal segment III with ventral bacilliform sensillum, inserted between phaneres d and e: Ma, Mb, seta c, Md (long with 2 distal barbs), sen. (not exceeding distal border of segment), seta e (smooth), Mf, Mg, Mh; length of d 1.6 times greater than c; b smooth or with 2 distal barbs, h smooth or with 1 distal barb, other long macrochaetae smooth. Length of latero-dorsal trichobothrium of segment V up to 188 microns, about 34 percent of head width. Segment X length 1.3 times width.

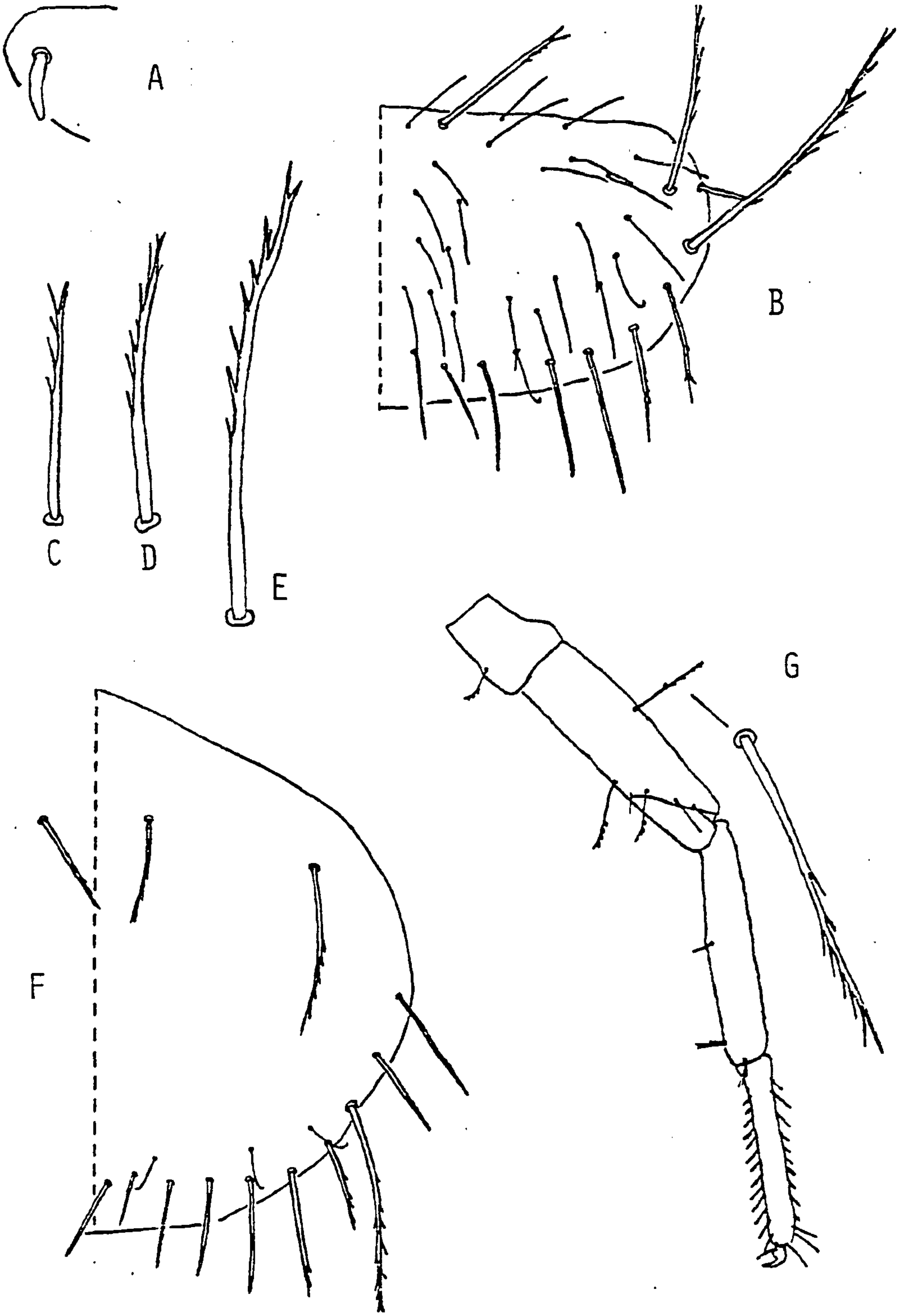
Frons with 3 macrochaetae on rostrum, few barbs on their distal half; anterior macrochaeta 1.3 times length of posterior pair. Macrochaetae bordering line of insertion of antennae 3 + 3; anterior macrochaeta approximately two-thirds as long as intermediate; anterior and posterior macrochaetae subequal, anterior slightly shorter than posterior; all three macrochaetae barbed on distal half. No macrochaetae anterior to arms of epicranial suture, near sagittal plane. Occipital setae barbed on their distal half; length about 54 percent as long as pronotal lp. Latero-anterior sensillum of labial palp long, subcylindrical, weakly curved (Fig. 22A). Posterior mental setae smooth; lateral submental macrochaetae smooth.

Thorax: Clothing setae smooth; notal chaetotaxy 3 + 3, 3 + 3, 2 + 2 (Fig. 22B-E). Pronotal ma with 4 long barbs on distal 47 percent, la with 7 barbs on distal 65 percent, lp with 8 barbs on distal 64 percent; mesonotal ma with 4 long barbs on distal 52 percent, la with 6 barbs on distal 58 percent, lp with 10 barbs on distal 62 percent; metanotal ma with 3 long barbs on distal 40 percent, lp with 9 long barbs on distal 65 percent.

Lengths and ratios of macrochaetae of specimen from Panther Creek Cave, as follows:

	ma	la	lp	ma/la	lp/ma
Th. I	88	103	168	0.85	1.91
Th. II	85	133	176	0.64	2.07
Th. III	88	--	161	--	1.83

FIGURE 22.--Litocampa inexspectata, new species. A, latero-anterior sensillum of right labial palp; B, pronotum (smooth clothing setae diagrammatic); C-E, ma, la, and lp of pronotum; F, mesonotum (clothing setae not shown); G, metathoracic leg (dorsal macrochaeta of femur enlarged). Female (3.7 mm; head width, 0.56 mm), Panther Creek Cave, Tennessee.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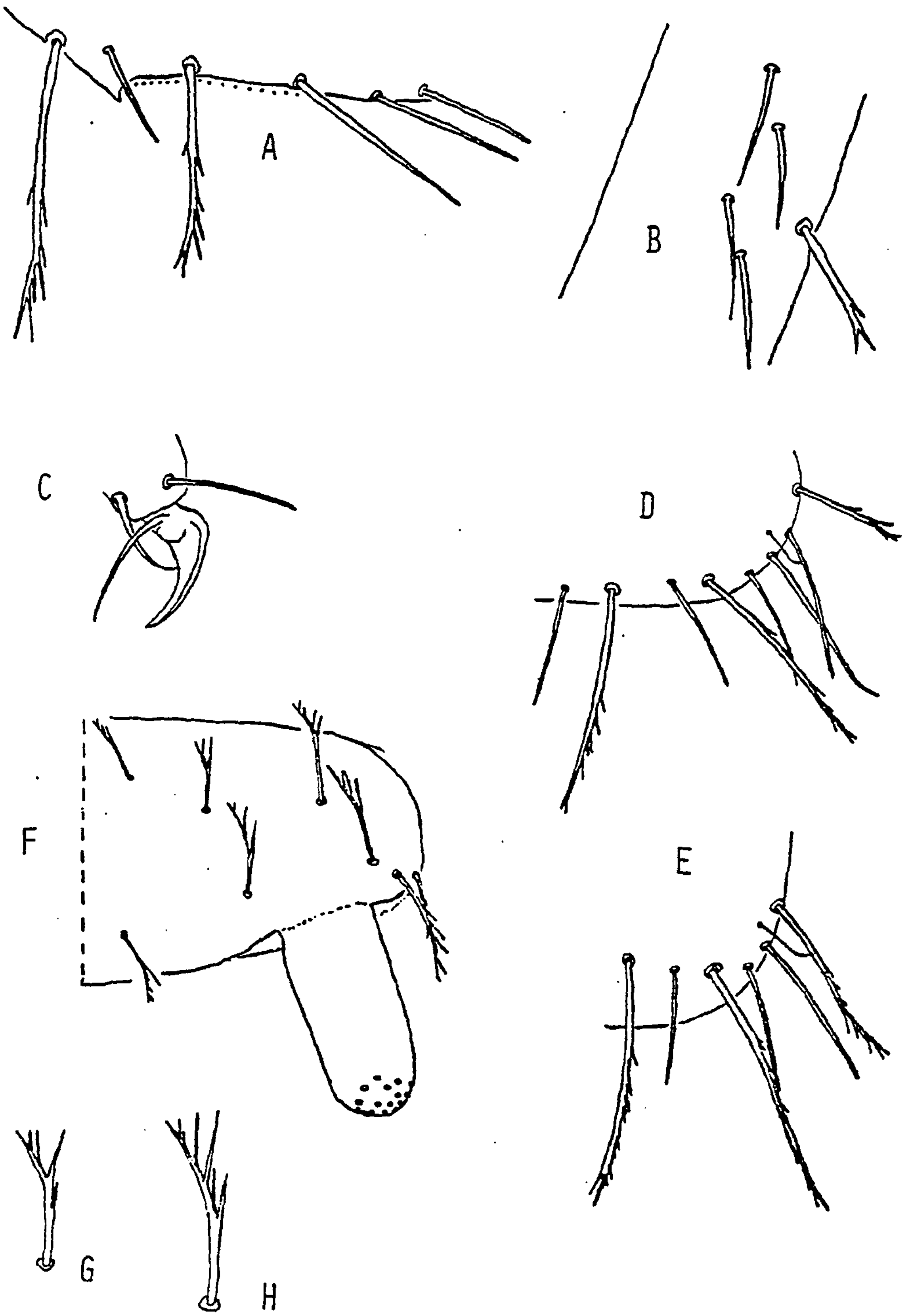
Mesonotum: ma/Sep ma-ma, 1.08; ma/Sep ma-la, 0.64; la/Sep ma-la, 1.00; lp_I/lp_{II}, 0.95; lp_{II}/lp_{III}, 1.09. Pronotum and mesonotum with 2 + 2 barbed posterior marginal setae and 10 smooth medial posterior marginal setae; metanotum with 1 + 1 barbed, 12 smooth posterior marginal setae.

Presternite of prosternum with 2 + 2 M; prosternite with 4 + 4 barbed precoxal M; 4 + 4 smooth precoxal setae; 1 + 1 subcoxal M; 2 + 2 lp. Meso- and metasternite with 4 + 4 barbed precoxal M; 4 + 4 smooth precoxal setae; 1 + 1 ma; 1 + 1 la; 1 + 1 subcoxal M; 2 + 2 lp.

Length of leg III about 35 percent of body length, reaching abdominal segment VI. Femur I without dorsal macrochaetae; femurs II and III with one dorsal macrochaeta. Dorsal macrochaeta inserted on proximal half of femur III, 1.1 times width of femur at point of insertion; barbed on its distal six-tenths (Fig. 22F). Femur III with 4 anterior marginal macrochaetae; 2 most ventral barbed on their distal 60 to 65 percent; distal pair smooth (Fig. 23A). Tibia III length 5.3 times width, with one bifurcated ventral macrochaeta with 1 small barb proximal to bifurcation (Fig. 23B); tibial spurs with 2 rows of long barbs. Tarsus III with 13 ventral setae in anterior row. Posterior claw only slightly longer than anterior; latero-tergal crests very reduced; no flange on posterior claw. Pretarsal appendices long, slender, and smooth; length exceeding tip of claws (Fig. 23C).

FIGURE 23.--<u>Litocampa inexspectata</u>, new species. A, anterior distal margin of femur III; B, ventral macrochaeta of tibia III; C, anterior view of anterior pretarsal claw of leg III; D, latero-posterior margin of tergite IV; E, latero-posterior margin of tergite V; F, urosternite I of female (glandular setae represented by their bases; clothing setae not shown); G-H, medial posterior macrochaeta and macrochaeta at base of eversible vesicle of urosternite III. Female (3.7 mm; head width, 0.56 mm), Panther Creek Cave, Tennessee.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Abdomen: Distribution of tergal macrochaetae (Fig. 23D,E):

	ma	la	lp	
Ab. I-III	1 + 1	0	0	
Ab. IV-VII	1 + 1	1 + 1	2 + 2	
Ab. VIII	1 + 1	0	3 + 3	
Ab. IX	1 + 1	0	5 + 5	(total)

Medial anterior macrochaetae slender, with 4 barbs on distal half; very slight increase in length posteriorly to Ab. VII; apex not reaching bases of posterior marginal setae. Length of ma on Ab. VIII and IX subequal,but less than on Ab. VII; apex exceeds bases of posterior marginal setae on Ab. VIII-IX. Lateral anterior macrochaetae very short on Ab. IV, subequal to ma; increases in length by two-thirds on Ab. V, by eight-tenths on Ab. VII. Lateral posterior macrochaetae long and robust, similar to thoracic lp; barbed on distal two-thirds. Lengths and ratios of certain tergal macrochaetae, as follows:

	ma	la	lp_1	lp_2	ma/D	ma/Sep ma-ma
Ab. I	64	--	--	--	0.74	0.60
Ab. IV	67	66	138	124	0.73	0.63
Ab. VII	70	121	173	173	0.72	0.64

Abdominal tergite IV with 13 ? posterior marginal setae separating sublateral posterior macrochaetae nearest sagittal plane; tergite V with ? such setae; VI with 15; VII with 16; VIII with 13; IX with 14.

Supra-anal valvule with 2 medial setae; subapical seta thicker and barbed.

Urosternite (coxosternite) I with 7 + 7 differentiated macrochaetae, 4 + 4 on middle portion; 1 + 1 submacrochaetae at latero-posterior angle of urosternite of female. Posterior margin without glandular setae on female. Lateral subcoxal appendages subcylindrical, moderately long, on female (Fig. 23F). Female with approximately 20 glandular setae on tip of appendages.

Urosternites II-VII with 4 + 4 well differentiated macrochaetae, with branches and barbs (Fig.23G,H); 2 + 2 weakly differentiated macrochaetae inserted at external and internal borders of each stylus. Styli essentially identical to those of L. keithi: apical seta of styli smooth or with 1 distal barbule and 2 short basal branches, proximal branch about one-half length of distal; subapical seta smooth or with 1 long barb on proximal half; medial ventral seta forked; clothing setae smooth. Stylus VII length 4.0 times width; apical seta about 50 percent as long as stylus; with 6 or 7 clothing setae and setiform sensilla. Urosternite VIII with 1 + 1 macrochaetae.

Cerci missing.

Variation: Right antenna with the normal arrangement of trichobothria on segments III-VI. Left antenna with only 1 dorsal trichobothrium on segment VI (instead of usual 2) and 1 dorsal trichobothrium on segments VII and VIII (usually without trichobothria).

TYPE LOCALITY.--Panther Creek Cave, 6 miles northeast of Sneedville, Hancock Co., Tennessee, and 0.6 mile south of the Virginia line. The cave is located on the south side of Newman Ridge, in the valley of the East Fork of Panther Creek which joins the Clinch River. The cave is reported to have about 900 feet of traversable passages and is developed in nearly vertical beds of the Newman linestone (Barr, 1961). The Mississippian aged Newman limestone is equivalent to the Greenbrier limestone and Bluefield shale farther north in Virginia and West Virginia (Butts, 1940; Schuchert, 1943).

DISTRIBUTION AND ECOLOGY.--Known only from the type locality. The single specimen of this species was collected by Dr. John R. Holsinger "at a damp place" (in litt.) in the cave, along with a specimen of *Litocampa cookei*. This represents only the second known occurrence in the United States of two campodeid species occupying the same cave, and the first occurrence for congeneric species (although *L. inexspectata* and *L. cookei* are phylogenetically widely separated within the genus). The other example of syntopy is that of *L. fieldingi* and a *Eumesocampa* sp. in Steeles Cave, Monroe Co., West Virginia (Ferguson, 1973; 1978; Holsinger et al., 1976).

REMARKS.--In Tennessee, Panther Creek Cave falls within the eastern edge of the extensive range of *L. cookei*. However, I believe that the species range of *L. inexspectata* will prove to be quite small, due to the disjunct relictal nature of the ranges of the other species in the *keithi* and closely related *bifurcata* groups.

ETYMOLOGY.--The epithet _inexspectata_ is from Latin, meaning "unexpected."

Litocampa welbourni, new species

(Figs. 24-26)

MATERIAL EXAMINED.--New Mexico: San Miguel Co.: Tererro Cave, Tererro, 1 immature (holotype), 18 June 1875, W. C. Welbourn, (LMF 473-1).

Holotype deposited in American Museum of Natural History.

DIAGNOSIS.--Distinguished from other species of *Litocampa* in the United States by presence of 3 + 3 and 2 + 2 macrochaetae on meso- and metanota, one dorsal macrochaeta on femur III, tibia III with 2 ventral macrochaetae, claws without well-developed latero-tergal crests, 1 + 1 medial anterior macrochaetae on abdominal tergites I-IX, 1 + 1 lateral anterior and 1 + 1 lateral posterior macrochaetae on tergites IV-VII, 7 + 7 macrochaetae on urosternite I, and 4 + 4 well differentiated macrochaetae on urosternites II-VII.

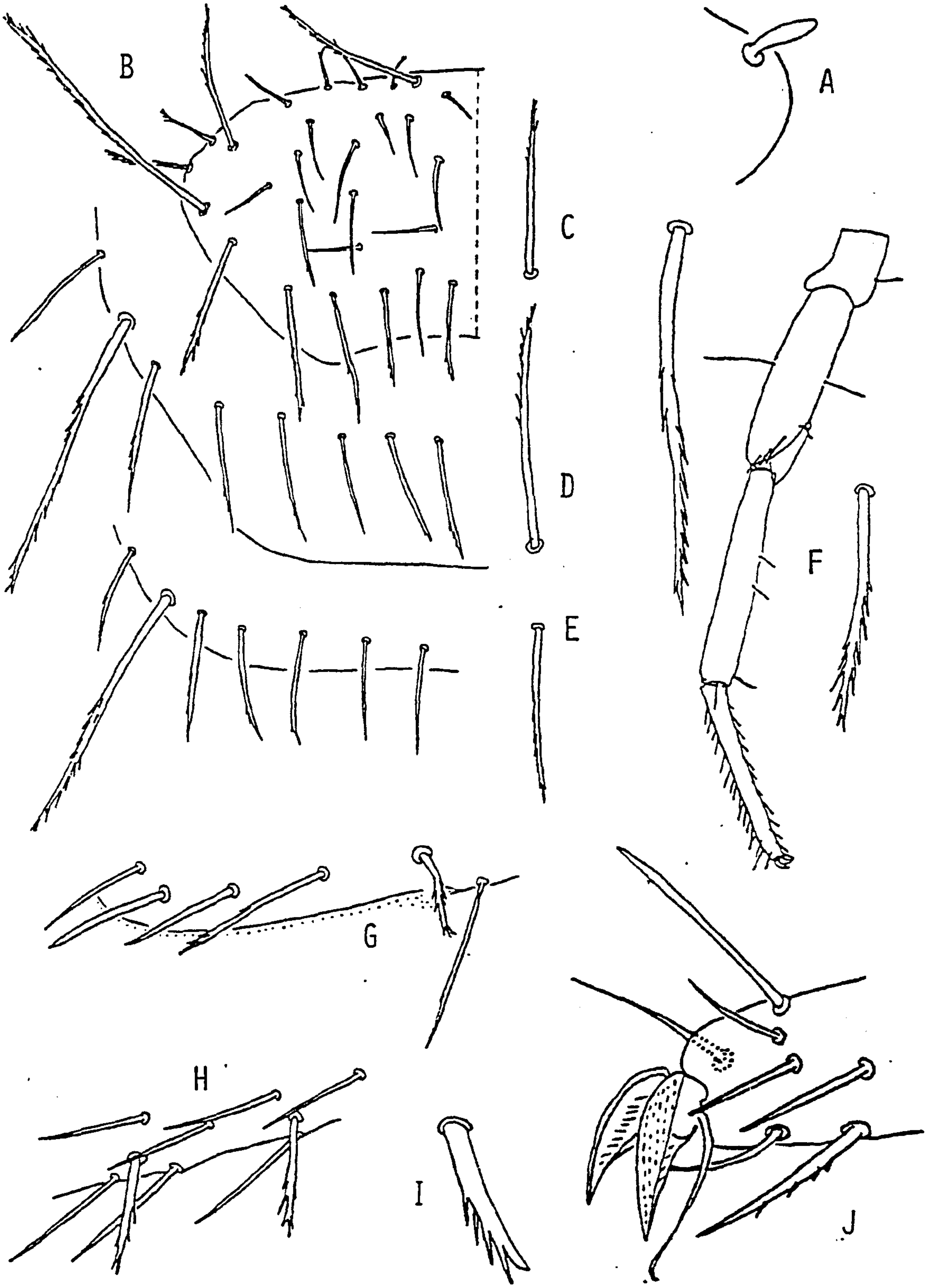
DESCRIPTION.--*Size*: Immature: body length, 3.4 mm; head width, 0.53 mm; pronotal width, 0.37 mm.

Head: Only complete antenna with 31 segments. Length of antenna 2.68 mm, or about 80 percent of body length, reaching abdominal segment VII. Antennal segment III with ventral bacilliform sensillum, inserted between phaneres *d* and *e*: M*a*, M*b*, seta *c* (smooth or with 2 barbules), M*d* (with 1-5 distal barbs), sen. (long, but not exceeding distal border of segment), seta *e* (smooth), M*f*, M*g*, seta or subM*h* (smooth or with 3 barbs); length of d greater than c; b smooth or with 1 minute barbule, other long macrochaetae smooth. Length of latero-dorsal trichobothrium of segment V 142 microns (probably broken), about 27 percent of head width. Segment X length 1.2 times width. Cupuliform organ of apical segment with approximately 7 sensilla.

Frons with 3 macrochaetae on rostrum, few barbules on their distal half; anterior macrochaeta 1.3 times length of posterior pair. Macrochaetae bordering line of insertion of antennae 3 + 3; anterior macrochaeta approximately two-thirds as long as intermediate; anterior and posterior macrochaetae subequal, anterior slightly shorter than posterior; all three macrochaetae barbed on distal one-third to one-half. No macrochaetae anterior to arms of epicranial suture, near sagittal plane. Occipital setae with several barbs on their distal two-thirds; length about 50 percent as long as pronotal lp. Latero-anterior sensillum of labial palp subcylindrical, slightly curved, swollen on distal half (Fig. 24A). Posterior mental setae smooth; lateral submental macrochaetae barbed.

Thorax: Clothing setae smooth; notal chaetotaxy 3 + 3, 3 + 3, 2 + 2 (Fig. 24B-E). Pronotal ma barbed on distal 64 percent, la on distal 68 percent, lp on distal 76 percent; mesonotal ma barbed on distal 64 percent, la on distal 63 percent, lp on distal 72 percent; metanotal ma barbed on distal 63 percent, lp barbed on distal 70 percent. Lengths and ratios of macrochaetae of only available specimen from Tererro Cave, as follows:

FIGURE 24.--Litocampa welbourni, new species. A, latero-anterior sensillum of left labial palp; B, pronotum, meso- and metanotal posterior margins; C, mesonotal ma; D, mesonotal la; E, metanotal ma; F, metathoracic leg (dorsal and anterior ventral macrochaetae of femur enlarged); G, anterior distal margin of femur III; H, ventral macrochaetae of tibia III; I, tibial spur of leg III, J, distal extremity of tarsus and pretarsus of leg III. Immature (3.4 mm; head width, 0.53 mm), Tererro Cave, New Mexico.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	ma	la	lp	ma/la	lp/ma
Th. I	99	94	189	1.05	1.90
Th. II	107	133	176	0.81	1.64
Th. III	105	--	163	--	1.56

Mesonotum: ma/Sep ma-ma, 1.62; ma/Sep ma-la, 1.02; la/Sep ma-la, 1.27; lp_I/lp_{II}, 1.07; lp_{II}/lp_{III}, 1.08. Pronotum with 3 + 3 barbed lateral posterior marginal setae and 6 medial posterior marginal setae with 1 or 2 barbules or smooth; mesonotum with 3 + 3 lateral, 5 medial posterior marginal setae; metanotum with 1 + 1 lateral, 7 medial posterior marginal setae.

Presternite of prosternum with 2 + 2 M; prosternite with 4 + 4 barbed precoxal M; 4 + 3 smooth precoxal setae; 1 + 1 subcoxal M; 2 + 2 lp. Meso- and metasternite with 4 + 4 barbed precoxal M; 4 + 3 smooth precoxal setae; 1 + 1 ma; 1 + 1 la; 1 + 1 subcoxal M; 2 + 2 lp.

Length of leg III about 45 percent of body length, reaching abdominal segment X. Femur I without dorsal macrochaetae; femurs II and III with one dorsal macrochaeta. Dorsal macrochaeta inserted on proximal half of femur III, length 1.4 times width of femur at point of insertion; barbed on its distal two-thirds (Fig. 24F). Femur III with 4 anterior marginal macrochaetae; most ventral macrochaeta inserted opposite dorsal macrochaeta; 2 most ventral barbed on their distal two-thirds; distal pair with 2 - 3 barbs (Fig. 24G). Tibia III length 6.3 times width, with 2 ventral macrochaetae with several barbs on their distal half (Fig. 24H); tibial spurs with 2 rows of long barbs (Fig. 24I).

Tarsus III with 13 ventral setae in anterior row. Posterior claw only slightly longer than anterior; latero-tergal crests reduced; no flange on posterior claw. Pretarsal appendices long, slender, and smooth; length easily exceeding tip of claws (Fig. 24J).

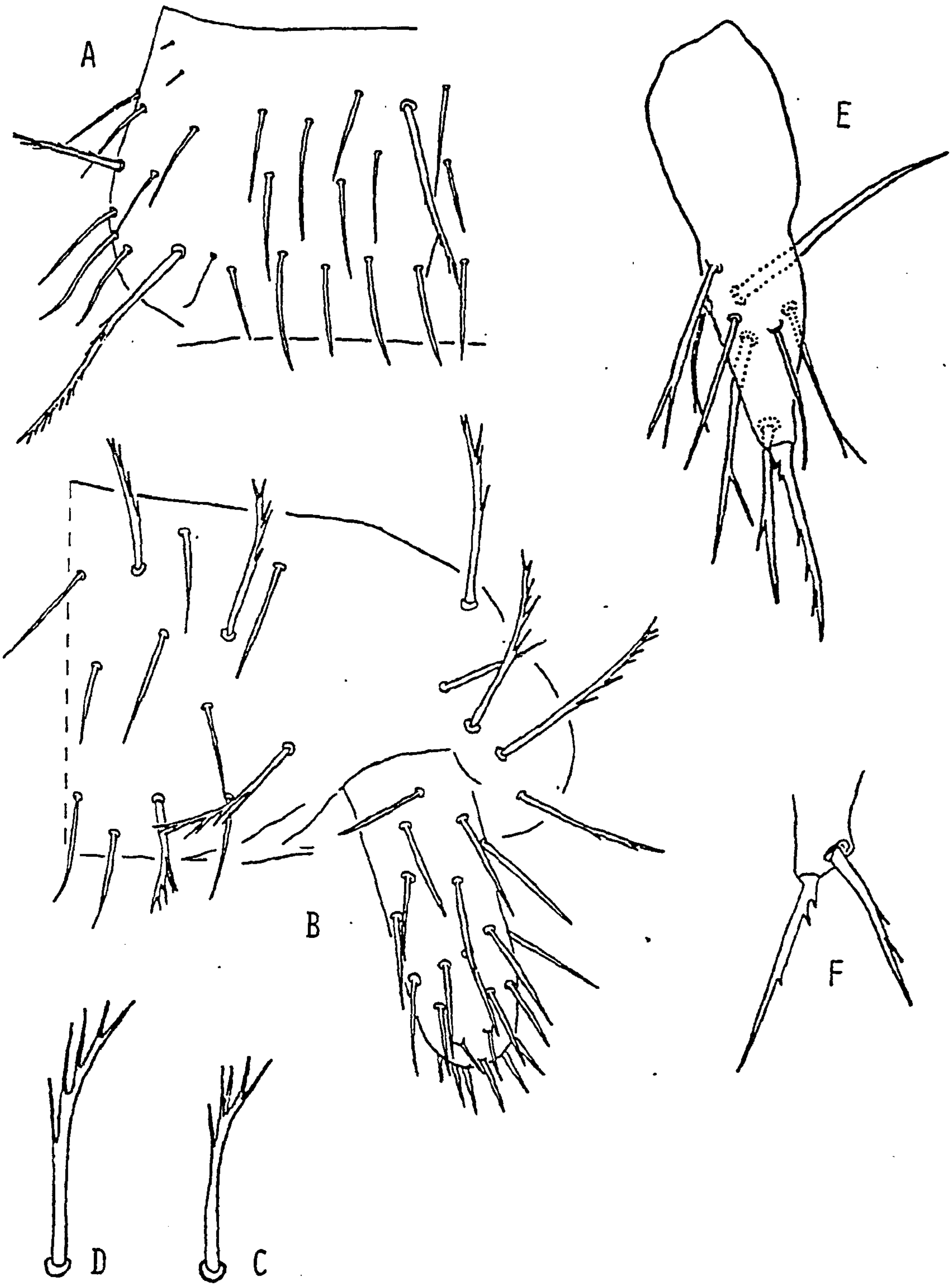
Abdomen: Distribution of tergal macrochaetae (Fig. 25A):

	ma	la	lp
Ab. I-III	1 + 1	0	0
Ab. IV-VII	1 + 1	1 + 1	1 + 1
Ab. VIII	1 + 1	0	3 + 3
Ab. IX	1 + 1	0	5 + 5 (total)

Medial anterior macrochaetae long, with several barbs on distal half; length increases 1.8 times by Ab. VI; slight decrease in length on Ab VII, more on Ab. VIII-IX; apex not reaching bases of posterior marginal setae on only Ab. I-II. Lateral anterior macrochaetae fairly short on Ab. IV, much shorter than ma; increases in length by one-half on Ab. V, by three-fourths on Ab. VII. Lateral posterior macrochaetae long and robust, similar to thoracic lp; barbed on distal two-thirds. Lengths and ratios of certain tergal macrochaetae, as follows:

	ma	la	lp	ma/D	ma/Sep ma-ma
Ab. I	78	--	--	0.87	0.85
Ab. IV	112	66	145	1.26	1.05
Ab. VII	122	115	186	1.55	1.12

FIGURE 25.--Litocampa welbourni, new species. A, tergite IV; B, urosternite I; C-D, medial posterior macrochaeta and macrochaeta at base of eversible vesicle of urosternite VI, right side; E, left stylus of urosternite II, posterior view; F, distal extremity of right stylus of urosternite IV. Immature (3.4 mm; head width, 0.53 mm), Tererro Cave, New Mexico.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Abdominal tergite IV with 11 posterior marginal setae separating sublateral posterior macrochaetae nearest sagittal plane; tergite V with 10 such setae; VI with 10; VII with 9; VIII with 5; IX with 5. Supra-anal valvule with 2 smooth setae; lateral proximal seta longer than subapical medial seta.

Urosternite (coxosternite) I with 7 + 7 differentiated macrochaetae, 4 + 4 on middle portion; 1 + 1 submacrochaetae at latero-posterior angle of urosternite. Posterior margin without glandular setae. Lateral subcoxal appendages subcylindrical; approximately 11 glandular setae on tip of appendages of immature (Fig. 25B).

Urosternites II-VII with 4 + 4 well differentiated macrochaetae, with branches or long barbs (Fig. 25C,D); 2 + 2 weakly differentiated macrochaetae inserted on either side of each stylus. Apical seta of styli with 1-4 distal barbules (3 most often) and 2 short basal branches, proximal branch about three-fourths length of distal; subapical seta with 1 long barb on proximal half, sometimes with 1 barbule or another barb distal to first; medial ventral seta forked, sometimes with barb proximal to bifurcation; clothing setae smooth, bifurcated only, or with 1 barbule proximal to bifurcation (Fig. 25E,F). Stylus VII length 3.5 times width; apical seta about 52 percent as long as stylus; with 8 clothing setae and setiform sensilla. Urosternite VIII with 1 + 1 macrochaetae.

Length of only complete cercus about 0.76 times body length, composed of a base, subdivided into 5 secondary segments, and 3 primary segments.

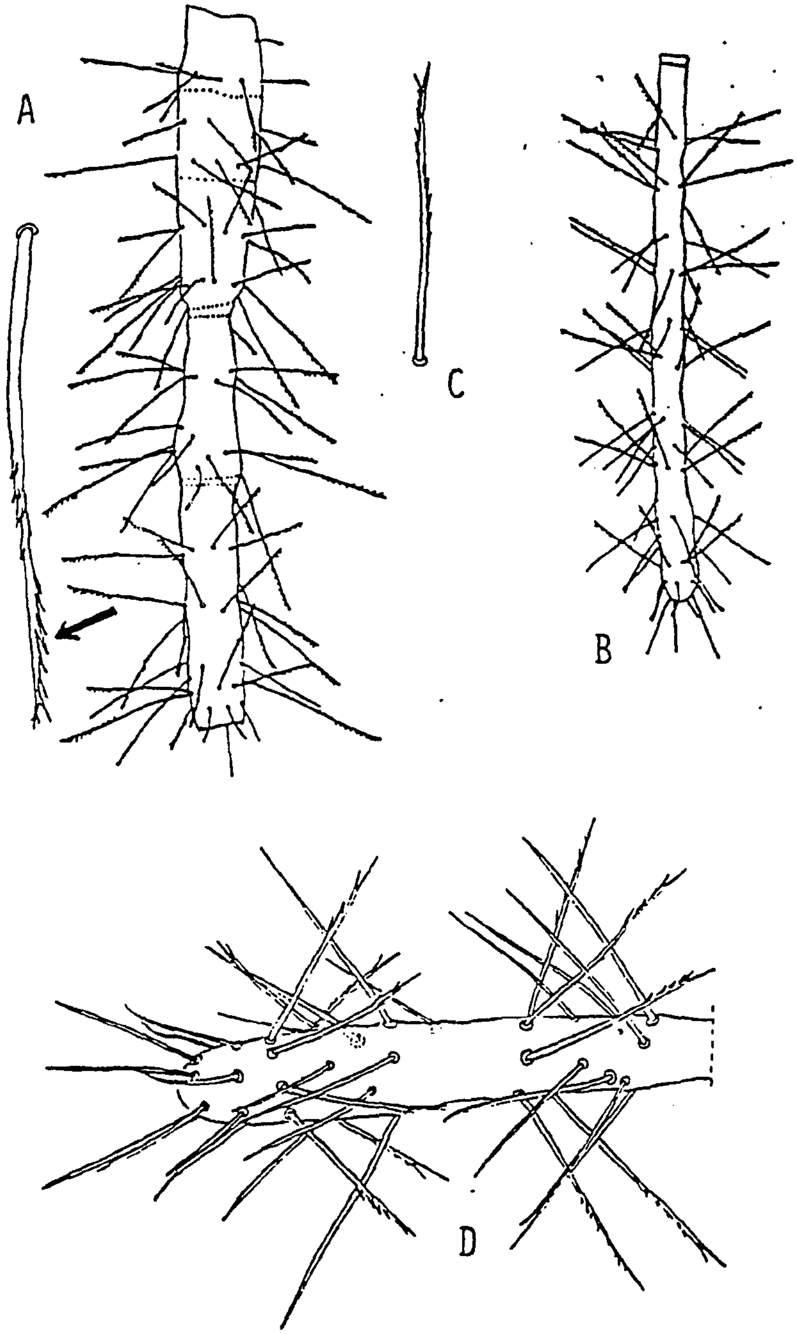
Segmental lengths (in mm): base = 0.89; primary segments = 0.45, 0.57, 0.69. Covering of base (Fig. 26A) and proximal segment composed of long macrochaetae, length of macrochaetae about 2.8 times width of segments, long barbs on their distal half. Proximal primary segments with whorls of 7 barbed macrochaetae, long smooth setae, and 6 short subapical setae. Penultimate segment length 13 times width, with 6 whorls of macrochaetae, alternating with whorls of long smooth setae; macrochaetae with long subapical barb and numerous smaller barbs on distal half to two-thirds; 7 short subapical setae. Macrochaetae of apical segment arranged in 6 whorls, length of macrochaeae about 3.1 times width of segment, alternating with whorls of long smooth setae (Fig. 26B-D); all macrochaetae barbed on distal half or more.

Variation: Phanere h is decidedly a seta on segment III of the left antenna, and a small macrochaeta or submacrochaeta on the right antenna. Whether or not this phanere would have differentiated into a distant macrochaeta with subsequent molts must await the examination of additional material.

TYPE LOCALITY.--Tererro Cave, 16 miles northeast of Santa Fe, in San Miguel Co., New Mexico. The cave is in the upper Pecos River drainage, at an altitude of 7500 feet.

DISTRIBUTION AND ECOLOGY.--Known only from the type locality. The single specimen of this species was found on a mud bank in the dark zone. There is no water in the cave at present, but the approximately one-half mile of passage appears to be an abandoned stream passage.

FIGURE 26.--Litocampa welbourni, new species. A, base of cercus (one macrochaeta enlarged); B, apical segment of cercus; C, macrochaeta of apical segment of cercus; D, distal portion of apical segment of cercus. Immature (3.4 mm; head width, 0.53 mm), Tererro Cave, New Mexico.


A
B
C
D

The entrance to the cave is about 40 feet above the present stream level outside. Other fauna in the cave include collembola, spiders, and an undescribed troglobitic species of harvestmen (W. C. Welbourn, personal communication).

ETYMOLOGY.--It is a distinct pleasure to name this species after its discoverer and former president of the Cave Research Foundation, W. Calvin Welbourn.

The *Virginiana* Group

DIAGNOSIS.--Antennal segment III with phanere *e*, metanotum with 1 + 1 lateral posterior macrochaetae, femur III with dorsal macrochaeta, pretarsal claws without large latero-tergal crests, abdominal tergites V-VII with 2 + 2 lateral posterior macrochaetae, medial anterior macrochaetae on abdominal tergites I-VII, 7 + 7 macrochaetae, and posterior margin of urosternite I of males with or without glandular setae.

REMARKS.--As presently defined, the *virginiana* group is composed of three species which are very similar morphologically. Two species occupy caves of southwestern Virginia and nearby West Virginia. The third species is known from caves in southern Tennessee and northern Alabama and Georgia. No specimens belonging to this group have been found in the intervening area of eastern Tennessee, producing a somewhat disjunct distribution for the species of this group.

Key to the Species of the *Virginiana* Group

1. Meso- and metasternites with 5 + 5 barbed precoxal macrochaetae.... .... *L. virginiana*

1'. Meso- and metasternites with 4 + 4 barbed precoxal macrochaeta....2

2. Posterior margin of urosternite I of males with glandular setae;

distal segments of cerci with 4 or more whorls of macrochaetae. Known only from caves in Ward Cove, Tazewell Co., Va. .... L. barringerorum, new species

2'. Posterior margin of urosternite I of males without glandular setae; distal segments of cerci with 2 whorls of macrochaetae. Known from caves in southern Tennessee and northern Alabama and Georgia........................... L. cherokeensis, new species

Litocampa virginiana Ferguson

(Fig. 27)

Plusiocampa sp., Ferguson, 1971a:34; 1979:179-182; Holsinger et al., 1976:6, 32, 62, 78.

Litocampa (Litocampa) virginiana (in part) Ferguson, (in press): figs. 3, 4.

MATERIAL EXAMINED.--VIRGINIA: Giles Co.: Starnes Cave 3♀, 1 immature, 19 May 1974, J. R. Holsinger, (LMF 446); Bland Co.: Newberry-Banes Cave, 2♂, 4♀, 30 Jan. 1977, B. L. Ferguson and B. Johnson, (LMF 540); Washington Co.: Perkins Cave, ca. 10 mi. NNE of Abingdon, 1♂, 24 Mar. 1979, J. R. Holsinger and V. Tipton, (LMF 565); plus the material reported on earlier (Ferguson, in press) except that now listed for L. barringerorum, n. sp. WEST VIRGINIA: Mercer Co.: Dyepot Cave, 1♀, 12 May 1966, J. R. Holsinger, (LMF 20).

DIAGNOSIS.--Distinguished from other species of Litocampa in the United States by presence of 3 + 3 and 2 + 2 macrochaetae on meso- and metanota, with 1 dorsal macrochaeta on femur III, tibia III with 1 ventral macrochaeta, claws without well-developed latero-tergal crests, medial anterior macrochaetae present on abdominal tergites I-VII, 1 + 1 lateral anterior and 2 + 2 lateral posterior macrochaetae on tergites IV-VII, 7 + 7 macrochaetae on urosternite I, and 4 + 4 well differentiated macrochaetae on urosternites II-VII.

DESCRIPTION.--Corresponding to the earlier description (Ferguson, in press), with the following additions.

Head: Antennal segment III with ventral bacilliform sensillum, inserted between phaneres d and e: Ma, Mb, seta c (smooth or with subapical barb), Md, sen. (apex exceeding distal border of segment), seta e (short), Mf, Mg, Mh; length of d slightly greater than c; d with 1 subapical barb, h smooth or with 2 barbs, other long macrochaetae smooth. Length of latero-dorsal trichobothrium of segment V up to 230 microns, about 28 percent of head width. Segment X length 1.6 times width. Cupuliform organ of apical segment with 8 sensilla.

Occipital setae with numerous barbs on their distal seven-tenths; length about 46 percent as long as pronotal lp.

Thorax: Additional macrochaetal ratios for specimens of the type series and new material from Starnes Cave, as follows: mesonotum: ma/Sep ma-ma, 1.78-2.00; ma/Sep ma-la, 1.00; la/Sep ma-la, 1.29-1.44.

Presternite of prosternum with 2 + 2 M; prosternite with 4 + 4 barbed precoxal M; 2 + 2 (on immature) to 4 + 4 smooth precoxal setae; 1 + 1 subcoxal M; 2 + 2 lp. Mesosternite with 5 + 5 barbed precoxal M; 2 + 2 to 4 + 4 smooth precoxal setae; 1 + 1 ma; 1 + 1 la; 1 + 1 subcoxal M; 2 + 2 lp. Metasternite with 5 + 5 barbed precoxal M; 2 + 2 to 4 + 4 smooth precoxal setae; 1 + 1 ma; 1 + 1 la; 1 + 1 subcoxal M; 1 + 1 lp, 1 + 1 slp.

Leg III with dorsal macrochaeta inserted on distal half of femur; length of macrochaeta 1.5-1.6 times width of femur at point of insertion; small barbs on its distal two-thirds (Fig. 27A). Tibia III length 6.3-6.9 times width, with one bifurcated ventral macrochaeta, sometimes with 1 small barb proximal to bifurcation. Tarsus III with 12-16 ventral setae in anterior row.

Abdomen: Additional ratios for certain tergal macrochaetae, as follows: ma/Sep ma-ma, 0.87-0.88 on Ab. I, 0.76-1.00 on Ab. IV, 0.97-1.16 on Ab. VII. Abdominal tergite IV with up to 14 posterior marginal setae separating pair of sublateral posterior macrochaetae nearest sagittal plane; tergite V with up to 14 such setae; VI with 14; VII with 15; VIII with 11; IX with 14.

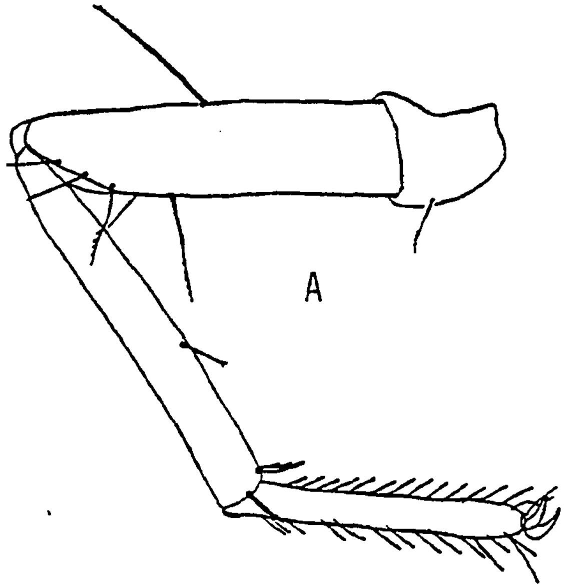
Urosternite (coxosternite) I of female with subcylindrical lateral subcoxal appendages (Fig. 27B).

Stylus VII length 3.2-4.1 times width; apical seta about 45-50 percent as long as stylus; with up to 13 clothing setae and setiform sensilla.

Proximal primary segments of cerci with whorls of 7 barbed macrochaetae, long smooth setae, and 7-9 small subapical setae. Penultimate segment length 18.75 times width, with 4-5 whorls of macrochaetae, alternating with whorls of long and shorter smooth setae; 7 small subapical setae.

Variation: As reported earlier (Ferguson, 1974), the most notable variation is that of the lengths of the medial anterior macrochaetae on the thoracic nota and abdominal tergites. Among certain clusters of cave populations there is also variation in the number of antennal segments and overall size. Due to a degree of morphological overlap

FIGURE 27.--Litocampa virginiana Ferguson. A. metathoracic leg; B, lateral posterior part of urosternite I of female (some glandular setae represented by their bases; simple clothing setae of subcoxal appendage diagrammatic). A, male (5.2 mm; head width, 0.72 mm); B, female (6.1 mm; head width, 0.86 mm), Starnes Cave, Virginia.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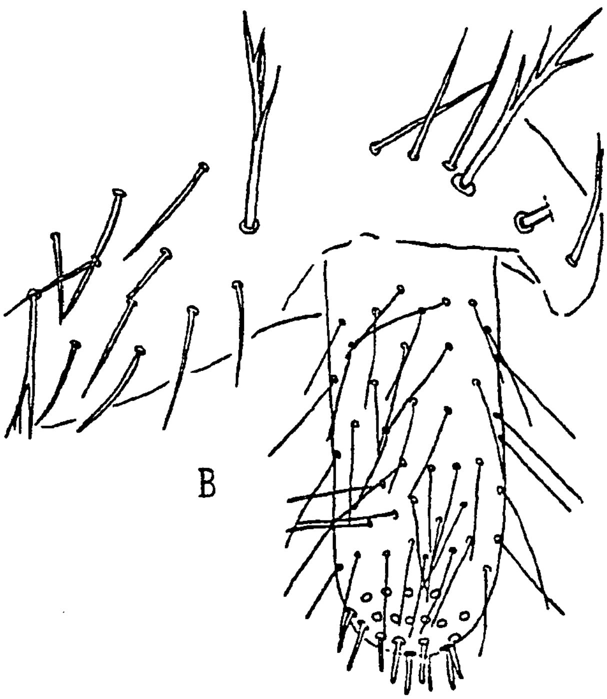

B

and the occurrence of widely separated populations with individuals possessing the same characteristics, it seems unwise to recognize even subspecies at this time.

TYPE LOCALITY.--Starnes Cave, 4.3 miles southwest of Pearisburg, in Giles Co., Virginia. The cave has about 3500 feet of passages and is developed in Middle Ordovician-aged limestones (Douglas, 1964; Holsinger, 1975).

DISTRIBUTION AND ECOLOGY.--Litocampa virginiana is presently known from 17 caves in Virginia and from one cave not far into West Virginia. This species occupies caves in the Ridge and Valley Province of southwestern Virginia (and southern West Virginia). The range of the species appears to be bounded to the northeast by the main channel of New River. To the southeast, Walker Mountain separates it from portions of the New River Valley and the Holston River Valley, whose caves are occupied by Litocampa bifurcata. While there are physical (stratigraphic and structural) barriers to the west, none are apparent to the south. I have anticipated that L. virginiana would be found in caves in northeastern Tennessee. So far such a discovery has not been made. Instead, Litocampa cookei and L. inexspectata have been found to occupy caves in Tennessee, close to the presently known southern border of the range of L. virginiana. Perhaps interspecific competition in the past, if not at present, accounts for the southern limits of its range.

Litocampa barringerorum, new species

(Figs. 28-29)

Plusiocampa sp., Ferguson, 1971a:34; 1979:179-180, 182.

Litocampa (Litocampa) virginiana (in part) Ferguson, (in press): figs. 3, 4.

MATERIAL EXAMINED.—VIRGINIA: Tazewell Co.: Fallen Rock Cave, 12 ♂, 14 ♀ (holotype and paratypes), 9 Nov. 1968, J. R. Holsinger, et. al., (LMF 13); 7 ♂, 15 ♀ (paratypes), 10 Oct. 1970, L. M. and B. L. Ferguson, (LMF 160); 2 ♂, 6 ♀, 1 immature (paratypes), 5 June 1971, L. M. and B. L. Ferguson, (LMF 165); Bowen's Cave, 3.5 mi. SW of Liberty, 2 ♀ (paratypes), 28 July 1963, J. R. Holsinger, (LMF 171); Lost Mill Cave No. 1, 1 ♂ (paratype), 28 May 1966, J. R. Holsinger, (LMF 1); 2 ♀ (paratypes), 2 May 1970, L. M. and B. L. Ferguson, (LMF 36); Lost Mill Cave No. 3, 1 ♂ (paratype), 28 May 1966, J. R. Holsinger and Russell Norton, (LMF 5); Gillespie Water Cave, 4.5 mi. SSE of Pounding Mill, 1 ♂, 1 ♀, 1 immature (paratypes), 23 July 1976, J. R. Holsinger and D. C. Culver, (LMF 546).

Holotype (LMF 13-10) and several paratypes deposited in the National Museum of Natural History (Smithsonian Institution); remaining paratypes deposited in American Museum of Natural History, B. Condé's collection, Université de Nancy, Nancy, France, and the author's collection.

DIAGNOSIS.--Similar to *Litocampa virginiana*, from which it can be distinguished by the presence of 4 + 4 barbed precoxal macrochaetae on the meso- and metasternite (instead of 5 + 5 on *L. virginiana*) and a field of glandular setae on the posterior margin of urosternite I of males (absent on males of *L. virginiana*). Known only from caves in the Ward Cove area of Tazewell County, Virginia.

DESCRIPTION.--*Size*: Males: body length, 3.7-6.9 mm; head width, 0.65-0.90 mm; pronotal width, 0.46-0.69 mm. Females: body length, 3.5-7.6 mm; head width, 0.54-1.03 mm; pronotal width, 0.38-0.75 mm. Immature: body length, 3.0 mm; head width, 0.50 mm; pronotal width, 0.27 mm.

Head: Antennal segments, 29-39 (mean, 33.7). Number of segments of 52 complete antennae, as follows:

No. segments:		29	30	31	32	33	34	35	36	37	38	39
Frequency:	♂	0	0	0	2	4	3	2	2	2	1	0
	♀	1	1	4	6	8	7	1	2	3	0	1
	immature	0	0	0	0	1	1	0	0	0	0	0

Length of longest antenna 7.05 mm, or about 93 percent of body length, reaching abdominal segment X. Antennal segment III with ventral bacilliform sensillum, inserted between phaneres *d* and *e*: M*a*, M*b*, seta *c*, M*d*, sen. (long, but not exceeding distal border of segment), M*e*, M*f*, M*g*, M*h*; length of *d* 1.21 times *c*; phaneres smooth. Cupuliform organ of apical segment with 12 sensilla.

FIGURE 28.--*Litocampa barringerorum*, new species. A, latero-anterior sensillum of right labial palp; B, pronotum (clothing setae omitted); C, mesonotum; D, right precoxal macrochaetae and setae of metasternite. Female (7.6 mm; head width, 0.75 mm), Fallen Rock Cave, Virginia.

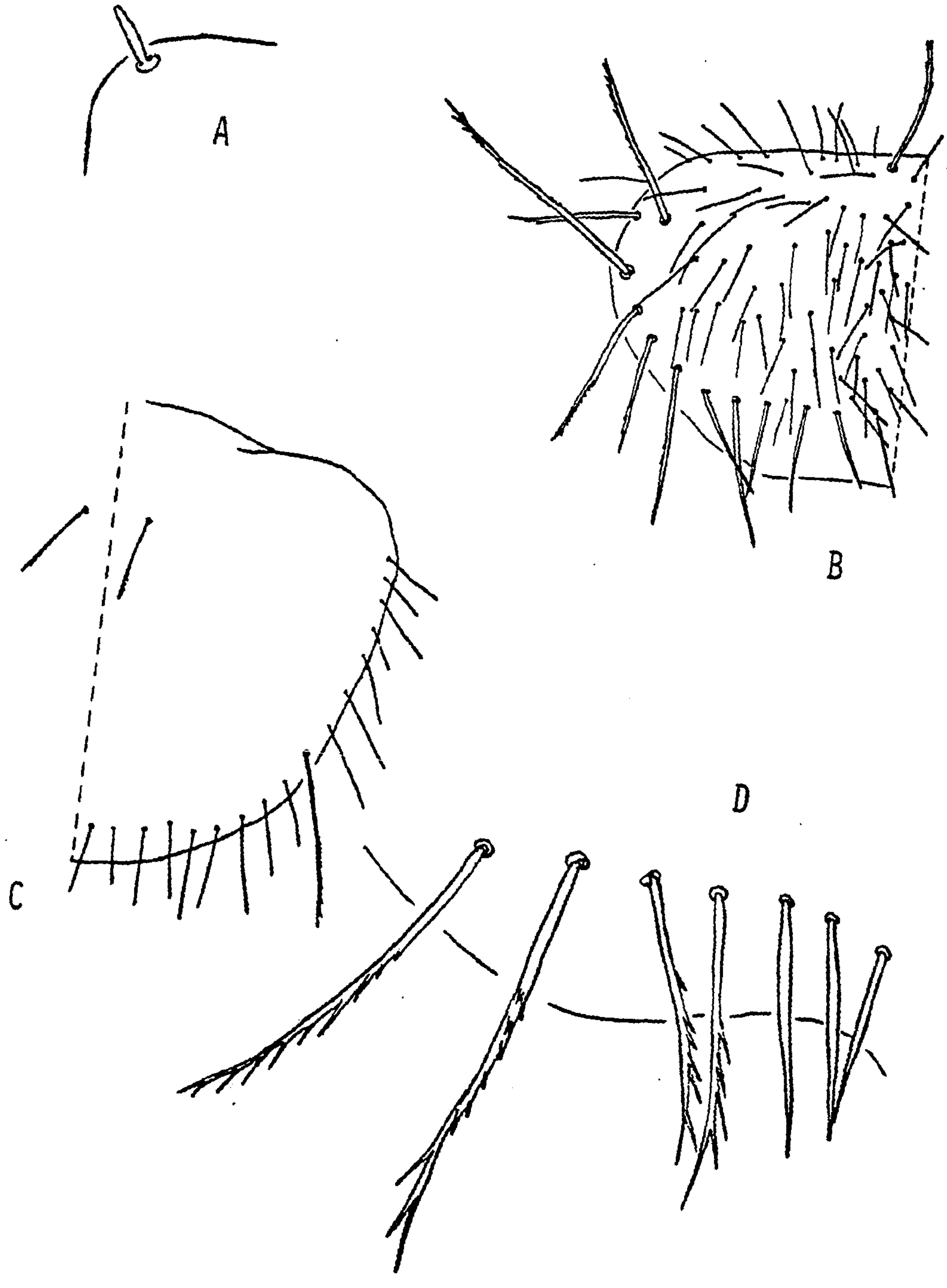
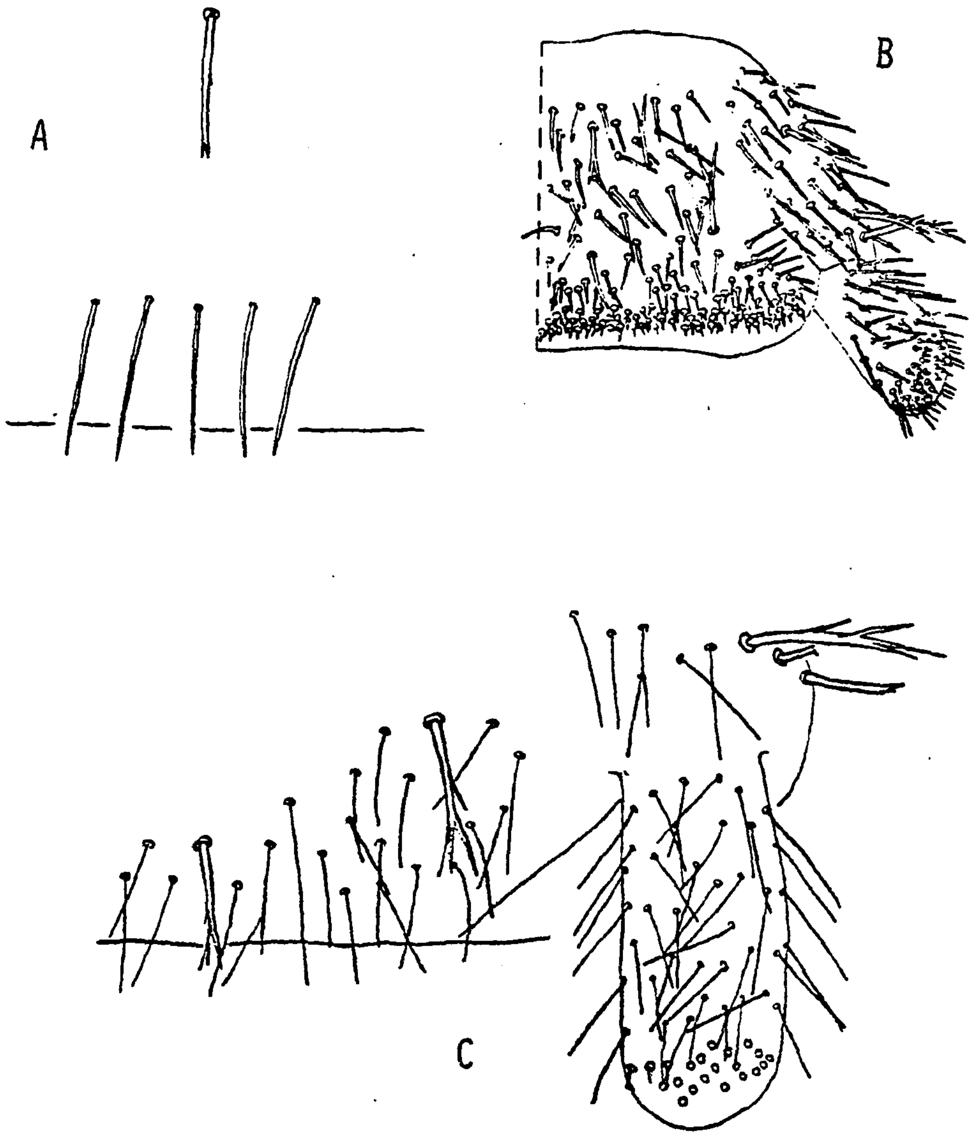

A
B
C
D

FIGURE 29.--*Litocampa barringerorum*, new species. A, medial anterior macrochaeta relative to the posterior marginal setae of tergite IV; B, urosternite I of male; C, latero-posterior part of urosternite I of female. B, male (6.9 mm; head width, 0.90 mm), Lost Mill Cave No. 1; others, female (7.6 mm; head width, 0.75 mm), Fallen Rock Cave, Virginia.


A
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C

Chaetotaxy of frons same as that of Litocampa virginiana. Latero-anterior sensillum of labial palp subcylindrical, straight. Posterior mental setae smooth; lateral submental macrochaetae smooth. Thorax: Clothing setae smooth; notal chaetotaxy 3 + 3, 3 + 3, 2 + 2. Lengths and ratios of macrochaetae of specimens from Fallen Rock Cave, as follows:

	ma	la	lp	ma/la	lp/ma
Th. I	97–173	108–194	194–292	0.72–1.00	1.53–2.28
Th. II	113–205	151–270	216–356	0.62–0.76	1.74–2.25
Th. III	103–205	—	205–335	—	1.63–2.29

Mesonotum; ma/Sep ma-ma, 1.38–1.43; ma/Sep ma-la, 0.75–0.76; la/Sep ma-la, 1.07–1.09; lp_{I}/lp_{II}, 0.81–0.96; lp_{II}/lp_{III}, 0.95–1.13. Pronotum of largest female with 5 + 5 barbed lateral posterior marginal setae and 7 smooth medial posterior marginal setae; mesonotum with 4 + 5 lateral, 9 medial posterior marginal setae; metanotum with 2 + 1 lateral, 12 medial posterior marginal setae.

Presternite of prosternum with 2 + 2 M; prosternite with 4 + 4 barbed precoxal M; 5 + 5 smooth precoxal setae; 1 + 1 subcoxal M; 2 + 2 lp. Meso- and metasternite with 4 + 4 barbed precoxal M; 4 + 4 to 5 + 5 smooth precoxal setae; 1 + 1 ma; 1 + 1 la; 1 + 1 subcoxal M; 2 + 2 lp.

Length of leg III about 38 percent of body length, reaching abdominal segment VI. Femur I without dorsal macrochaetae; femurs II and III with one dorsal macrochaeta. Dorsal macrochaeta inserted on distal half of femur III, 1.2-1.3 times width of femur at point of insertion; barbed on distal two-thirds. Femur III with 4 anterior marginal macrochaetae; 2 most ventral barbed on distal two-thirds; distal pair smooth. Tibia III length 6.75 times width, with one bifurcated ventral macrochaeta; tibial spurs with 2 rows of long barbs. Tarsus III with 15 ventral setae in anterior row. Posterior claw slightly longer than anterior; latero-tergal crests reduced; small flange on posterior claw. Pretarsal appendices long, slender, and smooth; length exceeding tip of claws.

Abdomen: Distribution of tergal macrochaetae same as for *Litocampa virginiana*. Lengths and ratios of certain tergal macrochaetae, as follows:

	ma	la	lp_1	lp_2	ma/D	ma/Sep ma-ma
Ab. I	65-97	—	—	—	0.44-1.00	0.52-0.77
Ab. VI	65-119	86-130	184-297	140-238	0.50-1.00	0.48-0.75
Ab. VII	97-140	130-259	216-340	211-335	0.67-1.20	0.63-1.00

Abdominal tergite IV with up to 16 posterior marginal setae separating sublateral posterior macrochaetae nearest sagittal plane; tergite V with up to 18 such setae; VI with 16; VII with 15; VIII with 12; IX with 14. Supra-anal valvule with barbed subapical medial seta, 1 + 1 barbed lateral setae (sometimes replaced by setiform sensilla), and 1 medial setiform sensillum.

Urosternite (coxosternite) I with 7 + 7 differentiated macro- 4 + 4 on middle portion; 1 + 1 submacrochaetae at latero-posterior angle of urosternite of males and females. Posterior margin with glandular setae on males. Lateral subcoxal appendages subcylindrical, short, among females and males. Females with glandular setae on tip of appendages only.

Urosternites II-VII with 4 + 4 well differentiated macrochaetae, with branches and barbs; 1 + 1 weakly differentiated macrochaetae inserted internally at base of each stylus. Apical seta of styli smooth and with 2 short basal branches, proximal branch about one-half length of distal; subapical seta smooth; medial ventral seta straight or bifurcated; clothing setae smooth. Stylus VII length 6.0 times width; apical seta about 46 percent as long as stylus. Urosternite VIII with 1 + 1 macrochaetae. Genital papilla of largest male with up to 16 short setae encircling gonopore.

Cerci and their covering like those of Litocampa virginiana.

TYPE LOCALITY.--Fallen Rock Cave, in Ward Cove, Tazewell Co., Virginia. The cave contains a large stream and is the major drainage of the upper end of Ward Cove. The cave has 6.39 miles of surveyed passage and is developed primarily in the Middle Ordovician-aged Lincolnshire formation (Holsinger, 1975).

DISTRIBUTION.--Litocampa barringerorum is known from 5 caves in Ward Cove of southwestern Tazewell Co., Virginia.

ETYMOLOGY.--It is a distinct pleasure to name this new species in honor of the Benjamin Barringer family, owners of Fallen Rock Cave.

This designation is a token of appreciation to Mr. and Mrs. Barringer and their son, Benjamin, Jr., for allowing me and other speleologists to study their cave and its animal life.

Litocampa cherokeensis, new species

(Fig. 30)

MATERIAL EXAMINED.—TENNESSEE: Maury Co.: Hobbs Cave, 2 ♀, (holotype and paratype), 26 July 1972, L. M. and B. L. Ferguson, (LMF 213): 1 ♂, 1 ♀ (paratypes), 29 Oct. 1969, J. R. Holsinger and R. A. Baroody, (LMF 33). ALABAMA: Colbert Co.: McKinney No. 2 Cave (Ala. #629), 3 mi. W. of Sheffield, 1 ♂, 19 Dec. 1965, S. B. Peck, (LMF 254): Dekalb Co.: Cherokee Cave (Ala. #806), 4.5 mi. NE of Ft. Payne, 1 ♂, 1 ♀, 15 July 1967, S. B. Peck and A. Fiske, (LMF 239): Jefferson Co.: Cedar Pole Cave, (Ala. #705), near Clay, 1 ♂, 10 Sept. 1965, S. B. Peck, (LMF 247). GEORGIA: Dade Co.: Johnson Crook Cave No. 2, 4.5 mi. NE of Rising Fawn, 1 ♀, 14 July 1967, S. B. Peck and A. Fiske, (LMF 27); Walker Co.: Cave Spring Cave, 2.5 mi. N. of Chicamauga, 2 ♂, 10 June 1967, S. B. Peck and A. Fiske, (LMF 29).

Holotype (LMF 213-1), paratype, and other material deposited in the American Museum of Natural History. Two paratypes retained in the author's collection.

DIAGNOSIS.—Distinguished from other species of *Litocampa* in the United States by presence of 3 + 3 and 2 + 2 macrochaetae on meso- and metanota, 4 + 4 barbed precoxal macrochaetae on meso- and metasternite, one dorsal macrochaeta on femur III, tibia III with 1 ventral macrochaeta, claws without well-developed latero-tergal crests, medial anterior macrochaetae present on abdominal tergites I-VII, 1 + 1 lateral anterior and 2 + 2 lateral posterior macrochaetae on tergites IV-VII, urosternite I with 7 + 7 macrochaetae and without glandular setae on males, and 4 + 4 well differentiated macrochaetae on urosternites II-VII.

DESCRIPTION.--Chaetotaxy and morphology most like that of Litocampa barringerorum, with the exception of glandular setae lacking on the posterior margin of urosternite I of males and the length (and number of whorls of macrochaetae) of the cercal segments. The meristic variation and measurements of specimens from Hobbs Cave are as follows:

Size: Male: body length, 5.0 mm; head width, 0.63 mm; pronotal width, 0.48 mm. Females: body length, 5.5-6.0 mm; head width, 0.73-0.85 mm; pronotal width, 0.51-0.58 mm.

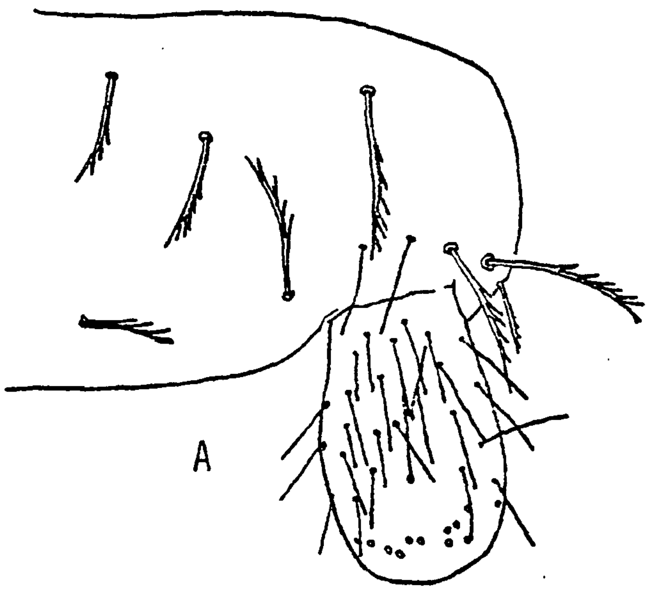
Head: Antennal segments, 26-31. Number of segments of 6 complete antennae as follows:

No. segments:		26	27	28	29	30	31
Frequency:	♂	0	0	0	0	1	0
	♀	1	1	0	1	1	1

Length of longest antenna 4.81 mm, or about 80 percent of body length, reaching abdominal segment VII. Cupuliform organ of apical segment with 11 sensilla.

Thorax: Clothing setae smooth; notal chaetotaxy 3 + 3, 3 + 3, 2 + 2.

FIGURE 30.--*Litocampa cherokeensis*, new species. A, urosternite I of male (some glandular setae of the subcoxal appendage represented by their bases; clothing setae not shown on sternite proper). Male (5.0 mm; head width, 0.63 mm), Hobbs Cave, Tennessee.



A

Lengths and ratios of macrochaetae as follows:

	ma	la	lp	ma/la	lp/ma
Th. I	97-162	130-173	238-281	0.75-0.94	1.73-2.44
Th. II	130-184	189-248	254-292	0.69-0.74	1.59-1.96
Th. III	119-167	—	248-281	—	1.68-2.09

Mesonotum; ma/Sep ma-ma, 1.70-1.85; ma/Sep ma-la, 0.75-0.94; la/Sep ma-la, 1.09-1.28; lp_I/lp_{II}, 0.94-0.96; lp_{II}/lp_{III}, 1.02-1.04. Pronotum of largest female with 4 + 5 barbed lateral posterior marginal setae and 8 smooth medial posterior marginal setae; mesonotum with 3 + 3 lateral, 10 medial posterior marginal setae; metanotum with 1 + 1 lateral, 11 medial posterior marginal setae.

Chaetotaxy of thoracic sternites same as for *L. barringerorum*.

Length of leg III about 40 percent of body length, reaching abdominal segment VII. Femur I without dorsal macrochaetae; femurs II and III wtih one dorsal macrochaeta. Dorsal macrochaeta inserted on distal half of femur III, 1.1 times width of femur at point of insertion; barbed on distal 0.6. Femur III with 4 anterior marginal macrochaetae; 2 most ventral barbed on distal two-thirds; distal pair smooth. Tibia III length 7.0 times width, with 1 or 2 barbed ventral macrochaetae; tibial spurs with 2 rows of long barbs. Tarsus III with 17 ventral setae in anterior row. Posterior claw slightly longer than anterior; latero-tergal crests reduced; no flange on posterior claw. Pretarsal appendices long, slender, and smooth; length exceeding tip of claws.

Abdomen: Distribution of tergal macrochaetae same as for *Litocampa virginiana* and *L. barringerorum*. Lengths and ratios of certain tergal macrochaetae, as follows:

	ma	la	lp_1	lp_2	ma/D	ma/Sep ma-ma
Ab. I	86-97	--	--	--	0.69-0.73	0.69-0.80
Ab. IV	92-113	103-119	227-270	189-216	0.72-0.74	0.66-0.71
Ab. VII	103-130	178-216	254-292	259-302	0.86-0.92	0.92-0.95

Abdominal tergite IV with up to 20 posterior marginal setae separating sublateral posterior macrochaetae nearest sagittal plane; tergite V with up to 19 such setae; VI with 17; VII with 17; VIII with 14; IX with 13. Supra-anal valvule with 2 proximal setae and 1 barbed subapical seta.

Urosternite (coxosternite) I with 7 + 7 differentiated macrochaetae, 4 + 4 on middle portion; 1 + 1 submacrochaetae at lateroposterior angle of urosternite of males and females. Posterior margin without glandular setae on males and females. Lateral subcoxal appendages subcylindrical, short, among both sexes. Females with glandular setae on tip of appendages only.

Urosternites II-VII with 4 + 4 well differentiated macrochaetae, with branches and barbs; 2 + 2 weakly differentiated macrochaetae inserted internally and externally at base of each stylus. Apical seta of styli smooth and 2 short basal branches, proximal branch about one-half length of distal; subapical seta smooth; medial ventral seta forked; clothing setae smooth. Stylus VII length 4.7

times width; apical seta about 45 percent as long as stylus. Urosternite VIII with 1 + 1 macrochaetae. Genital papilla of male with 15 short setae encircling gonopore.

Length of longest cercus about 0.76 times body length, composed of a base, subdivided into 5 secondary segments, and 13 primary segments. Segmental lengths (in mm): base = 0.18, 0.12, 0.13, 0.17, 0.19; primary segments = 0.21, 0.21, 0.23, 0.25, 0.27, 0.28, 0.33, 0.35, 0.35, 0.37, 0.35, 0.35, 0.44. Covering of base and proximal segments composed of long macrochaetae, length of macrochaetae about 1.6 times width of segments, barbs on distal half. Proximal primary segments with whorls of 7 barbed macrochaetae, long smooth setae, and 7 short subapical setae. Penultimate segment length 6.4 times width, with 2 whorls of macrochaetae, alternating with whorls of long smooth setae; macrochaetae with 4-5 barbs; 9 short subapical setae. Macrochaetae of apical segment arranged in 2 whorls, length of macrochaetae about 3.8 times width of segment, alternating with whorls of long smooth setae; macrochaetae of distal whorl smooth; macrochaetae of proximal whorl with 4-5 barbules.

Variation: Some specimens assigned to this species have shorter antennae (18 to 26 segments) than the specimens from the type locality. Future investigation may show that these other cave campodeid populations belong to one or more separate species within the *virginiana* group.

TYPE LOCALITY.—Hobbs Cave, 750 feet east of Campbells Station, at the southeast corner of Spencers Lake, in Maury Co., Tennessee. A large stream flows out the entrance of the cave, into the lake. The cave has 3200 feet of passage and is developed in the Middle Ordovician-aged Carters and Hermitage limestones (Barr, 1961).

DISTRIBUTION.—Litocampa cherokeensis is known from 2 caves in Georgia, 3 caves in Alabama, and 1 cave in Tennessee. The range of this spcies appears to be peripheral to that of the other cavernicolous campodeids in the region.

ETYMOLOGY.—The epithet cherokeensis was chosen for a variety of reasons. First, the species is known from Cherokee Cave in DeKalb County, Alabama. Second, it appears to exist in part in the original homeland of the Cherokee Indians, in the states of Tennessee, Alabama, and Georgia. And third, the name Cherokee is derived from the Choctaw chilukki for "cave people", that is, cave dwellers.

The *Hawksleyi* Group

DIAGNOSIS.--Antennal segment III with phanere *e*, metanotum with 1 + 1 lateral posterior macrochaetae, femur III with dorsal macrochaeta, pretarsal claws with large latero-tergal crests, abdominal tergites V-VII with 2 + 2 posterior macrochaetae, medial anterior macrochaetae on abdominal tergites I-II, urosternite I with 6 + 6 macrochaetae, and posterior margin of urosternite I of males with glandular setae.

REMARKS.--The two species included in this group are remarkably similar and were once considered by me to be conspecific. However, the absence of any overlap or variation in a key character displayed by individuals from the known 17 (12 + 5) populations of these two species, combined with some geographic and geological data, is taken to indicate at least two distinct species. These species occupy caves in the Ozark Plateau region of Missouri and Arkansas.

Key to the Species of the *Hawksleyi* Group

1. Abdominal tergite III with 1 + 1 posterior macrochaetae; tergite IV with 2 + 2 posterior macrochaetae........*L. hawksleyi*, new species

1'. Abdominal tergites III-IV with 1 + 1 posterior macrochaetae.........
....*L. ozarkensis*, new species

Litocampa hawksleyi, new species

(Figs. 31-32)

MATERIAL EXAMINED.--MISSOURI: Taney Co.: Tumbling Creek Cave (Ozark Underground Laboratory), 5 mi. NE of Protem, 2 ♂, 1 ♀ (holotype and paratypes), T. Aley, (LMF 485); 1 ♂, 2 ♀ (paratypes), 25 Apr. 1975, O. Hawksley, (LMF 455); Texas Co.: Cave, NE of Success, 1 ♀, 5 July 1940, L. Hubricht, (LMF 107); Pulaski Co.: McCann Cave No. 1, 4 mi. W. of Waynesville, 1 ♀, 6 Mar. 1976, J. L. Craig, (LMF 612). ARKANSAS: Boone Co.: Brewer Cave, T17N, R18W, sec. 5, SE 1/4, 1 ♂, 2 ♀, July-Aug. 1976, N. and J. Youngsteadt, (LMF 536); Newton Co.: Bat House Cave, T16N, R19W, sec. 18, NW 1/4, Center, 1 ♀, April 1977, N. and J. Youngsteadt, (LMF 534); Big Bear Cave, T16N, R20W, sec. 29, NE 1/4, Center, 2 ♂, 1 ♀, May 1977, N. and J. Youngsteadt, (LMF 542); Cave, T17N, R19W, 2 ♂, 1 ♀, June-July 1976, N. and J. Youngsteadt, (LMF 539); Lewis Spring Cave, T16N, R19W, sec. 12, Center, ♂♂♀♀, Jan. 1976, N. and J. Youngsteadt, (LMF 535); Little Bear Cave, T16N, R20W, sec. 20, SW 1/4, S. 1/2, 2 ♂, 1 ♀, Apr. 1976, N. and J. Youngsteadt, (LMF 532); Searcy Co.: Hurricane River Cave, T16N, R18W, sec. 7, N. 1/2, Center, ♂♂♀♀, Dec. 1975/Feb. 1976, N. and J. Youngsteadt, (LMF 533); Potato Cave, T16N, R18W, sec. 8, SW 1/4, SE 1/4, NE 1/4, 1 ♂, Feb. 1976, N. and J. Youngsteadt, (LMF 538); Stone Co.: Alexander's Cave, about 4-5 mi. W. of Fifty-Six, 1 , Feb. 1977, N. and J. Youngsteadt, (LMF 537).

Holotype (LMF 485-2) and paratypes deposited in American Museum of Natural History; remaining paratypes deposited in B. Condé's collection, Université de Nancy, Nancy, France, and the author's collection.

DIAGNOSIS.--Distinguished from other species of Litocampa in the United States by presence of 3 + 3 and 2 + 2 macrochaetae on meso- and metanota, one dorsal macrochaeta on femur III, tibia III with 1 ventral macrochaeta, claws with well-developed latero-tergal crests, medial anterior macrochaetae present on abdominal tergites I-II, 1 + 1 posterior macrochaetae on tergite III, 2 + 2 posterior macrochaetae on tergite IV, 1 + 1 lateral anterior and 2 + 2 posterior macrochaetae on tergites V-VII, 6 + 6 macrochaetae on urosternite I, and 4 + 4 well differentiated macrochaetae on urosternites II-VII.

DESCRIPTION.--Size: Males: body length, 4.6-6.3 mm; head width, 0.71-0.80 mm; pronotal width, 0.49-0.57 mm. Females: body length, 5.1-6.6 mm; head width, 0.69-0.82 mm; pronotal width, 0.45-0.57 mm.
Head: Antennal segments, 23-29. Number of segments of 22 complete antennae, disregarding one regenerating antenna of 26 segments which has a long apical segment and is paired with an antenna of 28 segments, as follows:

		23	24	25	26	27	28	29
No. segments:		23	24	25	26	27	28	29
Frequency:	♂	0	0	1	5	5	2	0
	♀	1	0	4	2	0	1	1

FIGURE 31.--Litocampa hawksleyi, new species. A, latero-anterior sensillum of right labial palp; B, pro-, meso-, and metanotum; C-E, ma, la, and lp of mesonotum; F-G, ma and lp of metanotum; H, pronotum (enlarged); I, posterior margin of abdominal tergite III. A, I, female (6.6 mm; head width, 0.82 mm); others, female (5.1 mm; head width, 0.69 mm), Tumbling Creek Cave, Missouri.

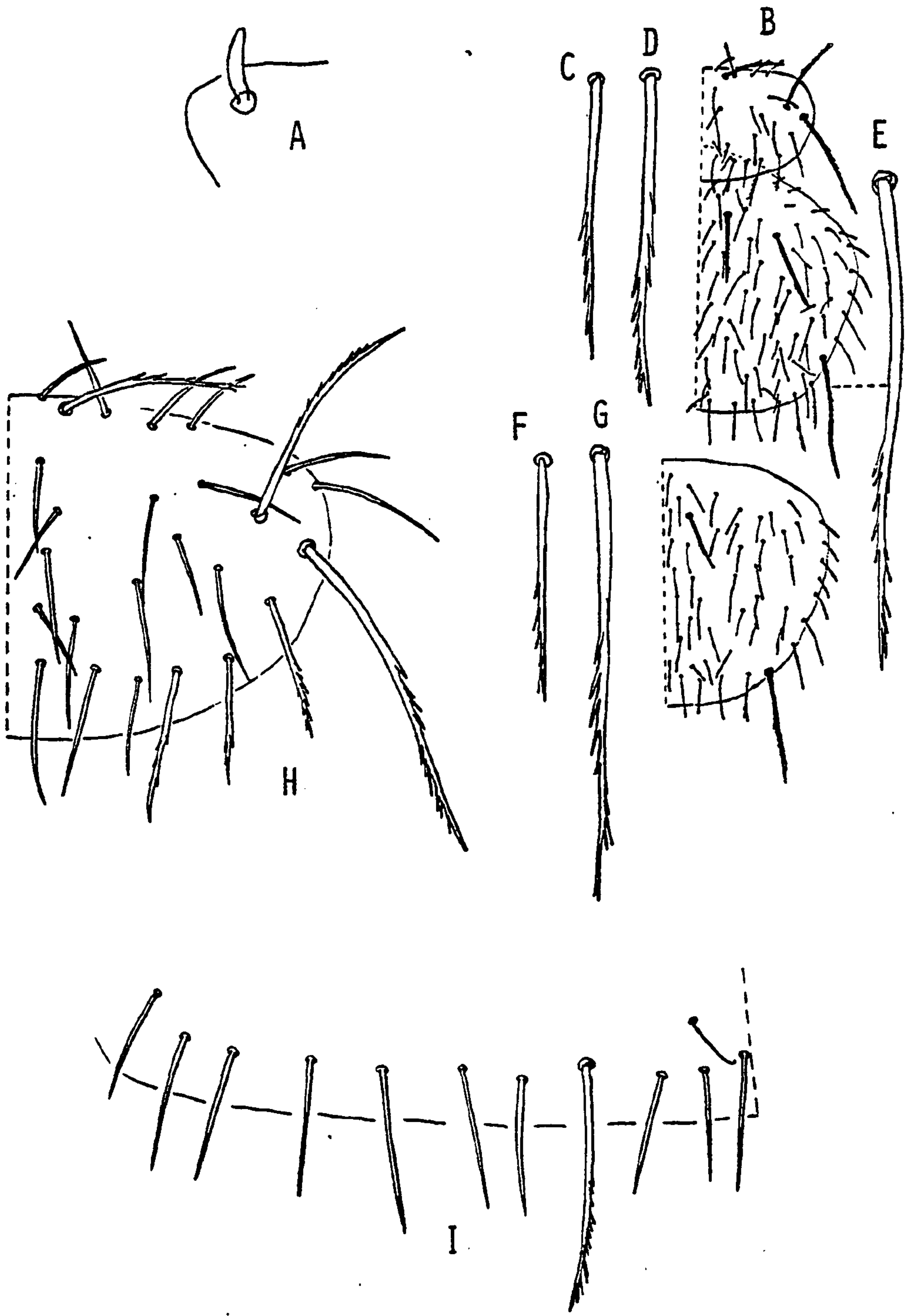
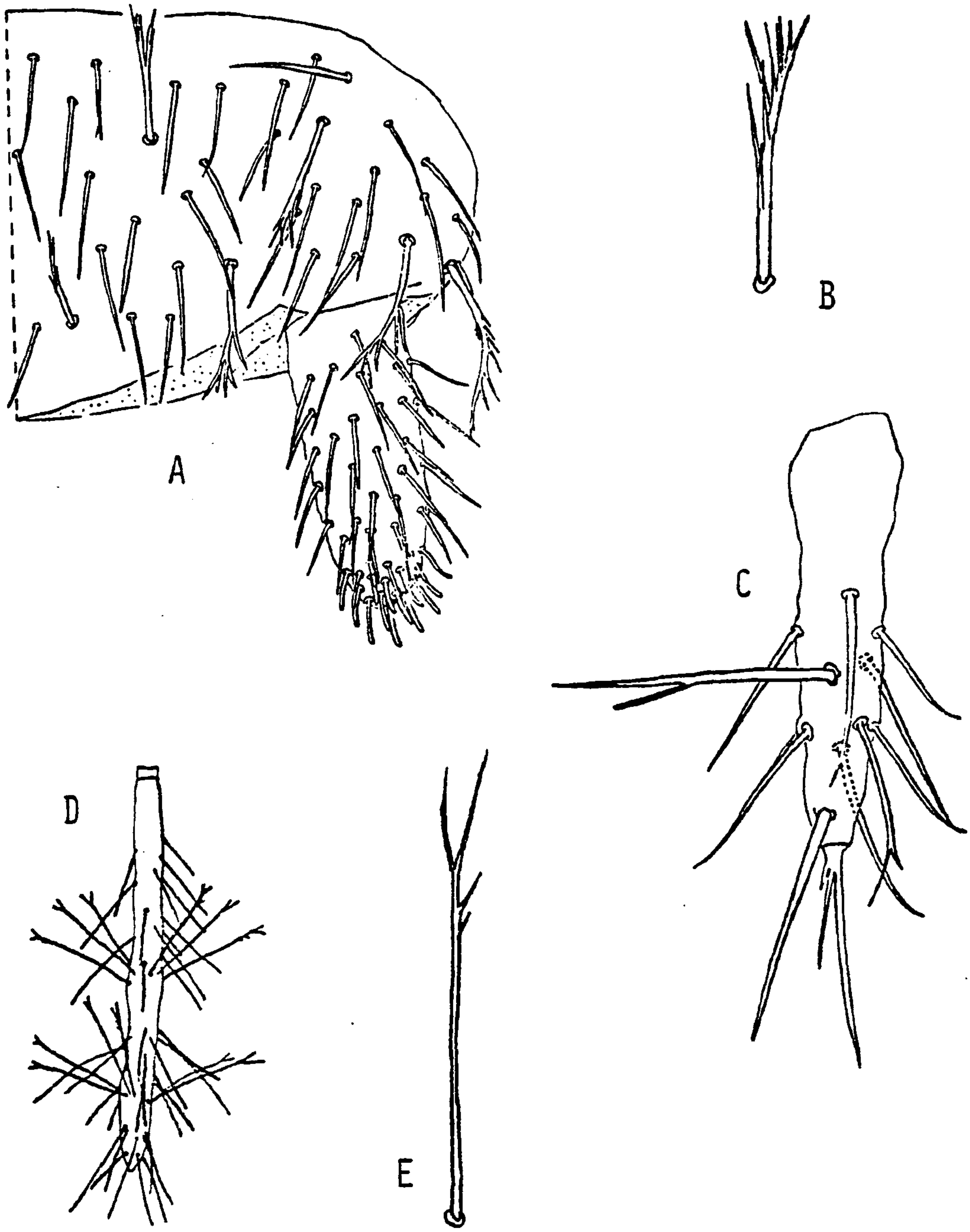

A
B
C
D
E
F
G
H
I

FIGURE 32.--Litocampa hawksleyi, new species. A, urosternite I of female; B, macrochaeta at base of eversible vesicle of urosternite V; C, left stylus of urosternite V; D, apical segment of cercus; E, macrochaeta from apical segment of cercus. A, C, female (5.1 mm; head width, 0.69 mm); others, female (6.6 mm; head width, 0.82 mm), Tumbling Creek Cave, Missouri.


A
B
C
D
E

Length of longest antenna 5.25 mm, or 83 percent of body length, reaching abdominal segment VIII. Antennal segment III with ventral bacilliform sensillum, inserted between phaneres d and e: Ma, Mb, seta c, Md, sen. (long, but not exceeding distal border of segment), Me, Mf, Mg, Mh; length of d 1.4 times c; phaneres smooth. Cupuliform organ of apical segment with 9 sensilla.

Frons with 3 macrochaetae on rostrum. Macrochaetae bordering line of insertion of antennae 3 + 3; anterior macrochaeta approximately three-fourths as long as intermediate; anterior and posterior macrochaetae subequal, anterior slightly shorter than posterior; all three macrochaetae barbed on distal half. No macrochaetae anterior to arms of epicranial suture, near sagittal plane. Occipital setae barbed on distal 0.8; length about 52 percent as long as pronotal lp. Latero-anterior sensillum of labial palp long, subcylindrical, slightly curved towards sagittal plane. Posterior mental setae smooth; lateral submental macrochaetae with long barbs.

Thorax: Clothing setae smooth; notal chaetotaxy 3 + 3, 3 + 3, 2 + 2. Lengths and ratios of macrochaetae of specimens from Tumbling Creek Cave, as follows:

	ma	la	lp	ma/la	lp/ma
Th. I	135–157	162	243–292	0.83–0.97	1.80–1.86
Th. II	151–162	184–194	259–292	0.82–0.83	1.71–1.80
Th. III	140–146	—	238–275	—	1.63–1.96

Mesonotum; ma/Sep ma-ma, 1.43–1.65; ma/Sep ma-la, 1.00–1.22; la/Sep ma-la, 1.20-1.48; lp_I/lp_{II}, 0.94-1.00; lp_{II}/lp_{III}, 1.06-1.09. Pronotum of largest female with 3 + 4 barbed lateral posterior marginal setae and 4 smooth medial posterior marginal setae; mesonotum with 3 + 3 lateral, 6 medial posterior marginal setae; metanotum with 9 medial posterior marginal setae.

Presternite of prosternum with 2 + 2 M; prosternite with 4 + 4 barbed precoxal M; 4 + 4 smooth precoxal setae; 1 + 1 subcoxal M; 2 + 2 lp. Meso- and metasternite with 4 + 4 barbed precoxal M; 4 + 5 smooth precoxal setae; 1 + 1 ma; 1 + 1 la; 1 + 1 subcoxal M; 2 + 2 lp on mesosternite, 1 + 1 lp on metasternite.

Length of leg III about 38 percent of body length, reaching abdominal segment VII. Femur I without dorsal macrochaetae; femurs II and III with one dorsal macrochaeta. Dorsal macrochaeta inserted on distal half of femur III, 1.03 times width of femur at point of insertion; barbed on distal 0.7. Femur III with 4 anterior marginal macrochaetae; 2 most ventral barbed on distal two-thirds; distal pair smooth. Tibia III length 7.5 times width, with one bifurcated ventral macrochaeta with several small barbs proximal to bifurcation; tibial spurs with 2 rows of long barbs. Tarsus III with 14 ventral setae in anterior row. Posterior claw longer than anterior; latero-tergal crests well-developed; flange on posterior claw. Pretarsal appendices long, slender, and smooth; length exceeding tip of claws.

Abdomen: Distribution of tergal macrochaetae:

	ma	mp	la	lp	
Ab. I-II	1 + 1	0	0	0	
Ab. III	0	1 + 1	0	0	
Ab. IV	0	1 + 1	0	1 + 1	
Ab. V-VII	0	1 + 1	1 + 1	1 + 1	
Ab. VIII	0	1 + 1	0	3 + 3	
Ab. IX	0	1 + 1	0	5 + 5	(total)

Lengths and ratios of certain tergal macrochaetae, as follows: Abdominal tergite I: ma, 81–97; ma/D, 0.65–0.82; ma/Sep ma-ma, 0.90–0.94.

	la	mp	lp	mp/Sep mp-mp
Ab. IV	--	194–227	184–227	0.68–0.69
Ab. V	130–162	194–227	227–259	0.58–0.62
Ab. VII	173–211	216–238	254–270	0.70–0.75

Abdominal tergite III with up to 5 posterior marginal setae separating medial posterior macrochaetae; tergite IV with up to 7 such setae; V with 8; VI with 8; VII with 6; VIII with 5; IX with 7. Supra-anal valvule with 7 setae; subapical seta barbed.

Urosternite (coxosternite) I with 6 + 6 differentiated macrochaetae, 3 + 3 on middle portion; 1 + 1 submacrochaetae at latero-posterior angle of urosternite of males and females. Posterior margin with glandular setae on males. Lateral subcoxal appendages subcylindrical among females; rounded in shape on mature males. Females with glandular setae on tip of appendages only.

Urosternites II-VII with 4 + 4 well differentiated macrochaetae, with branches and barbs; 2 + 2 weakly differentiated macrochaetae inserted internally and externally at base of each stylus. Apical seta of styli smooth and with 2 long basal branches, proximal branch about one-third length of distal; subapical seta smooth; medial ventral seta forked; clothing setae smooth, some bifurcated. Stylus VII length 4.0 times width; apical seta about 55 percent as long as stylus. Urosternite VIII with 1 + 1 macrochaetae. Genital papilla of largest male with 18 short setae encircling gonopore.

Length of longest cercus about 0.80 times body length, composed of a base, subdivided into 4 secondary segments, and 9 primary segments. Segmental lengths (in mm): base = 0.17, 0.17, 0.22, 0.28; primary segments = 0.33, 0.37, 0.41, 0.45, 0.50, 0.54, 0.59, 0.63, 0.63. Covering of base and proximal segments composed of long macrochaetae, length of macrochaetae about 2.3 times width of segments, barbs on distal half to two-thirds. Proximal primary segments with whorls of 8 barbed macrochaetae, long smooth setae, and 7 short subapical setae. Penultimate segment length 11.6 times width, with 2 whorls of macrochaetae, alternating with whorls of long and short smooth setae; macrochaetae with long subapical barb (i.e., bifurcated) and 5 or more long barbs below subapical; 6 short subapical setae. Macrochaetae of apical segment arranged in 2 whorls, length of macrochaetae about 4.25 times width of segment, alternating with whorls of long and short smooth setae; all macrochaetae bifurcated, with 1 or more barbules.

TYPE LOCALITY.--Tumbling Creek Cave, 25 miles east of Forsyth and 5 miles northeast of Protem, in Taney Co., Missouri. The cave has over 9000 feet of passages, part of which make up the Ozark Underground Laboratory, a privately owned and operated facility for cave studies. Tumbling Creek Cave has a variety of cave life, including the Ozark blind salamander, Typhlotriton spelaeus, and a nursery colony of about 150,000 gray bats, Myotis grisescens (Weaver and Johnson, 1980; Rhodes, 1974).

DISTRIBUTION AND ECOLOGY.--Litocampa hawksleyi is known from 3 caves in Missouri and from 9 caves in northern Arkansas. Most of the caves are located approximately 35 miles south of the type locality, with one cave 30 miles to the southeast. All of these caves, as well as the type locality, are in the White River drainage system, which flows to the southeast. The other two Missouri caves are as far as 100 miles NNE of the type locality and in the Gasconade River drainage, which flows to the northeast.

ETYMOLOGY.--This species is named in honor of Dr. Oscar Hawksley, for his many contributions to Missouri speleology.

Litocampa ozarkensis, new species

(Fig. 33)

MATERIAL EXAMINED.--ARKANSAS: Newton Co.: Fitton Cave, 7 ♂, 7 ♀ (holotype and paratypes), P. Lindsley, (LMF 294); 2 ♀, 1 immature (paratypes), "found in July on dry limestone rocks, approx. 1 mi. from mouth of cave; total darkness," J. J. Burch, (LMF 95); Boone Co.: Major's Cave, T16N, R20W, sec. 16, NW 1/4, 3 ♂, 1 ♀, July 1977, N. and J. Youngsteadt, (LMF 541); Independence Co.: Foushee Cave, about 6 mi. west of Locust Grove, 1 ♂, 4 ♀, May 1978, N. and J. Youngsteadt, (LMF 548); Searcy Co.: Back and Beyond Cave, Buffalo National River, 1 ♀, 18 Feb. 1979, W. C. Welbourn, (LMF 627); Fallout Cave, Buffalo National River, 1 ♀, 28 Oct. 1977, W. C. Welbourn, (LMF 626).

Holotype (LMF 294-10) and paratypes deposited in American Museum of Natural History; remaining paratypes deposited in B. Condé's collection, Universite de Nancy, Nancy, France, and the author's collection.

DIAGNOSIS.--Distinguished from other species of Litocampa in the United States by presence of 3 + 3 and 2 + 2 macrochaetae on meso- and metanota, one dorsal macrochaeta on femur III, tibia III with 1 ventral macrochaeta, claws with well-developed latero-tergal crests, medial anterior macrochaetae present on abdominal tergites I-II, 1 + 1 posterior macrochaetae on tergites III-IV, 1 + 1 lateral anterior and 2 + 2 posterior macrochaetae on tergites V-VII, 6 + 6 macrochaetae on urosternite I, and 4 + 4 well differentiated macrochaetae on urosternites II-VII.

DESCRIPTION.—Size: Males: body length, 3.6-6.1 mm; head width, 0.63-0.92 mm; pronotal width, 0.41-0.63 mm. Females: body length, 4.5-9.3 mm; head width, 0.75-1.05 mm; pronotal width, 0.48-0.73. Immature: body length, 4.4 mm; head width, 0.58 mm; pronotal width, 0.36 mm.

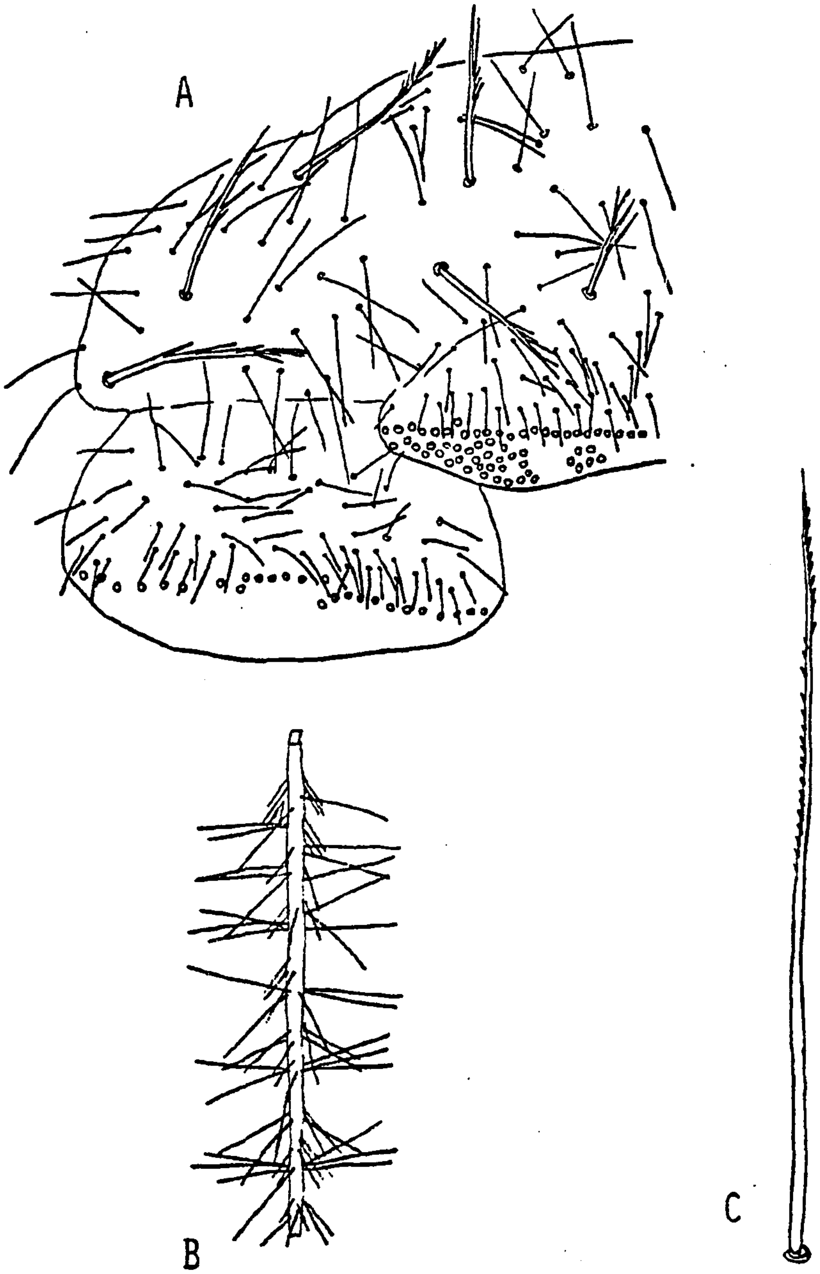
Head: Antennal segments, 37-41. Number of segments of 13 complete antennae, disregarding 3 antennae of 33, 34, and 35 segments which were obviously regenerating (they are paired with longer antennae and have very long apical segments), are as follows:

No. segments:		37	38	39	40	41
Frequency:	♂	0	1	5	0	0
	♀	3	1	0	2	1

Length of longest antenna 7.20 mm, or 1.17 times body length. Antennal segment III with ventral bacilliform sensillum, inserted between phaneres d and e: Ma, Mb, seta c, Md, sen. (long, reaching distal border of segment), Me, Mf, Mg, Mh; lengths of c and d subequal; long macrochaetae smooth. Cupuliform organ of apical segment with 9 sensilla.

Frons with 3 macrochaetae on rostrum. Macrochaetae bordering

FIGURE 33.--Litocampa ozarkensis, new species. A, urosternite I of male (glandular setae represented by their bases; many not shown); B, distal segment (tenth) of longest cercus (broken); C, macrochaeta from tenth segment of cercus. A, male (6.1 mm; head width, 0.92 mm); B, female (8.4 mm; head width, 1.03 mm), Fitton Cave, Arkansas.


A
B
C

line of insertion of antennae 3 + 3; anterior macrochaeta approximately 0.8 as long as intermediate; intermediate and posterior macrochaetae subequal; all three macrochaetae barbed on distal half. Sometimes with 1 + 1 macrochaetae anterior to arms of epicranial suture, near sagittal plane; shorter than macrochaetae at posterior border of antennal insertion; barbed. Occipital setae with few barbs on distal half; length about 50 percent as long as pronotal lp. Latero-anterior sensillum of labial palp subcylindrical, weakly curved towards sagittal plane. Posterior mental setae smooth; lateral submental macrochaetae barbed.

Thorax: Some clothing setae with distal barbules; notal chaetotaxy 3 + 3, 3 + 3, 2 + 2. Lengths and ratios of macrochaetae of mature specimens from Fitton Cave, as follows:

	ma	la	lp	ma/la	lp/ma
Th. I	119–184	130–194	221–302	0.89–1.00	1.75–1.86
Th. II	184–259	157–254	270–367	1.02–1.17	1.42–1.47
Th. III	173–221	—	248–335	—	1.44–1.51

Mesonotum: ma/Sep ma–ma, 1.55–1.89; ma/Sep ma–la, 1.85–2.00; la/Sep ma–la, 1.71–1.81; lp_I/lp_{II}, 0.82; lp_{II}/lp_{III}, 1.09–1.10. Pronotum of largest female with 5 + 5 barbed lateral posterior marginal setae and 4 barbed medial posterior marginal setae; mesonotum with 4 + 4 lateral, 4 medial posterior marginal setae; metanotum with 8 medial posterior marginal setae.

Presternite of prosternum with 2 + 2 M; prosternite with 4 + 4 barbed precoxal M; 5 + 5 smooth precoxal setae; 1 + 1 subcoxal M; 2 + 2 lp. Meso-and metasternite with 4 + 4 barbed precoxal M; 5 + 5 smooth precoxal setae; 1 + 1 ma; 1 + 1 la; 1 + 1 subcoxal M; 1 + 1 lp.

Length of leg III 50 percent of body length, reaching abdominal segment X. Femur I without dorsal macrochaetae; femurs II and III with one dorsal macrochaeta. Dorsal macrochaeta inserted on distal half of femur III, 1.64 times width of femur at point of insertion; barbed on distal half. Femur III with 4 anterior marginal macrochaetae; 2 most ventral barbed on distal 0.6; distal pair barbed. Tibia III length 13 times width, with one ventral macrochaeta with 2 rows of small barbs; tibial spurs with 2 rows of long barbs. Tarsus III with 23 ventral setae in anterior row. Posterior claw longer than anterior; latero-tergal crests well-developed; flange on posterior claw. Pretarsal appendices long, slender, and smooth; length exceeding tip of claws.

Abdomen: Distribution of tergal macrochaetae:

	ma	mp	la	lp
Ab. I-II	1 + 1	0	0	0
Ab. III-IV	0	1 + 1	0	0
Ab. V-VII	0	1 + 1	1 + 1	1 + 1
Ab. VIII	0	1 + 1	0	3 + 3
Ab. IX	0	1 + 1	0	5 + 5

Lengths and ratios of certain tergal macrochaetae, as follows: Abdominal tergite I: ma, 86-130; ma/D, 0.55-0.76; ma/Sep ma-ma, 0.74-0.75.

	la	mp	lp	mp/Sep mp-mp
Ab. IV	--	189-270	--	1.17-1.19
Ab. V	97-205	200-281	167-308	0.84-1.03
Ab. VII	140-254	205-302	200-329	0.78-1.03

Abdominal tergite III with up to 4 posterior marginal setae separating medial posterior macrochaetae; tergite IV with up to 4 such setae; V with 5; VI with 6; VII with 6; VIII with 5; IX with 5. Supra-anal valvule with 9 setae; subapical seta barbed.

Urosternite (coxosternite) I with 6 + 6 differentiated macrochaetae, 3 + 3 on middle portion. Posterior margin with glandular setae on males. Lateral subcoxal appendages subcylindrical, small, among females; greatly expanded laterally, width 1.8 times length, on mature males. Females with glandular setae on tip of appendages only.

Urosternites II-VII with 4 + 4 well differentiated macrochaetae, with branches and barbs; 2 + 2 weakly differentiated macrochaetae inserted internally and externally at base of each stylus. Apical seta of styli with 1-3 distal barbules and 2 long basal branches, proximal branch about one-third length of distal; subapical seta with 1 long medial barb and several smaller barbs; medial ventral seta forked; clothing setae smooth or bifurcated and with 1 barbule. Urosternite VIII with 1 + 1 macrochaetae. Genital papilla of largest male with 20 short setae encircling gonopore.

Length of longest cercus (incomplete) about 1.20 times body length, composed of a base, subdivided into 4 secondary segments, and 10 primary segments. Segmental lengths (in mm): base = 0.22, 0.22, 0.29, 0.39; primary segments = 0.44, 0.53, 0.57, 0.69, 0.75, 0.89, 0.98, 1.19, 1.35, 1.59. Covering of base and proximal segments composed of long macrochaetae, length of macrochaetae about 3.5 times width of segments, small barbs on distal two-thirds. Proximal primary segments with whorls of 7 barbed macrochaetae, long smooth setae, and 7 short subapical setae. Last primary segment length 32.7 times width, with 6 whorls of macrochaetae, alternating with whorls of short smooth setae; macrochaetae without prominent subapical barb and with many small barbs; length of macrochaetae about 6.7 times width of segment; 7 short subapical setae.

TYPE LOCALITY.--Fitton Cave, 7.5 miles west of Dogpatch (Marble Falls), in Newton Co., Arkansas. With 8.14 miles of surveyed passages, Fitton Cave (also known as Beauty Cave) is the longest known cave system in Arkansas. The cave is developed in the Middle Mississippian-aged Boone limestone (Looney and Looney, 1980; Smith, 1970).

DISTRIBUTION AND ECOLOGY.--*Litocampa ozarkensis* is known from five caves in northern Arkansas. The caves are south and west of those containing the closely related *L. hawksleyi*.

ETYMOLOGY.--The specific name refers to the occurrence of this species in the Ozark Plateau region of Arkansas.

The *Valentinei* Group

DIAGNOSIS.--Antennal segment III with phanere *e*, metanotum without lateral posterior macrochaetae, pretarsal claws with large latero-tergal crests, abdominal tergites VI-VII with 2 + 2 lateral posterior macrochaetae, medial anterior macrochaetae on abdominal tergites I-VII, urosternite I with 7 + 7 macrochaetae, and posterior margin of urosternite I of males without glandular setae.

REMARKS.--The two species in this group are very similar morphologically. *Litocampa pecki* is known from two caves in the upper Coosa River drainage basin of Georgia. *L. valentinei* has been found in many caves of the Cumberland Plateau region of Alabama and south central Tennessee. Expect for one locality in DeKalb County, Alabama, all locations of *L. valentinei* are north of the Tennessee River.

Key to the Species of the *Valentinei* Group

1. Abdominal tergite V with 1 + 1 medial anterior and 1 + 1 lateral anterior macrochaetae ....*L. valentinei*

1'. Abdominal tergite V with 1 + 1 medial anterior and 1 + 1 lateral posterior macrochaetae......................*L. pecki*, new species

Litocampa valentinei (Condé)

(Figs. 34-35)

Plusiocampa valentinei Condé, 1949b:130-132, fig. 2F-H. [Cave Spring Cave, Madison Co., Alabama; repository unknown]; 1956a:128, 132. 170, 171, 187; Nicholas, 1960:140; Ferguson, 1973:18-19; (in press).

Litocampa (*Cocytocampa*) *valentinei* (Condé), Paclt, 1957:27.

MATERIAL EXAMINED.—ALABAMA: *DeKalb Co.*: Stanley-Carden Cave (Ala. #730), ca. 4 mi. NE of Ft. Payne, 1 sex ?, 3 Sept. 1967, J. E. and M. R. Cooper, (LMF 192); 1 ♂, 1 ♀, 16 July 1967, S. B. Peck and A. Fiske, (LMF 283); *Jackson Co.*: Boulder Sink Cave (Ala. #1020), ca. 3 mi. WSW of Scottsboro, 1 ♂, Aug. 1969, J. Wilson and R. C. Graham, (LMF 199); Crossings Cave (Ala. #310), 2 ♂, 1 ♀, 9, 18 May 1972, S. B. and J. Peck, (LMF 329); Crow Creek Cave (Ala. #1074), ♂♂♀♀, Dec. 1969, R. C. Graham and J. Wilson, (LMF 552); Edgefield Cave (Ala. #614), 3 mi. NNE of Stevenson, 1 ♂, 1 Aug. 1967, S. B. Peck and A. Fiske, (LMF 262); 1 ♀, 11 Aug. 1967, S. B. Peck and A. Fiske, (LMF 233); Fern Cave (Ala. #597), Lower level, ♂♂♀♀, July 1969, R. C. Graham, (LMF 557); Indian Rock Cave (Ala. #535), ca. 4 mi. W. of Tupelo, 1 ♂, 11 May 1969, R. C. Graham and W. Torode, (LMF 197); Larkins Cave (Ala. #537), Limrock, 5 ♂, 11 ♀, 23 Aug., 14 Sept. 1968, S. B. Peck, (LMF 241); Limrock Blowing Cave (Ala. #311), 1 ♀, 1 June 1968, R. C. Graham, (LMF 195); New Fern Cave System (Ala. #597N), 1.5 mi. ENE of Paint Rock, on Nat Mtn., 1 ♀, 10 Feb. 1969, R. C. Graham, (LMF 198); ♂♂♀♀, July 1969, W. Torode, (LMF 555); Pig Pen Cave (Ala. #519), 2 mi. NNE of Woodville, 1 ♀, 26 Nov. 1967, "Elliot Res.", (LMF 196); 2 ♀, 28 July 1967, S. B. Peck and A. Fiske, (LMF 251); Roadside Cave (Ala. #826), 2 ♂, 1 ♀, 7 July 1973, S. B. Peck, (LMF 358); Rousseau Cave (Ala. #81), 2 mi. N. of Garth, 1 ♂, 1 ♀, 6 Sept. 1965, S. B. Peck, (LMF 253); Russell Cave (Ala. #169), Pig Entrance, Russell Cave National Monument, 1 ♂, 17 Aug. 1967, S. B. Peck and A. Fiske, (LMF 277); Sheldons Cave (Ala. #166), 1 mi. N. of Scottsboro, 1 ♀, trap #225, 4-8 Apr. 1967, S. B. Peck, (LMF 243); 1 ♂, 2 ♀, 25 Jan. 1967, S. B. Peck, (LMF 258); Valhalla Cave (Ala. #691), ♂♂♀♀, Apr. 1970, C. Warren, Hall, and W. Torode, (LMF 553); Madison Co.: Cave Spring Cave (Herrin or Hering Cave) (Ala. #6), 5 mi. N. of New Hope, 1 ♂, 1 ♀, 30 Dec. 1965, J. E. and M. R. Cooper, (LMF 30); 1 ♀, 16 July 1972, L. M. and B. L. Ferguson, (LMF 207); 3 ♂, 4 ♀, 1 immature, 20 July 1972, L. M. and B. L. Ferguson, (LMF 208); 1 ♂, 1 ♀, 1 immature, 30 Aug. 1968, S. B. Peck, (LMF 231); 1 ♂, 2 ♀, 25 Aug., 11 Sept. 1968, S. B. Peck, R. C. Graham, and A. Dobson, (LMF 232); Grayson Spring Cave (Ala. #122), ca. 2 mi. SW of Gurley, 1 ♂, 15 Dec. 1968, R. C. Graham, (LMF 194); Styles Spring Cave (Ala. #968), Sharp Cove, Hollytree Quadrangle, 1 ♂, 31 Aug. 1968, S. B. Peck, R. C. Graham, and W. Torode, (LMF 245); Marshall Co.: Cathedral Caverns (Ala. #165), 1 ♀, 15 July 1972, L. M. and B. L. Ferguson and K. Gurley,

(LMF 206); 3 ♂, 5 ♀, 20 July 1972, L. M. and B. L. Ferguson, (LMF 209); 2 ♂, 17 Aug. 1965, S. B. Peck, (LMF 263); 2 ♂, 5 ♀, 20-30 Dec. 1965, carrion trap, S. B. Peck, (LMF 272); Kellers Cave (Ala. #326), 2.5 mi. S. of New Hope, 1 ♂, 26 June 1967, S. B. Peck and A. Fiske, (LMF 278); Kristy's Cave (Ala. #700), ♂♂♀♀, Aug. 1969, J. Wilson, (LMF 554); ♂♂♀♀, 16 Apr. 1970, W. Torode, (LMF 558); Ledbetter Cave (Ala. #319), ca. 5 mi. WNW of Colombus City, 1 ♀, 1 immature 1 sex ?, 27 Jan. 1968, G. Wyman and R. C. Graham, (LMF 193); Roaring River Cave (Ala. #1031), ♂♂♀♀, Sept. 1969, R. C. Graham, (LMF 556). TENNESSEE: Franklin Co.: Caroline Cove Cave, 5.5 mi. SE of Belvidere, 2 ♂, 4 ♀, 11 July 1967, S. B. Peck and A. Fiske, (LMF 244); 1 ♂, 31 July 1967, S. B. Peck and A. Fiske, (LMF 249); Putnam Spring Cave, 9 mi. S. of Belvidere, 1 ♂, 9 July 1967, S. B. Peck and A. Fiske, (LMF 276); Ranie Willis Cave, 1 mi. SE of Anderson, 1 ♂, 2 ♀, 11 Aug. 1967, S. B. Peck and A. Fiske, (LMF 280); Round Mountain Cave, 7 mi. NE of Estill Fork, 1 ♀, 1 immature, 30 July 1967, S . B. Peck and A. Fiske, (LMF 238); Grundy Co.: Partin Spring Cave, 1 ♀, 5 July 1973, S. B. Peck, (LMF 348).

Most material will be deposited in the American Museum of Natural History, the remainder in the author's collection.

DIAGNOSIS.—Distinguished from other species of *Litocampa* in the United States by presence of 3 + 3 and 1 + 1 (ma) macrochaetae on meso- and metanota, one dorsal macrochaeta on femur III, tibia III with 1 or 2 ventral macrochaetae, claws with well-developed latero-tergal crests, medial anterior macrochaetae present on abdominal tergites I-VII, 1 + 1 lateral anterior and 2 + 2 lateral posterior macrochaetae on tergites V-VII (lateral posterior macrochaetae often lacking on tergite V), 7 + 7 macrochaetae on urosternite I, and 4 + 4 well differentiated macrochaetae on urosternites II-VII.

DESCRIPTION.--Corresponding to the description of *Plusiocampa valentinei* (2 female specimens) by Condé (1949b).

Size: Males: body length, 4.2-6.2 mm; head width, 0.60-0.82 mm; pronotal width, 0.42-0.54 mm. Females: body length, 6.0-7.8 mm; head width, 0.73-0.98 mm; pronotal width, 0.52-0.66 mm. Immatures: body length, 4.0-4.7 mm; head width, 0.54-0.57 mm; pronotal width, 0.35-0.37 mm.

Head: Antennal segments, 40-49. Number of segments of 19 complete antennae, disregarding 1 antenna of 42 segments which was paired with an antenna of 47 segments and was obviously regenerating, are as follows:

No. segments:		40	41	42	43	44	45	46	47	48	49
Frequency:	♂	0	0	0	1	0	1	3	3	0	0
	♀	1	1	0	1	1	0	0	2	4	0
	immature	0	0	0	0	0	0	0	0	0	1

Length of longest antenna 7.94 mm, or about 1.03 times body length. Antennal segment III with ventral bacilliform sensillum, inserted between phaneres *d* and *e*: M*a*, M*b*, seta *c*, M*d*, sen. (long, exceeding

FIGURE 34.--*Litocampa valentinei* (Condé). A, latero-anterior sensillum of left labial palp; B, pronotum (clothing setae omitted); C-E, *ma*, *la*, and *lp* of pronotum; F, mesonotum (clothing setae omitted). Female (7.8 mm; head width, 0.98 mm), Cave Spring Cave, Alabama.

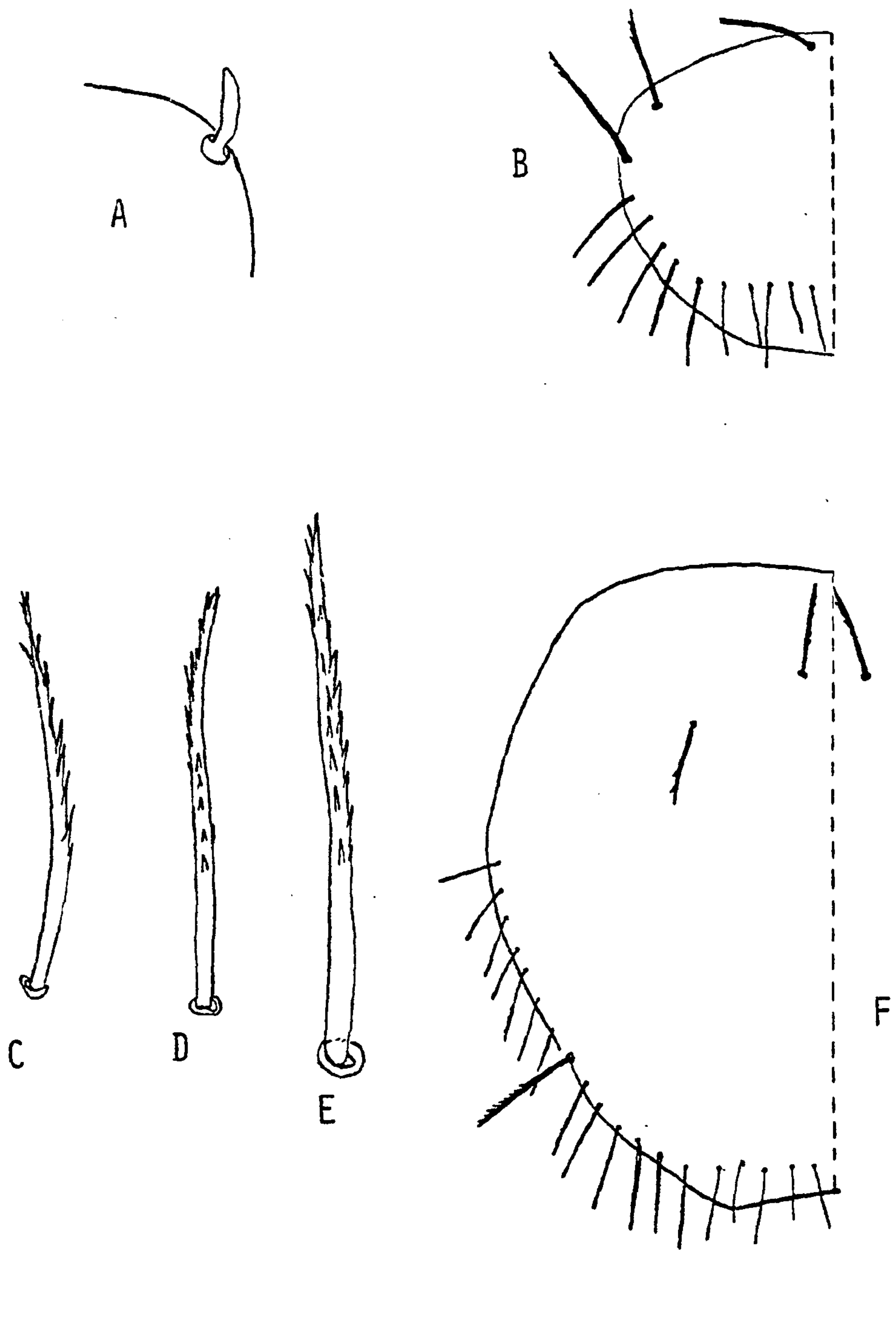
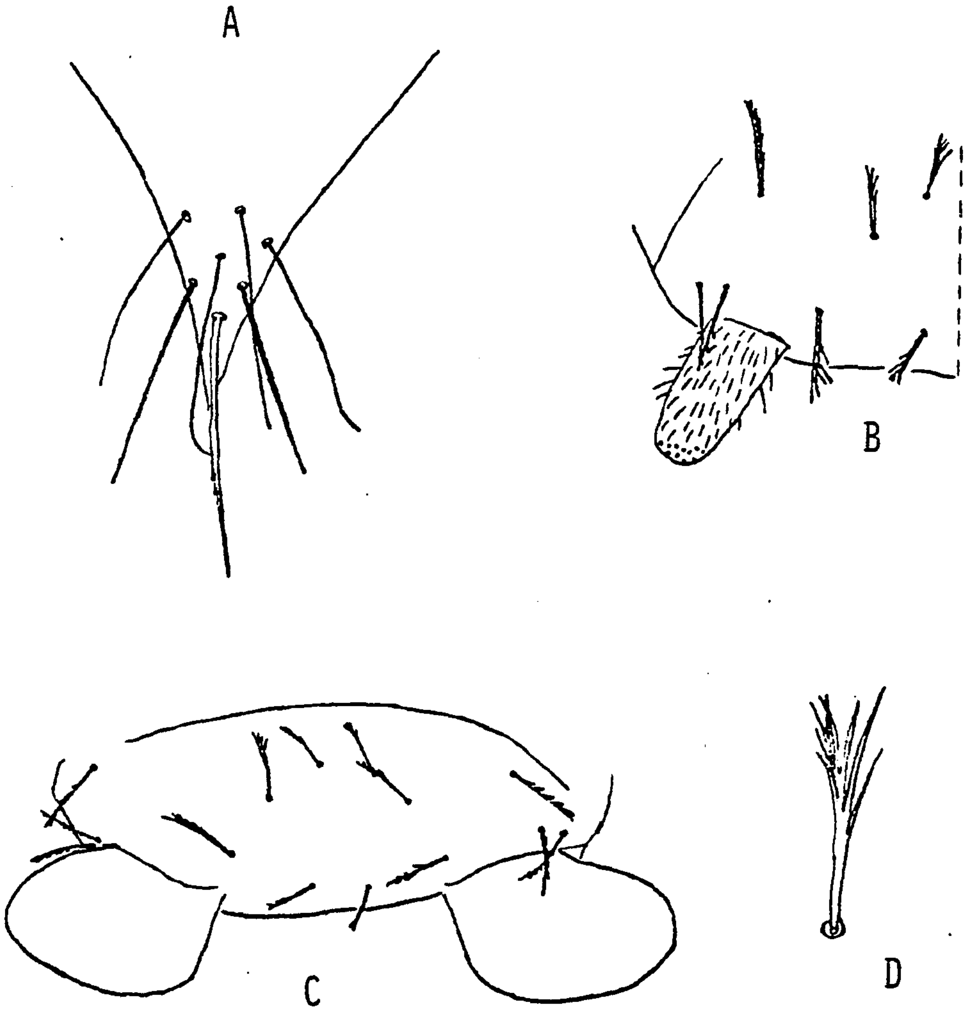

A
B
C
D
E
F

FIGURE 35.--*Litocampa valentinei* (Condé). A, supra-anal valvule; B, urosternite I of female; C, urosternite I of male; D, macrochaeta at base of eversible vesicle of urosternite VI. C, male (6.2 mm; head width, 0.82 mm); others, female (7.8 mm; head width, 0.98 mm), Cave Spring Cave, Alabama.


A
B
C
D

distal border of segment), seta e, Mf, Mg, Mh; length of d 1.9 times c; b with 3 distal barbules, other phaneres smooth. Cupuliform organ of apical segment with 10 sensilla. Latero-anterior sensillum of labial palp subcylindrical, weakly curved towards sagittal plane. Posterior mental setae smooth; lateral submental macrochaetae smooth. Thorax: Clothing setae smooth; notal chaetotaxy 3 + 3, 3 + 3, 1 + 1. Lengths and ratios of macrochaetae of mature specimens from Cave Spring Cave, as follows:

	ma	la	lp	ma/la	lp/ma
Th. I	86-151	97-162	162-211	0.89-0.93	1.39-1.88
Th. II	108-151	92-130	140-184	1.17-1.18	1.21-1.30
Th. III	76-103	—	—	—	—

Mesonotum: ma/Sep ma-ma, 1.65-1.67; ma/Sep ma-la, 0.82-1.00; la/Sep ma-la, 0.71-0.85; lp_I/lp_{II}, 1.15. Pronotum of largest female with 5 + 7 barbed lateral posterior marginal setae and 9 smooth medial posterior marginal setae; mesonotum with 7 + 7 lateral, 10 medial posterior marginal setae; metanotum with 6 + 7 lateral, 13 medial posterior marginal setae.

Presternite of prosternum with 2 + 2 M; prosternite with 4 + 4 barbed precoxal M; 5 + 5 smooth precoxal setae; 1 + 1 subcoxal M; 2 + 2 lp. Meso-and metasternite with 4 + 4 barbed precoxal M; 5 + 5 smooth precoxal setae; 1 + 1 ma; 1 + 1 la; 1 + 1 subcoxal M; 2 + 2 lp on mesosternite, 1 + 1 lp on metasternite.

Length of leg III about 45 percent of body length, reaching abdominal segment VII. Femur I without dorsal macrochaetae; femurs II and III with one dorsal macrochaeta. Dorsal macrochaeta inserted on proximal half of femur III, 0.66 times width of femur at point of insertion; barbed on distal 0.6. Tibia III length 9.6 times width, with one, sometimes two, bifurcated ventral macrochaeta with 1 small barb proximal to bifurcation.

Abdomen: Distribution of tergal macrochaetae:

	ma	la	lp
Ab. I-IV	1 + 1	0	0
Ab. V	1 + 1	1 + 1	0 (2 + 2)
Ab. VI-VII	1 + 1	1 + 1	2 + 2
Ab. VIII	1 + 1	0	3 + 3
Ab. IX	1 + 1	0	5 + 5 (total)

Lengths and ratios of certain tergal macrochaetae, as follows:

	ma	la	lp_1	lp_2	ma/D	ma/Sep ma-ma
Ab. I	54-76	--	--	--	0.34-0.43	0.50-0.53
Ab. V	70-92	76-108	--	--	0.40-0.57	0.52-0.57
Ab. VII	76-103	124-189	162-227	162-248	0.51-0.67	0.51-0.67

Abdominal tergite VI with up to 18 posterior marginal setae separating sublateral posterior macrochaetae nearest sagittal plane; tergite VII with up to 15 such setae; VIII with 14; IX with 16. Supra-anal valvule with 5-7 setae; subapical seta barbed.

Urosternite (coxosternite) I with 7 + 7 differentiated macrochaetae, 4 + 4 on middle portion. Posterior margin without glandular setae on males and females. Lateral subcoxal appendages subcylindrical, small, among females; appendages greatly expanded laterally on mature males. Females with glandular setae only on tip of appendages.

Urosternites II-VII with 4 + 4 well differentiated macrochaetae, with branches and barbs; 1 + 1 weakly differentiated macrochaetae inserted internally and externally at base of each stylus. Urosternite VIII with 1 + 1 macrochaetae. Genital papilla of male with up to 18 short setae encircling gonopore.

Length of longest cercus about 1.58 times body length, composed of a base, subdivided into 15 secondary segments, and 8 primary segments. Segmental lengths (in mm): base = 0.25, 0.13, 0.16, 0.19, 0.23, 0.26, 0.29, 0.33, 0.34, 0.36, 0.38, 0.42, 0.43, 0.45, 0.47; primary segments = 0.65, 0.76, 0.81, 0.90, 1.03, 1.09, 1.17, 1.29. Covering of base and proximal segments composed of long macrochaetae, length of macrochaetae about 2.2 times width of segments. Numerous barbs on distal half or two-thirds. Proximal primary segments with whorls of 7 barbed macrochaetae, long smooth setae, and 11 short subapical setae. Penultimate segment length 21.6 times width, with approximately 9 whorls of macrochaetae, alternating with whorls of long smooth setae near distal whorls of macrochaetae; macrochaetae with long subapical barb and numerous barbules below subapical; 11 short subapical setae. Macrochaetae of apical segment arranged in approximately 10 whorls, length of macrochaetae about 4.0 times width of segment; macrochaetae smooth in apical whorl only.

TYPE LOCALITY.—Condé (1949b) did not designate a type locality; he had specimens from two caves in Madison Co., Alabama: Cave Spring Cave and Aladdin Cave. These caves are approximately 15 miles apart and are developed in the same geologic horizon, the Upper Mississippian-aged Gasper formation (Jones and Varnedoe, 1968; Varnedoe, 1973; 1975). Cave Spring Cave (also known as Hering Cave) is a long cave (6100 feet of passages surveyed) from which issues a large subterranean stream. Aladdin Cave had been sealed shut by its owner at the time of my visit in 1972, in a desperate attempt to prevent further vandalism to what seems to have been a beautiful small cave (479 feet long). Therefore, I am designating as the type locality the first locality mentioned by Condé (1949b), Cave Spring Cave, due in part to its size and its continued availability to zoological investigators.

DISTRIBUTION AND ECOLOGY.—*Litocampa valentinei* is known from 24 caves in northeastern Alabama and 5 caves in southern Tennessee. These caves are in the Cumberland Plateau, and all but one, Stanley-Carden Cave, DeKalb Co., Alabama, are north of the Tennessee River.

Members of this species appear to be quite active and agile. They were observed congregating on over-hanging walls at bait stations in two Alabama caves: Cave Spring Cave in Madison County and Cathedral Caverns in Marshall County. I suspect that this agility may be an adaptation for escaping periodic flooding of the cave passages. Both caves have active streams (Jones and Varnedoe, 1968; Kenneth Gurley, personal communication). This ability or tendency to walk on over-hanging walls (in a sense, the ceiling) has not been reported by others or observed by the writer in other species of campodeids.

Litocampa pecki, new species

(Figs. 36-37)

MATERIAL EXAMINED.--GEORGIA: Chattooga Co.: Blowing Spring Cave, 12 ♂, 9 ♀, 1 immature (holotype and paratypes), 11 June 1967, J. R. Holsinger, S. B. Peck, A, Fiske, and R. A. Baroody, (LMF 25); Walker Co.: Pettijohn Cave, 5 mi. SW of LaFayette, 3 ♂, 9 ♀, 10 June 1967, J. R. Holsinger, S. B. Peck, A. Fiske, and R. A. Baroody, (LMF 22); 4 ♀, 10-21 June 1967, (trap #272), S. B. Peck and A. Fiske, (LMF 23).

Holotype (LMF 25-2) and paratypes to be deposited in the American Museum of Natural History.

DIAGNOSIS.--Distinguished from other species of Litocampa in the United States by presence of 3 + 3 and 1 + 1 macrochaetae on meso- and metanota, one dorsal macrochaeta on femur III, tibia III with 1 ventral macrochaeta, claws with well-developed latero-tergal crests, medial anterior macrochaetae present on abdominal tergites I-VII, 1 + 1 lateral posterior macrochaetae on tergite V, 1 + 1 lateral anterior and 2 + 2 lateral posterior macrochaetae on tergites VI-VII, 7 + 7 macrochaetae on urosternite I, and 4 + 4 well differentiated macrochaetae on urosternites II-VII.

DESCRIPTION.--Morphologically similar to Litocampa valentinei, differing primarily by the chaetotaxy of the abdominal tergites and by the number of antennal segments.

FIGURE 36.--Litocampa pecki, new species. A, metathoracic leg; B, dorsal macrochaeta of femur III; C, anterior distal margin of femur III. Female (6.6 mm; head width, 0.89 mm), Blowing Spring Cave, Georgia.

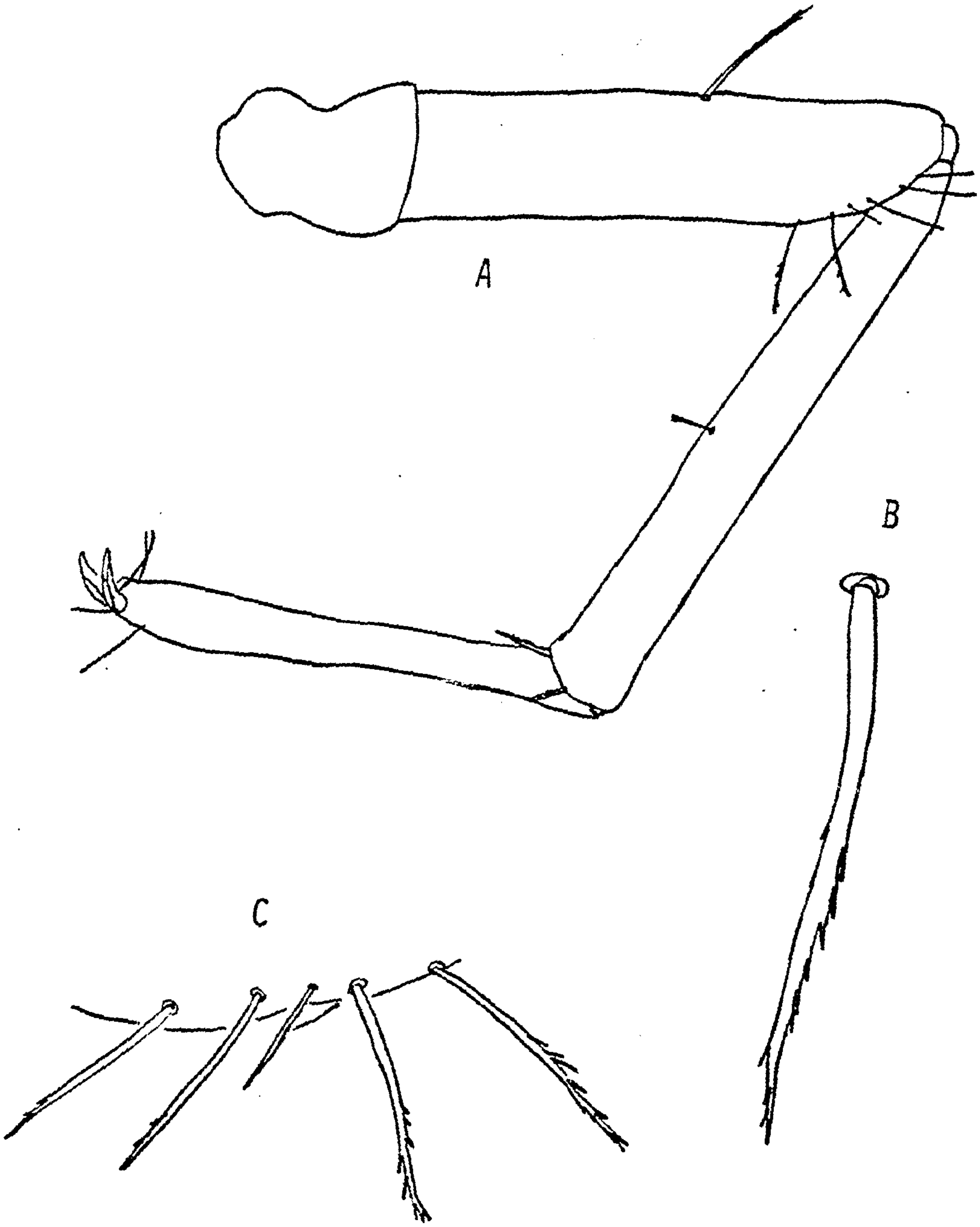
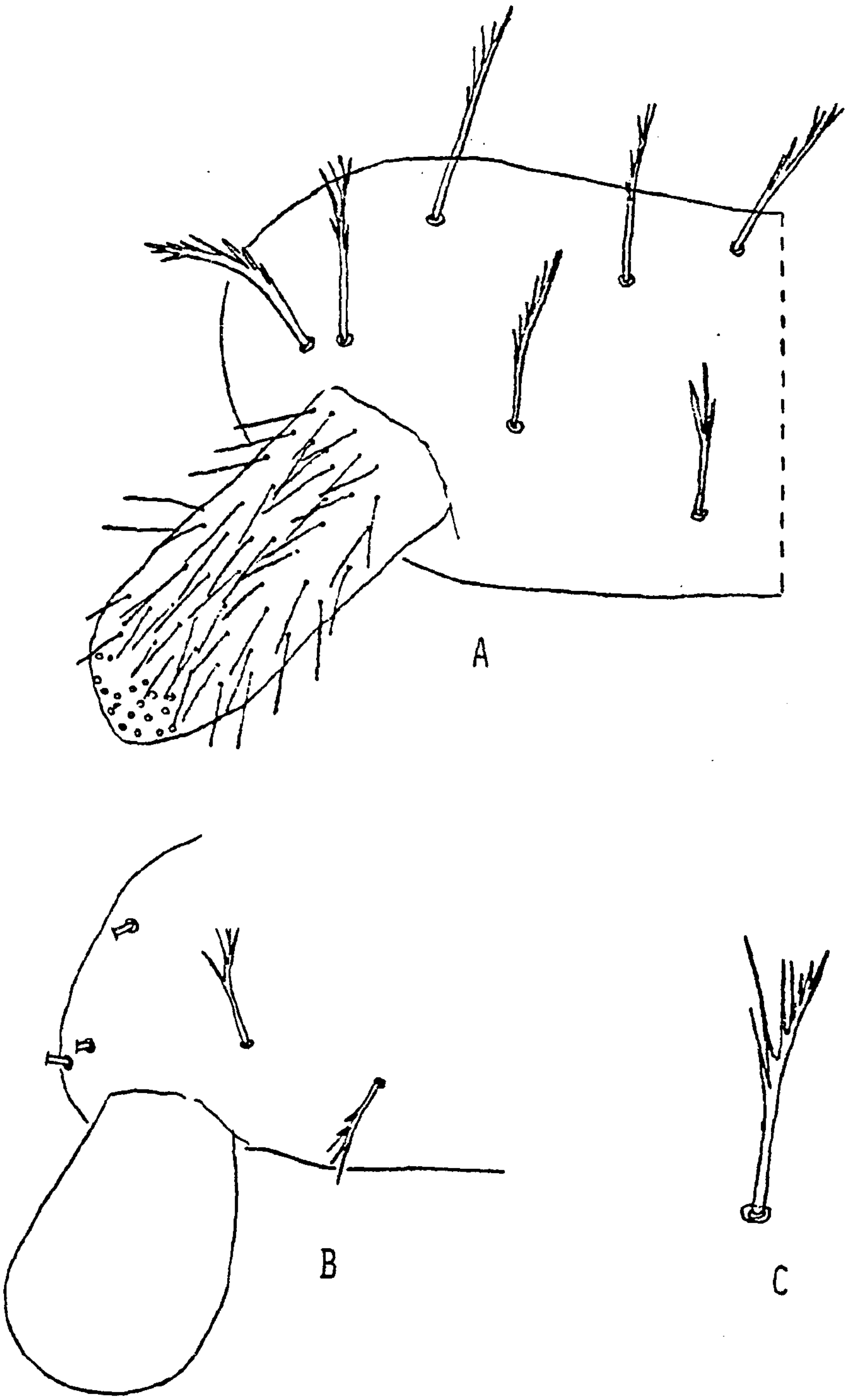

A
B
C

FIGURE 37.—*Litocampa pecki*, new species. A, urosternite I of female; B, latero-posterior part of urosternite I of male, showing shape of subcoxal appendage; C, macrochaeta at base of eversible vesicle of urosternite VI. B, male (6.1 mm; head width, 0.74 mm); others, female (6.6 mm; head width, 0.89 mm), Blowing Spring Cave, Georgia.


A
B
C

Size: Males: body length, 3.2-6.1 mm; head width 0.55-0.74 mm; pronotal width, 0.36-0.55 mm. Females: body length, 3.9-6.6 mm; head width, 0.62-0.89 mm; pronotal width, 0.43-0.65 mm. Immature: body length, 4.0 mm; head width, 0.55 mm; pronotal width, 0.33 mm.

Head: Antennal segments, 34-38. Number of segments of 33 complete antennae, disregarding 2 antennae of 31 and 34 segments which were obviously regenerating, as follows:

		34	35	36	37	38
No. segments:		34	35	36	37	38
Frequency:	♂	0	0	0	11	7
	♀	3	2	0	7	1
	immature	0	0	0	0	2

Length of longest antenna 5.87 mm, or about 89 percent of body length, reaching abdominal segment X. Antennal segment III with ventral bacilliform sensillum, inserted between phaneres d and e: Ma, Mb, seta c, Md (long, smooth), sen. (long, exceeding distal border of segment, seta e (weakly developed), Mf, Mg, Mh; length of d 1.84 times c; b and h with 1-3 distal barbules, other macrochaetae smooth. Segment X length 1.4-1.8 times width. Cupuliform organ of apical segment with 10 sensilla. Latero-anterior sensillum of labial palp subcylindrical, weakly curved. Posterior mental setae smooth; lateral submental macrochaetae smooth.

Thorax: Clothing setae smooth; notal chaetotaxy 3 + 3, 3 + 3, 1 + 1. Lengths and ratios of macrochaetae of mature specimens from Blowing Spring Cave, as follows:

	ma	la	lp	ma/la	lp/ma
Th. I	92-130	92-173	157-248	0.69-1.00	1.71-2.09
Th. II	81-119	86-124	151-227	0.94-1.05	1.50-1.95
Th. III	70-86	—	—	—	—

Mesonotum; ma/Sep ma-ma, 0.92-0.94, ma/Sep ma-la, 0.69-1.00; la/Sep ma-la, 0.69-0.89; lp_{I}/lp_{II}, 1.00-1.07. Pronotum with 3 + 3 barbed lateral posterior marginal setae and 8 medial posterior marginal setae; mesonotum with 1 + 1 to 4 + 4 lateral, 10 to 12 medial posterior marginal setae; metanotum with 1 + 1 to 3 + 3 lateral, 11 to 13 medial posterior marginal setae.

Presternite of prosternum with 2 + 2 M; prosternite with 4 + 4 barbed precoxal M; 5 + 6 smooth precoxal setae; 1 + 1 subcoxal M; 2 + 2 lp or 1 + 1 lp and 1 + 1 slp. Meso- and metasternite with 4 + 4 barbed precoxal M; 6 + 6 smooth precoxal setae; 1 + 1 ma; occasionally 1 mi; 1 + 1 la; 1 + 1 subcoxal M; 1 + 1 lp.

Length of leg III about 45 percent of body length, reaching abdominal segment IX. Femur I without dorsal macrochaetae; femurs II and III with one dorsal macrochaeta. Dorsal macrochaeta inserted on distal half of femur III, 1.1-1.3 times width of femur at point of insertion; barbed on distal 0.6. Femur III with 4 anterior marginal macrochaetae; 2 most ventral barbed on their distal 60 to 70 percent; distal pair smooth. Tibia III length 8.4-9.2 times width, with one smooth bifurcated ventral macrochaeta; tibial spurs with 2 rows of long barbs. Posterior claw longer than anterior; latero-tergal crests well-developed; flange on posterior claw. Pretarsal appendices long, slender, and smooth; length exceeding tip of claws.

Abdomen: Distribution of tergal macrochaetae:

	ma	la	lp
Ab. I-IV	1 + 1	0	0
Ab. V	1 + 1	0 (1 + 1)	1 + 1
Ab. VI-VII	1 + 1	1 + 1	2 + 2
Ab. VIII	0	0	3 + 3
Ab. IX	0	0	5 + 5 (6 + 6) (total)

Lengths and ratios of certain tergal macrochaetae, as follows:

	ma	la	lp_1	lp_2	ma/D	ma/Sep ma-ma
Ab. I	43-65	—	--	—	0.32-0.61	0.36-0.52
Ab. V	54-90	—(97-119)	76-178	—	0.50-0.63	0.50-0.53
Ab. VII	59-86	92-184	151-270	140-265	0.50-0.88	0.47-0.64

Abdominal tergite V with up to 17 posterior marginal setae separating sublateral posterior macrochaetae nearest sagittal plane; tergite VI with up to 16 such setae; VII with 15; VIII with 13; IX with 13. Supra-anal valvule with 1 barbed subapical seta, 1 or 2 smooth setae or setiform sensilla.

Urosternite (coxosternite) I with 7 + 7 differentiated macrochaetae, 4 + 4 on middle portion; 1 + 1 submacrochaetae at latero-posterior angle of urosternite of males and females. Posterior margin without glandular setae on both sexes. Lateral subcoxal appendages cylindrical, moderately long, among females; rounded, expanded laterally on mature males. Females with glandular setae only on tip of appendages.

Urosternites II-VII with 4 + 4 well differentiated macrochaetae, with branches and barbs. Apical seta of styli smooth and with 2 short basal branches, proximal branch about one-third length of distal; subapical seta smooth or 1-2 distal barbules; medial ventral seta bifurcated; clothing setae smooth. Stylus VII length 4.1-5.5 times width; apical seta about 45 percent as long as stylus. Urosternite VIII with 1 + 1 macrochaetae. Genital papilla of largest male with 17 short setae encircling gonopore.

Length of cercus of largest male 1.60 times body length, composed of a base, subdivided into 4 secondary segments, and 16 primary segments. Segmental lengths (in mm): base = 0.77 mm; primary segments = 0.28, 0.31, 0.36, 0.42, 0.46, 0.51, 0.55, 0.58, 0.59, 0.62, 0.63, 0.64, 0.66, 0.75, 0.84, 0.85. Covering of base and proximal segments composed of long macrochaetae, length of macrochaetae about 2.8 times width of segments, long barbs on distal half. Proximal primary segments with whorls of 7 barbed macrochaetae, long smooth setae, and 7 short subapical setae. Penultimate segment length 25.8 times width, with 5 whorls of macrochaetae, alternating with whorls of long smooth setae; macrochaetae smooth or with 2-3 distal minute barbules on macrochaetae of proximal two whorls; 10 short subapical setae. Macrochaetae of apical segment arranged in 5 whorls, length of macrochaetae about 6.6 times width of segment, alternating with whorls of long smooth setae; all macrochaetae smooth.

REMARKS.--Except for the ma macrochaetae, the la are the more constant macrochaetae on abdominal tergite V of Litocampa valentinei, with an occasional lp. In L. pecki, again except for the ma, the lp are the more constant macrochaetae on tergite V, with an occasional la. Also, when the la are present on tergite V of L. pecki, there is usually an extra pair of lp on abdomen IX.

TYPE LOCALITY.--Blowing Spring Cave, 2.5 miles east of Cloudland, in Chattooga Co., Georgia.

DISTRIBUTION AND ECOLOGY.--Litocampa pecki is known from two caves, approximately 10 miles apart, in the Valley and Ridge Province of Georgia. Both caves are in part of the drainage system of the Coosa River, which flows southwest and south, eventually into the Gulf of Mexico. Lookout Mountain appears to separate this species from its closest related species, L. valentinei, which occurs in neighboring DeKalb Co., Alabama. The range of L. pecki probably extends southwest for some distance into Alabama.

ETYMOLOGY.--It is a real pleasure to name this species in honor of Dr. Stewart B. Peck. Dr. Peck, a leader in the study of cavernicole zoogeography, has collected cave organisms from many regions. He collected this species as well as many others which are new to science.

The *Henroti* Group

DIAGNOSIS.--Antennal segment III with phanere *e*, meso- and metanotum with 1 + 1 lateral posterior macrochaetae and with or without 1 + 1 medial posterior macrochaetae, pretarsal claws with large latero-tergal crests, abdominal tergites V-VII with 2 + 2 lateral posterior macrochaetae, medial anterior macrochaetae on abdominal tergite I-VII, urosternite I with 7 + 7 macrochaetae, and posterior margin of urosternite I of males without glandular setae.

REMARKS.--The two species currently included in this group are quite similar morphologically, with the exception of the presence of medial posterior macrochaetae on the meso- and metanota of *L. henroti*. The known range of *L. henroti* is quite small and limited to Madison County, Alabama. *L. davisi* is not as specialized morphologically and is more widespread, being found in caves of the Eastern Highland Rim of Tennessee, southeast across the Cumberland Plateau of Tennessee, and in caves in the Valley and Ridge Province of Georgia and Alabama.

Key to the Species of the *Henroti* Group

1. Meso- and metanota with 1 + 1 medial posterior macrochaetae.........
 ....*L. henroti*

1'. Meso- and metanota without medial posterior macrochaetae...........
 ....*L. davisi*, new species

Litocampa henroti (Condê)

(Figs. 38-39)

Plusiocampa henroti Condê, 1949:127-130, figs. 2A-E, 3. [Shelta Cave, Madison Co., Alabama; repository unknown]; 1956:62, fig. 15B, 128, 132, 170, 175, 187; Nicholas, 1960:140; Ferguson, 1973:18-19; (in press).

Litocampa (*Tychocampa*) *henroti* (Condê), Paclt, 1957:27.

MATERIAL EXAMINED.--ALABAMA: *Madison Co.*: Shelta Cave (Ala. #4), 5 ♂, 2 ♀, at bait near lake, 21 July 1972, L. M. and B. L. Ferguson, (LMF 210); 1 ♂, 25 Sept. 1966, L. Hubricht, (LMF 256); Green Grotto (Ala. #229), 1 ♀, 22 Mar. 1966, S. B. Peck, (LMF 261); Matthews Cave (Ala. #23) 4 mi. E. of Madison, 1 ♀, 22 Aug. 1968, S. B. Peck, (LMF 236).

Two topotypes retained in author's collection; remaining material deposited in American Museum of Natural History.

DIAGNOSIS.--Distinguished from other species of *Litocampa* in the United States by presence of 4 + 4 (*ma*, *mp*, *la*, *lp*) and 3 + 3 (*ma*, *mp*, *lp*) macrochaetae on meso- and metanota, one dorsal macrochaeta on femur III, tibia III generally with 2 (occasionally with 1) ventral macrochaetae, claws with well-developed latero-tergal crests, medial anterior macrochaetae present on abdominal tergites I-VII, 1 + 1 lateral posterior macrochaetae on tergite IV, 1 + 1 lateral anterior and 2 + 2 lateral posterior macrochaetae on tergites V-VII, 7 + 7 macrochaetae on urosternite I, and 4 + 4 well differentiated macrochaetae on urosternites II-VII.

DESCRIPTION.--Chaetotaxy identical to that described for Plusiocampa henroti (young male specimen) by Condé (1949b). The meristic variation, measurements, and additional characters for 10 specimens belonging to this species are given below.

Size: Males: body length, 4.8-6.8 mm; head width, 0.60-0.80 mm; pronotal width, 0.42-0.56 mm. Females: body length, 6.3-8.0 mm; head width, 0.79-0.96 mm; pronotal width, 0.56-0.64 mm.

Head: The number of segments on complete antennae are as follows:

No. segments:		33	34	35	36	37	38	39	40
Frequency:	♂	0	1	0	0	0	4	0	0
	♀	1	0	0	2	1	0	0	1

Of these, one antenna with 34 segments and another with 36 were apparently regenerating (they were paired with antennae of 38 and 40 segments, respectively). Length of longest antenna 7.58 mm, or about 95 percent of body length, reaching abdominal segment X. Antennal segment III with ventral bacilliform sensillum, inserted between phaneres d and e: Ma, Mb (with 5 barbules), seta c, Md (with 2 barbules), sen. (long, but not exceeding distal border of segment), M e, Mf, Mg, Mh; other phaneres smooth; length of d 1.8 times c. Cupuliform organ of apical segment with 14 sensilla. Latero-anterior sensillum of labial palp subcylindrical, weakly curved, slightly

FIGURE 38.--*Litocampa henroti* (Condé). A, pronotum; B-D, *ma*, *la*, and *lp* of pronotum; E, mesonotum; F, supra-anal valvule. Female (8.0 mm; head width, 0.96 mm), Shelta Cave, Alabama.

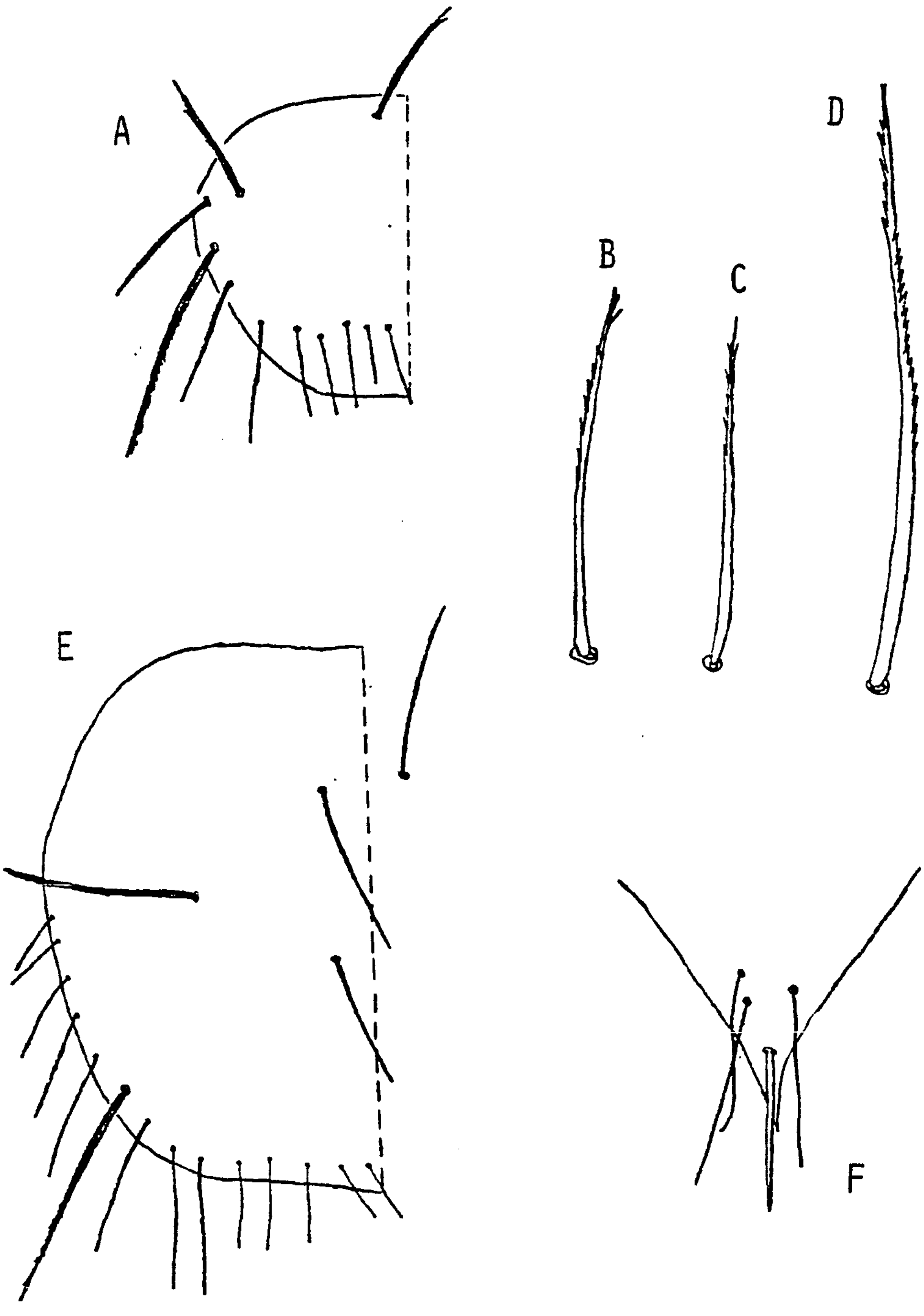
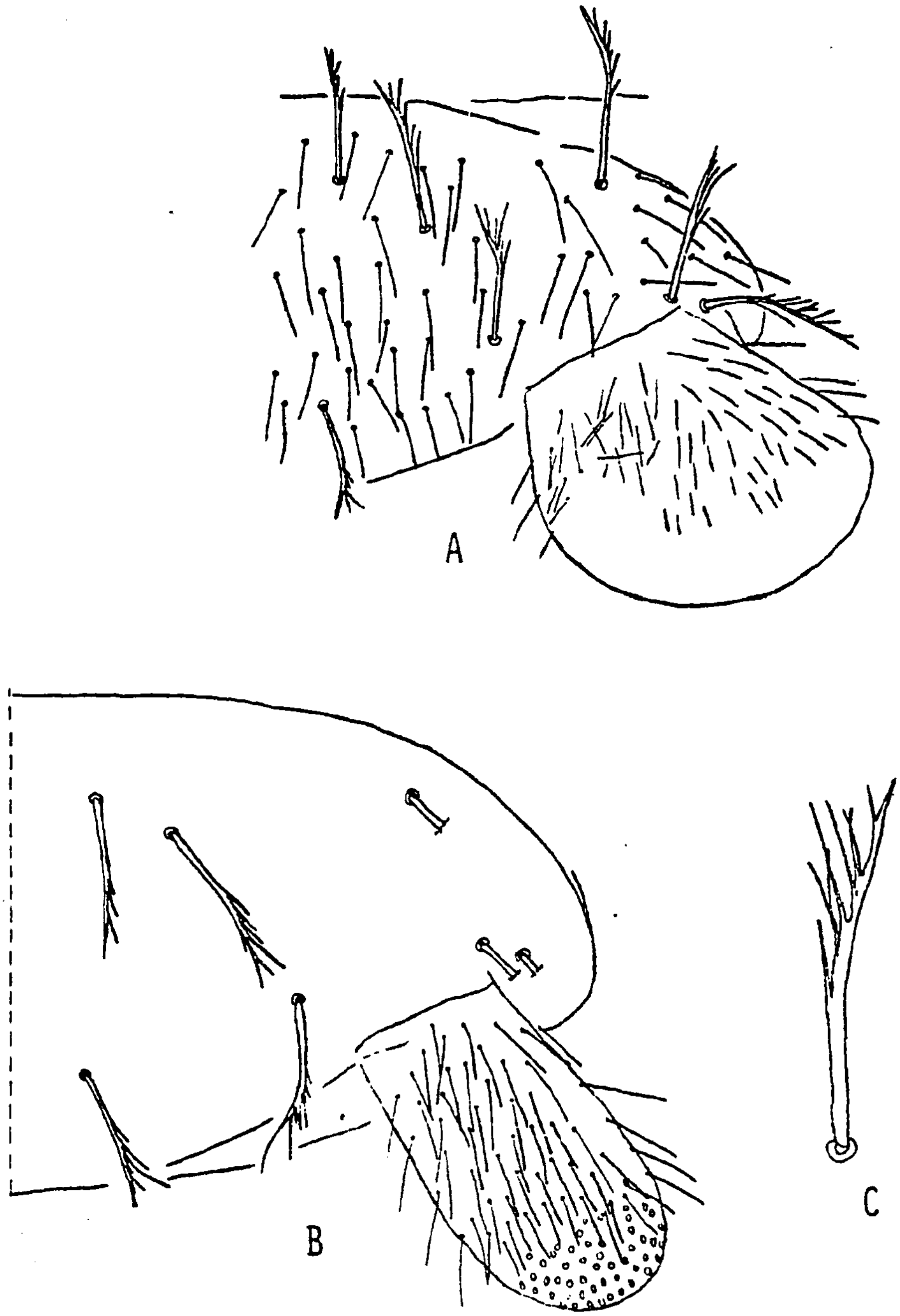

A
B
C
D
E
F

FIGURE 39.--Litocampa henroti (Condé). A, urosternite I of male (glandular setae on tip of subcoxal appendage not shown); B, urosternite I of female (clothing setae of sternite proper not shown); C, macrochaeta at base of left eversible vesicle of urosternite VII. A, male (6.8 mm; head width, 0.80 mm); others, female (8.0 mm; head width, 0.96 mm), Shelta Cave, Alabama.


A
B
C

swollen in middle region. Posterior mental setae smooth; lateral submental macrochaetae smooth.

Thorax: Clothing setae smooth; notal chaetotaxy 3 + 3, 4 + 4, 3 + 3. Lengths and ratios of macrochaetae of specimens from Shelta Cave, as follows:

	ma	mp	la	lp	ma/la	lp/ma
Th. I	162-238	--	140-205	238-246	1.15-1.16	1.45-1.47
Th. II	189-265	133-205	194-297	265-362	0.89-0.97	1.37-1.40
Th. III	194-281	157-227	--	248-351	--	1.25-1.28

Mesonotum: ma/Sep ma-ma, 2.23-2.50; ma/Sep ma-la, 1.09-1.21; la/Sep ma-la, 1.22-1.24; lp_I/lp_{II}, 0.90-0.96; lp_{II}/lp_{III}, 1.03-1.07. Pronotum with 2 + 3 barbed lateral posterior marginal setae and 4 to 8 medial posterior marginal setae; mesonotum with 2 + 2 to 3 + 3 lateral, 6 to 10 medial posterior marginal setae; metanotum with 1 + 1 lateral, 6 to 8 medial posterior marginal setae.

Presternite of prosternum with 2 + 2 M; prosternite with 4 + 4 barbed precoxal M; 4 + 4 to 5 + 5 smooth precoxal setae; 1 + 1 subcoxal M; 2 + 2 lp. Meso- and metasternite with 4 + 4 barbed precoxal M; 3 + 3 to 5 + 5 smooth precoxal setae; 1 + 1 ma; 1 + 1 la; 1 + 1 subcoxal M; 2 + 2 lp on mesosternite, 1 + 1 lp on metasternite.

Length of leg III about 40 percent of body length, reaching abdominal segment VII. Femur I without dorsal macrochaetae; femurs II and III with one dorsal macrochaeta. Dorsal macrochaeta inserted on distal half of femur III, 1.3 times width of femur at point of insertion; barbed on its distal 0.6. Tibia III length 9.0 times width, with one or two bifurcated ventral macrochaeta with several small barbs proximal to bifurcation.

Abdomen: Distribution of tergal macrochaetae:

	ma	la	lp	
Ab. I-III	1 + 1	0	0	
Ab. IV	1 + 1	0	1 + 1	
Ab. V-VII	1 + 1	1 + 1	2 + 2	
Ab. VIII	0	0	3 + 3	
Ab. IX	0	0	5 + 5	(total)

Lengths and ratios of certain tergal macrochaetae, as follows:

	ma	la	lp_1	lp_2	ma/D	ma/Sep ma-ma
Ab. I	146-227	--	--	--	1.31-1.42	1.50-1.69
Ab. IV	140-232	--	227-335	--	1.26-1.53	1.23-1.30
Ab. VII	146-243	162-270	248-346	243-346	1.50-1.59	1.32-1.50

Abdominal tergite IV with up to 13 posterior marginal setae separating sublateral posterior macrochaetae nearest sagittal plane; tergite V with up to 13 such setae; VI with 12; VII with 14; VIII with 9; IX with 11. Supra-anal valvule with barbed subapical seta, and up to 2 setiform sensilla and 1 barbed proximal seta.

Urosternite (coxosternite) I with 7 + 7 differentiated macrochaetae, 4 + 4 on middle portion; 1 + 1 submacrochaetae at latero-posterior angle of urosternite of males and females. Posterior margin without glandular setae on both sexes. Lateral subcoxal appendages of females subcylindrical, expanded slightly at tip; broader, more rounded on mature males; glandular setae only at tips of appendages.

Urosternites II-VII with 4 + 4 well differentiated macrochaetae, with branches and barbs; 1 + 1 weakly differentiated macrochaetae inserted internally and externally at base of each stylus.

Urosternite VIII with 1 + 1 macrochaetae. Genital papilla of male with up to 14 short setae encircling gonopore.

Longest cerci compared to body length are those of smallest female, length about 1.58 times body length, composed of a base, subdivided into 4 secondary segments, and 15 primary segments. Segmental lengths (in mm): base = 0.14, 0.17, 0.18, 0.27; primary segments = 0.29, 0.29, 0.40, 0.46, 0.50, 0.55, 0.59, 0.63, 0.65, 0.70, 0.73, 0.80, 0.86, 0.88, 0.85. Covering of base and proximal segments composed of long macrochaetae, length of macrochaetae about 3.1 times width of segments, 2 rows of small barbs on distal half. Proximal primary segments with whorls of 7 barbed macrochaetae, long smooth setae, and 7-9 short subapical setae. Penultimate segment length 23.3 times width, with 6-7 whorls of macrochaetae, sometimes alternating with whorls of long smooth setae; macrochaetae with long subapical barb and several barbules below subapical; 8 short subapical setae. Macrochaetae of apical segment arranged in 6 whorls, length of macrochaetae about 4.9 times width of segment, alternating with whorls of long and short smooth setae; all macrochaetae with several distal barbules except on 2 apical whorls.

Incertae sedis.--A single female specimen from Monteagle Saltpeter Cave, 4.5 miles southeast of Monteagle, Marion Co., Tennessee, collected by Stewart B. Peck on August 28, 1968, may belong to this species. However, there are only 2 small medial posterior macrochaetae on the mesonotum and apparently none on the metanotum. The abdominal chaetotaxy also differs slightly from either *Litocampa henroti* or *L. davisi* by having only 1 + 1 *ma* on tergite IV.

TYPE LOCALITY.--Shelta Cave, located in Huntsville, Madison Co., Alabama. The cave has 2500 feet of passages and is developed in the Middle Mississippian-aged Warsaw limestone (Varnedoe, 1973; 1975). Shelta Cave is a nature preserve owned by the National Speleological Society, and has a diverse and unique fauna. It is notable for its three species of crayfish and the rare atyid shrimp, *Palaemonias alabamae*.

DISTRIBUTION AND ECOLOGY.--*Litocampa henroti* is known from three caves, all in a relatively small area of Madison Co., Alabama. Matthews Cave is located 4.8 miles southeast of Shelta Cave and is developed in the Middle Mississippian-aged Tuscumbia limestone, which is stratigraphically below the Warsaw limestone (Schuchert, 1943). Matthews Cave has 1752 feet of surveyed passages and reportedly has a rich fauna including crayfish, *Pseudanophthalmus* beetles, spiders, and fish (Jones and Varnedoe, 1968). Green Grotto is located approximately 12 miles southwest of Shelta Cave and is small (304 feet long). It is developed in the Upper Mississippian-aged Bangor limestone (Varnedoe, 1973; 1975).

All three caves are situated in the Highland Rim, north of the Tennessee River.

Litocampa davisi, new species

(Figs. 40-41)

MATERIAL EXAMINED.--TENNESSEE: *Warren Co.*: Cumberland Caverns, near old Higginbottom entrance, 1 ♂ (holotype), 27 July 1972, L. M. and B. L. Ferguson, (LMF 216); 1 ♀ (paratype), near commercial entrance, 26 July 1972, L. M. and B. L. Ferguson, (LMF 215); *Bedford Co.*: Ward Cave, 1 ♂, 7 July 1972, T. C. Barr, Jr., (LMF 590). ALABAMA: *Blount Co.*: Bryant Cave (Ala. #355), 3 ♀, 19 Mar. 1966, S. B. Peck, (LMF 269); Catfish Cave (Ala. #640), 0.5 mi. SW of Bangor, 1 ♂, 28 June 1967, S. B. Peck and A. Fiske, (LMF 265); *DeKalb Co.*: Goat House Cave (Ala. #741), 4 mi. N. of Sulfur Springs, 1 ♀, late 1968, T. Iles, (LMF 191); *Jackson Co.*: Salt River Cave (Ala. #221), 4 mi. W. of Anderson, Tenn., 1 ♂, 17 Aug. 1967, S. B. Peck and A. Fiske, (LMF 248). GEORGIA: *Dade Co.*: Morrison Cave, 2 mi. E. of Trenton, 1 ♂, 1 ♀, 1 immature, 13 July 1967, S. B. Peck and A. Fiske, (LMF 28); *Walker Co.*: Bible Springs Cave, 2 mi. NE of Lookout, 2 ♀, 11 June 1967, J. R. Holsinger, S. B. Peck, A. Fiske, and R. A. Baroody, (LMF 26); Mt. Cove Farm Cave, 1.5 mi. E. of Lookout, 1 ♂, 1 ♀, 11 June 1967, J. R. Holsinger, S. B. Peck, A. Fiske, and R. A. Baroody, (LMF 24).

Paratype retained in the author's collection; holotype and remaining material deposited in American Museum of Natural History.

DIAGNOSIS.--Distinguished from other species of *Litocampa* in the

United States by presence of 3 + 3 and 2 + 2 macrochaetae on meso- and metanota, one dorsal macrochaeta on femur III, tibia III with 1 ventral macrochaeta, claws with well-developed latero-tergal crests, medial anterior macrochaetae present on abdominal tergites I-VII, 1 + 1 lateral anterior and 1 + 1 lateral posterior macrochaetae on tergite IV, 1 + 1 lateral anterior and 2 + 2 lateral posterior macrochaetae on tergites V-VII, 7 + 7 macrochaetae on urosternite I, and 4 + 4 well differentiated macrochaetae on urosternites II-VII.

DESCRIPTION.--Morphologically similar to *Litocampa henroti*, differing primarily in the thoracic tergal and sternal chaetotaxy and in the lengths of cercal segments.

Size: Male: body length, 5.0 mm; head width, 0.66 mm; pronotal width, 0.47 mm. Female: body length, 6.6 mm; head width, 0.87 mm; pronotal width, 0.57 mm.

Head: Among type specimens from Cumberland Caverns, male has 2 complete antennae with 41 segments each; female has 1 complete antenna with 38 segments. Length of longest antenna 5.04 mm, or about 1.02 times body length. Antennal segment III with ventral bacilliform sensillum, inserted between phaneres *d* and *e*: M*a*, M*b*, seta *c*, M*d* (with 3 distal barbs), sen. (long, reaching distal border of segment), M *e* (short, smooth), M*f*, M*g*, M*h*; length of *d* 1.81 times *c*; *b* with 5-6 distal barbules, other macrochaetae smooth. Cupuliform organ of apical segment with 12 sensilla.

Frons with 3 macrochaetae on rostrum, barbed on their distal

FIGURE 40.--*Litocampa davisi*, new species. A, latero-anterior sensillum of right labial palp; B, pro-, meso-, and metanotum (clothing setae not shown); C, pronotum (clothing setae diagrammatic); D, metathoracic leg; E, dorsal macrochaeta of femur III; F, anterior distal margin of femur III; G, ventral macrochaeta of tibia III; H, tibial spur; I, posterior pretarsal claw. Female (6.6 mm; head width, 0.87 mm), Cumberland Caverns, Tennessee.

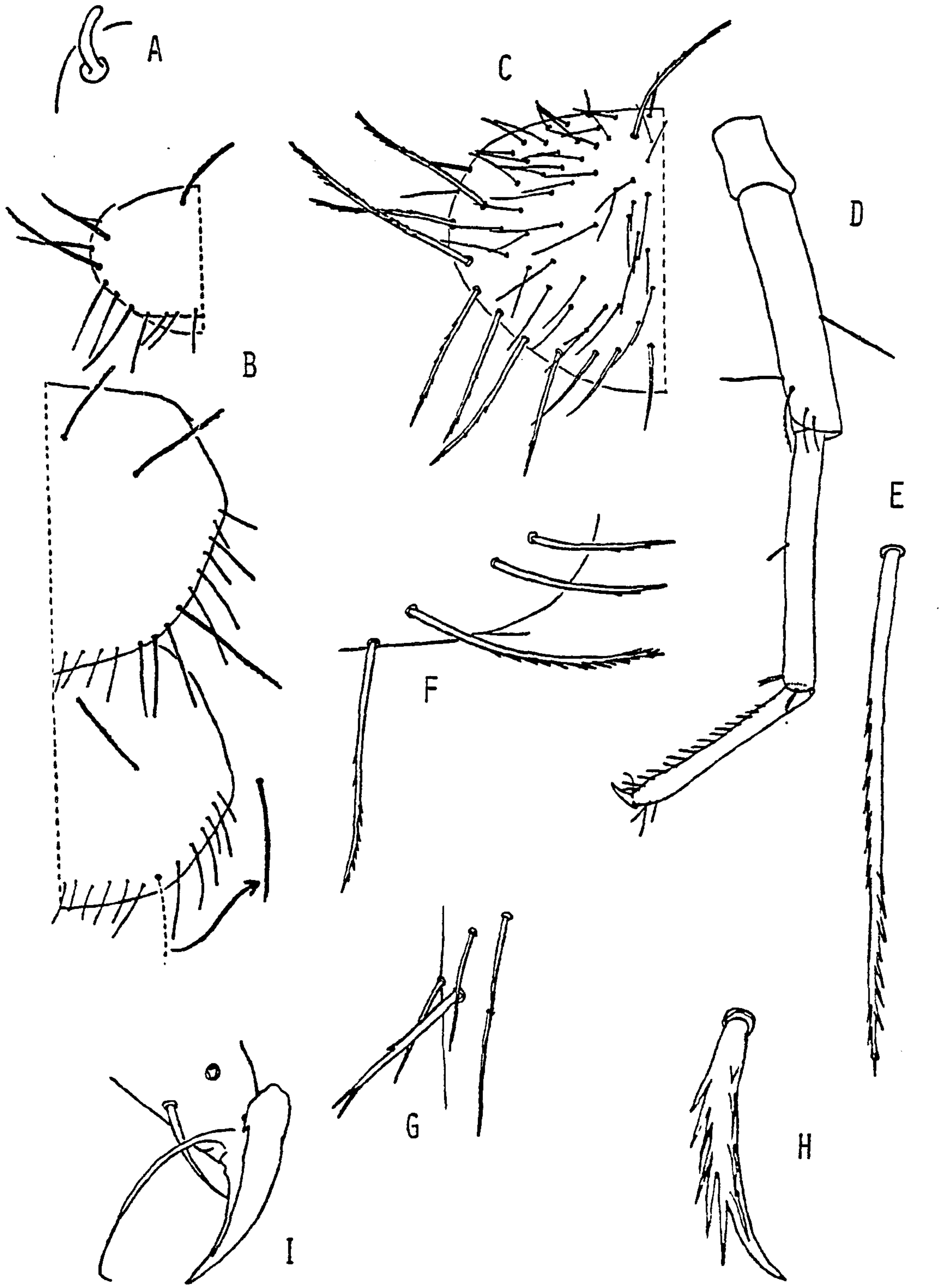

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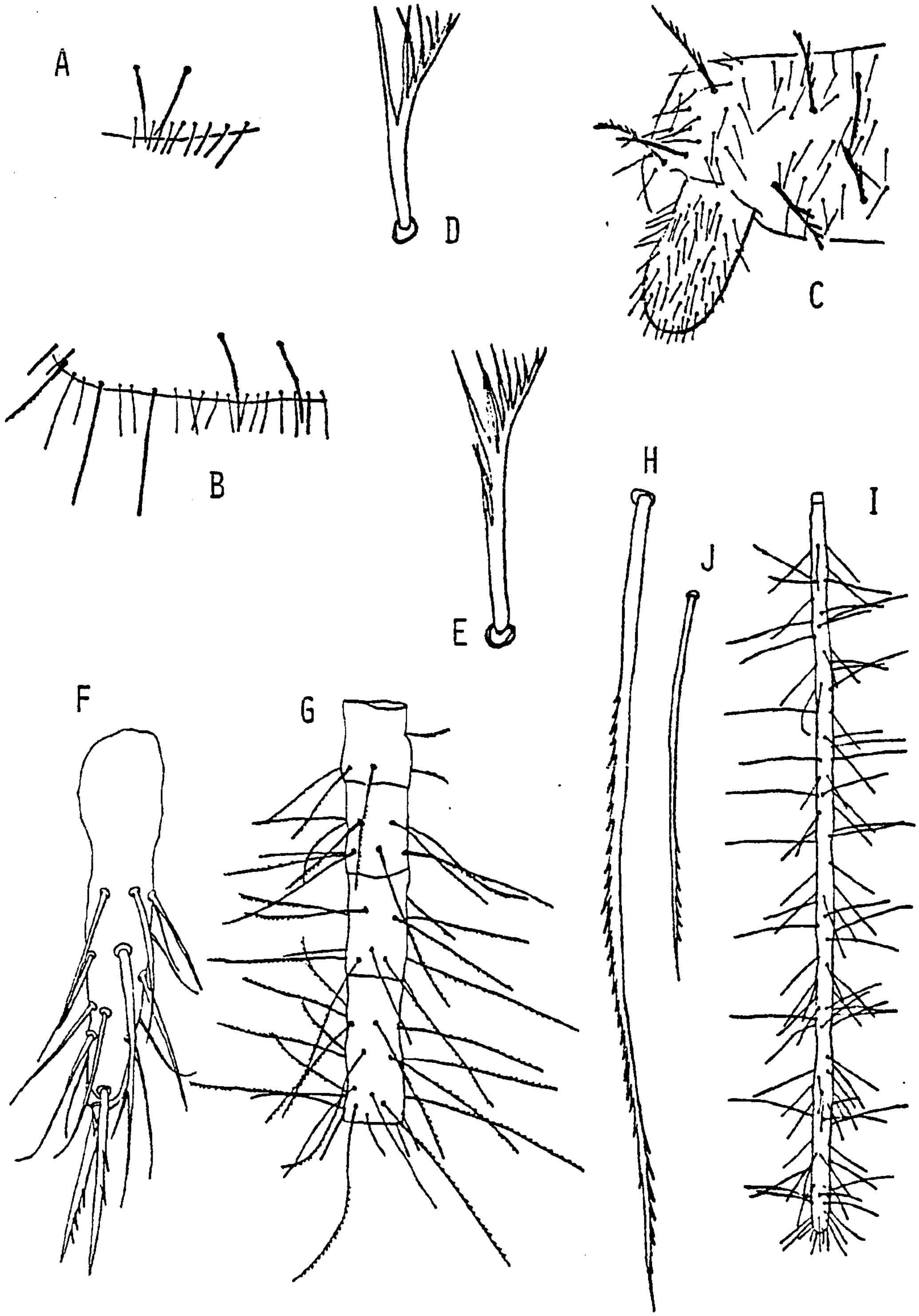
FIGURE 41.--Litocampa davisi, new species. A, medial anterior macrochaetae relative to posterior marginal setae of abdominal tergite I; B, tergite VII; C, urosternite I of female; D-E, medial posterior macrochaeta and macrochaeta at base of eversible vesicle of urosternite VII; F, left stylus of urosternite VII (ventral view); G, base of cercus; H, macrochaeta from cercal base; I, apical segment of cercus; J, macrochaeta from distal segment of cercus. Female (6.6 mm; head width, 0.87 mm), Cumberland Caverns, Tennessee.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two-thirds; anterior macrochaeta 1.3-1.5 times length of posterior pair. Macrochaetae bordering line of insertion of antennae 3 + 3; anterior macrochaeta approximately two-thirds as long as intermediate; posterior macrochaetae 1.3 times length of anterior; all three macrochaetae barbed on distal two-thirds. Macrochaetae anterior to arms of epicranial suture, near sagittal plane, 1 + 1; equal in length to macrochaetae at anterior border of antennal insertion; barbed on distal half. Occipital setae with many barbs on their distal 0.8; length about 55 percent as long as pronotal lp. Latero-anterior sensillum of labial palp subcylindrical, slightly curved towards sagittal plane. Posterior mental setae smooth; lateral submental macrochaetae smooth.

Thorax: Clothing setae smooth; notal chaetotaxy 3 + 3, 3 + 3, 2 + 2. Lengths and ratios of macrochaetae of specimens from Cumberland Caverns, as follows:

	ma	la	lp	ma/la	lp/ma
Th. I	184-200	189-211	286-313	0.95-0.97	1.56-1.57
Th. II	194-221	248-275	319-329	0.78-0.80	1.49-1.64
Th. III	216-243	--	313-319	--	1.29-1.48

Mesonotum: ma/Sep ma-ma, 2.56-2.57; ma/Sep ma-la, 1.14-1.24, la/Sep ma-la, 1.42-1.59; lp_I/lp_{II}, 0.90-0.95; lp_{II}/lp_{III}, 1.00-1.05. Pronotum with 3 + 4 barbed lateral posterior marginal setae and 8 medial posterior marginal setae; mesonotum with 3 + 3 lateral, 8 medial posterior marginal setae; metanotum with 1 + 1 lateral, 9 medial posterior marginal setae.

Presternite of prosternum with 2 + 2 M; prosternite with 4 + 4 barbed precoxal M; 3 + 4 smooth precoxal setae; 1 + 1 subcoxal M; 2 + 2 lp. Meso- and metasternite with 5 + 5 barbed precoxal M; 5 + 5 smooth precoxal setae; 1 + 1 ma; 1 + 1 la; 1 + 1 subcoxal M; 2 + 2 lp on mesosternite, 1 + 1 lp and 1 + 1 slp on metasternite.

Length of leg III about 58 percent of body length, reaching abdominal segment X. Femur I without dorsal macrochaetae; femurs II and III with one dorsal macrochaeta. Dorsal macrochaeta inserted on distal half of femur III, 1.6 times width of femur at point of insertion; barbed on distal three-fourths. Femur III with 4 anterior marginal macrochaetae; 2 most ventral barbed on distal two-thirds; distal pair with 2-3 barbs. Tibia III length 10.2 times width, with one bifurcated ventral macrochaeta with 1 small barb proximal to bifurcation; tibial spurs with 2 rows of long barbs. Posterior claw longer than anterior; latero-tergal crests well developed; flange on posterior claw. Pretarsal appendices long, slender, and smooth; length exceeding tip of claws.

Abdomen: Distribution of tergal macrochaetae:

	ma	la	lp	
Ab. I-III	1 + 1	0	0	
Ab. IV	1 + 1	0	1 + 1	
Ab. V-VII	1 + 1	1 + 1	2 + 2	
Ab. VIII	0	0	3 + 3	
Ab. IX	0	0	5 + 5	(total)

Lengths and ratios of certain tergal macrochaetae, as follows:

	ma	la	lp_1	lp_2	ma/D	ma/Sep ma-ma
Ab. I	162-189	--	--	--	1.46-1.50	1.58-1.59
Ab. IV	167-184	--	259-281	--	1.26-1.35	1.26-1.29
Ab. VII	173-194	189-221	302-324	302-319	1.64-1.78	1.23-1.38

Abdominal tergite IV with up to 11 posterior marginal setae separating sublateral posterior macrochaetae nearest sagittal plane; tergite V with up to 12 such setae; VI with 12; VII with 13; VIII with 9; IX with 14. Supra-anal valvule with 1 barbed subapical medial seta, 1 + 1 barbed lateral subapical setae, 2 + 2 smooth lateral setae, 1 medial setiform sensillum.

Urosternite (coxosternite) I with 7 + 7 differentiated macrochaetae, 4 + 4 on middle portion; 1 + 1 submacrochaetae at latero-posterior angle of urosternite of male and female. Posterior margin without glandular setae on both sexes. Lateral subcoxal appendages subcylindrical on female, broader on mature male. Female with glandular setae on tip of appendages only.

Urosternites II-VII with 4 + 4 well differentiated macrochaetae, with branches and barbs; 2 + 2 weakly differentiated macrochaetae inserted internally and externally at base of each stylus. Apical seta of styli with 4 distal barbules and 2 short basal branches, proximal branch about one-half length of distal; subapical seta with 2 long barbs; medial ventral seta forked; clothing setae smooth. Stylus VII length 4.2 times width; apical seta about 45 percent as long as stylus; with 15 clothing setae and setiform sensilla. Urosternite VIII with 1 + 1 macrochaetae. Genital papilla of male with 16 short setae encircling gonopore.

Length of longest cercus 1.48 times body length, composed of a base, subdivided into 4 secondary segments, and 10 primary segments. Segmental lengths (in mm): base = 0.15, 0.17, 0.21, 0.30; primary segments = 0.35, 0.45, 0.54, 0.69, 0.80, 0.99, 1.09, 1.32, 1.43, 1.50. Covering of base and proximal segments composed of long macrochaetae, length of macrochaetae about 3.8 times width of segments, many barbs on distal two-thirds. Proximal primary segments with whorls of 7 barbed macrochaetae, long smooth setae, and 7 short subapical setae. Penultimate segment length 37.7 times width, with 7 whorls of macrochaetae, alternating with whorls of long smooth setae; macrochaetae with many barbules on distal half; 7 short subapical setae. Macrochaetae of apical segment arranged in 8 whorls, length of macrochaetae about 4.9 times width of segment, alternating with whorls of long and short smooth setae; macrochaetae of apical whorl smooth; macrochaetae of penultimate whorl with 2-5 barbules; 7-10 barbules on other macrochaetae.

Variation: Male from Cumberland Caverns with 2 macrochaetae on each tibia III; female with 1 macrochaeta on each tibia III. Specimens from other caves with 1 macrochaeta on tibia (one specimen with 1 and 2 macrochaetae on tibias).

TYPE LOCALITY.--Cumberland Caverns, 1.8 miles west of Shellsford, in

Warren Co., Tennessee. Cumberland Caverns, with 28 miles of surveyed passages (Looney and Looney, 1980), is the longest known cave system in Tennessee. The cavern is developed in the Middle Mississippian-aged Ste. Genevieve-Gasper limestone (Barr, 1961). Part of the system is shown commercially.

DISTRIBUTION AND ECOLOGY.--Known from 9 caves in Tennessee, Alabama, and Georgia. The range of this species appears to be peripheral to that of *Litocampa henroti* in northern Alabama.

The specimen from Ward Cave, Bedford Co., Tennessee, has many linear septate spores of soil fungi (order Moniliales, family Dematiaceae) in its gut. A female specimen from Bryant Cave, Blount Co., Alabama, has a nematode in its mesothorax (right side).

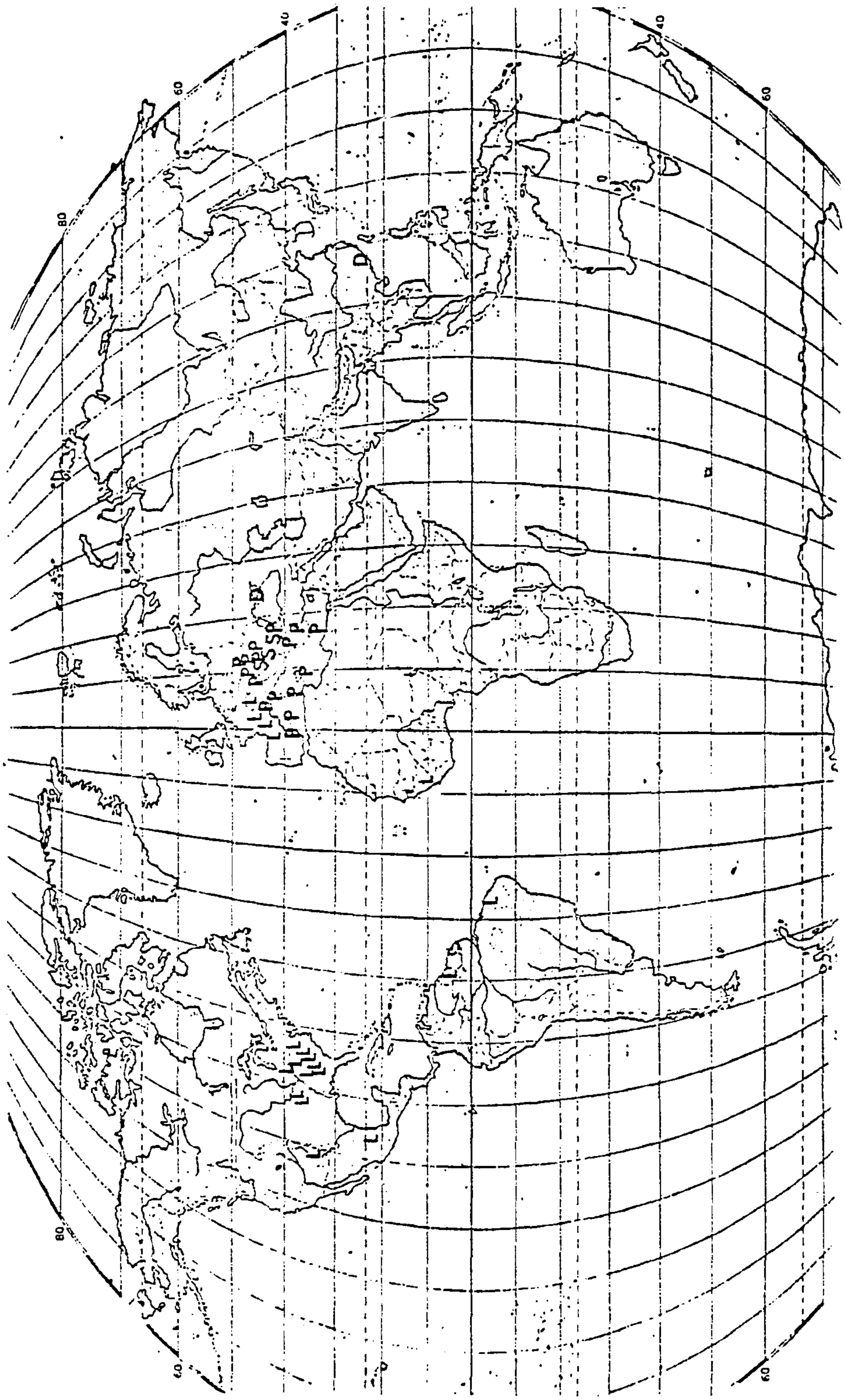
ETYMOLOGY.--It is a pleasure to name this species in honor of Roy A. Davis, owner and operator of Cumberland Caverns.

ZOOGEOGRAPHY

World-Wide Distribution

The genus _Litocampa_ (Appendix II) and the apparently closely related genus _Plusiocampa_, with which the former was originally included as a subgenus (Silvestri, 1933d), show a wide-ranging disjunct distribution. Present day species are found in the southeastern United States, in the Mediterranean region, and elsewhere (Fig. 42). A similar distribution for related cave beetles in the Mediterranean area of Europe and in the southeastern United States prompted René Jeannel in his book _Les Fossiles Vivants des Cavernes_ (1943) to suggest that the widely separated disjunct distribution was due to continental drift. If the disjunct distribution of the _Litocampa_ species on either side of the Atlantic Ocean is due to plate tectonics (of which continental drift is a part), then, the genus _Litocampa_ originated before or during the Mesozoic Era. This would also imply that at least some populations have undergone little morphological change during the last 180 million years, enabling us to still distinguish related species. There is abundant evidence for continental drift from deep sea-floor drilling, paleomagnetism, seismic studies, magnetic anomalies, radioactive dating, and stratigraphy (Dott and Batten, 1981). There is a wealth of paleobiogeographical data as well (Hallam, 1967, 1973).

FIGURE 42.--Geographic distribution of the subgenera of *Plusiocampa* and *Litocampa*. P, *Plusiocampa* (*Plusiocampa*); S, *P.* (*Stygiocampa*); D, *P.* (*Didymocampa*); L, *Litocampa* (*Litocampa*).



But do campodeid diplurans, and in particular the genus Litocampa, represent ancient organisms?

First, the fossil record is of little help in answering this question. The only known campodeid fossil is that of a large individual (a troglobite?) found in onyx marble in Arizona (Pierce, 1951). This specimen is believed to be Miocene in age, or slightly older.

Based on morphology, diplurans have been considered anything from the most primitive living insects, to offshoots of the ancestral stock that gave rise to the true insects. A popular view (Mackerras, 1970) is that they might be an offshoot from protomachiloid stock, but probably diverged from earlier protohexapods that failed to escape the ancestral environment. Paleontologists infer that the Diplura originated in the Late Silurian Period (Tasch, 1973). A fossil collembolan is known from Devonian or Early Mississippian-aged strata. Although the Collembola show considerably more specialized features than do Diplura, the fossil springtail is supposedly very much like the forms living today. Also, there are well known cases of contemporary organisms which have good fossil records back into the Paleozoic Era, and yet show little overall morphological change (e.g., the brachiopod, Lingula, Foraminifera, the horseshow crab, Limulus, the coelacanth, Latimeria, the Ginkgo, cockroaches, etc.). Mayr (1963) suggested that the more "primitive" the group of animals, the greater the number of forms that have existed for long periods of time.

Species of Litocampa are mainly distinguished by the morphology of their pretarsal claws and the possession of a generalized (primitive?) chaetotaxy, which is present in other members of the family. It is likely that these few conditions might survive for long periods of time.

Finally, there is further evidence from the extant Diplura that suggests that they do indeed predate the breakup of Pangaea. Among the primitive Projapygidae only seven species of the genus *Projapyx* are known, from Guinea of West Africa, from neighboring Cameroon, and from Brazil. The nineteen species of the other genus (Smith, 1960) of this family, *Symphylurinus*, are found in China, India, Africa, Australia, South America, and southern Mexico. Except for the latter, all of these land masses are part of the old Gondwanaland. In another primitive dipluran family, Anajapygidae, the five species of *Anajapyx* are found in Italy, Mexico, California, and Guinea of West Africa. This distribution is quite similar to that of the *Litocampa* and *Plusiocampa* combined. The similarities, mentioned earlier under Systematics, between certain species groups of *Litocampa* on either side of the Atlantic, again, might be explained by plate tectonics. Finally, as to the primitiveness of the genus *Litocampa*, Condé (1956a, freely translated) wrote that "their wide distribution on the surface of the earth leads me to believe that these little evolved forms are very ancient, much more so than *Plusiocampa* of the *corcyraea* type, and this agrees well with the interpretation of the colonization of the French caves."

Distribution in the United States

In the contiguous United States, species of _Litocampa_ have been found in the following karst areas (Davies and Le Grand, 1972). In the Appalachian region they are known from caves in the Valley and Ridge Province, the Cumberland Plateau, and even from the Blue Ridge Province of Tennessee and North Carolina (Fig. 43). They are also found in caves of the Highland Rim, the Nashville Basin, the Pennyroyal Plain, the Mammoth Cave Plateau, and the Crawford Upland of the Interior Lowlands. Finally, they are known from the Interior Highlands of Missouri and Arkansas (Fig. 44) and from north-central New Mexico, north of the Pecos Plains (Fig. 45). The presently known locations for each species of a species group yield information which, when combined with the analysis of morphological data that follows, may provide insight into past dispersal patterns.

Bifurcata group.--In this species group, _Litocampa bifurcata_ is the least specialized, or rather, has the least number of cave-associated characters (Ferguson, 1974). Known from seven caves in the eastern most part of the Valley and Ridge Province (Fenneman, 1938) of southwestern Virginia (Figs. 43, 46), it also has the largest range of any species in its group. _Litocampa barryi_ is found in two caves, approximately 40 miles SSW from the southern most location of _L. bifurcata_. Morphologically, _L. barryi_ is closest to _L. bifurcata_; however, the form of its pretarsal claws shows somewhat more cave adaptation than does that of _L. bifurcata_. _Litocampa barryi_ is located in the western

FIGURE 43.--Distribution of the cavernicolous species of *Litocampa* in the eastern United States. Bifurcata Group: A1, *L. bifurcata*; A2, *L. barryi*; A3, *L. holleri*; Fieldingi Group: B, *L. fieldingi*; Keithi Group: C1, *L. inexspectata*; C2, *L. keithi*; Virginiana Group: D1, *L. virginiana*; D2, *L. barringerorum*; D3, *L. cherokeensis*; Cookei Group: E1, *L. jonesi*; E2, *L. cookei*; E3, *L. sperkai*; E4, *L. holsingeri*; Henroti Group: F1, *L. davisi*; F2, *L. henroti*; Valentinei Group: G1, *L. valentinei*; G2, *L. pecki*. (Shown on "Landform Map" by Erwin Raisz).

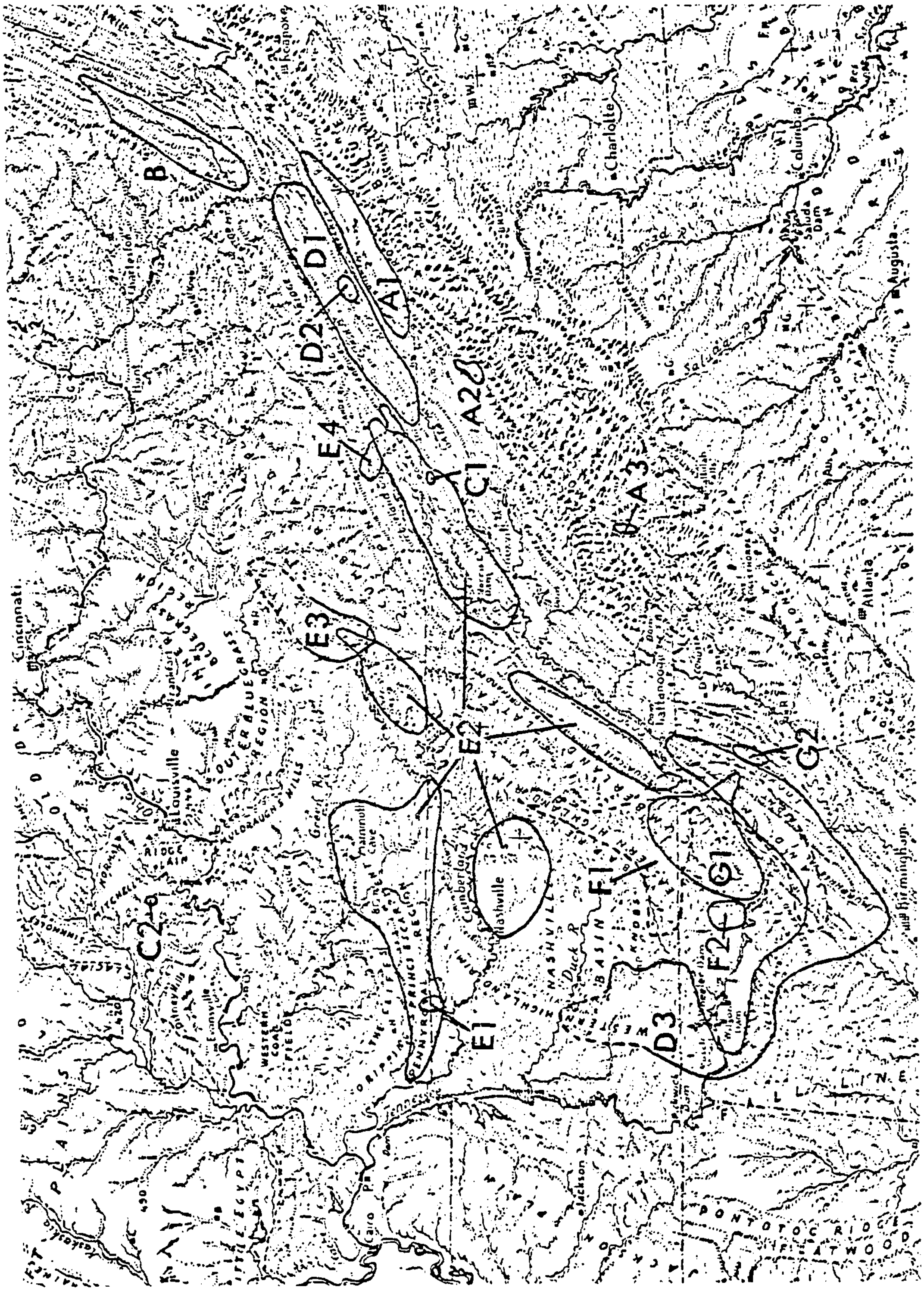

B
D1
D2
A1
A2
A3
E4
C1
E3
E2
E1
C2
F1
F2
G1
G2
D3
Cincinnati
Louisville
Nashville
Charlotte
Columbia
Augusta
Atlanta
Birmingham
Chattanooga
Cairo
OUTER BLUEGRASS REGION
PONTOTOC RIDGE
FLATWOODS

FIGURE 44.--Distribution of the Hawksleyi Group of Litocampa in Missouri and Arkansas: *L. hawksleyi* (H) and *L. ozarkensis* (O). (Shown on "Landform Map" by Erwin Raisz).

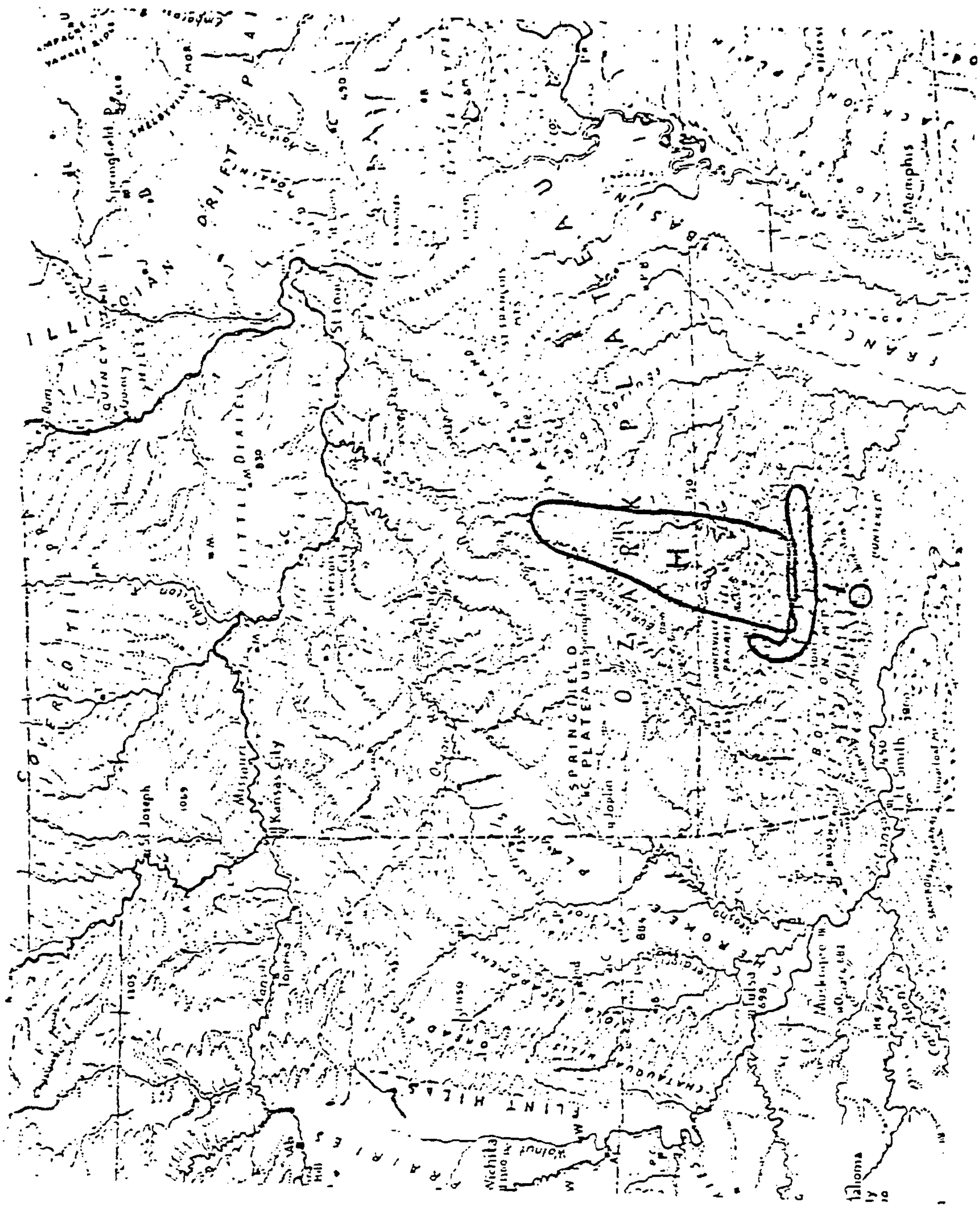
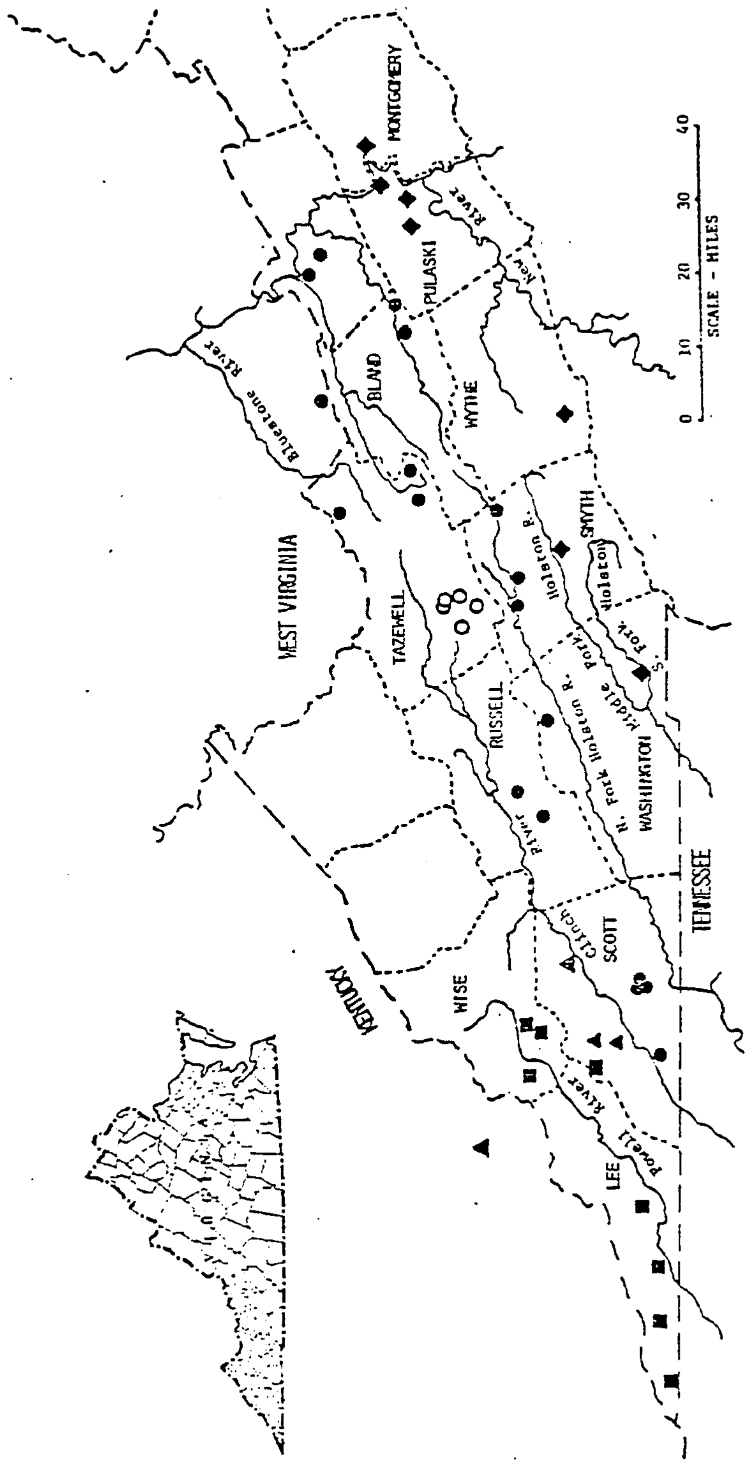

Memphis
St Joseph
Kansas City
Joplin
Tulsa
Muskogee
Wichita
FLINT HILLS

FIGURE 45.--New Mexico and the Guadalupe area of Texas, showing the distribution of _Litocampa welbourni_ (solid circle). (Shown on "Landform Map" by Erwin Raisz).


Gallup
Chama
Santa Fe
Las Vegas
Tucumcari
Albuquerque
Socorro
Deming
El Paso
Alamogordo
Raton
Trinidad
Chacra Mesa
Zuni
Plains of San Augustine
Tularosa Basin
Rio Grande
Toyah Basin
Presidio
Bofecillos Mts
Rio Conchos
Grand Canyon de Sta Helena
Sierra del Carmen
Boquillas C.
Mariscal Mt.
Llano Estacado

FIGURE 46.--Southwestern Virginia and adjacent areas, showing the distribution of species of *Litocampa*: *L. virginiana* (solid circles), *L. barringerorum* (open circles), *L. bifurcata* (diamonds), *L. holsingeri* (triangles), and *L. cookei* (squares).


MONTGOMERY
PULASKI
New River
BLAND
Bluestone River
WYTHE
SMYTH
WEST VIRGINIA
TAZEWELL
Holston R.
Holston
Fork
S.
Middle Fork
RUSSELL
N. Fork Holston R.
WASHINGTON
TENNESSEE
Clinch River
SCOTT
WISE
KENTUCKY
Powell River
LEE
0 10 20 30 40
SCALE - MILES

edge of the Blue Ridge Province in Tennessee (Figs. 43, 47). *Litocampa holleri* is currently known from a single cave in the Nantahala Gorge area of Swain Co., North Carolina. The cave is formed in the Murphy marble. Due to fairly extensive exposures of this formation only five miles to the southwest in Cherokee Co., North Carolina, one might expect to find this species in any caves that may have developed in that area. Due to the presumably high degree of cave adaptation displayed by this species, and the geographical and geological nature of the area, I would not expect it to have an extensive range. The presently known location of *L. holleri* is about 90 miles SSW of that of *L. barryi*. *Litocampa holleri* is found SE of the Great Smoky Mountains and SW of the Nantahala Mountains in the Blue Ridge Province of North Carolina (Figs. 43, 47).

Fieldingi group.--Represented by a single species, this group is known from 13 caves in the Greenbrier River drainage basin. *Litocampa fieldingi* possesses several cave-associated characters. The species is located about 25 miles NW of the present range of *L. bifurcata*, from which I believe it is derived (Figs. 43, 48).

Keithi group.--The eastern most species of the *keithi* group, *L. inexspectata*, is the most generalized of the three species included in the group. This species is known from a single cave in northeastern Tennessee, in the Valley and Ridge Province (Figs. 43, 47). *Litocampa inexspectata* is separated by 235 miles from *L. keithi* in southern Indiana with which it shows closest affinity. *Litocampa keithi* is located in the eastern edge of the Crawford Upland, below

FIGURE 47.--Eastern Tennessee and western North Carolina, showing distribution of species of *Litocampa*: *L. cookei* (solid squares), *L. inexspectata* (open circle), *L. barryi* (open diamonds), and *L. holleri* (solid diamond). Open hexagon indicates the location of a related, undescribed genus and species. Two symbols in a circle indicate two species from the same locality.

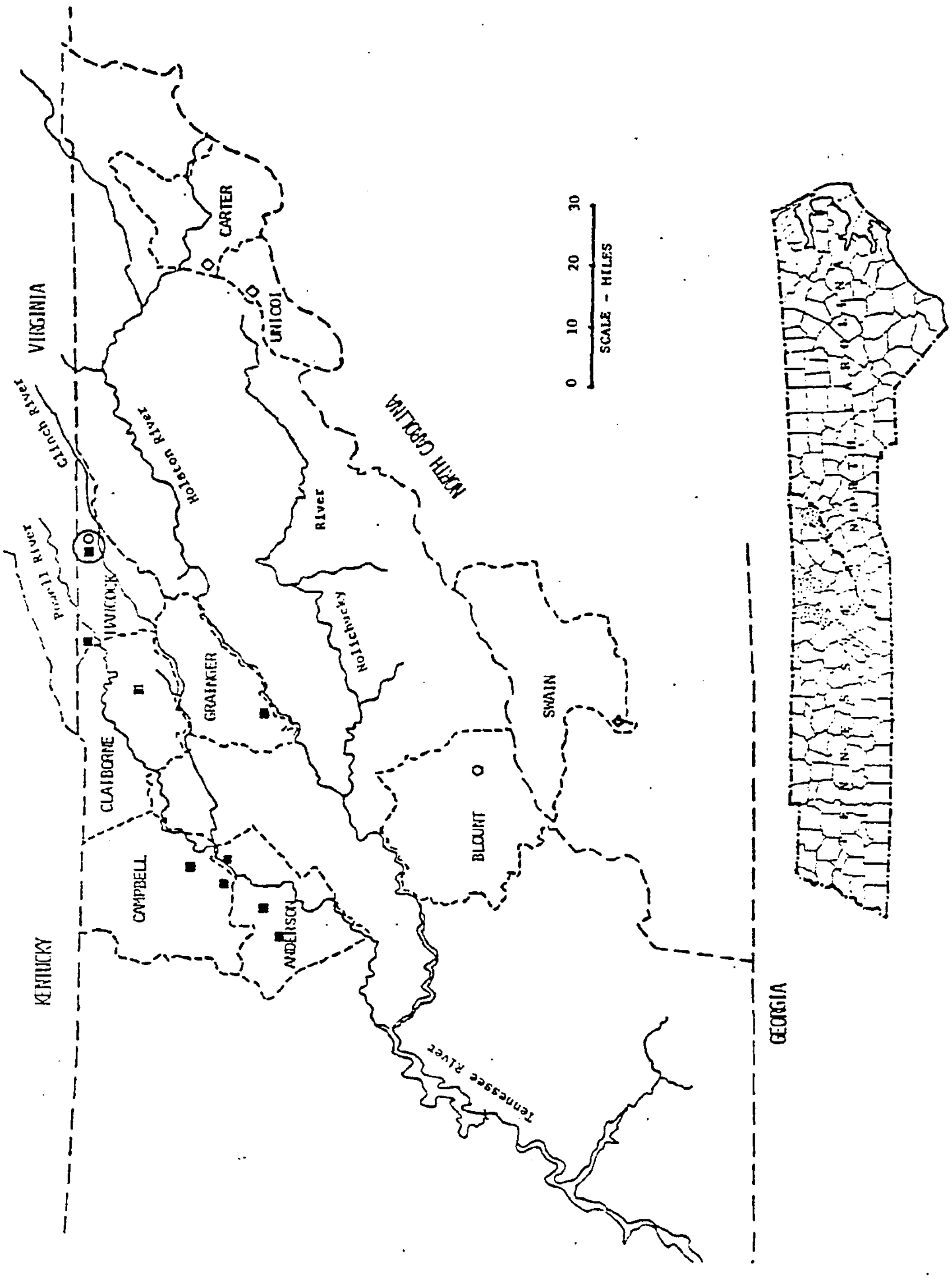
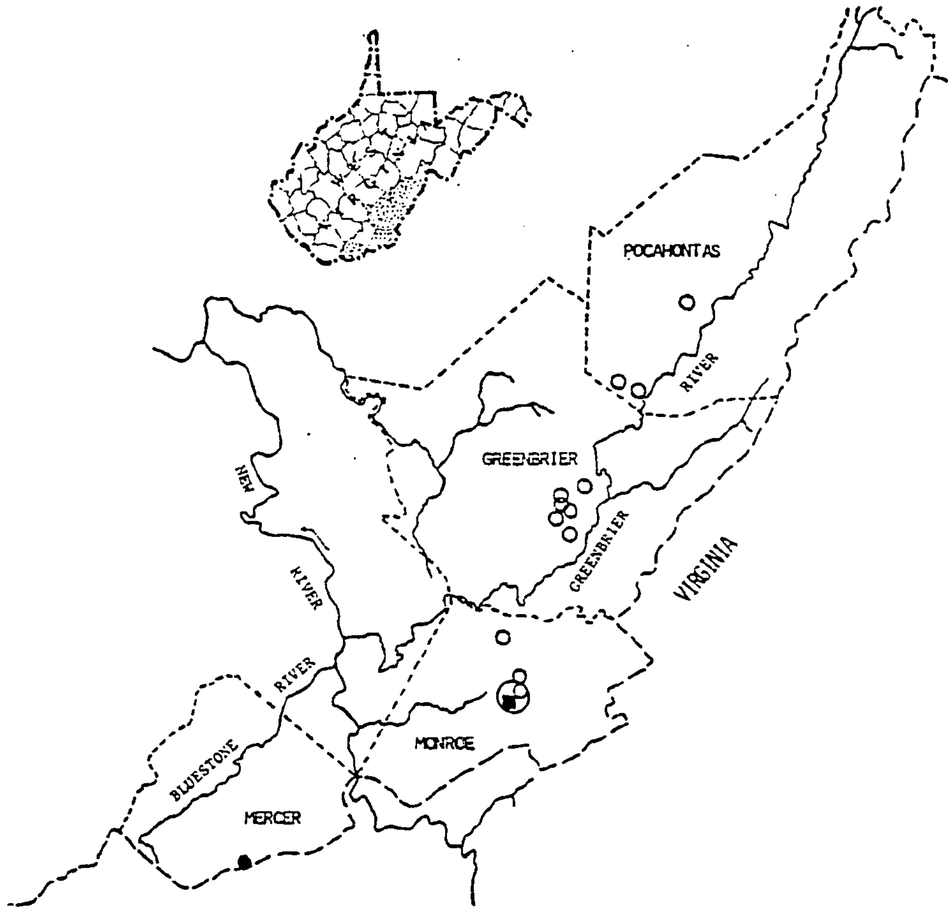

VIRGINIA
KENTUCKY
NORTH CAROLINA
GEORGIA
CARTER
UNICOI
HANCOCK
CLAIBORNE
GRAINGER
CAMPBELL
ANDERSON
BLOUNT
SWAIN
Clinch River
Powell River
Holston River
Nolichucky
River
Tennessee River
0 10 20 30
SCALE - MILES

FIGURE 48.--Southeastern West Virginia, showing distribution of *Litocampa fieldingi* (open circles), *L. virginiana* (solid circle), and *Eumesocampa* sp. (square). Two symbols in a circle indicate two species from the same locality.

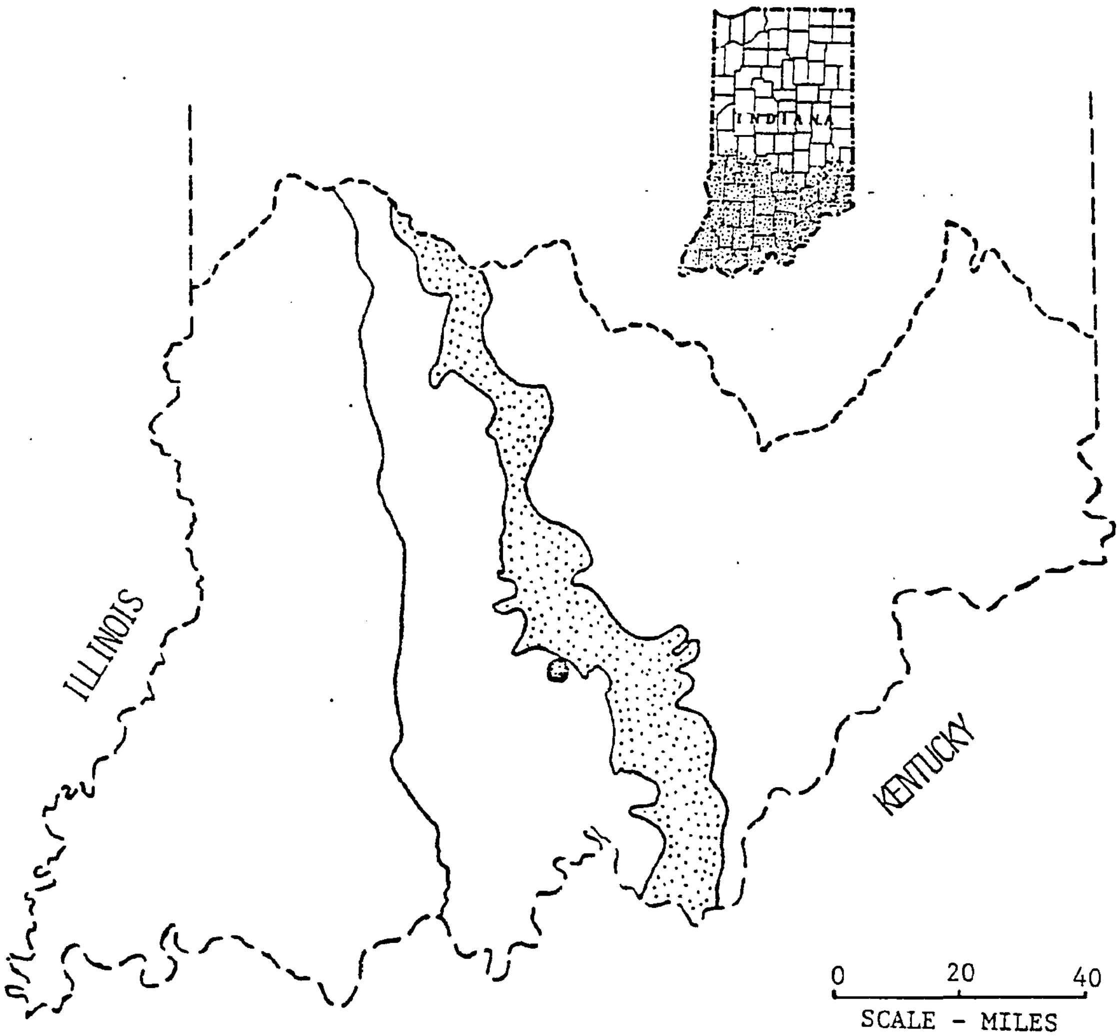

POCAHONTAS
RIVER
GREENBRIER
NEW
RIVER
GREENBRIER
VIRGINIA
RIVER
MONROE
BLUESTONE
MERCER

the southern most extent of the Wisconsin glaciation in Indiana (Figs. 43, 49). Although only known from a single cave, the geological nature of the area and the extensive cavern development suggests that the range could be much larger, as mentioned earlier in the species description. Although it does not possess large latero-tergal crests generally associated with cave adaptation in campodeids, *L. keithi* nevertheless displays ample morphological evidence of being an advanced obligate cavernicole.

The third species of the *keithi* group, *L. welbourni*, is known known only from a single cave north of the Pecos Plains (Fenneman, 1931). Due to the morphologically primitive nature of *L. welbourni* and the isolated pattern of cave distributions in New Mexico (except for the Carlsbad Caverns-Guadalupe Mountains area), I would expect a very insular range for this species.

Virginiana group.--Three species are presently recognized in this group. *Litocampa virginiana* is known exclusively from southwestern Virginia and neighboring Mercer Co., West Virginia (Fig. 48). It has been found in caves in an area southwest of the New River in Giles County, southeast of the Clinch River, and northwest of Walker Mountain (and the Middle Fork of the Holston River). Surprisingly, it has not yet been found in the adjacent areas of Tennessee (Figs. 43, 46). As reported earlier (Ferguson, 1974), there is difficulty in subdividing *L. virginiana* further, although a statistical analysis of the number of antennal segments and of the lengths of various macrochaetae relative to the sizes of individual specimens indicated some

FIGURE 49.--Location of Litocampa keithi (solid circle) in southern Indiana. Dashed line indicates the southern limit of the Wisconsin glaciation. Solid lines delineate the eastern Mitchell Plain (stippled) and the western Crawford Upland.


INDIANA
ILLINOIS
KENTUCKY
0 20 40
SCALE - MILES

genetic variability between certain clusters of populations. The utilization of additional taxonomic characters has helped in recognizing one such cluster (which was recognized earlier as having specimens that were "most unlike" the others) as a distinct species, *L. barringerorum*. *Litocampa barringerorum* is confined to caves of the Wards Cove area of Tazewell Co., Virginia, in the headwaters of the Clinch River (Figs. 43, 46).

Two hundred sixty miles to the south in northwestern Georgia, and even farther in south central Tennessee and northern Alabama (Figs. 43, 50, 51, 52), occurs the third member of the species group, *L. cherokeensis*. Morphologically, *L. cherokeensis* is virtually identical to *L. barringerorum*, differing primarily by the relative lengths of certain macrochaetae.

The range of *L. cherokeensis* forms a big arc passing from northwestern Georgia southwest to a cave northeast of Birmingham, Alabama. It then extends northwest to a cave in Colbert County, Alabama. Finally, the range must be continued across the Tennessee River to Hobbs Cave, Maury Co., Tennessee. How much further to the north the range might extend is unknown. This large range is situated mainly in the Valley and Ridge Province and the immediately adjacent outer edge of the Cumberland Plateau of Georgia and Alabama (peripheral to the locations of *L. davisi*), and extends into the Western Highland Rim of Tennessee.

Henroti group.--This group contains two species, *L. davisi* and *L. henroti*. *Litocampa davisi* shows fewer specialized (new) characters,

FIGURE 50.--Northwestern Georgia, showing distribution of species of *Litocampa*: *L. davisi* (hexagons), *L. cherokeensis* (solid circles), and *L. pecki* (triangles).

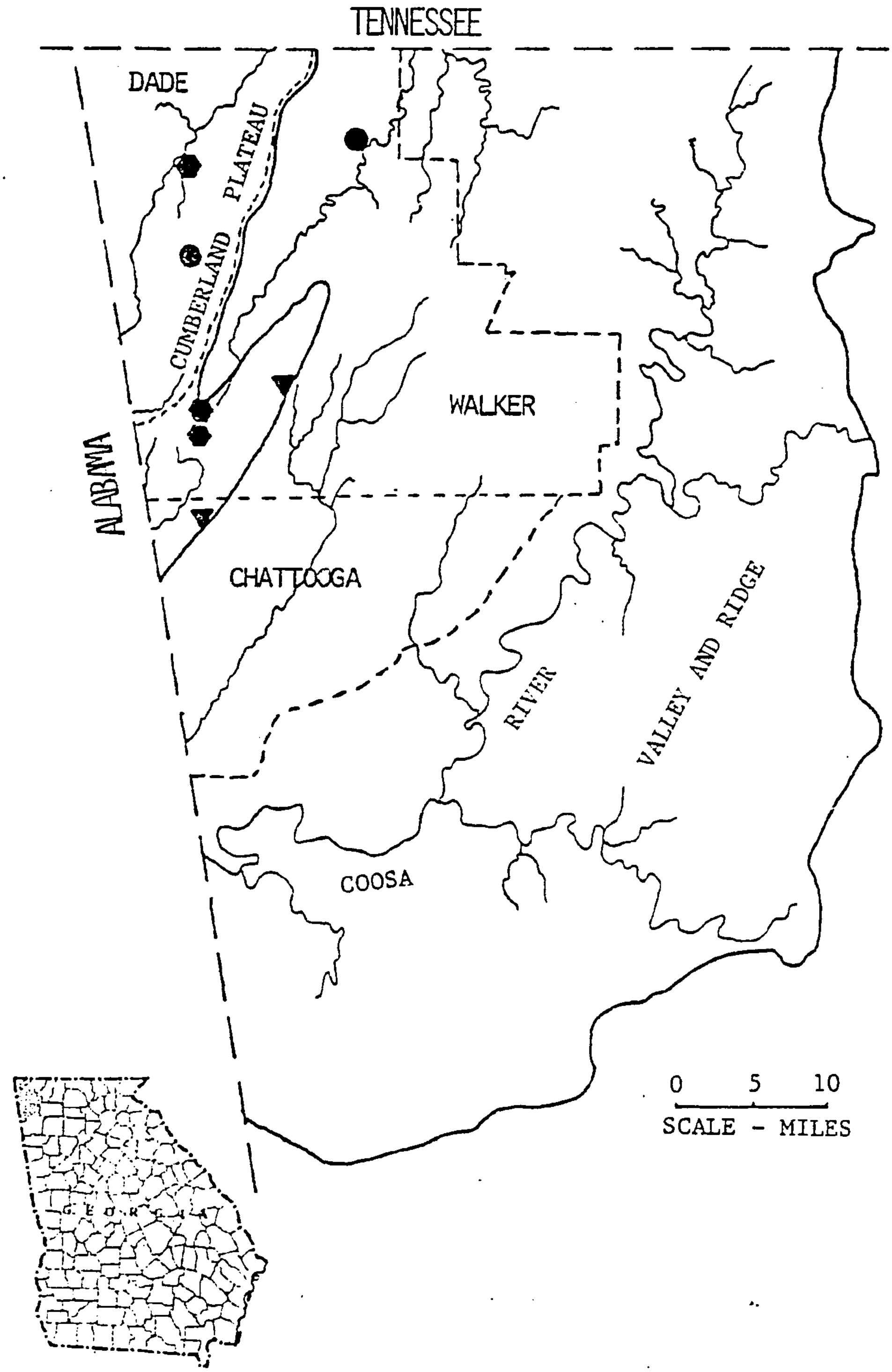

TENNESSEE
DADE
CUMBERLAND PLATEAU
WALKER
ALABAMA
CHATTOOGA
RIVER
VALLEY AND RIDGE
COOSA
0 5 10
SCALE - MILES
GEORGIA

FIGURE 51.--Northern Alabama, showing distribution of species of *Litocampa*: *L. davisi* (solid hexagons), *L. valentinei* (triangles), *L. henroti* (open hexagons), and *L. cherokeensis* (solid circles).

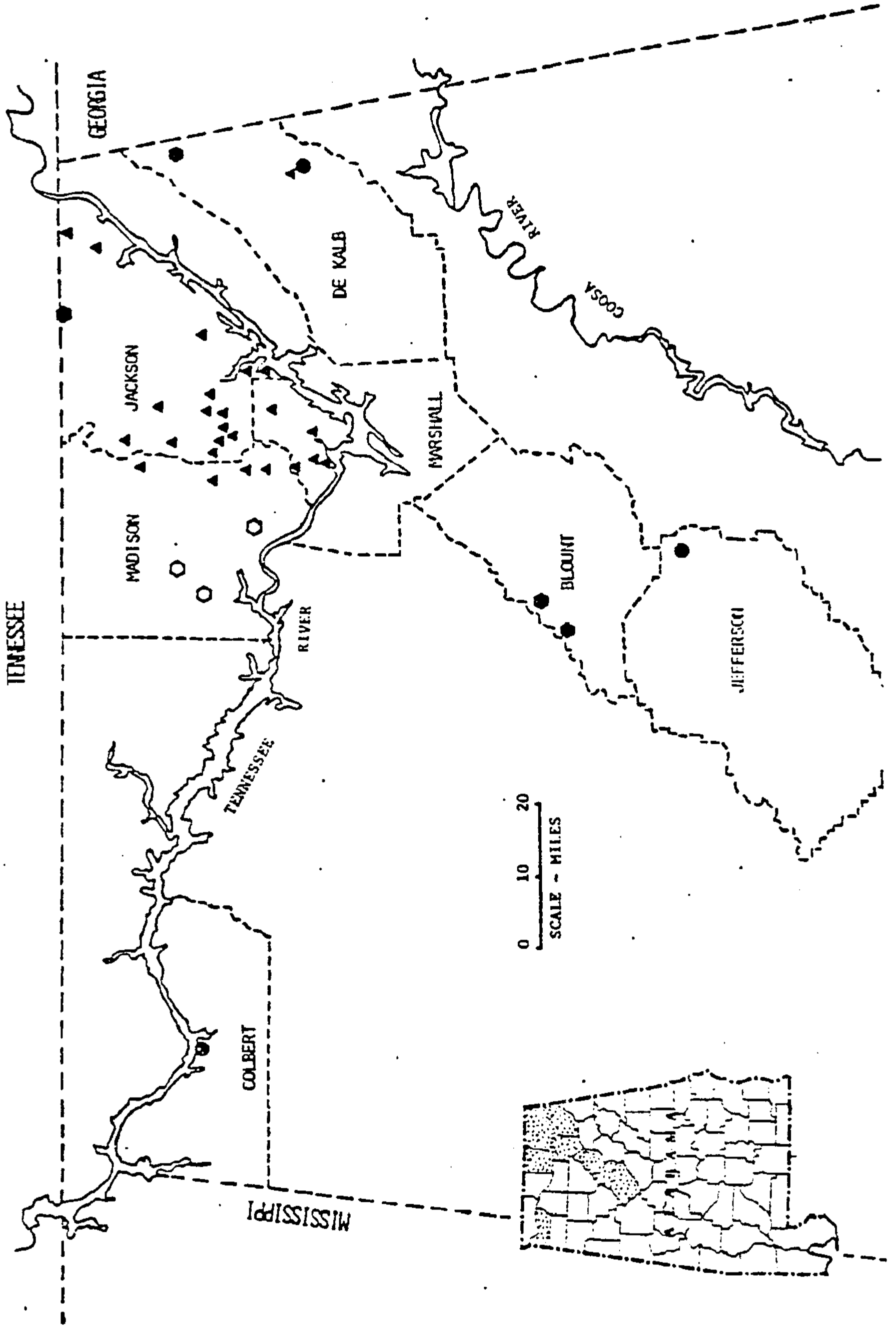
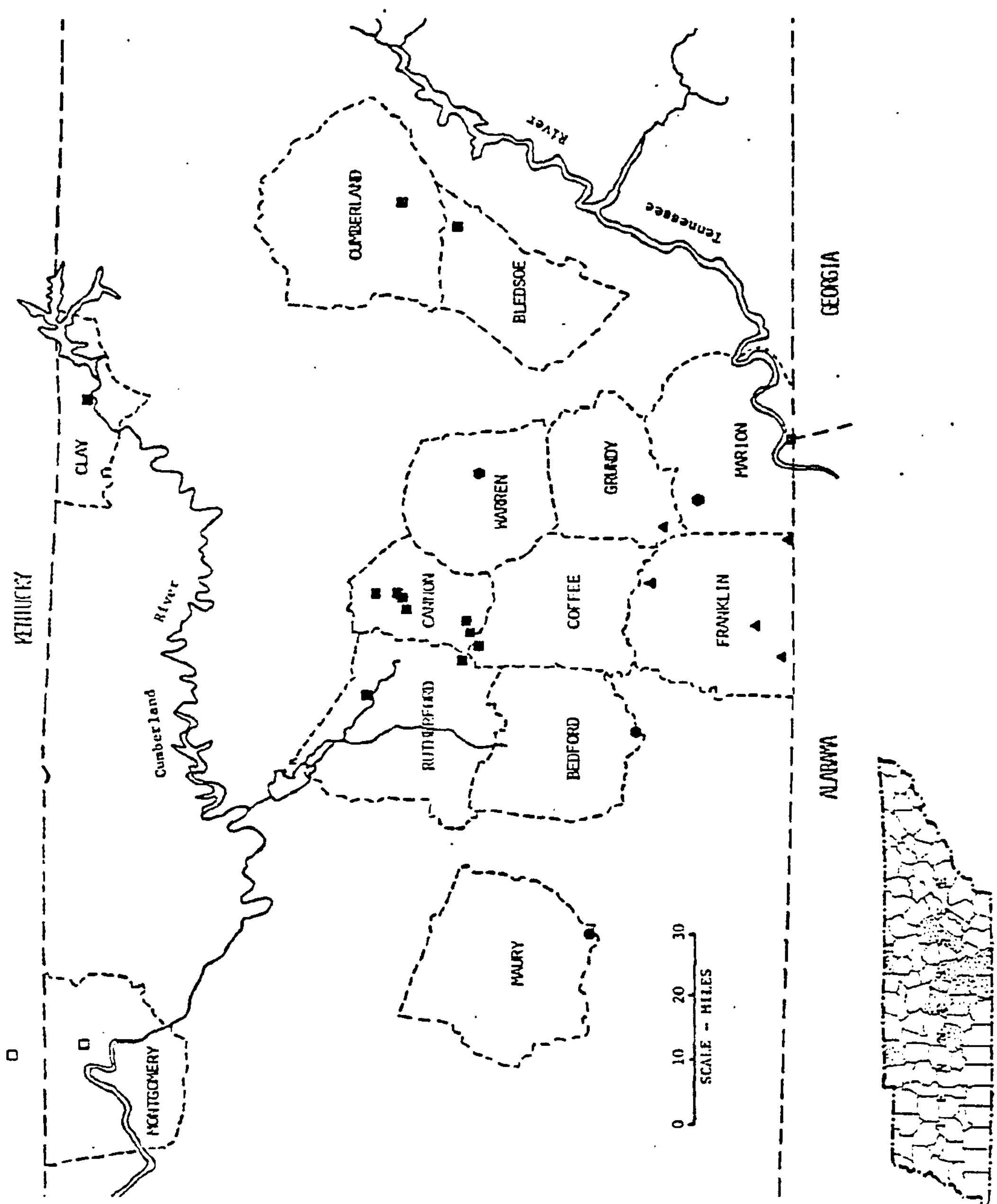

GEORGIA
TENNESSEE
MISSISSIPPI
DE KALB
JACKSON
MADISON
MARSHALL
BLOUNT
JEFFERSON
COLBERT
COOSA RIVER
TENNESSEE RIVER
0 10 20
SCALE - MILES

FIGURE 52.--Central Tennessee and adjacent areas, showing distribution of species of *Litocampa*: *L. jonesi* (open squares), *L. cookei* (solid squares), *L. davisi* (solid hexagons), *L. cherokeensis* (solid circles), and *L. valentinei* (triangles).


KENTUCKY
CLAY
Cumberland
River
MONTGOMERY
CUMBERLAND
BLEDSOE
Tennessee
River
GEORGIA
WARREN
GRUNDY
MARION
CANNON
COFFEE
FRANKLIN
RUTHERFORD
BEDFORD
ALABAMA
MAURY
0
10
20
30
SCALE - MILES

and has a larger, more scattered distribution (Figs. 43, 50, 51, 52). It occupies caves in the southeastern portion of the Highland Rim of Tennessee, and enters the Cumberland Plateau of southeastern Tennessee, northwestern Georgia, and Alabama. Litocampa henroti appears confined to a small area west and south of Huntsville, in the Highland Rim area of Alabama (Figs. 43, 51). A damaged specimen from Monteagle Saltpeter Cave in Marion Co., Tennessee may be either L. henroti or a distinct species intermediate between L. henroti and L. davisi.

Valentinei group.--This group, possibly closely related to the henroti group, also contains two species, L. valentinei and L. pecki. Both species possess apparently derived characters (discussed in the next section of this paper), such as the loss of the metanotal lateral posterior macrochaetae. In other characters the two species are remarkably identical. Litocampa valentinei is known from many cave locations in northeastern Alabama and southern Tennessee (Figs. 43, 51, 52). All but one location are confined to the Cumberland Plateau north of the Tennessee River. The one exception is in Stanley-Carden Cave, DeKalb Co., Alabama. This cave may be located near the headwaters of a tributary to the Tennessee, whereas the two locations for L. pecki are near streams which drain into the Coosa River (Figs. 43, 50). It also appears that Lookout Maountain separates the two ranges. The two Georgia cave locations for L. pecki occur along the eastern edge of the Cumberland Plateau; the range of the species probably extends for some distance into Alabama.

Cookei group.--Litocampa cookei of the cookei group has the largest range of any recognized species (Figs. 43, 46, 47, 52, 53, 54). The greatest straight-line expanse is about 280 miles, from a cave in Trigg Co. of western Kentucky to several caves in Wise County of southwestern Virginia. It is also known from caves in the Mammoth Cave region, south to Nickajack Cave at the southern border of Tennessee, where Georgia, Alabama, and Tennessee meet. The latter location is south of the Tennessee River. All others are west of the upper Tennessee River and its tributary, the Holston River (Fig. 47). For the majority of cases in northeastern Tennessee, *L. cookei* occurs west of the Clinch River, as it does in Virginia (Fig. 46).

On the range map (Fig. 43), it is projected that *L. cookei* will be found north of Mammoth Cave in the northern extension of the Pennyroyal Plain and Mammoth Cave Plateau, as well as further to the west in the same regions.

Litocampa sperkai occurs in caves of the Highland Rim section in eastern Kentucky. All but one location are north of the Cumberland River in Pulaski and Rockcastle Counties (Fig. 43, 54). The locality south of the river is Sloans Valley Cave, one of the largest cave systems in the state. Specimens from this cave display a trend toward the loss of the metanotal lateral posterior macrochaetae, which is not evident in other populations of the species. There is also one known population of *L. cookei* north of the Cumberland River in eastern Kentucky, in Richardson Cave, Pulaski County.

While both *L. cookei* and *L. sperkai* display the usual characters associated with cave inhabiting campodeids (*L. sperkai*

FIGURE 53.--South-Central Kentucky and adjacent areas, showing distribution of species of *Litocampa*: *L. cookei* (solid squares) and *L. jonesi* (open squares).

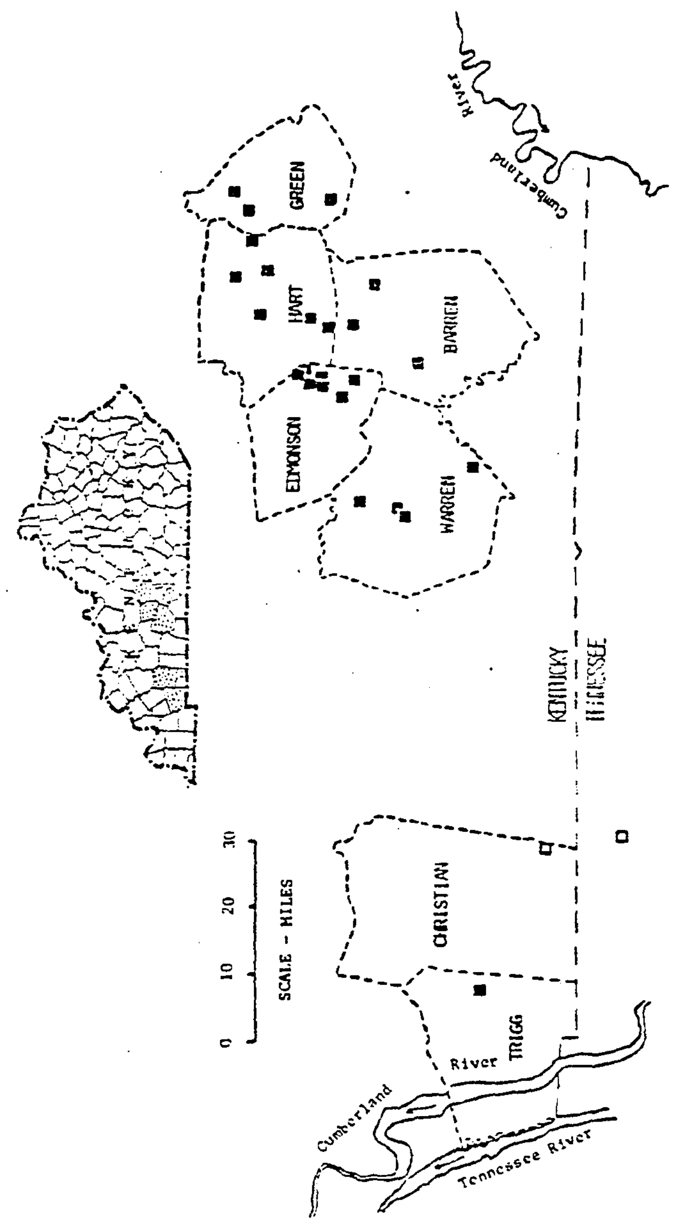
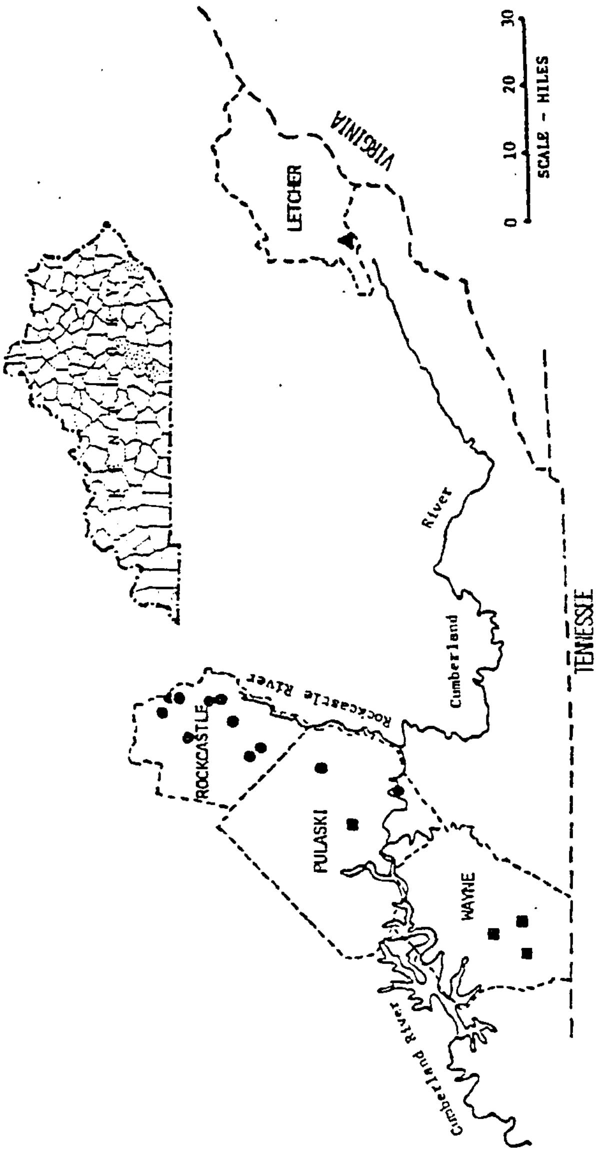

GREEN
HART
BARREN
EDMONSON
WARREN
CHRISTIAN
TRIGG
KENTUCKY
TENNESSEE
Cumberland River
Cumberland River
Tennessee River
SCALE - MILES
0
10
20
30

FIGURE 54.--Southeastern Kentucky, showing distribution of species of *Litocampa*: *L. cookei* (squares), *L. sperkai* (solid circles), and *L. holsingeri* (triangle).

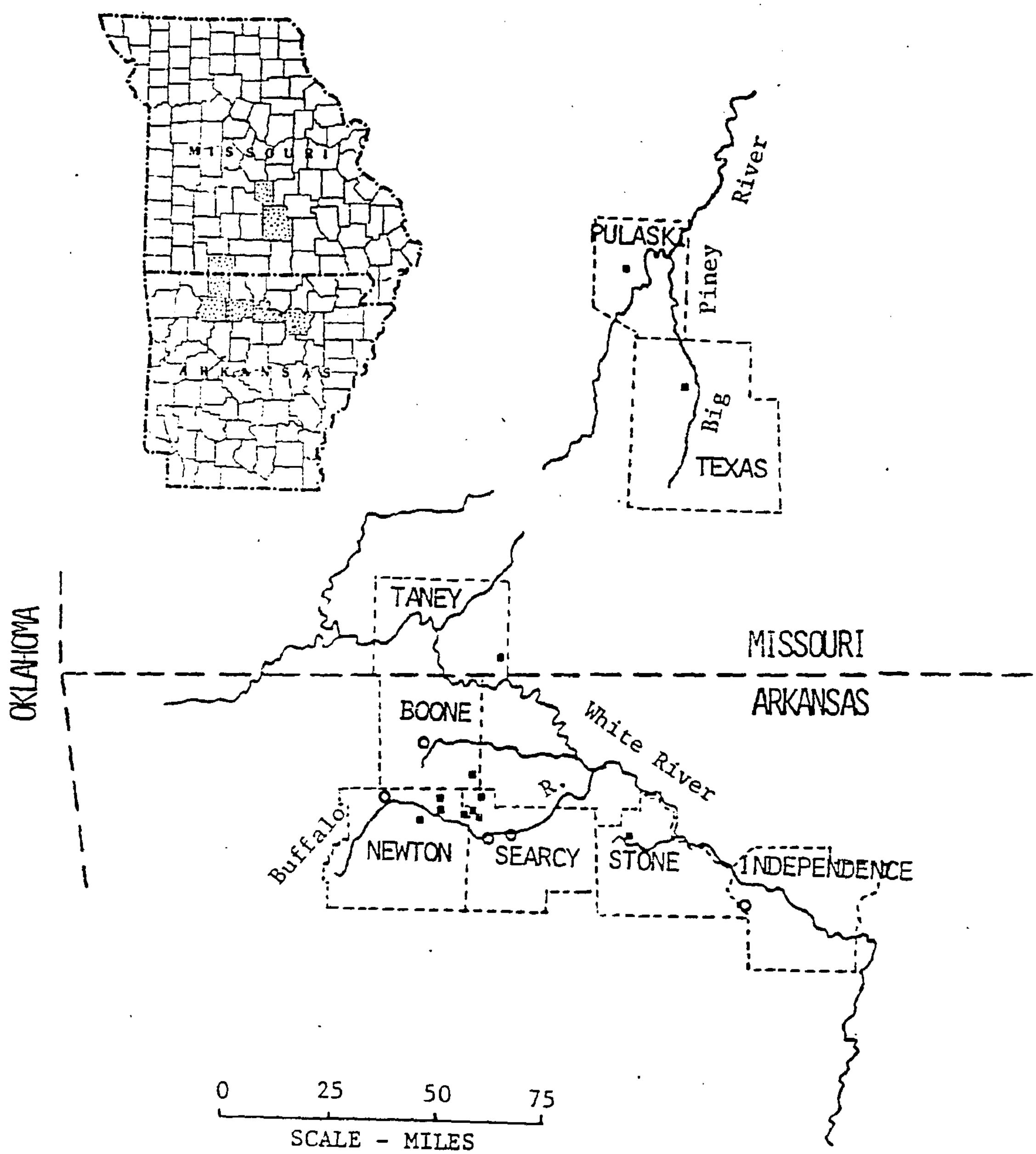

VIRGINIA
LETCHER
0 10 20 30
SCALE - MILES
River
Cumberland
TENNESSEE
Rockcastle River
ROCKCASTLE
PULASKI
WAYNE
Cumberland River

may be slightly less specialized), L. jonesi is the least specialized of all. It does not have large latero-tergal crests on the claws, the number of sensilla in the cupuliform organ of the apical segment of the antenna is small, sternal macrochaetae are branched, not plumose as in the other species of the group, and it has a more normal abdominal chaetotaxy. It also has the smallest range, being known from two caves about 11 miles apart, on either side of the Tennessee-Kentucky border (Figs. 43, 53). The caves are in the southern-most portion of the Pennyroyal Plain, north of the Cumberland River (Fig. 52).

Lastly, L. holsingeri is found in southwestern Virginia in the Rye Cove area of Scott County, and slightly to the northeast, still west of the Clinch River (Figs. 43, 46, 54). Surprisingly, specimens which appear to belong to this species are known from a cave 25 miles to the northwest in Kentucky. If they are conspecific, then the views put forth earlier (Ferguson, 1974) concerning the origin of L. holsingeri must be modified. Litocampa holsingeri is the most cave-adapted species in the group.

Hawksleyi group.--The final species group contains two species, L. hawksleyi and L. ozarkensis. Morphologically the species are very similar, except for the number of macrochaetae on the fourth abdominal tergite. Members of both species have characteristics attributed to a high degree of cave adaptation. They both occupy caves in the Springfield-Salem plateaus section of the Ozark Plateau, north of the Boston Mountains (Figs. 44, 55).

FIGURE 55.--Southern Missouri and northern Arkansas, showing distribution of species of *Litocampa*: *L. hawksleyi* (squares) and *L. ozarkensis* (circles).


MISSOURI
ARKANSAS
River
PULASKI
Piney
Big
TEXAS
OKLAHOMA
TANEY
MISSOURI
ARKANSAS
BOONE
White River
R.
Buffalo
NEWTON
SEARCY
STONE
INDEPENDENCE
0
25
50
75
SCALE - MILES

The Ozark Region represents an uplifted structural dome composed of gently inclined strata of Paleozoic age, with a core of Precambrian rocks represented by the St. Francois Mountains situated in a southeastern portion of Missouri (King, 1977; Atwood, 1940). Through erosion and lowering of the dome (probably accompanied by continued uplift), a series of more or less concentric strata (some cavernous) has been exposed. Different degrees of dissection and down-cutting by streams crossing the area have further produced a jagged series of concentric strata.

It appears that the caves containing _L. ozarkensis_ in Searcy and Independence Counties, Arkansas, may be formed in lower Ordovician Beekmantown limestone south of the Buffalo and White Rivers (Stose, 1960). The exposed strata then loop around the headwaters of Buffalo River in Newton County, where Fitton Cave is located, and continue northward into Boone County where the final location of this species is known. _Litocampa hawksleyi_, which has by far the larger range, is found in caves in strata of different ages, or if in the same strata, at different locations. One location of _L. hawksleyi_ in Newton County, south of Buffalo River, contradicts this attempt to envision some type of geographic isolation for the two species.

Discussion.--For the most part, the _Litocampa_ species in the United States (Figs. 43, 44) are found rather far south of the southern-most extension of the last glacial advance, as compared to other cavernicoles, such as amphipods (see distribution in Holsinger, 1978). This is in agreement with Vandel's observation (1965) that terrestrial troglobites are generally found south of the northern range extensions of aquatic troglobites. The genera of duplurans in North American caves (see Map IA in Appendix I) which extend north of *Litocampa* are all genera with epigean representatives. Therefore, they may be troglophiles in that part of their range, not having had time to become completely "cave-adapted" since the retreat of the glaciers. Looking more specifically at the *Litocampa* ranges, an example of a cavernicole which has a range nearly as extensive as *L. cookei* is that of another apterygote insect, the collembolan *Pseudosinella hirsuta* (Christiansen and Culver, 1968). Among the cave beetles in Kentucky, *Darlingtonia* is known only from caves in the eastern Highland Rim, while other closely related genera are found in caves of the Pennyroyal Plain and Mammoth Cave Plateau to the west. The similarity in the range of *Litocampa jonesi* and that of *Pseudanopthalmus c. ciliaris* has already been mentioned with the species description of *Litocampa jonesi*.

There is considerable similarity between the ranges of certain species of cave crickets of the tribe Hadenoecini (Hubbell and Norton, 1978) and those of *Litocampa* species. Hubbell considers the cricket species mentioned here to be obligatory trogloxenes, organisms that reproduce only in caves but emerge from them at night to feed. The range of *Hadenoecus jonesi* is identical to that of *Litocampa valentinei*, with the exception of the single population of *L. valentinei* in DeKalb County, Alabama. *Hadenoecus subterraneus* is found in the Mammoth Cave region of Kentucky, and *H. cumberlandicus* is found in caves of the Highland Rim in eastern Kentucky. The two species are said to be morphologically very similar. This is essentially the situation found for Litocampa cookei and L. sperkai, although the range of L. cookei is considerably greater than that of Hadenoecus subterraneus.

The range of the crickets, Euhadenoecus fragilis and E. insolitus are quite similar to that for species of the virginiana group. However, E. fragilis extends farther north into Virginia and West Virginia than does Litocampa virginiana. And E. insolitus has a verified more northern extension from Alabama through Tennessee to the southern border of central Kentucky. Hubbell suggests that the range extends through the eastern Highland Rim of Tennessee (Hubbell and Norton, 1978). Finally he says that the two species are morphologically very similar and that the genus Euhadenoecus is the more primitive of the two genera of cave crickets in the tribe Hadenoecini. In the next section I will present material suggesting that the members of the virginiana group are more primitive than, for example, members of the cookei group (particularly L. cookei, L. sperkai, and L. holsingeri). Therefore, there is again a similarity in range and in degree of morphological variation for these cave crickets and cave campodeids. In addition, Herbert H. Ross (personal communication) has indicated that some species of primitive Trichoptera show a distribution pattern quite like that of the virginiana group.

T. C. Barr, Jr. (personal communication) commented on the similarity in the distributional patterns of the Hadenoecus species, Phalangodes (harvestmen), and Orconectes (crayfish) from caves.

Also, the genus *Kleptochthonius* (*Chamberlinochthonius*) of the cavernicolous pseudoscorpions has a range similar to that of *Litocampa cookei* (species of cave pseudoscorpions are highly endemic). According to Muchmore (1973), the cave-adapted *Apochthonius* and *Mundochthonius* seem to be restricted to the periphery of the area occupied by *Kleptochthonius*. A general pattern such as this occurs for the species of *Litocampa*. Finally, the occurrence of *Litocampa* species in the Ozark Plateau, when most species of the genus are located in the southern Appalachians, is in agreement with the findings of J. L. Craig (unpublished manuscript) who suggests that most Ozark cavernicoles originated in the southern Appalachians. Peck and Lewis (1978) gave similar interpretations for the source of the cave fauna of Illinois and southeastern Missouri.

EVOLUTION

Phylogeny

In an effort to reconstruct a more accurate phylogeny for the species groups under study, a cladogram was constructed (Fig. 56 ; Table 1). The difficulty is the scarcity of taxonomic characters which can be established as "ancestral" or "derived" with any degree of certainty. The apparent state or degree of primitiveness of several characters used in the cladogram have been mentioned by a few authors and are summarized and discussed by Condé (1956a).

The cosmopolitan genus *Campodea* contains species which most likely possess the characters one would expect to have been found in a generalized ancestral campodeid. If this genus is chosen as being nearest to the ancestral type, then the following might be considered plesiomorphic characters: pro-, meso-, and metanota with 3 + 3 (*ma*, *la*, *lp*), 3 + 3, and 2 + 2 (*ma*, *lp*) macrochaetae; femur III without dorsal macrochaetae; pretarsal claws without latero-tergal crests; abdominal tergites with 1 + 1 lateral posterior macrochaetae; and 6 + 6 macrochaetae on urosternite I.

The presence of glandular setae on the posterior border of urosternite I (character 9 of cladogram) of mature male campodeids appears to occur more often (in species of all genera) than the alternate state. Their presence has been considered ancestral by others (Pagés, 1951; Condé, 1956a).

Epigean species of *Litocampa* have pretarsal claws with very

FIGURE 56.--Cladogram of the species groups of *Litocampa* in the United States, using characters described in Table 1. Half shaded boxes indicate that only some members of the species group possess the derived state. Boxes marked with an X represent a probable character state reversal.

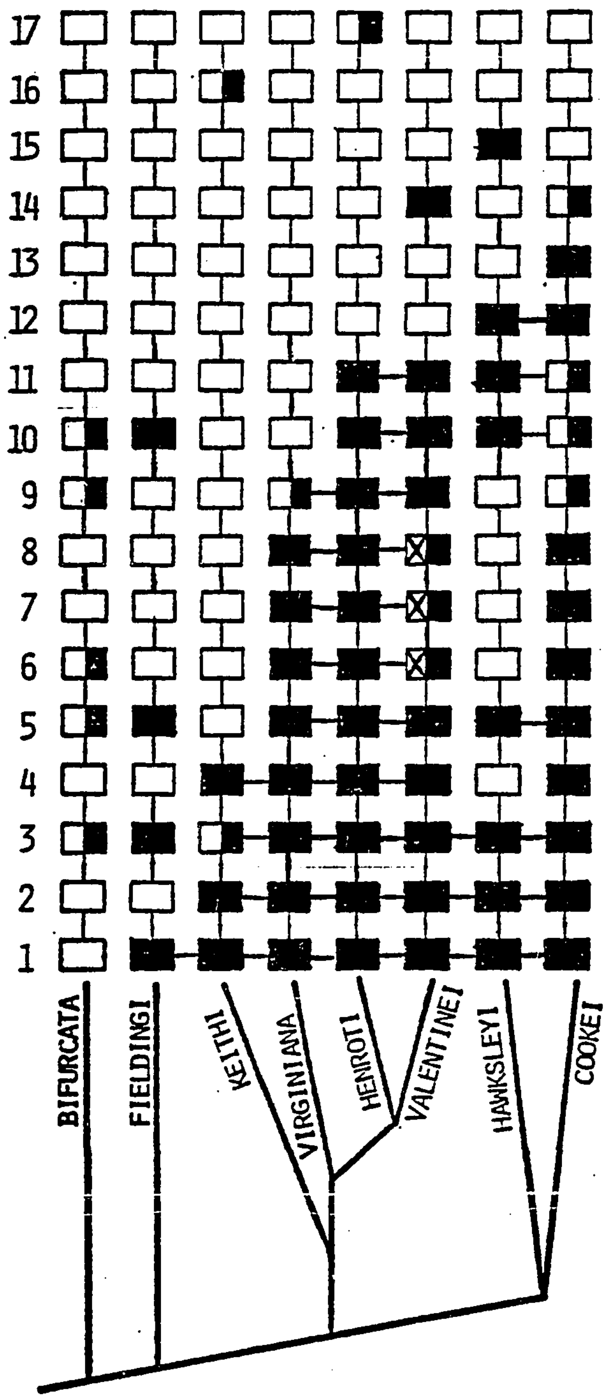

17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
BIFURCATA
FIELDINGI
KEITHI
VIRGINIANA
HENROTI
VALENTINEI
HAWKSLEYI
COOKEI

TABLE 1.--Characters Used in Cladogram of Figure 56.

	Character	Ancestral ☐	Derived ■
1.	Dorsal macrochaeta on femur III	Absent	Present
2.	Phanere e of antennal segment III	Absent	Present
3.	Lateral posterior macrochaetae on tergites VI-VII	1 + 1	2 + 2
4.	Macrochaetae of urosternite I	6 + 6	7 + 7
5.	ma macrochaetae on tergite IX	Present	Absent
6.	ma or mp macrochaetae on tergite IX	Present	Absent
7.	ma or tergite VIII or ma (mp) on tergite IX	Present	Absent
8.	ma or mp on tergite VIII, or ma(mp) on tergite IX	Present	Absent
9.	Glandular setae on urosternite I	Present	Absent
10.	Latero-tergal crests of pre-tarsal claws	Reduced	Large
11.	Lateral anterior macrochaetae on tergite IV	Present	Absent
12.	ma macrochaetae on tergites III-VII	Present	Absent
13.	ma macrochaetae on tergites I-II	Present	Absent
14.	Lateral posterior macrochaetae on metanotum	Present	Absent
15.	Basal branches of apical seta of styli	Short	Long
16.	Macrochaetae on urosternites II-VII	4 + 4	5 + 5
17.	Medial posterior macrochaetae on meso- and metanota	Absent	Present

reduced latero-tergal crests (character 10), and, therefore, the presence of large crests is a derived state. This latter condition occurs frequently among the cavernicolous *Litocampa*, *Plusiocampa*, and other genera. The large crests appear to be a type of cave adaptation similar to that recognized for the claws of cave inhabiting Collembola (Christiansen, 1965). *Haplocampa* is the only genus with a number of epigean species possessing large latero-tergal crests. However, as presented later, it is possible that they had cavernicolous ancestors. Since all of the species of the groups under examination are cave inhabitants, it is not surprising that most groups have at least one or more members with the large crests (exceptions are the primitive *keithi* and *virginiana* groups).

The state of some other characters seem rather apparent, such as the elaborate, long basal branches of the apical seta of the styli belonging to the species of the *hawksleyi* group. If the *hawksleyi* group (stock) was ancestral to many of the other groups, one might expect this character to appear in some of them, but it does not. The state of other characters was decided in part by association with other characters believed to be either ancestral or derived.

One very important character (or group of characters) is the presence of medial anterior macrochaetae on the abdominal tergites. Condé (1956a) has stated that the generalized or primitive state is the absence of medial anterior macrochaetae on the abdominal tergites. I suggest that just the opposite is true for two reasons. First, the single species (*Litocampa bifurcata*) which has the largest assemblage of plesiomorphic characters has medial anterior macrochaetae on tergites I-IX (other members of its species group have these macrochaetae on tergites I-IX and I-VIII). Second, if one considers the abdominal segments to be serially homologous to the thoracic segments, the nearly universal occurence of medial anterior macrochaetae on the thoracic nota (ancestral state) would be expected to have homologs on the abdominal tergites. I have observed such a repetitive pattern for the tergal chaetotaxy of symphylans.

When compared to similar structures on the thysanurans, there is much about the abdominal morphology of campodeids to suggest that they were once leg bearing segments which have lost their larger appendages through tagmentation and specialization of the anterior segments (thorax) for locomotion. Campodeids still support their long abdomens on six pairs of styli and move with a worm-like motion (campo is Greek for bending or flexible) which must enhance their movement through soil, humus, and cave sediment.

From the most primitive condition of having medial anterior macrochaetae on tergites I-IX, there are several possible derived states worth considering. There appears to be a tendency for the medial anterior macrochaetae of the eighth and ninth tergites to become modified into medial posterior macrochaetae or to be progressively lost. A scheme was devised on the cladogram so that a species group which had a more primitive state would illustrate this even though other less primitive states were considered as characters.

Finally, if one applies the idea of serial homologs to the thoracic and abdominal segments, then it supports the belief mentioned earlier that the ancestral state for the abdominal tergites is the possession of 1 + 1 lateral posterior macrochaetae, because that is the number commonly found on the thoracic tergites.

The cladogram also indicates certain characters which vary within the species groups. Examples are: the degree of development of the latero-tergal crests of the claws; specific variation in the abdominal chaetotaxy (but the general pattern is the same); the presence of glandular setae on the posterior border of urosternite I of the males; chaetotaxy of the urosternites II-VII; and slight thoracic macrochaetal variations (in number). Other examples are: variations in the number of ventral macrochaetae on the tibias; chaetotaxy of thoracic sternites; body size; number of antennal segments; lengths of macrochaetae, legs, cerci, and so forth.

Some major characters which appear to be constant for the species groups are: the number of macrochaetae on urosternite I; the presence or absence of a dorsal macrochaeta on femur III; the number of phaneres on antennal segment III; the presence or absence of medial anterior macrochaetae on the abdominal tergites, and their general pattern of distribution; and the morphology of the abdominal styli. Using these major characters one can construct the phyletic dendrogram shown in Figure 57. No time scale is to be inferred; the dendrogram simply indicates the hypothesized sequence of branching and relative affinity of the included taxa.

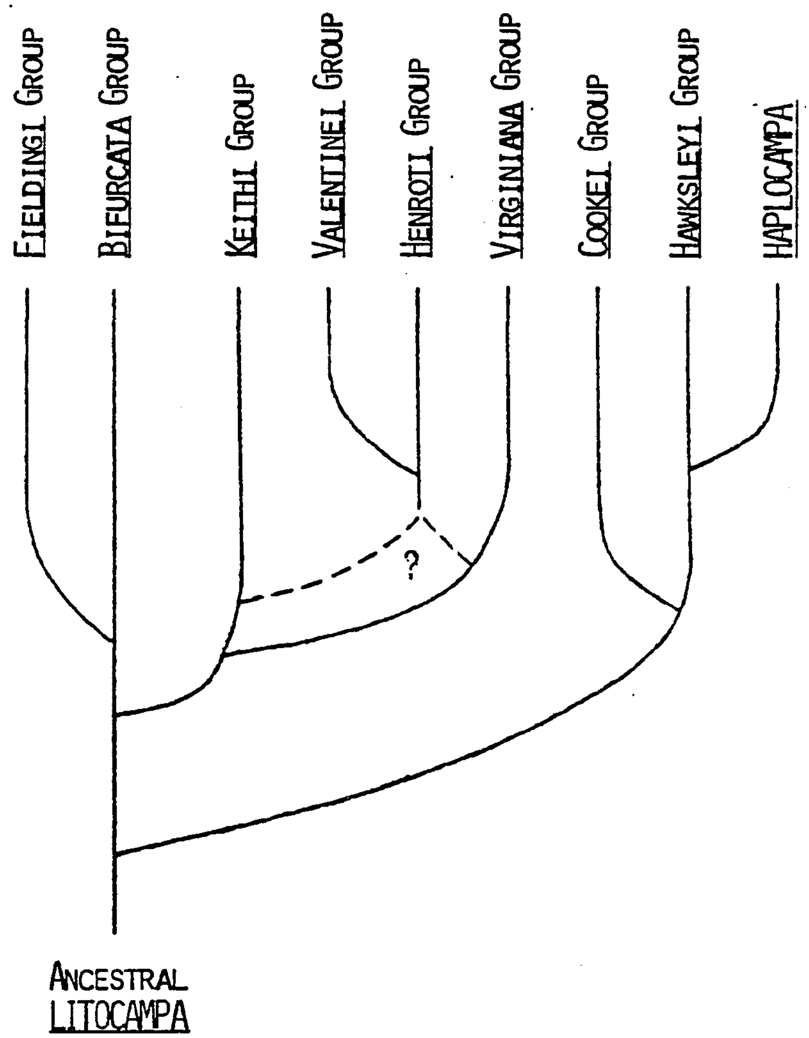


FIGURE 57.--Suggested phylogeny of the species groups of Litocampa and the related genus Haplocampa in the United States.

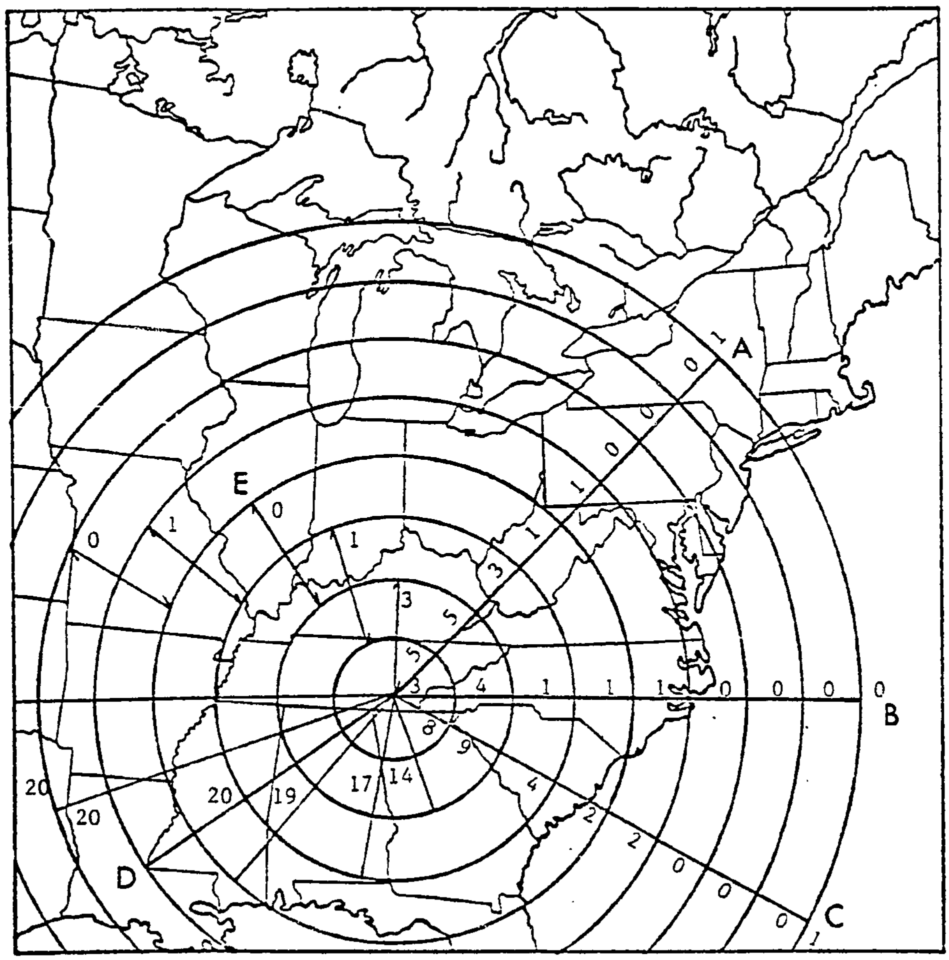
Center of Distribution

An examination of the preceding distribution maps (Figs.43 -55) suggests that the center of distribution of the genus Litocampa in the United States lies in the southern Appalachians, in southeastern Tennessee.

In an attempt to more precisely determine the center, a set of concentric circles was drawn, using radii with increments of approximately 100 miles. These circles were transferred to a transparent film and centered over various points in eastern Tennessee, northern Alabama, and Georgia. The numbers of species of Litocampa (plus a closely related, undescribed monotypic genus in Blount County, Tennessee) known to occur within the area of the center circle and in that of each of the succeeding bands were counted. Figure 58 represents the optimum arrangement in which the numbers of species decrease progressively from the center. Approximately 38 percent of the 21 known species considered here occur within the inner circle, and 67 percent within the area bounded by the second 100-mile band. The second 100-mile band from the center encompasses the range of six more species than does the area of the center circle, but the two share three species in common. The second and third band have one species in common, and bands further removed from the center share one or none. Furthermore, the highest number of endemics are located in the center circles, and the number decreases outwardly.

This pattern of distribution adds supporting evidence for the hypothesis that the major center of speciation and subsequent range

FIGURE 58 .--Distribution of the numbers of species of *Litocampa* and a closely related undescribed genus. Numbers along lines indicate numbers of species; distance between concentric circles is approximately 100 miles. A, endemics in areas between circles; B, non-endemics in areas between circles; C, totals in areas between circles; D, totals within limits of circles indicated; E, taxa shared by two concentric bands spanned by lines.


A
B
C
D
E
0
1
3
5
4
8
9
14
17
19
20
2

expansion in the United States was the southern Appalachian Mountains. Similar patterns have been found for millipedes (Hoffman, 1969; Shear, 1972) and crayfishes (Hobbs, 1969).

Evolution and Dispersal

If the genus Litocampa does predate the breakup of Pangaea, then one can look at the inferred paleogeography and paleoclimatology of the North American region prior to and since the rifting of the supercontinent and get some idea of the conditions under which the ancestral Litocampa lived, and some of the possibilities for dispersal.

The collision of Gondwanaland with North America (then part of Laurasia) to form Pangaea also formed the folded and faulted Appalachian Mountains (Dott and Batten, 1981). During the Permian and Early Triassic Periods the Appalachian Mountains were situated immediately south of the equator and are believed to have been covered by humid tropical forests, with arid regions to the "west". By Late Triassic times the Appalachian Mountains were situated north of the equator due to continued movement of the continent by plate tectonics. Also, from the Triassic to the present the rocks of the Blue Ridge may have been at the surface continuously, and if so were probably forming a mountain range (Gathright, 1976).

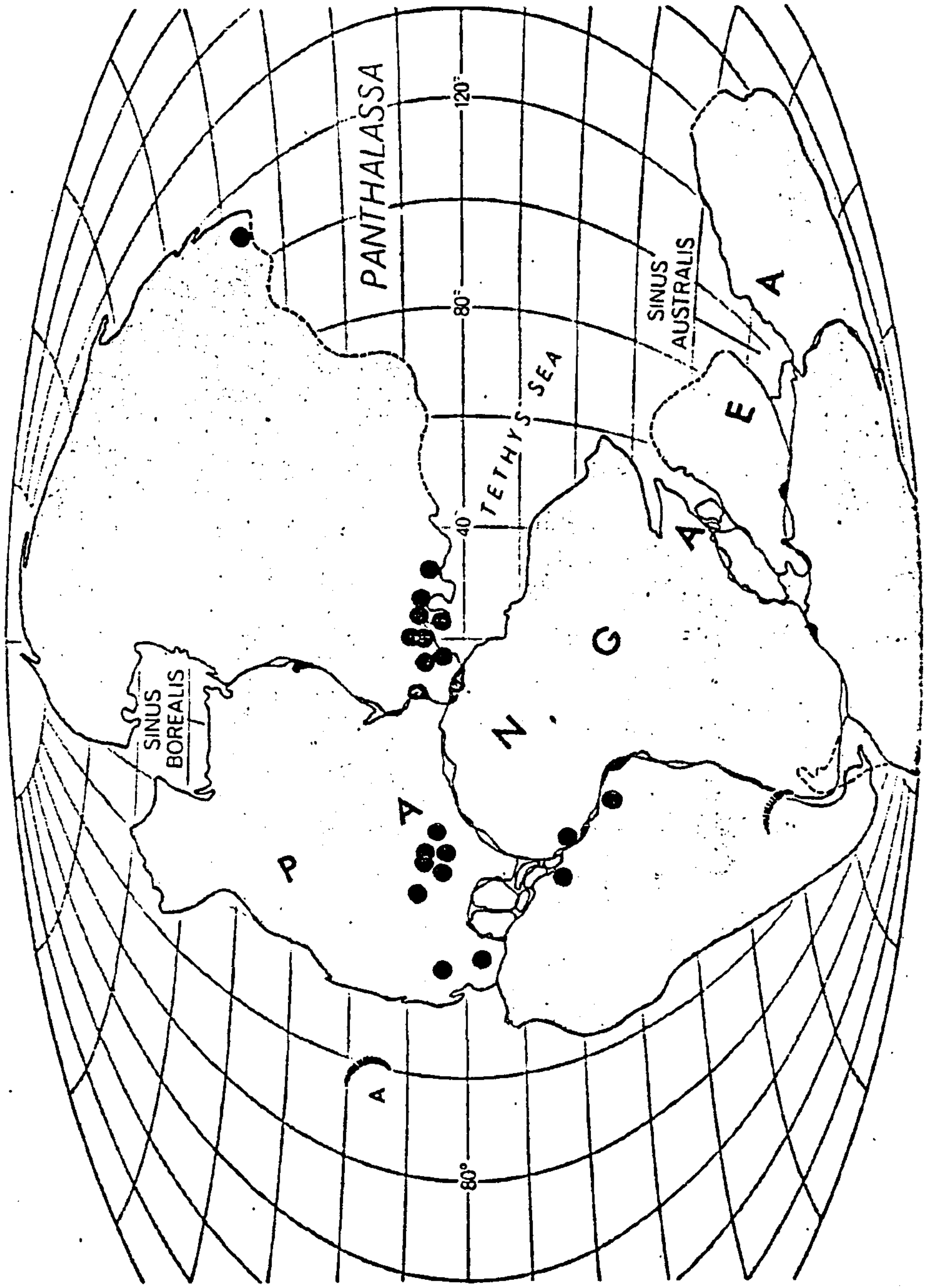
By Late Triassic times, the breakup of Pangaea was underway and was complete by the end of the Mesozoic. During the Jurassic and much of the Cretaceous a shallow inland sea extended from the Artic to the current Gulf regions. This sea would have surrounded the Ozark region on nearly three sides, preventing dispersal to or from the west, but allowing it to the east.

Although North America had moved considerably farther north by early Cenzoic time (50-60 million years ago), the location of land and sea and the movement of air masses suggest that the southern Appalachians were still covered with tropical forests which extended "west" to the Ozark Region. This would have been the optimal time for the dispersal of campodeids to or from the southwestern United States or Mexico. By Late Cenozoic (about 20 million years ago) a hot dry climate prevailed in the southwestern United States and Mexico, but the Appalachian Mountains still had subtropical conditions.

Therefore, it appears that the ancestral Litocampa were thermophiles. When plotted on a map of Pangaea prior to its breakup in the Mesozoic Era (Fig. 59), the distribution of recent Litocampa and Plusiocampa species show that most of these campodeids are found along the equator or between 30° N. and S. latitude. On a more recently constructed map of Pangaea (Seyfert and Sirkin, 1973) the Plusiocampa location in southeastern Asia would also be below 30° N. latitude, instead of near 40° N. as it appears on the map in Figure 59. The glacial advances at the end of the Cenozoic must have had a devastating effect on any epigean members of the genus. It is interesting to note that the three endogean species of the genus today are found in the tropics, while the cavernicoles are in the temperate zone.

Many "schemes" and routes were considered in an attempt to explain the evolution, dispersal, and distribution of the species of

FIGURE 59.--The present distribution of Litocampa and Plusiocampa superimposed on a map of Pangaea during the Mesozioc Era. (After Dietz and Holden, 1970).


PANTHALASSA
TETHYS SEA
SINUS AUSTRALIS
SINUS BOREALIS
P A N G A E A
120°
80°
40°
80°
A

Litocampa in the United States. Particular attention was given to trying to explain the introduction of the species from Mexico. Only one species of Litocampa has been described from Mexico (Wygodzinsky, 1944b); however, it lacks medial anterior macrochaetae on the abdominal tergites, a trait which Conde (1956a) suggests as primitive. However, there were many problems inherent with such a hypothesis.

Due to the intermediate nature of its abdominal chaetotaxy and its intermediate geographical location (to Mexico), I hypothesized that the hawksleyi stock in the Ozark Plateaus gave rise to both the cookei group and the other groups. This implied a loss of several characters in some cases and the acquisition of characters in others. In view of the variability of the abdominal chaetotaxy as compared to other morphological characters, this hypothesis had a weak basis. And there was always the problem of the unique (for a Litocampa) characters belonging to the hawksleyi group which it shares with the Haplocampa. Morphologically, I feel a better case can be made for the radiation of species from the southern Appalachian region. The zoogeographical data may also support such a claim.

If my phylogenetic interpretations presented earlier are valid, there seems to exist a general pattern regarding related species. Members of a species group, which appear to be primitive, have larger ranges than do the related species judged to be morphologically advanced (derived). For example, (primitive versus advanced): L. davisi vs. L. henroti, L. valentinei vs. L. pecki, L. cookel vs. L. holsingeri and L. sperkai(?), and L. bifurcata vs. L. barryi and L. holleri.

The general pattern applies fairly well to the species groups. If one calculates the distances between the most wide-spread locations for the different species of a group (Figs. 43, 44), the order of most wide-spread to least is the following: keithi, virginiana, cookei, bifurcata, hawksleyi, fieldingi, davisi, and valentinei groups. In this list fieldingi appears out of order, being included near the younger groups as presented in the cladogram (Fig. 56). In fact, this is probably close to where it really belongs in the evolution of these groups. Some other morphological and zoogeographical data presented below support this sequence.

If it were not for the wide east-west expanse of the range of the cookei group, the primitive bifurcata group would easily have the next largest range. The known range of the hawksleyi group is probably artifically limited in size due to the lack of collecting in other areas of the Ozark Plateau. In all, the agreement between the sizes of the ranges and the interpretation of the relative ages of the groups that was presented earlier, based entirely on morphology, is quite good.

The history of Litocampa in the United States appears long and varied. There have probably been several periods of expansion by some groups and extinctions, or displacements, of others. How these events all fitt together will probably never be known with any degree of certainty. Trying to establish precise time intervals for these events is even more speculative. The best that can be done at present is to try to interpret some of the patterns in light of the available morphological, geological, and zoogeographical evidence.

Due to the close similarity between Litocampa bifurcata in America and L. vandeli in the central Pyrenees of France, and the large number of probable ancestral characters shared by these species, I hypothesize that the bifurcata stock is representative of the most primitive forms occupying the area now recognized as the United States at the breakup of Pangaea. Whether the forms we find in the United States are all derived from the ancestral bifurcata stock in unknown. There is good morphological and zoogeographical evidence that it did give rise to L. fieldingi, or its immediate ancestors. And it seems possible that it could have given rise to the keithi or virginiana stocks, which geographically are still its neighbors. It could have even given rise to the ancestral hawksleyi stock, but a lot of modification and subsequent evolution had to follow to produce the present species of that group.

First, the most primitive Litocampa stock (bifurcata group), or its descendants, appears to have occupied at least the southern Appalachian Mountains, particularly the Blue Ridge Province (Fenneman, 1938) of Tennessee, North Carolina, and southwestern Virginia. They ranged as far north as the divide between the drainage systems of the New River and the James and Roanoke Rivers. New River is analogous to the ancient Teays River (Ross, 1969). And they probably ranged southward as far as the presently recognized extent of the Blue Ridge Province in northern Georgia. Such forested upland would have provided moist, thick humus and soil in which the early Litocampa stock could live.

At some undetermined time, this earliest stock gave rise to

L. fieldingi whose range is in the limestone valleys north of New River in West Virginia. This event could have preceeded or followed the origin of some other stocks. However, due to the wide range of *L. fieldingi*, with little evidence of additional variation, I feel at present that its origin probably occurred sometime later in the evolution of the *Litocampa* groups. It is without question derived from *bifurcata*-like ancestors. *Bifurcata* stock also appears to have given rise to a quite distinct undescribed genus located in caves in the western edge of the Great Smoky Mountains.

Two species groups are candidates for the second derived species group. Of the two, the *keithi* group displays the more primitive characters. But, the *hawksleyi* group displays some equally primitive characters, along with a number of uniquely derived characters. *Keithi* stock was wide ranging. It occupied the eastern most Valley and Ridge and spread far, into Indiana for certain, and perhaps as far west as New Mexico and Nevada. It may be shown in the future that *L. welbourni* radiated from a Mexican center of distribution; nevertheless, it appears to show affinity to the *keithi* group. Also, an undescribed genus (genus A on Map IA of the Appendix), found in a cave of southern Nevada, could have had a *keithi* stock ancestor as well.

Either members of the *bifurcata* stock ranged as far as the Interior Highlands (the Ozarks) and established the *hawsleyi* group, or members of the *keithi* stock did so. Another alternative is that the group had ancestors of some unknown stock. If *keithi* stock was ancestral to the *hawksleyi* group, then there must have been a character reversal regarding the chaetotaxy of the first abdominal sternite. Due to the degree of morphological deviation of the hawksleyi group from the other species groups, and my belief, for morphological and zoogeographical reasons, that this stock was ancestral to the Haplocampa, the hawksleyi stock would have had to originate quite early in order to have time for the subsequent evolution. It may, as well, have given rise to the cookei stock of Litocampa.

The wide-ranging keithi stock was probably ancestral to the virginiana group. This group appears to have occupied the Valley and Ridge Province (relict populations of these are found in Virginia and Georgia today), the adjacent areas of the Cumberland Plateau in Georgia and Alabama, with a northward extension through northwestern Alabama into the Western Highland Rim of Tennessee, and probably further. However, most of the area of the Interior Low Plateaus and the Cumberland Plateau of Kentucky, Georgia, and Alabama eventually were occupied by other stocks. Morphologically and zoogeographically, keithi stock could have been ancestral to the virginiana group and the henroti group. Keithi stock might have given rise to the ancestral virginiana group in the Valley and Ridge section of the southern Appalachians and to the ancestral henroti group in the adjacent areas of the Interior Lowlands. However, the cladogram suggests a closer affinity between the henroti group and the virginiana group. Finally, the henroti group appears to possess a few more primitive characters than the valentinei group, and could be ancestral to it.

I hypothesize that the cookei group evolved from hawksleyi stock.

Supporting this view is the intermediate nature of the abdominal tergal chaetotaxy of the *hawksleyi* group as compared to the *cookei* group and all other species lumped together. In addition, the most primitive member of the *cookei* group, *L. jonesi*, is situated geographically close to the *hawksleyi* group range. Dispersal from the Ozark Plateaus along Shawneetown Ridge in southern Illinois could have introduced *Litocampa* to Kentucky. Faunal movement in the opposite direction appears to be the case in most instances, according to J. L. Craig (unpublished manuscript). His voluminous data on other cavernicoles of the Ozarks supports the view that the *hawksleyi* stock reached the Ozarks from the east. If the *hawksleyi* stock reached the Ozarks from the west and central highlands of Mexico, it would have to have done so prior to the formation of the Cretaceous sea. Also, if the *hawksleyi* stock gave rise to the *cookei* stock, the divergence had to occur prior to the appearance on the abdominal styli of apical setae with long basal branches.

If the reverse was true, and an ancestor of the *cookei* group reached the Ozarks and subsequently evolved into the *hawksleyi* group, then one is confronted with several problems. Assuming the ancestral *cookei* had already lost the medial anterior macrochaetae on all abdominal tergites, it is difficult to consider the medial anterior macrochaetae of the *hawksleyi* group as new acquisitions, in light of the number of other primitive characters they display. The *hawksleyi* pattern of abdominal chaetotaxy is known to the writer in only three epigean species of *Haplocampa* from Washington, Oregon, and Alberta, Canada (Silvestri, 1912a, 1933e; Bareth and Conde, 1958). Also, there is an undescribed species of Haplocampa in eastern Missouri and southwestern Illinois which has characters intermediate, or similar, to the cookei group. For example, it lacks medial anterior macrochaetae on the abdominal tergites, which is the same condition found in members of the cookei group.

Forms similar to L. jonesi, the most primitive member of the cookei group, might then have given rise to the more specialized L. cookei. Subsequently, this species (or its immediate ancestor) must have spread throughout the Interior Lowlands, but did not go north of the present day Ohio River. (The remark that "C. cookei" had been sighted in Wyandotte (Cope, 1872) has no basis in fact.) It also reached as far east as southwestern Virginia, and probably to southern Tennessee. Whether it displaced other species in these areas at that time is unknown. I interpret the syntopic occurrence of L. cookei and L. inexspectata in a northeastern Tennessee cave as evidence that L. cookei did spread eastward, into the ranges of other campodeid species. However, I believe this particular invasion occurred at a more recent time. Possibly the spread of L. cookei was in some way limited by the presence of other campodeid species - note the ranges of L. davisi and the species of the virginiana group relative to that of L. cookei (Fig. 43).

As a result of climatic changes in the Pleistocene, it is possible that some fragmentation of the L. cookei range occurred, forming at least two peripherally isolated populations. Subsequent speciation in these isolated populations (see Mayr, 1963, 1970) produced *L. holsingeri* in southwestern Virginia (and neighboring Kentucky?). The other became *L. sperkai* in eastern Kentucky. With the return of favorable (humid?) conditions for above ground dispersal, *L. cookei* may have repopulated certain areas abandoned earlier. The overlapping ranges of *L. holsingeri* and particularly, *L. sperkai*, with that of *L. cookei* is taken to mean that reproductive isolation has developed for the species in question. No morphological intergradation is known.

This lack of intergradation is not the case for some campodeid populations in Coffee County, Tennessee. Some specimens of these populations have an abdominal chaetotaxy similar (not identical) to that of *L. holsingeri*. This suggests that the Letcher County, Kentucky, population of *L. holsingeri* might be a case of parallel evolution, since *L. cookei* could have been ancestral to both. In the Tennessee example, there is every conceivable gradation between the new forms and pure *L. cookei* (most are pure *cookei*). The caves in which these specimens were found appear to be in an erosional remnant or outlyer of the Highland Rim, which has been detached by past erosion and degradation.

I propose that here the populations of *L. cookei* were isolated for some time from the rest of the range (subterranean dispersal was probably impossible), allowing genetic changes and the development of some new characters. The variation seen today suggests that speciation was not complete, and, with the reintroduction of *L. cookei* recently (see below), the gene pool of the former geographical isolate has been swamped.

The population of *L. sperkai* that is south of the Cumberland River in Pulaski County (Fig. 54) shows signs of diverging from those populations north of the river. Rivers have been shown to act as barriers to dispersal of terrestrial cavernicoles (Barr, 1959a, 1959b). Whether the above case is due to a shifting in the stream channel, stream piracy, of a fortuitous crossing by *L. sperkai* is not known.

The Nickajack Cave locality for *L. cookei* in southernmost Tennessee, on the south side of the Tennessee River, might be explained by dispersal of *L. cookei* prior to the capture of the headwaters of the old Appalachian River (former Tennessee River when it flowed south into the Coosa River) by the Sequatchie River (Ross, 1971). Stream piracies probably played a role in the separation of *L. valentinei* from the populations which were to become *L. pecki*. This kind of reasoning suggests that the ranges of some of the cavernicolous campodeids, such as *L. cherokeensis* and *L. davisi*, are quite old.

The ideas presented above to explain the *cookei* stock evolution requires overland movement of the cavernicoles. Pertinent to this discussion is the role of temperature and humidity in limiting the dispersal of cavernicolous campodeids. The temperature and humidity data for Steeles Cave (presented with the species description of *L. fieldingi*) does little to decide which climatic factor is more important. Campodeids probably cannot withstand subfreezing temperatures. They are exothermic and normally inhabit the soil which provides some insulation from the surface temperature extremes. The absence or reduction in numbers of species of campodeids in more polar regions of the earth (Paclt, 1957; Condé, 1956a) might support this statement. They certainly can withstand cool conditions since they live in caves where temperatures normally range from about 10 to 15°C (Moore and Sullivan, 1978). And some campodeids are known from lava tube caves which have temperatures of 5°C or less (some lava tubes act as cold traps and may have ice in them all year).

Campodeids have an exceedingly thin cuticle, and even though they live as endogeans and cavernicoles in a humid environment, they still have special organs (the eversible vesicles) for the absorption of water (Drummond, 1953). The most widely ranging species of the campodeidae in the hot regions of the earth are the Lepidocampa, which are believed to be protected from dessication in part by their scales and large body size (Silvestri, 1899; Condé, 1956a). The campodeids' method of reproduction and development may also restrict them to humid environments. They reproduce by externally placed spermatophores, some of which are later discovered and picked up by the females (Bareth, 1964). The females later attach their eggs to a short stalk in a small "brood chamber" in the soil (Wygodzinsky, 1941). The first instar (called a prelarva) is completely quiescent and not fully developed. The second instar (larva I) is active and takes food for the first time.

Although caves maintain a nearly constant temperature year round, there are temperature fluctations, particularly in those with large sinking streams which results in an influx of cold surface water during the winter. In such wet caves one tends to find the larger populations of campodeids. Collection records do not give much insight into whether cave campodeids are more abundant during certain times of the year. This is because most collections have been made during the warmer months. It has been my experience that cave campodeids can be found in relative abundance at any time of the year. However, there are large fluctuations in the apparent size of populations. John R. Holsinger (personal communication) has commented on this for *L. barringerorum* in Fallen Rock Cave, Tazewell County, Virginia.

On over a half dozen trips to Fallen Rock Cave, I have found many campodeids crawling on the high silt banks of the stream passage near the cave's entrance. However, in October, 1979, only a few individuals were found after hours of searching. Cheese bait used over night attracted only one more specimen. Although there had been some recent large rains, this part of Virginia had experienced a drought, and the cave streams were appreciably low. In Fallen Rock Cave, the silt banks were noticeably drier than I had ever seen them before, which must have accounted for the lack of campodeids. At the same time in nearby Lawson Cave, there were many hundreds of campodeid diplurans on the wet clay banks and floor of that cave.

It appears to me that the campodeids which have survived in caves as relicts are much more likely to have dispersed above ground during cool, moist glacial periods of the Pleistocene Epoch, than during the warmer, but dryer, interglacials. Using methods employed by

Peck (1973, 1978) and Ferguson (1974) to correlate the timing of morphological changes in cavernicoles with the climatic fluctuations of the Pleistocene, I suggest that some *bifurcata* stock reached West Virginia and founded *L. fieldingi* no later than the Illinoian glacial period. During the following interglacial period, *L. fieldingi* evolved and acquired cave adaptations. Some surface dispersal during the Wisconsin glacial period would help to account for the present range of *L. fieldingi* in West Virginia.

Litocampa cookei probably spread widely during the Illinoian glacial period, establishing populations in southwestern Virginia, eastern Kentucky, and elsewhere. During the last interglacial period (Sangamon) some populations became isolated and diverged enough to be regarded as distinct species: *L. sperkai* and *L. holsingeri*. *Litocampa holsingeri* may have dispersed via above ground routes during the following Wisconsin glaciation. This may account for the two populations outside of Rye Cove, in Scott County, Virginia. Any subterranean dispersal by *L. holsingeri* would have been severely limited by highly folded and thrust faulted strata of southwestern Virginia. As a more advanced cavernicole than *L. cookei*, *L. holsingeri* may have been less likely to disperse above ground. *Litocampa sperkai* may have also had limited dispersal above ground during the Wisconsin, thus establishing a population south of the present day Cumberland River. One could also suggest that *L. cookei* managed to reenter the east Kentucky caves as well.

From Craig's interpretation of the faunal data and information on the glacial history of the area (unpublished manuscript), he proposes that the terrestrial troglobites of the south slope of the Ozark Plateau (location of L. hawksleyi and L. ozarkensis) probably invaded the subterranean habitat prior to the Illinoian glaciation, during the Kansan glaciation or earlier. I would push the time back even further, possibly into the Mesozoic for the founding of the hawksleyi stock. Time is needed for the evolution of the genus Haplocampa and its spread and speciation throughout the northwest and west.

CONCLUSIONS

The cavernicolous campodeids found in the eastern part of Kentucky, which very closely resemble certain forms of Litocampa cookei from the Mammoth Cave region, are shown to belong to a distinctly different species. It is concluded, therefore, that only one species of campodeid occupies Mammoth Cave. If the wide-ranging L. cookei represents a complex of morphologically similar species, then a more detailed examination, probably including the use of electrophoretic techniques to analyze the genetic variation of different populations, will be required to separate the species.

Additional information on the previously described eight species has been presented, including new localities and range extensions for each species. Twelve new species have been described. The species of Litocampa in the United States were assigned to eight species groups, and these groups were compared by cladistic analysis in an attempt to work out a more satisfactory phylogeny. The insight gained from this analysis, along with the zoogeographical data and a knowledge of the past geologic events, indicates that the genus Litocampa predates the beginning of the breakup of Pangaea at the onset of the Jurassic Period. Presently known distributions show that the range of the genus during the Early Mesozoic was probably subtropical to equatorial. Following the breakup of the supercontinent, the land masses were rafted on lithospheric plates into higher latitudes while speciation and dispersal of Litocampa undoubtedly continued. The cladistic analysis of the species groups and the zoogeographical data suggest that in the United States the southern Appalachian Mountains have been a focal point for the dispersal of species of the genus Litocampa.

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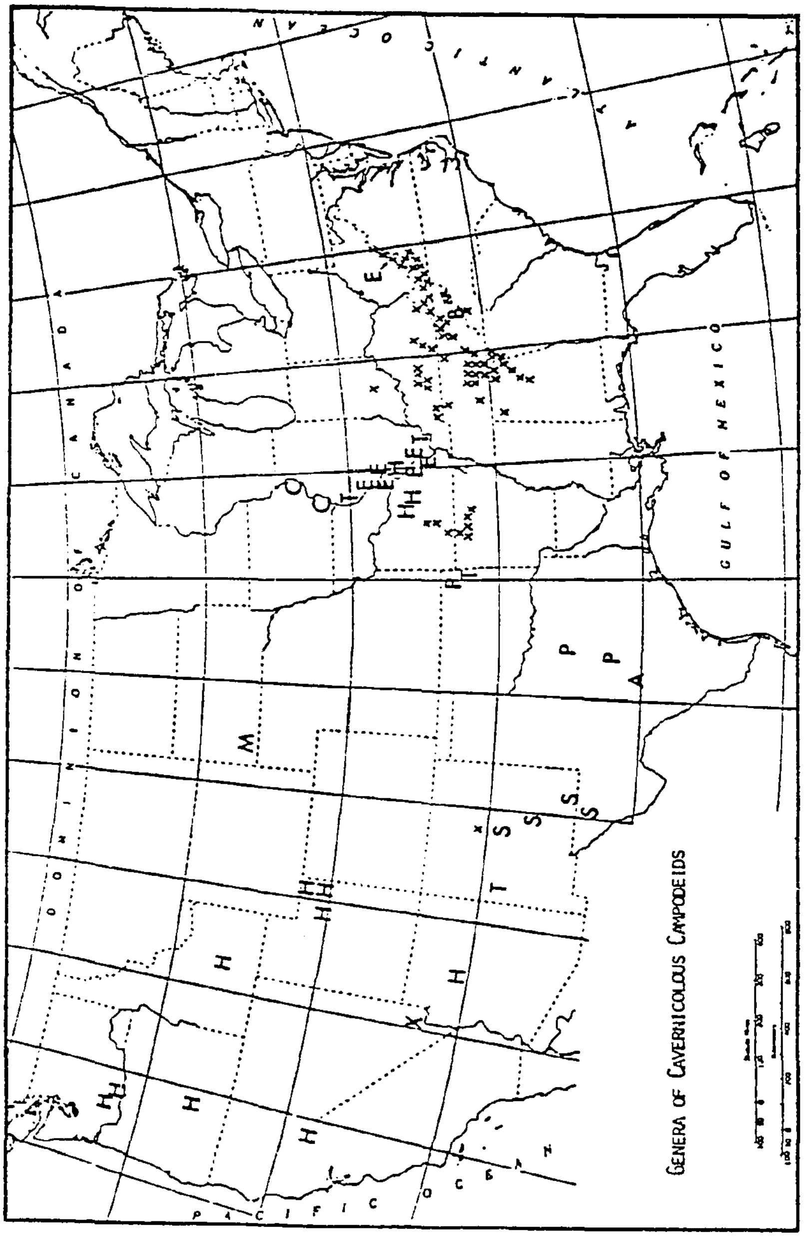
APPENDIX I

Appendix I.--Geographic distribution of cavernicolous campodeids in the United States, excluding _Litocampa_.

By referring to Map IA, one can determine the presently known genera of cavernicolous campodeids in the United States and their relative locations. For a more detailed listing of locations, consult the following table by genus and state. The genera are listed alphabetically, as are the states, counties, and caves under their respective categories. _Litocampa_ is not included in the list. For its locations, consult the maps in the Zoogeography section and the individual cave locations for each species in the Systematics section.

MAP IA.--United States, showing distribution of genera of cavernicolous campodeids: Litocampa (small x), Eumesocampa (E), Campodea (C), Metriocampa (M), Tricampa (T), Podocampa (P), Haplocampa (H), Allocampa ? (A), undescribed genus A (large X), undescribed genus B (B), and undescribed genus S (S).



GENERA OF CAVERNICOLOUS CAMPODEIDS

Appendix I.--Geographic distribution of cavernicolous campodeids in the United States, excluding Litocampa.

Genus	State	County	Cave	Species
Allocampa (?)	Texas	Kendall	Kirschky Ranch	1 sp.
Campodea	Iowa	Jackson	Dancehall	1 sp.
		Lee	Horsethief	"
Eumesocampa	Illinois	Monroe	Camp Vandeventer Horsethief Madonnaville	n. sp. A
		Pike	Lost Creek Twin Culvert	"
		Union	Sensemeyer	"
	Missouri	Jefferson	Cave, S. of Antonia	"
		Perry	Berome Moore Mystery	"
		St. Geneviere	Battys Buddys Kohms	"
	West Va.	Monroe	Steeles	n. sp. B
Haplocampa	Arizona	Coconino	Tapeats	n. sp. A
	California	Plumas	Sunnyside Mine	n. sp. B
	Idaho	Butte	Boy Scout	n. sp. C
	Illinois	Monroe	Illinois Mammoth	n. sp. D
	Missouri	Crawford	Bear Jagged Canyon	"
		Washington	Green Hamilton Spring	"
	Oregon	Lake	South Ice (No. 1)	n. sp. E

Genus	State	County	Cave	Species
Haplocampa	Utah	Daggett	Sheep Creek	n. sp. F
		Duchesne	Pole Creek	n. sp. G
		Uintah	Big Brush Creek Little Brush Creek	n. sp. F
	Washington	Klickitat	Cheese	n. sp. H
		Skamania	Ape	n. sp. I
			Dead Horse Creek Dry Creek Lower Falls Creek Upper Falls Creek	n. sp. H
Metriocampa (n. subgen.)	South Dakota	Custer	Wind	n. sp.
Podocampa	Oklahoma	Delaware	Junk Yard Kyle Nichols	sp. A
	Texas	Palo Pinto	Manley Water	sp. B
		Travis	Tooth	sp. A
Tricampa	Illinois	Adams	Burton	1 or more sp.
		Hardin	Equality	"
	New Mexico	Valencia	Caves near Ice Caves	"
	Oklahoma	Delaware	Kyle Nichols	"
Undescribed Genus A	Nevada	Lincoln	Whipple	n. sp.
Undescribed Genus B	Tennessee	Blount	Tuckaleechee Caverns	n. sp.
Undescribed Genus S	New Mexico	Eddy	Black Carlsbad Caverns Cave Tree Cave Cottonwood Decorated Dry	1 or more n. sp.

Genus	State	County	Cave	Species
Undescribed Genus S	New Mexico	Eddy	Hell Below	1 or more n. sp.
			Hermit	
			Hidden	
			Jurnigen No. 1	
			Lake	
			Midnight Goat	
			Mudgett's	
			Musk Ox	
			New	
			Ogle	
			Pink Dragon	
			Pink Panther	
			Rainbow	
			Ringtail (Flea)	
			Scout	
			Sentinel	
			Spider	
			Three Fingers	
			Watertank	
		Lincoln	Fort Stanton	"
		Torrance	Lobo	"
	Texas	Culberson	Chiveros	"

APPENDIX II

Appendix II.--Geographic distribution of the known species and subspecies of Litocampa and Plusiocampa.

Taxon and Citation	More than 3+3 Macrochaetae on Pronotum	Number of Dorsal Machrochaetae on Femur III	Location
P. corcyraea Silvestri, 1912b	+	1	Aegean Isls.
P. festai Silvestri, 1933c	+	1	"
P. festai coi Silvestri, 1933c	+	1	"
P. lagoi Silvestri, 1933c	+	1	"
P. solerii Silvestri, 1933c	+	1	"
P. caprai Condé, 1950a	+	1	Austria
P. corcyraea Silvestri, 1912b	+	1	"
P. erebophila (Hamann, 1896)[1]	+	0	"
P. exsulans Condé, 1947b	+	1	"
P. nivea (Joseph, 1882)[2]	+	0	"
P. strouhali Silvestri, 1933b	+	1	"
P. strouhali cavicola Silvestri, 1942[3]	+	1	"

[1]Junior synonym of P. nivea (Joseph, 1882), Paclt, 1957.

[2]Redescribed by Denis, 1923, and Silvestri, 1948; also a descriptive note by Condé, 1947b.

[3]Descriptive notes given by Condé in Franz, 1954.

Appendix II.--Continued.

Taxon and Citation	More than 3+3 Macrochaetae on Pronotum	Number of Dorsal Machrochaetae on Femur III	Location
P. breuili Condé, 1954b	+	1	Balearic Isls.
P. fagei Condé, 1954b	+	1	"
L. brasiliensis (Wygodzinsky, 1944a)	-	0	Brazil
P. bulgarica Silvestri, 1931a	+	1	Bulgaria
P. bureschi Silvestri, 1931a	+	0	"
P. montana Drenovski, 1937[4]	+	?	"
P. rauseri Rusek, 1965	+	0	"
P. sinensis Silvestri, 1931b[5]	+	2	China
P. corcyraea cyrnensis Condé, 1952	+	1	Corsica
P. notabilis Silvestri, 1912b	+	1	"
P. rybaki Condé, 1956b	+	1	Crete
P. evallonychia Silvestri, 1949	+	2	Crimea

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[4]Location data, Drenovski, 1939; nom. nud., Paclt, 1957.
[5]Descriptive notes in Condé, 1956a, and Paclt, 1957.

Appendix II.--Continued.

Taxon and Citation	More than 3+3 Macrochaetae on Pronotum	Number of Dorsal Machrochaetae on Femur III	Location
P. spelaea Stach, 1929[6]	+	1	Czechoslovakia
P. balsani Condé, 1947c	+	1	France
P. bonadonai Condé, 1948d	+	1	"
L. bourgoini (Condé, 1948a)	-	0	"
L. cognata (Condé, 1948d)	-	0	"
L. coiffaiti (Condé, 1948a)	-	1	"
P. dargilani (Moniez, 1893)[7]	+	1	"
L. drescoi (Condé, 1949c)	-	1	"
L. humilis (Condé, 1948a)	-	0	"
P. magdalenae Condé, 1957b	+	1	"
P. pouadensis (Denis, 1930)	+	1	"
P. pouadensis bonneti Condé, 1948d	+	1	"
P. provincialis Condé, 1949a	+	1	"

[6]Redescribed in Paclt, 1957, p. 45.
[7]Redescribed by Condé, 1946.

Appendix II.--Continued.

Taxon and Citation	More than 3+3 Macrochaetae on Pronotum	Number of Dorsal Machrochaetae on Femur III	Location
P. provincialis praedita Condé, 1949a	+	1	France
L. sollaudi (Denis, 1930)	-	0	"
P. suspiciosa Condé and Mathieu, 1958	+	1	"
L. vandeli (Condé, 1947a)[8]	-	0	"
L. vandeli longiseta (Condé, 1948a)	-	0	"
P. lindbergi Condé, 1956b	+	1	Greece
P. rybaki Condé, 1956b	+	1	"
L. neotropica (Silvestri, 1933d)	-	1	Guyana
L. perkinsi (Silvestri, 1934c)	-	0	Hawaii
P. spelaea Stach, 1929[9]	+	1	Hungary
P. bonadonai lanzai Condé, 1962	+	1	Italy
P. caprai Condé, 1950a	+	1	"
P. grandii Silvestri, 1933a	+	1	"

[8]Illustrations and descriptive notes in Condé, 1956a.
[9]See footnote 6.

Appendix II.--Continued.

Taxon and Citation	More than 3+3 Macrochaetae on Pronotum	Number of Dorsal Machrochaetae on Femur III	Location
P. notabilis Silvestri, 1912b	+	1	Italy
P. romana Condé, 1954a	+	1	"
L. atoyacensis (Wygodzinsky, 1944b)	-	0	Mexico
L. aethiopica (Silvestri, 1933f)	-	0	Rep. of Guinea
P. elongata Ionescu, 1955	+	1	Rumania
P. humicola Ionescu, 1951[10]	+	1	"
P. spelaea Stach, 1929[11]	+	1	"
P. provincialis Condé, 1949a	+	1	Sardinia
P. suspiciosa Condé and Mathieu, 1958	+	1	Sicily
L. solomonis Bareth and Condé, 1972	-	0	Solomon Isls.
L. espanoli (Condé, 1949c)	-	1	Spain
P. pouadensis bonneti Condé, 1948d	+	1	"
P. pouadensis leoni Condé, 1951	+	1	"

[10]Junior synonym, P. spelaea Stach, 1929 (Paclt, 1957).
[11]See footnote 6.

Appendix II.--Continued.

Taxon and Citation	More than 3+3 Macrochaetae on Pronotum	Number of Dorsal Machrochaetae on Femur III	Location
L. bourgeoini (Condé, 1948a)	-	0	Switzerland
L. sollaudi (Denis, 1930)	-	0	"
L. barringerorum n. sp.	-	1	U.S.A.
L. barryi n. sp.	-	0	"
L. bifurcata Ferguson (in press)	-	0	"
L. cherokeensis n. sp.	-	1	"
L. cookei (Packard, 1871)	-	1	"
L. davisi n. sp.	-	1	"
L. fieldingi (Condé, 1949b)	-	1	"
L. hawksleyi n. sp.	-	1	"
L. henroti (Condé, 1949b)	-	1	"
L. holleri n. sp.	-	0	"
L. holsingeri Ferguson (in press)	-	1	"
L. inexspectata n. sp.	-	1	"

Appendix II.--Continued.

Taxon and Citation	More than 3+3 Macrochaetae on Pronotum	Number of Dorsal Machrochaetae on Femur III	Location
L. jonesi (Condé, 1949b)	-	1	U.S.A.
L. keithi n. sp.	-	1	"
P. nearctica Silvestri, 1934b[12]	-	1	"
L. ozarkensis n. sp.	-	1	"
L. pecki n. sp.	-	1	"
L. sperkai n. sp.	-	1	"
L. valentinei (Condé, 1949b)	-	1	"
L. virginiana Ferguson, (in press)	-	1	"
L. welbourni n. sp.	-	1	"
P. affinis Condé, 1947b	+	1	Yugoslavia
P. dalmatica Condé, 1959	+	0	"
P. denisi Condé, 1947b	+	0	"
P. exsulans Condé, 1947b	+	1	"
P. latens Condé, 1948b	+	1	"

[12]Junior synonym, *L. cookei* (Packard, 1871).

Appendix II.--Continued.

Taxon and Citation	More than 3+3 Macrochaetae on Pronotum	Number of Dorsal Machrochaetae on Femur III	Location
P. remyi Condé, 1947b	+	0	Yugoslavia
P. schweitzeri Condé, 1947b	+	1	"

VITA

Lynn Milton Ferguson was born on January 12, 1944, in Rocky Mount, Virginia. He graduated from Franklin County High School in 1962. He attended the University of Virginia for three years, and after transferring to East Tennessee State University, received the Bachelor of Science degree in 1968, majoring in biology and geology. After teaching at South Salem School of the Roanoke County School System, he attended Virginia Polytechnic Institute and State University, receiving the Master of Science degree in Zoology in 1974. In 1976 he accepted a faculty position at Longwood College where he teaches biology, geology, entomology, and speleology. He is a member of Sigma Xi, the Association of Southeastern Biologists, the National Association of Geology Teachers, the National Speleological Society, and other organizations. He is also a member of Sigma Gamma Epsilon (Honorary Earth Science) and Phi Sigma (Honorary Life Science) societies. Lynn is married to the former Lucie Scott Lancaster, and they have two children, Lucie Scott, age 12, and Lynn Martel, age 6.

Lynn M. Ferguson

SYSTEMATICS, EVOLUTION, AND ZOOGEOGRAPHY OF THE CAVERNICOLOUS CAMPODEIDS OF THE GENUS *LITOCAMPA* (DIPLURA: CAMPODEIDAE) IN THE UNITED STATES

by

Lynn Milton Ferguson

(ABSTRACT)

Three hundred seventy-two collections of campodeid diplurans from 268 caves in 22 states were examined. Forty species belonging to 10 genera are represented. The majority of the collections (268) consists of species in the genus *Litocampa*, which is found in 174 caves east of the Mississippi River (out of 185 caves from which collections were taken), as well as in 17 caves of the Ozarks Plateau region of Arkansas and Missouri and in one cave in New Mexico. Twelve new species of *Litocampa* are described and illustrated. Additional information and illustrations are provided for the eight previously described species belonging to this genus in the United States. Two undescribed genera related to *Litocampa* are recognized.

Based on the new data, the subfamilies of the Campodeidae are redefined, and the Plusiocampinae and Syncampinae are synonomized with the Campodeinae and Hemicampinae, respectively. The genera *Plusiocampa* and *Litocampa* are also redefined. The subgenus *Cocytocampa*, in part, is raised to generic status. The remaining species of this former subgenus

and the subgenus *Tychocampa* are included with the *Litocampa* s. str. Eight species groups are proposed for *Litocampa* in the United States. The taxonomic position of the genus *Litocampa* is illustrated by means of keys. A key to all related or similar genera and keys to the species of *Litocampa* in the United States are included.

The geographic range of each species is presented, as well as lists of all known cavernicolous campodeids in the United States and the world-wide distribution of all species of *Litocampa* and *Plusiocampa*. The dispersal, evolution, and phylogenetic relationships of the North American species of *Litocampa* are discussed, in light of the past tectonic and climatic changes affecting North America.