MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN NO. 156

The Systematics and Biology of the Cave-Crickets of the North American Tribe Hadenoecini (Orthoptera Saltatoria: Ensifera: Rhaphidophoridae: Dolichopodinae)

by
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and
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Yale University

Ann Arbor
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
August 1, 1978

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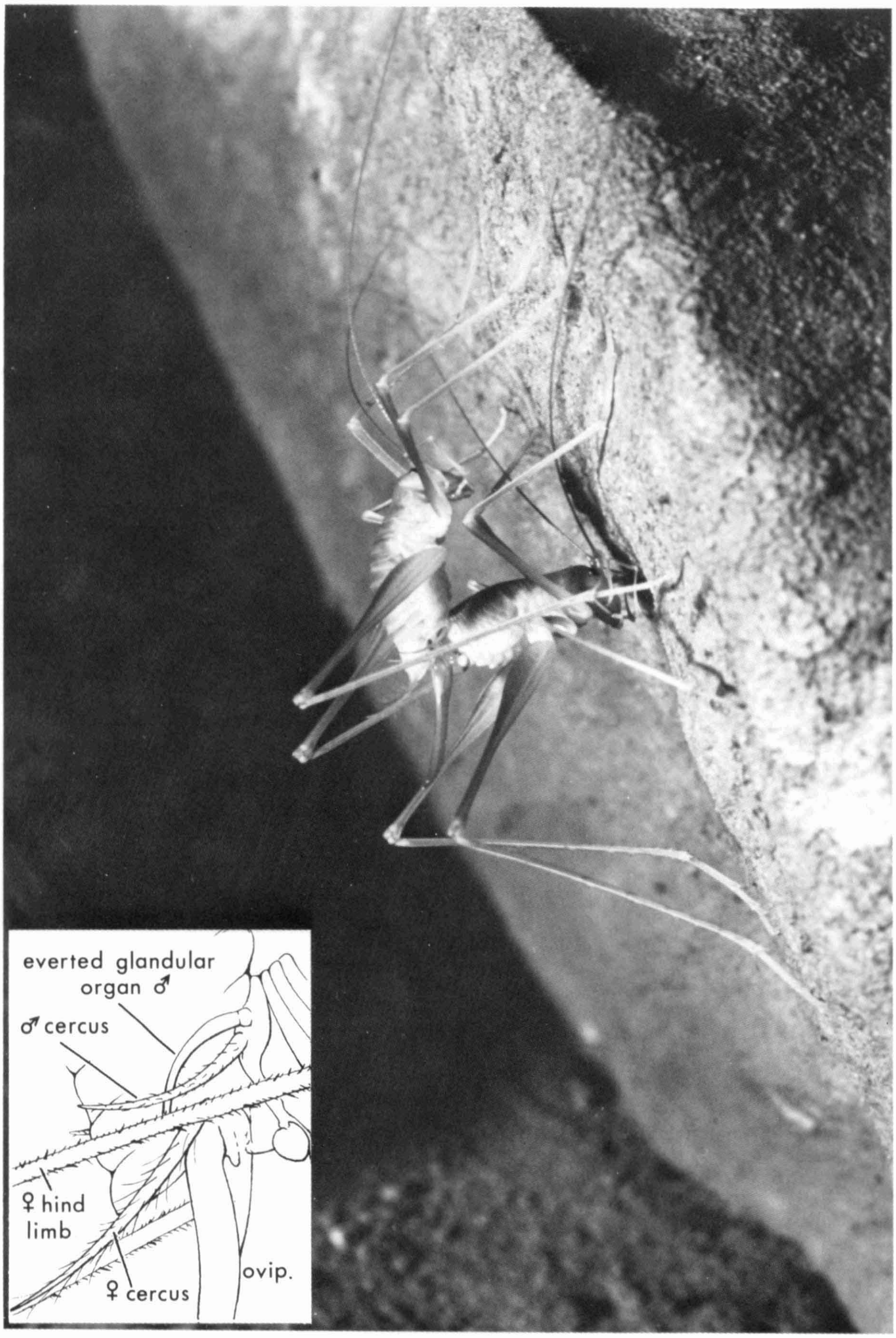
PLATE I

Hadenoecus subterraneus, mating pair, Mammoth Cave, Kentucky, January, 1968
(photo by Norton)

Hadenoecus copulates with the female above. The inset shows the position of the eversible elongate dorsolateral organs of the male enclosing the end of the female's abdomen.


everted glandular organ ♂
♂ cercus
♀ hind limb
♀ cercus
ovip.

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ABSTRACT

The rhaphidophorid tribe Hadenoecini, restricted to the eastern United States, comprises two genera—*Euhadenoecus* gen. nov., with four species of which three are new, and *Hadenoecus* Scudder, with five species of which four are new. Two of the species of *Euhadenoecus* are forest-dwellers; all the other members of the tribe are obligatory cavernicoles that reproduce only in caves but emerge from them at night to feed. In parts I and II of this study, by T. H. Hubbell, the tribe, genera and species are described, and their distribution, phylogeny and evolutionary history are discussed. Part III, by R. M. Norton, deals with the life history, behavior and ecology of the two best-known species, *H. subterraneus* and *H. cumberlandicus*.

INTRODUCTION

Among the larger, more conspicuous and more often observed of the insects that inhabit caves in the eastern United States are the pale, spidery "cave-crickets"[1] of the rhaphidophorid subfamily Dolichopodinae, tribe Hadenoecini. Commonly seen clinging singly or in groups to the cavern walls and ceilings, they are wingless, with compact bodies and very long, slender legs and antennae, and have small but functional dark eyes. The guides in commercial caves often refer to them as "white cave-crickets" to distinguish them from the more robust, shorter-legged, brown-maculate "camel-crickets" of the genus *Ceuthophilus* that frequent cave entrances and the twilight zones. Actually they are not white; adults are pale yellowish or yellowish-brown, but small nymphs are very light in color and almost translucent.

Hitherto only a single cave-inhabiting species of this tribe has been recognized—*Hadenoecus subterraneus* (Scudder). A second smaller, darker, sylvicolous species, *puteanus* Scudder, has until now been placed in the same genus but is here made the type of *Euhadenoecus* gen. nov. *Hadenoecus* Scudder, with *subterraneus* as type, includes in

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[1] The term "cricket" properly applies only to the members of the Grylloidea, but the common names "camel-cricket" and "cave-cricket" are so firmly attached to the rhaphidophorids that it is useless to try to change them.

addition four new species; all its members are cave-dwellers. *Euhadenoecus* has four species, three of them new; two of its species are cavernicoles. The insects of this tribe pose many interesting problems in evolutionary systematics, zoogeography, ecology and behavior, some of which are discussed herein.

HISTORICAL REVIEW. The earliest mention of a member of the Hadenoecini was by Thompson (1844), who reported the presence in Mammoth Cave, Kentucky, of what he identified as a species of *Phalangopsis* Serville, a genus of long-legged Gryllidae. In 1861 Scudder described the Mammoth Cave insect as *Rhaphidophora subterranea*, and in the following year it was again described by Saussure as *Rhaphidophora cavernarum*. In 1862 Scudder erected the genus *Hadenoecus* for *subterraneus*, and he also tentatively placed in it the European *Rhaphidophora palpata* (Sulzer). Walker (1869) added to *Hadenoecus* the European *Rhaphidophora cavicola* (Kollar), and in the same year Scudder described *Hadenoecus edwardsii* from New Zealand, confirmed the position of *palpatus* in the genus, and erroneously synonymized his *subterraneus* under Saussure's *cavernarum*. A fifth species, *H. poduroides*, was described by Walker (1871) from Australia. All four of the extra-American species have since been removed from *Hadenoecus*—*cavicola* became the type of *Troglophilus* Krauss 1879, *palpata* that of *Dolichopoda* Bolivar 1880; *edwardsii*, after a complicated nomenclatural history, is now recognized as the type of *Gymnoplectron* Hutton 1897; and *poduroides*, obviously a member of the Macropathinae, was dubiously and doubtless incorrectly assigned to *Talitropsis* Bolivar 1883 by Kirby in 1906.

In 1877 Scudder described *Hadenoecus puteanus* from North Carolina and Mississippi. Bolivar (1880) distinguished the genera *Dolichopoda* Bolivar, *Hadenoecus* Scudder, *Rhaphidophora* Serville, *Troglophilus* Krauss and *Ceuthophilus* Scudder in a key. Brunner von Wattenwyl, in his "Monographie der Stenopelmatiden und Gryllacriden" (1888), presented the first comprehensive classification of the gryllacridoid Ensifera. He treated what we now recognize as the family Rhaphidophoridae as Section II of his Stenopelmatidae and divided this section into three groups, the Rhaphidophorae, Dolichopodae and Ceuthophilae. Although his classification brought order out of confusion, it associated unrelated genera because it was based primarily on the spur and spine armature of the legs, in which parallel modifications are common. Thus his Ceuthophili was based on the presence of large "spines" in addition to small teeth on the dorsal carinae of the hind tibiae and was made to include, besides *Ceuthophilus*, the North American *Hadenoecus*, *Udeopsylla* and *Gammarotettix*, the European *Troglophilus*, the South American *Heteromallus* and the Australian *Talitropsis*—genera which are today placed in four subfamilies.

Barr (1966) has described the development of cave biology in the United States, and the history of work on the Hadenoecini can be discussed in terms of the stages into which he divides it. The "early period" begins with the visit of A. S. Packard to Mammoth Cave in 1871 and extends into the early 1900's. This was a time of active exploration, during which collections of *Hadenoecus* were made in many caves, mostly in Kentucky, by Packard, Cope, Hubbard, Hyatt, Ortmann, Putnam and Sanborn. Packard (1888) and other authors published many of the resulting records, always under the name *subterraneus* or its synonym *cavernarum*, although some of them were based on other species. The Mammoth Cave species was also mentioned and sometimes figured in various textbooks and general works.

During the next two decades interest in cave biology declined in the United States, although this was the time it reached its height in Europe under the influence of E. G. Racovitza and R. Jeannel. Aside from the publication of a few additional records of *puteanus* and *subterraneus*, of a key to the North American rhaphidophorid genera by Caudell (1916), and a redescription by Blatchley (1920) of *Hadenoecus* and the two species it then contained, cave-crickets received no attention in this interval.

LATER STUDIES. During Barr's "middle period," between 1930 and 1955, interest in North American biospeleology again increased, cave exploration was resumed on an extensive scale, and taxonomic studies of cave animals multiplied. The most important event, so far as our knowledge of the Hadenoecini is concerned, was the inception and active prosecution of an extensive program of cave collecting by Dr. Walter B. Jones, then State Geologist of Alabama and Director of the Alabama Museum of Natural History. Much of the material here recorded was collected by Dr. Jones and others associated with him in that project.

The initial stimulus for this renewed interest in cave faunas may have been the publication in 1931 by C. Bolivar and R. Jeannel of their "Campaigne Spéologique dans l'Amerique du Nord en 1928." In this report Chopard recorded the cave Orthoptera collected by Bolivar and Jeannel in Indiana, Kentucky and Virginia, and gave the first detailed and accurate descriptions of the two species then recognized in *Hadenoecus*. He also cited reasons for believing that genus to be closely related to the European *Dolichopoda* and not a member of the Ceuthophilinae, as was then generally assumed. Chopard assigned these two genera to a single tribe, the Dolichopodini, an action accepted by Hubbell (1936) and reaffirmed by Chopard in 1938. But in 1934 H. H. Karny, the leading authority on the gryllacridoid Orthoptera, argued against Chopard's conclusion, and then as well as in his 1937 Genera Insectorum monograph retained *Hadenoecus* as a member of his tribe Ceuthophilini, a placement that has been followed in subsequent publications by most authors, including Beier (1955).

Kjell Ander's very important 1939 work, "Vergleichend-anatomische und phylogenetische Studien über die Ensifera (Saltatoria)," greatly advanced our understanding of the relationships of these insects. In it he presented the results of years of meticulous and exacting investigation of the morphology of many genera and species of Ensifera. Among the taxonomic and phylogenetic conclusions he reached were (1) that *Hadenoecus* cannot be a member of the Ceuthophilini and (2) that it is not so closely related to *Dolichopoda* as Chopard thought; according to Ander, *Dolichopoda* is the most primitive of living Rhaphidophoridae. In this family he recognized two subfamilies—the Macropathinae, circum-Antarctic in distribution, and the Rhaphidophorinae, confined to the northern hemisphere. The Rhaphidophorinae were divided into the North American tribes Hadenoecini, Ceuthophilini, Tropidischiini and Gammarotettigini, and the Palearctic tribes Dolichopodini, Troglophilini and Rhaphidophorini, the last of which has also penetrated the tropics in southeastern Asia and spread as far as New Guinea and its associated archipelagoes.

The results of a computerized multicharacter analysis of the phyletic relationships within the Rhaphidophoridae made by the senior author are as yet unpublished but are briefly summarized in what follows. They are in general agreement with Ander's views, but do support Chopard's conclusion that *Hadenoecus* s.l. is more closely related to *Dolichopoda* than to any other taxon.

The "modern period" in North American biospeleology began, according to Barr, about 1956. It has been characterized by an accelerating growth of interest in the study of cave faunas, by a shift in emphasis from taxonomic to ecological, physiological and evolutionary studies, and by an exponential increase in the number of publications. Although taxonomic and faunistic contributions no longer predominate, they have shared in this increase, and as a result most of the important groups of cave animals have by now received attention. Some of the more recent studies have dealt with the biology of *Hadenoecus subterraneus*—its reproduction, life cycle, behavior, and role in the cave ecosystem; the findings are summarized in Part III. Similar studies, of interest for comparison with those on *Hadenoecus*, had already been made in Europe on species of *Dolichopoda, Troglophilus* and *Tachycines* (by, among others, Boldyrev 1915, Chopard 1917, 1918, and Remy 1931), and in recent years more detailed observations have been published on various New Zealand and Australian macropathine rhaphidophorids by Richards (1954, 1961, 1962, 1965, 1970). Leroy (1967) has summarized most of the resulting information. Sbordoni et al. (1976) discussed the evolutionary implications of the distribution of two electrophoretically distinguishable alleles at one gene locus in populations of the Italian *Dolichopoda geniculata* Costa; situations such as that which they describe doubtless exist also in *Hadenoecus.*

ACKNOWLEDGEMENTS

In making the studies on which this report is based the authors received help from many sources for which our thanks are here expressed. Foremost among those persons to whom the senior author is indebted is the late Dr. Walter B. Jones, who not only provided the largest and most comprehensive collection yet made of the cave species of *Hadenoecus,* with field data, but also served as host and guide on a visit to Alabama caverns. Both of us are grateful to Dr. Thomas C. Barr, Jr., and Dr. Terrence G. Marsh, who not only supplied specimens from many caves but also cave locations throughout Kentucky and information on the distribution of *Hadenoecus subterraneus* and *H. cumberlandicus* and their beetle predators.

The systematic study by the senior author was supported in part by NSF Research Grant 14012, and James J. Friauf and Theodore J. Cohn assisted in the early stages of the work. Field data on collections and information about caves inhabited by Hadenoecini were furnished by the following persons in addition to those already mentioned: L. G. K. Carr, K. Dearolf, D. C. Eades, L. M. Ferguson, R. E. Gordon, J. R. Holsinger, L. Hubricht, R. Y. Lamb, D. Merkle, Bro. G. Nicholas, H. F. Strohecker, E. S. Thomas and H. K. Wallace. By far the greater part of the material used in the systematic revision was either lent to the senior author by various museums or was deposited by its collectors in the University of Michigan Museum of Zoology. The institutions and individuals that provided such help are listed in Part I.

To Arnold G. Kluge, Curator of Reptiles and Amphibians in the University of Michigan Museum of Zoology, the senior author is much indebted for advice, criticism and indispensable help in making the computerized multiple character analysis of phyletic relationships within the Rhaphidophoridae mentioned in the introduction. This constitutes the basis for the hypotheses about the evolutionary and distributional history of the family presented in Part II.

Much of the field work of the junior author was done at Mammoth Cave National Park, to the successive superintendents of which and to the National Park Service he expresses his appreciation of the opportunities they afforded him. His work was supported by a one-year fellowship from the Cave Research Foundation, to which he is also indebted for use of their facilities at Mammoth Cave National Park. Numerous private landowners allowed access to caves on their property and numerous "cavers" helped him in the field.

The illustrations are for the most part the work of Suzanne Runyon Moore, Martha B. Lackey, Patricia J. Wynne and Mark Orsen, past and present staff artists of the University of Michigan Museum of Zoology.

PART I. A REVISION OF THE RHAPHIDOPHORID TRIBE HADENOECINI

by Theodore H. Hubbell

With the general acceptance in recent years of the family status of the Rhaphidophoridae, its subdivisions have either all been elevated to subfamilial rank or have, except for the Macropathinae, all been treated as tribes of the single subfamily Rhaphidophorinae. Uncertainty about the relationships of the group here recognized as the tribe Hadenoecini led me to make a computerized analysis of the phyletic relationships within the family, using multiple morphological characters. The results of this study will be separately published, but the dendrogram obtained is shown in the present paper as Figure 1. In the classification based on this analysis the Rhaphidophoridae are divided into five subfamilies: Macropathinae, Tropidischiinae, Dolichopodinae with tribes Dolichopodini and Hadenoecini, Rhaphidophorinae with tribes Troglophilini, Rhaphidophorini and Gammarottettigini, and Ceuthophilinae with tribes Pristoceuthophilini, Argyrtini and Ceuthophilini. In redescribing the Dolichopodinae to include the Hadenoecini, and in defining the latter tribe, the similarities, differences and distinctive features of the subfamilies are noted.

MATERIAL STUDIED. About 7,600 specimens of Hadenoecini were examined, some pinned but most of them preserved in alcohol. Of these the greater number are in the University of Michigan Museum of Zoology (UMMZ), including the types of the new species; when, in recording specimens, no indication of ownership is given, they are in that collection. Most of the material in other North American and European museums has been seen, either on visits to those museums or by means of loans from them. For this cooperation thanks are expressed to the following institutions and individuals (listed under the abbreviations used to denote ownership of specimens). Personal collections are also included.

Sources of Material Studied

ALA—Alabama Museum of Natural History, University, Ala. (W. B. Jones). AMNH—American Museum of Natural History, New York, N. Y. (J. Rozen). ANSP—Academy of Natural Sciences, Philadelphia, Pa. (H. R. Roberts, D. G. Rentz). Includes the Scudder and Morse collections, formerly in the Museum of Comparative Zoology, Harvard University. AU—Auburn University Department of Entomology, Auburn, Ala. (K. L. Hays). B—Collection of Thomas C. Barr, Jr., School of Biological Sciences, University of Kentucky, Lexington, Ky. BMNH—British Museum (Natural History), London, England. (D. R. Ragge). CAS—California Academy of Sciences, San Francisco, Cal. (H. B. Leech). CM—Carnegie Museum, Pittsburgh, Pa. (G.

Netting, G. Wallace). CNC—Canadian National Collection, Ottawa, Ontario. (J. E. H. Martin). CU—Cornell University Department of Entomology, Ithaca, N. Y. (H. Diettrich). D—Collection of Kenneth Dearolf. FMNH—Field Museum of Natural History, Chicago, Ill. (R. L. Wenzel, H. Dybas). H—Collection of John R. Holsinger, Department of Biology, Old Dominion University, Norfolk, Va. INHS—Illinois Natural History Survey, Urbana, Ill. (M. W. Sanderson). ISU—Iowa State University Department of Entomology, Ames, Iowa. (J. L. Laffoon). K—Collection of Carl H. Krekeler, Department of Biology, Valparaiso University, Valparaiso, Ind. M—Collection of Terrence G. Marsh, North Central College, Naperville, Ill. MHNG—Museum d'Histoire Naturelle, Geneve, Switzerland. (Bernd Hauser). MINN—University of Minnesota Department of Entomology, St. Paul, Minn. (E. F. Cook). NCA—North Carolina Department of Agriculture, Raleigh, N. C. (D. L. Wray). NHW—Naturhistorisches Museum, Wien, Austria. (Max Beier). OSM—Ohio State Museum, Columbus, Ohio. (E. S. Thomas). OSU—Ohio State University Department of Entomology, Columbus, Ohio. (C. A. Tripplehorn). OU—Ohio University Department of Entomology, Athens, Ohio. (W. C. Stehr). PU—Purdue University Department of Entomology, Lafayette, Ind. (L. Chandler). Includes the Blatchley collection of Orthoptera. S—Collection of Thomas Siebert, Department of Biology, University of Kentucky, Lexington, Ky. ST—Collection of H. F. Strohecker, Department of Zoology, University of Miami, Coral Gables, Fla. UK—University of Kansas, Snow Entomological Museum, Lawrence, Kansas. (G. W. Byers). USNM—U.S. National Museum (Natural History Museum), Washington, D.C. (J. F. G. Clarke, A. B. Gurney). VPI—Virginia Polytechnic Institute Department of Entomology, Blacksburg, Va. (L. M. Ferguson). WVAC—West Virginia Association for Cave Studies, Charleston, W. Va. (J. M. Rutherford).

Abbreviations of Collectors' Names

Full collection data are recorded only for the new species described herein. In order to conserve space the most frequently recurring collectors' names are abbreviated as follows:

A—Adler, K. K. Ba—Bailey, J. R. B—Barr, T. C. Jr. Be—Bell, L. N. Bl—Bellamy, R. E. Ca—Carpenter, J. H. Co—Cooper, J. C—Culver, D. C. D—Dearolf, K. Di—Dickson, G. F—Fiske, A. Fr—Friauf, J. J. He—Hebard, M. Ho—Holsinger, J. R. H—Hubbell, T. H. J—Jones, W. B., et al. L—Lamb, R. Y. M—Marsh, T. G. Ma—Matthews, L. E., et al. Mc—McLennon, L. Me—Merkle, D. N—Norton, R. M. Ne—Neff, Brad Pa—Packard, A. S. Pl—Paulson, D. P—Peck, S. B. R—Reese, A. M. Ru—Rutherford, J. M., Jr. S—Sanborn, F. G. V—Valentine, J. M. W—Wallace, H. K.

The collections studied were made by more than 180 persons, including those already mentioned, some of whom are (or were) professional biologists. But a large part of the material was collected by amateurs interested primarily in cave exploration and only incidentally in cave faunas, often in caves that would otherwise have remained unsampled. Since they cannot all be individually thanked, and since most of them are members of the National Speleological Society, appreciation of their valuable contributions is expressed to the membership of that society collectively.

The records for two of the species treated below, *Euhadenoecus puteanus* and *Hadenoecus subterraneus,* are so numerous and so often repetitious that only localities and ownership of specimens are listed for them; additional information derived from labels or associated field notes is merely summarized.

METHODS OF STUDY. In addition to examining the external features, numerous internal structures were studied by dissection, verifying and extending observations made by Ander (1939). Measurements and spine counts were made on many specimens to determine the nature and amount of individual and regional variation in body proportions and leg armature within the species. The dimensions and indices used are for the most part those described by Hubbell (1936).

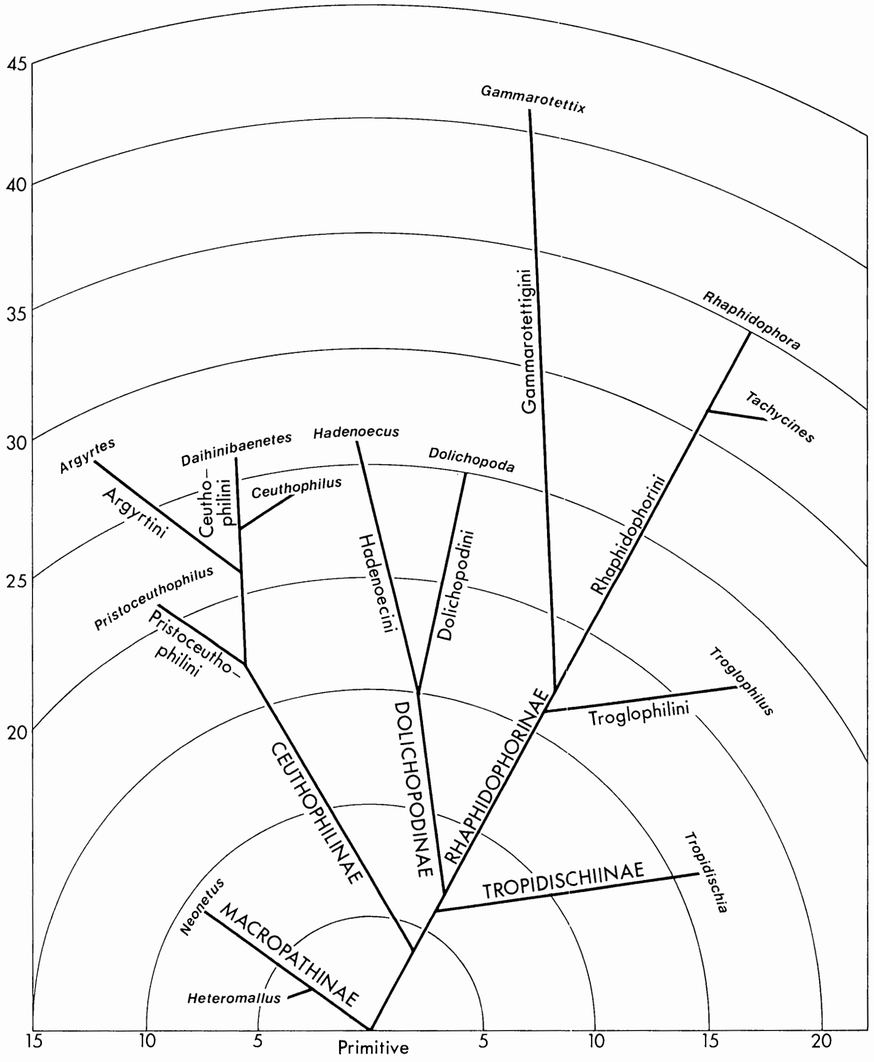

Fig. 1. Diagram of phyletic relationships within the Rhaphidophoridae. A Wagner Tree, based on computerized analysis of the distribution of 129 character states of 42 external and internal characters in 13 genera representing all the major subdivisions of the family. Concentric numbered arcs show the number of steps of advancement over the primitive condition.

DOLICHOPODINAE

The subfamily Dolichopodinae is here redefined to include the Hadenoecini and Dolichopodini as tribes. It is characterized by the following combination of characters, only a few of which are unique to it. Those which represent advances over the primitive condition are marked with an asterisk.

EXTERNAL CHARACTERS. Body compact, with small thorax and large plump abdomen; legs and antennae very long and slender; dorsum dull to weakly polished, subglabrous to very minutely setose. *Head* with fastigium verticis bipartite; sensory area of maxillary palpi terminal. *Thorax* with relatively shallow pronotum exposing parts of pleurites, meso- and metanotum very shallow, exposing greater parts of pleurites; *metasternal foramen strongly transverse, *entire region between mesosternum and metasternum sclerotized with median sclerite (Ander's terminology) forming only the central part of this sclerotization. *Abdomen* with *pseudotympanal organ reduced, inconspicuous; *ventromesal angles of 10th tergite prolonged mesad as narrow sclerotized bands beneath paraprocts, their mesal ends fused or attingent; cerci tapering, flexible, unspecialized. *Legs:* *femora without movable genicular spurs; *basitarsus III unarmed; tarsal pulvilli narrow, compressed; tarsal claws with basal seta. *Male terminalia:* *styles more or less reduced, often partly fused with subgenital plate; phallus lobes short, without dorsal eversible glands. *Female terminalia:* ovipositor with long inner valves; ventral ovipositor valves armed distoventrad with crenulate or serratocrenulate teeth.

INTERNAL CHARACTERS. Cryptopleura of pronotum large; collum proventriculi with 6-7 posteriorly denticulate "cushions" in each sector; proventriculus well developed, its rods not expanded or angulate at cephalic end; trachea cephalica ventralis relatively short, with lower branch issuing before the upper two branches; ventral nerve cord with abdominal *ganglia 2 and 3 fused, *ganglion 7 fused with 8-11; testis long, narrow, flattened, without tunic, its *tubules very narrow, thin and short; male accessory glands consisting of a pair of very large "coarse" and many "thin" ones on each side; spermatophore without spermatophylax; *spermatheca with left arm reduced; *ovipositor gland apparently absent.

Of the above characters only the sternal sclerotization, specialized 10th abdominal tergite and structure of the testis and male accessory glands are unique to the subfamily. The distribution among the subfamilies and tribes of the Rhaphidophoridae of character states in 13 of the 43 characters used in the previously mentioned phyletic analysis is shown in Table 1.

TABLE 1

DISTRIBUTION OF CHARACTER STATES AMONG THE RHAPHIDOPHORIDAE

		DOLICHOPODINAE			CEUTHOPHILINAE			RHAPHIDOPHORINAE		
	MACRO-PATHINAE	Dolicho-podini	Hadenoe-cini	TROPIDI-SCHIINAE	Pristoceutho-philini	Argyrtini	Ceutho-philini	Troglo-philini	Rhaphido-phorini	Gammaro-tettigini
1. Fastigium verticis	•	•	•	•	A	A	A	•	•	•
2. 5th segment maxillary palpus	•	*B*	•	•	B	B	B	B	•	•
3. Exposed propleura	•C	•	C	C*	C*	C*	C*	C*	C*	C*
4. Tibia III, dorsal armature	•D*	*D*	•	D*	•	•	•	D	D*	D**
5. Basitarsus III, armature	•	E	E	E*	E	E*E	E	E*	E*	E*
6. Claw, basal seta	•	•	•	•	F	F	F	•	•	•
7. Styles	•	G	G	•	•	•	G*	•	•	G*
8. Ovipositor, inner valves	H	•	•	•	H	H	H	H*	•	H
9. Ovipositor, ventral valves	•	I	I*	•	•	*I*	*I*	II	•	*I*
10. Cryptopleura	•	•	•	•	•	J	J	J	J	J
11. Proventricular valves	K	*K*	•	•	•	•	•	•	K	•
12. Abdominal ganglia 2,3	•L	L*	L	L	L	L	L	L	L	L
13. Abdominal ganglion 7	•	M*	M*	M	•	•	•	M	M*	M

Explanation of Table 1. Presence of the primitive condition is shown by a dot, advanced conditions by capitals; a star indicates a more advanced state. Roman and italic characters show divergence from the primitive condition in different directions.

1. *Fastigium verticis:* Primitively bipartite; A—undivided, subconical (sometimes weakly sulcate in Argyrtini and Ceuthophilini).
2. *Fifth Segment of maxillary palpus:* Primitively with apical sensory area; *B*—sensory area elongate, constricted at base, forming an apparent sixth segment; B—sensory area prolonged proximad along ventral surface.
3. *Exposed propleura:* Primitively broad; C—narrowed; C*—not exposed below line of attachment of pronotum.
4. *Tibia III, dorsal carinal armature:* Primitively with a series of denticles interrupted by larger socketted spurs; *D*—denticles lost, spurs numerous, short, weakly socketted;[1] D—denticles in groups within which size increases distad, end spine of each group often faintly socketted, a distal pair of socketted spurs preceding dorsal calcars; D*—only denticles or fixed spines present except for socketted distal pair; D**—only fixed spines of irregularly alternating length present, including distal pair.

5. *Basitarsus III, dorsal armature:* Primitively with paired distodorsal spines, often biseriately spinose; E—unarmed; E*—tip conically produced or spinose.
6. *Tarsal claws, basal seta:* Primitively present; F—absent.
7. *Styles:* Primitively well-developed, socketted; G—moderately or strongly reduced, often more or less fused with subgenital plate; G*—lost.
8. *Ovipositor, inner valves:* Primitively nearly as long as the others; H—much shorter than others; H*—rudimentary.
9. *Ovipositor, armature of ventral valves:* Primitively unarmed or weakly denticulate on distoventral margin; I—with many closely spaced serratocrenulate teeth at ends of oblique striae on inner surface; I*—with fewer and coarser crenulate teeth; *I*—with sharply triangular, aciculate or hooked teeth; II—with widely separated peg-like teeth along most of their length.
10. *Prothoracic cryptopleura:* Primitively large with epimeral portion broad and shallowly emarginate; J—moderately to strongly reduced with epimeral portion narrow and considerably to strongly emarginate.
11. *Proventricular valves:* Primitively consisting of six small equal folds or short lobes; K—dorsal and ventrolateral lobes large and petal-like, others rudimentary; *K*—all six lobes large and petal-like, all alike except that the ventral one is smaller and mesally grooved.
12. *Abdominal ganglia 2 and 3:* Primitively separate and separate from the fused metathoracic and first abdominal ganglia; L—fused, but separate from M+1; L*—fused, and fused with M+1 to form M+1-3.
13. *Abdominal ganglion 7:* Primitively distant from fused ganglion 8-11; M—separate, but shifted toward 8-11; M*—fused with 8-11 to form 7-11.

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[1] Dolichopodini, usually described as having an armature of fixed spines.

HADENOECINI Ander 1939

This tribe includes only two genera, *Hadenoecus* Scudder, the type genus, and the new genus *Euhadenoecus*, both restricted to the eastern United States. Its members differ from those of the Dolichopodini in six of the characters tabulated above (structure of the maxillary palpus, reduction of the free propleura, presence of freely movable spurs on the dorsal carinae of tibia III, armature of the ventral ovipositor valves, structure of the proventricular valve, and lack of fusion of abdominal ganglia 2 and 3 with M+1), and in other features pertaining to the thorax, epiphallus, phallic lobes, testis, spermatheca, labrum, proventriculus, midgut coeca and malpighian tubules as noted below. In habitus and many structural details the Hadenoecini closely resemble the Dolichopodini, and most of its species, like those of the latter tribe, are cavernicolous and pale in color.

Head: Tall, subvertical, subovate in cephalic aspect. Vertex high, rising above eyes to nearly twice their vertical diameter, in side view strongly convex above and steeply declivent cephalad to base of very small, anteriorly projecting fastigium verticis. Latter divided, consisting of two subconical prominences or low ridges separated by a V-shaped groove, basal outline of entire fastigium subtriangular or ovate; lateral ocelli absent or faintly indicated by pale spots on caudal portions of lateral faces. Eyes small, narrow, moderately prominent, half or less than half as tall as distance from lower angle to anterior mandibular condyle, wholly pigmented except, in some species, the upper angle. Interocular distance distinctly greater than height of eye; antennal fossae nearly contiguous. Frons nearly twice as broad as tall, its triangular interantennal projection separated from fastigium verticis by a very narrow connection extending between the antennal fossae; median ocellus obsolete. Maxillary palpus extremely long and slender; third segment slightly longer than fourth, distal (fifth) segment longest, gently upcurved and slightly broadened distad, its membranous sensory area small, apical, extending very briefly onto ventral surface. Labrum with distal lips produced as a pair of short, narrow, incurved admesal lobes separated by a deep emargination and with outer edges slightly undercut at base (in Dolichopodini short, rounded-triangular, separated by a shallow V-shaped notch). Antennae very long (80-100 mm.), basal segment in dorsal aspect longer than broad, subquadrate with mesal face gently to rather strongly convex; second segment less than half as long as first and narrower; third segment still narrower and about twice as long as second; remaining segments all similar, diminishing in size distad, their surfaces minutely setose.

Thorax: Pronotum relatively shallow, deepest at caudal third, semicylindrical or weakly sellate, foveolae over muscle insertions weakly impressed; in dorsal view fore margin straight, hind margin weakly convex, side margins evenly convex or a little more strongly so at caudal third; in side view ventrocephalic angle very broadly, ventrocaudal angle more abruptly rounding into ventral margin, latter almost evenly and strongly convex or its anterior portion oblique and only weakly curved; cephalic and ventral edges marginate. Proepimeron narrowly exposed below attachment of pronotum. Mesonotum and metanotum very shallow, exposing greater part of pleura; caudal edge of mesonotum convex, of metanotum nearly straight in dorsal view, lower edge of mesonotum but not of metanotum weakly marginate. Mesosternal fovea widely transverse with open furcal pits at ends; metasternal fovea about half as wide, with furcal pits slightly overhung by its side walls; entire region between mesosternum and metasternum weakly sclerotized, its surface elevated in front of metasternal fovea into a low pyramidal or apiculate prominence (in Dolichopodini forming a transverse ridge with rounded summit).

Legs: *Coxa I* with a short pyramidal spine at middle of cephalic carina (in Dolichopodini carina curved, without spine). All *femora* unarmed, or femora II and III with a minute caudogenicular spine (in Dolichopodini all sometimes unarmed, usually with minute paired distodorsal spines and femora II and III with minute caudogenicular spine; femur III with ventral carinae spinose in subgenus *Chopardina*). *Tibiae* I and II unarmed above except for a pair of short distodorsal (apical) spurs, ventral carinae with 4-8 similar spurs including an apical pair (in Dolichopodini dorsal carinae of tibia II and often of tibia I spinose). Tibia III carinate on each dorsal margin, convex beneath; each carina with 5-8 small, straight, dorsally bicarinate movable spurs, between and proximad of which are many short, sharp, distally inclined and more or less overlapping spinose denticles, this armature resembling that of the Ceuthophilinae (in Dolichopodini carinae armed with short socketted spurs, all alike and without intervening denticles); ventral surface with a few small spurs on cephalic and usually a smaller number on caudal margin proximad of the short paired distoventral calcars (more numerous on both margins in Dolichopodini); distal calcars gently curved, externally setose, dorsocaudal one-third to one-half as long as basitarsus, slightly longer than dorsocephalic, intermediate calcars less than half as long as dorsals, ventral calcars short, subequal, one-half to two-thirds as long as intermediates. *Tarsi* long, slender, tarsus I twice to nearly three times as long as pronotum and slightly longer than tarsus III; tarsal segments compressed, setose above and on sides, ventral edges narrowly membranous, appearing carinate in dried material; basitarsus on all legs about as long as remaining segments taken together, unarmed; tarsus III with second segment briefly apiculate distodorsad, all other tarsal segments truncate; claws slender, gently curved, one-third to nearly one-half as long as fourth segment, with basal seta.

Abdomen: Pleural membranes of anterior segments with sparse, minute nodular setae; pseudotympanal organ (Ander 1939: 39) not evident; cerci in both sexes slightly longer than to half as long again as pronotum, slender, flexible, tapering to a minute sharp point; paraprocts sexually dimorphic, in both sexes enclosed ventrad by a narrow, inconspicuous sclerotized band formed of an extension of the ventromesal angles of the tenth tergite, as first noted by Ander (1957: 91).

Terminal abdominal structures of male: Basal part of 10th tergite unspecialized, its caudal margin truncate or nearly so. Epiproct subtriangular or paraboloid in outline. Paraprocts large, their apices projecting beyond end of epiproct, weakly to distinctly decurved and differing specifically in form. Epiphallus absent.[1] Phallus short, flattened subconical, with transverse apical phallotreme enclosed (in resting condition) by the sides of the dorsal lobe, and with dorsal and ventral lobes differently modified in the two genera. Subgenital plate distally bilobate, the lobes bearing styles, which may be small but distinct and socketted, or more or less reduced and fused to the apices of the lobes.

Terminal abdominal structures of female: Ovipositor with dorsal valves somewhat narrowed beyond base and with sides thence subparallel for half or more than half length, distal portion tapering and upcurved to the narrowly acute tip, these valves along part of their length with upper and lower portions separated by a low angulation; ventral valves armed distoventrad with 5-8 more or less strongly scoop-shaped teeth separated by oblique ventral grooves, appearing crenulate in side view. Paraprocts smaller and their apices less distinctively modified from species to species than in male. Subgenital plate small, its distal margin broadly convex, ventral surface either without (*Euhadenoecus*) or with (*Hadenoecus*) an intramarginal sclerite of species-specific form.

Key to the Genera and Species of Hadenoecini

1. Male with a pair of pale membranous glandular areas at sides of epiproct (Fig 2, c-g; Pl. IV, a,b) and without eversible tubular organs between 9th and 10th tergites; subgenital plate trapezoidal, with distolateral portions set off by oblique sulci and bearing small socketted styles; paraprocts with ends little decurved, narrow and incurved or bulbous. Female subgenital plate without intramarginal sclerite; ovipositor teeth (Fig. 3; Pl. IV, c-e) without distal process. Femur II without caudogenicular spinule. Legs relatively shorter (see Table 2 below). Epigeic or cavernicolous . . . . EUHADENOECUS new genus 2

1'. Male without pale areas at sides of epiproct; a pair of fleshy elongate tubular organs protrusible from slits between 9th and 10th tergites cephalad of cercal bases (Fig. 5, j); subgenital plate subtriangular, terminating in a pair of subconical lobes bearing small, partly fused styles at their tips; paraprocts more or less strongly decurved distad, their apices in side view broad and subplanate or narrowed to ventrally projecting points. Female subgenital plate with an intramarginal ventral sclerite (Fig. 13); ovipositor teeth (Fig. 14; Pl. IV, f-h) with a minute hairlike process extending distad from their distoventral angles. Femur II nearly always with a minute caudogenicular spinule. Legs relatively longer (see Table 2 below). Cavernicolous. . . . . HADENOECUS Scudder 5

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[1] What might be mistaken for an epiphallus in *Euhadenoecus* is the bracket-shaped edge of the dorsal lobe of the phallus, shown in Fig. 5, a-e, and Pl. II,b.

2 (1). Male paraprocts not enlarged or bulbous distad, mostly brown; epiproct (Fig. 2, c,d) mostly brown with contrastingly pale proximolateral glandular areas; subgenital plate with sides and distal folds brown, latter projecting distinctly beyond mesal part of distal margin and set off by deep sulci; dorsal lip of phallus more broadly sclerotized, its edge bracket-shaped with mesal point (Fig. 5, a-c). Coloration more intensive, pronotum and basal part of femur III usually with a distinct pattern of brownish markings. Legs averaging shorter relative to pronotal length (see Table 2 below); tibia III without a predistal spur on ventrocaudal margin. Primarily epigeic, in forests 3

2'. Male paraprocts with distal ends projecting more strongly beyond epiproct, bulbous, usually pale; epiproct (Fig. 2, e-g) pale or mesal portion light brown, contrasting little with pale proximolateral glandular areas; subgenital plate entirely pale, its distolateral folds small, projecting little beyond mesal part of distal margin and bounding sulci less deep; dorsal lip of phallus narrowly sclerotized, its edge tectate in distal view. Coloration paler, pronotum and base of femur III with only a faint pattern, abdominal dorsum pale or with faint darker banding along caudal margins of tergites. Legs averaging longer relative to pronotal length (see Table 2 below); tibia III usually with a predistal spur on ventrocaudal margin (sometimes absent in *insolitus*). Cavernicolous 4

3 (2). Male epiproct (Fig. 2, c) with pale glandular areas broad, rounded subquadrate or subcircular in outline, their mesal edges slightly elevated as a narrow dark rim separating them from the usually pale, hourglass-shaped intervening area, which at its narrowest point is narrower than the breadth of one of them. Fastigial ridges (Fig. 2, a) more or less suffused with brown on sides and cephalad, sides often with a faintly indicated pale ocellar spot. Distinctly smaller than *adelphus* wherever the two occur together (see Fig. 8). Southern New York and northeastern Ohio to Georgia and Mississippi. . . . . *Euhadenoecus puteanus* (Scudder)

3'. Male epiproct (Fig. 2, d) with pale glandular areas small, narrowly triangular or subcrescentic, their mesal edges not outlined by a dark line, intervening space brown, usually about twice as broad as one of them. Fastigial ridges (Fig. 2, b) entirely pale or their sides sometimes brownish, ocellar spots rarely indicated. Anterior abdominal tergites paler dorsad than laterad, rarely with a weak median brownish stripe. Size larger than *puteanus* wherever the two occur together. Appalachian Mountains in North Carolina and Georgia. . . . . *Euhadenoecus adelphus* n. sp.

4 (2'). Male epiproct (Fig. 2, e) about four-fifths as long as broad, subquadrate with nearly straight convergent sides or nearly ellipsoidal, distal margin gently convex or faintly emarginate, surface longitudinally grooved between large pale tumid glandular areas that extend along full length of sides; male paraprocts projecting only about one-fourth their length beyond epiproct, their bulbous distal ends smaller, not divaricate. Caves of Appalachian Ridge and Valley Province in Virginia, West Virginia, Kentucky and northeastern Tennessee. . . . . *Euhadenoecus fragilis* n. sp.

4'. Male epiproct (Fig. 2, f,g) short, one-half to three-fifths as long as broad, rounded-triangular or paraboloid with convex-obtuseangulate apex, surface shallowly grooved or basally impressed, pale glandular areas small, subtriangular or lunate, seldom more than three-fifths as long as epiproct, sometimes scarcely distinguishable; male paraprocts projecting one-third to one-half their length beyond epiproct, their bulbous distal ends larger, usually distinctly divaricate. Caves in northeastern Alabama (mostly south of the Tennessee River), the Nashville Basin and bordering Highland Rim in central Tennessee, and adjoining south-central Kentucky; parthenogenetic in some caves in the northern part of its range. . . . . *Euhadenoecus insolitus* n. sp.

5 (1'). Females 6

5'. Males 10

6 (5). Subgenital plate sclerite either with proximolateral incurvate arms with attingent tips or with a continuous proximal rim, the arms or rim enclosing an oval or ovate membranous or excavate area; or else subquadrate, without incurvate arms or raised proximal rim and without a membranous or excavate mesoproximal area. 7

6'. Subgenital plate sclerite with space between proximal arms widely open cephalad. . . . 8

7 (6). Subgenital plate sclerite (Fig. 13, a-d) enclosing a deeply to shallowly impressed, sclerotized, transversely elliptic or ovate area that has a more or less distinctly elevated rim, or subquadrate without distinct impressed mesodistal area; base of sternite VII with a pair of small dark sclerotizations near sides and without a mesal prominence. Femur I 3.3-

4.2 times as long as pronotum, femur III 6.7-8.3 times as long as broad. Mammoth and other caves of the Pennyroyal Plateau in south-central Kentucky. . . . .*Hadenoecus subterraneus* (Scudder)

7′. Subgenital plate sclerite (Fig. 13, j) enclosing a planate membranous area that is widest distad and lacks a distinctly raised rim; sternite VII without dark lateral sclerotizations but with a mesal prominence with short, rounded transverse crest. Femur I 4.2-4.8 times as long as pronotum, femur III 8.9-10.9 times as long as broad. Caves of the Cumberland Plateau and Highland Rim in Alabama north of the Tennessee River, and in adjacent south-central Tennessee. . . . . *Hadenoecus jonesi* n. sp.

8 (6′). Subgenital plate sclerite (Fig. 13, e) with enclosed area quadrate, wider than long, bounded laterad by short, subtriangular projections of sclerite, these projections with straight inner and convex outer edges and subacute apices at cephalic margin of subgengenital plate. Caves of western edge of Cumberland Plateau and eastern edge of Bluegrass Region in eastern Kentucky; the northernmost populations parthenogenetic. . . . .*Hadenoecus cumberlandicus* n. sp.

8′. Subgenital plate sclerite with enclosed area semicircular, semielliptic or subtriangular; proximolateral projections of sclerite not as in alternative 9

9(8′). Subgenital plate sclerite (Fig. 13, f-h) an arcuate bar with subquadrate or rounded distolateral expansions and its proximolateral ends subacute and more or less incurvate but widely separated, partly enclosing a semicircular or semielliptic membranous area. Caves of western edge of Cumberland Plateau and adjoining Highland Rim in northern Tennessee. . . . . *Hadenoecus opilionoides* n. sp.

9′. Subgenital plate sclerite (Fig. 13, i) comprising a pair of subtriangular lateral portions with narrowly rounded, widely separated proximal apices, the two parts narrowly connected distad and distal margin of sclerite transverse and slightly sinuate; membranous mesoproximal area V-shaped with narrowly rounded distal angle. Caves of western edge of Cumberland Plateau and adjoining Highland Rim in south-central Tennessee. . . . . *Hadenoecus barri* n. sp.

10 (5′). Paraprocts (Pl. II, e) narrowing distad to base of narrow, abruptly decurved, obliquely truncate distal portion, the ventral angle of which in both distal and lateral aspects forms a narrow, subacute ventrally directed point . . . .
—Mammoth Cave region (see 7 above) . . . .*Hadenoecus subterraneus* (Sc.)
—Eastern Kentucky (see 8 above) . . . . *Hadenoecus cumberlandicus* n. sp.

10′. Paraprocts either narrowing in basal half and thence subequal or ventrally widened, or of subequal breadth to just before distal end. Tennessee and Alabama 11

11 (10′). Paraprocts (Pl. II, f) broad in side view, outer face with an oblique ridge extending from base near cercus to junction with dorsal edge, latter thence strongly convex-declivent to somewhat produced ventral tip and narrowly sclerotized along edge, lateral surface below ridge and dorsal edge membranous and concave, broadly lunate in outline; in distal view subvertical distodorsal edge narrow, with ventral end slightly produced and subacute. Distribution as given in 7′ . . . . *Hadenoecus jonesi* n. sp.

11′. Paraprocts narrowing to midlength, thence subequal or widening before end, lower ridge of outer face decurved, its distal portion forming lower edge of decurved tip; distodorsal edges in distal view not narrowly sclerotized nor straight and subvertical 12

12 (11′). Ends of paraprocts broadened (Pl. II, g), tips in distal aspect narrowly attingent mesad, ventral edges convex or ventrolaterally obtuseangulate, together subtruncate or forming a shallowly angulate emargination, admesal ventral angles not produced. Distribution as given in 9 . . . . *Hadenoecus opilionoides* n. sp.

12′. Distal part of paraprocts of subequal breadth, ends obliquely subtruncate and attingent, with subacute, narrowly rounded admesal ventral tips, which together form a convex or obtuseangulate projection. Distribution as given in 9′ . . . . *Hadenoecus barri* n. sp.

TABLE 2

BODY PROPORTIONS IN *EUHADENOECUS* AND *HADENOECUS*[1]

	EUHADENOECUS					HADENOECUS					
		Means					Means				
MALE	Range in genus	puteanus	adelphus	fragilis	insolitus	Range in genus	subterraneus	cumberlandicus	opilionoides	barri	jonesi
Fem.I/Pron.	2.6 -3.9	2.99	2.92	3.47	3.28	3.3 - 5.1	3.72	3.65	4.11	3.99	4.38
Fem.III/Pron.	4.2 -6.5	4.79	4.70	5.55	5.22	5.2 - 7.2	5.83	5.80	6.21	6.05	6.51
Fem.III L/Br.	5.6 -8.8	6.24	6.25	7.94	6.71	6.6 -10.4	7.66	7.68	8.93	8.69	9.67
Basit.I/Pron.	0.93-1.49	1.20	1.03	1.26	1.34	1.45- 2.24	1.61	1.58	1.84	1.84	2.01
Basit.III/Pron.	0.82-1.42	1.10	0.98	1.20	1.17	1.12- 1.69	1.37	1.26	1.40	1.31	1.49
Max.palp.5/Pron.	0.69-1.09	0.88	0.76	0.98	0.95	1.06- 1.42	1.22	1.20	1.24	1.22	1.26
FEMALE											
Fem.I/Pron.	2.3 -3.8	2.72	2.65	3.42	3.20	3.2 - 4.8	3.57	3.56	3.87	3.89	4.34
Fem.III/Pron.	3.8 -5.8	4.62	4.54	5.38	5.13	5.0 - 7.3	5.72	5.87	5.78	5.79	6.46
Fem.III L/Br.	4.9 -8.3	5.71	5.76	7.46	6.81	6.7 -10.9	7.51	8.23	8.57	8.29	9.72
Basit.I/Pron.	0.77-1.43	1.09	1.03	1.24	1.30	1.30- 2.16	1.55	1.63	1.68	1.72	1.93
Basit.III/Pron.	0.83-1.34	1.02	0.95	1.13	1.16	1.00- 1.64	1.35	1.26	1.31	1.27	1.52
Max.palp.5/Pron.	0.69-10.4	0.85	0.74	0.96	0.95	1.00- 1.48	1.24	1.21	1.19	1.25	1.30
Ovip./Pron.	1.8 -2.9	2.04	2.04	2.51	2.57	2.7 - 3.9	3.22	3.42	3.41	3.40	3.09
Ovip./Fem.I	0.63-0.88	0.76	0.75	0.75	0.80	0.77- 1.11	0.90	0.92	0.88	0.86	0.71
Ovip./Fem.III	0.35-0.56	0.44	0.43	0.47	0.50	0.43- 0.65	0.55	0.57	0.59	0.57	0.48

[1] The species means are the averages of the regional means for the entire geographic range of each species.

EUHADENOECUS[1] Hubbell, new genus

Type species: *Hadenoecus puteanus* Scudder.

GENERAL FEATURES. Size smaller and legs shorter relative to pronotal length than in *Hadenoecus* (see Table 2 above). Femora II and III without a caudogenicular spinule. Tibia III (Fig. 4, b-f) with denticles of dorsal carinae close-set, strongly overlapping, the series extending from near base of tibia almost to its end, terminating abruptly at or beyond predistal dorsal spur; predistal ventral spurs normally 2 on cephalic, 0 or 1 on caudal margin.

MALE CHARACTERS. Intersegmental membrane between 9th and 10th abdominal tergites without a pair of slit-like openings from which tubular organs can be evaginated. *Epiproct* with proximolateral areas set off from rest of sclerite, their surfaces membranous, planate or tumid, minutely setose and nearly always paler than rest of epiproct, their form species-specific (Fig. 2, c-g; Pl. II, a-d; Pl. IV, a,b); these areas believed to be pheromone organs.[2] Distal ends of *paraprocts* (Pl. II, a-d) obliquely subtruncate or rounded, in some species bulbous; not strongly decurved nor with subacute ventrally directed tips. *Subgenital plate* (Pl. III, a-d) with distolateral portions set off by sulci to form marginal plicae, the mesal ends of which are separated by a subquadrate or arcuate emargination and bear small but socketted, mesodistally directed *styles*. Dorsal lobe of *phallus* with mesal portion weakly sclerotized, its margin bracket-shaped with a short mesal angulate point; in unevaginated state, as seen in distal view when subgenital plate is depressed (Fig. 5, a-e; Pl. II, b), edges of dorsal lobe curled around ends of transverse phallotreme, forming short caudally rounded lobes on either side of ventral margin that border the short, narrow, distally rounded ventral lobe proper; extruded ventral bulla ample, pouch-shaped, nonsetose.

FEMALE CHARACTERS. *Subgenital plate* simple, its ventral surface without an intra-marginal sclerotization. *Spermatheca* bilobate, its right lobe a large, rather thick finger-like pouch curved to the left and with bluntly rounded end, its left lobe reduced to a small ovoid or subspherical diverticulum from near the base of the right lobe; the common stalk short, rather broad. *Ovipositor* (Fig. 3; Pl. IV, c-e) relatively shorter than that of *Hadenoecus* (see Table 1 above), the teeth of its ventral valves relatively larger and separated by deeper grooves than those of that genus, the larger proximal ones in side view trapezoidal or rounded-triangular in outline, sometimes slightly retrorse, and their distal margins without a minute, distally projecting hairlike process.

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[1] Gr. *Eu*, original, primitive, + *Hadenoecus*.

[2] Stained serial sections of the male terminalia of *E. puteanus* prepared for me by Dr. John B. Burch show that these areas of the epiproct are underlain not by normal hypodermal tissue but by a single layer of tall columnar cells probably secretory in function.

COMMENTS. Two of the four species of this genus, *puteanus* Scudder and *adelphus* n. sp., are forest inhabitants and primarily epigeic, although both frequent cave entrances; the other two, *fragilis* and *insolitus* nn. spp., are obligatory trogloxenes like the species of *Hadenoecus*.

The members of *Euhadenoecus* are more primitive in a number of respects than are those of *Hadenoecus*, if one takes as the criterion of primitiveness the presence of a given characteristic in several rhaphidophorid tribes besides the Hadenoecini. Such primitive features include, in the male, the socketted styles, and in the female, the crenulate ovipositor teeth without appendage, the simple subgenital plate and the basally furcate spermatheca. The fact that two of the species are still epigeic and retain the deeper coloration and stronger dark pattern associated with that ancestral mode of life, and that the two cavernicolous species are neither as pale nor as long-legged as are those of the wholly cavernicolous genus *Hadenoecus*, fits with this conclusion and also indicates that *Hadenoecus* has been a cave-inhabitant longer than have the cavernicolous species of *Euhadenoecus*.

EUHADENOECUS PUTEANUS (Scudder) (Figs. 2, a,c; 3, a-f; 4, b-d; 5, a,b; 8 (graph); 7, 9 (maps); Pl. II, a,b; Pl. III, a,b; Pl. IV, a,c-e).

1877. *Hadenoecus puteanus* Scudder, Proc. Bost Soc. Nat. Hist., 19: 37 (♂, ♀—North Carolina (types); Monticello, Miss.).

Lectotype, here selected: Male, with labels "N.C., Scudder's Type 1876, *Had. puteanus* Scudd., [MCZ] type 14159, S. H. Scudder Coll.;" *lectallotype* an identically labelled female; both pinned, in ANSP ex MCZ.[1]

This forest-inhabiting, saxicolous and arenicolous species is the most widely distributed, abundant and variable member of the Hadenoecinae. Its closest relative is the very similar *adelphus,* with which it occurs in the southern Appalachians and with which it is compared under that species. These two differ from the other members of the genus by their brownish color and more distinct dorsal pattern, the contrastingly pale lateral glandular areas of the male epiproct, presence of a mesal point on the dorsal lip of the phallus, and the usual absence of a predistal ventrocaudal spur on tibia III which is almost always present in the others.

DESCRIPTION OF PLESIOTYPIC MALE:[2] Length of body ca. 12.6, of pronotum 3.7 (3.9), of femur I 10.4 (10.4), of femur III 16.3 (16.5), of tibia III 19.9 (20.7), of antenna ca. 92 mm; proximal breadth of femur III 2.9 (3.0), distal breadth 0.7 mm.

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[1] The type series was collected in an old well in the mountains of western North Carolina by H. K. Morrison in 1876.

[2] Approximately topotypic, from Arrowwood Glade, Macon Co., N.C.; in alcohol, UMMZ. Parenthesized figures in the following description apply to the type.

General color of dorsum ochraceous buff, thoracic nota and abdominal tergites broadly bordered with dilute reddish brown; meso- and metathoracic episterna pale except ventrad. Vertex with five narrow brown longitudinal lines, the outer two extending to upper angles of eyes, a similar line on rear of genae; anterior portions of fastigium brownish. Pronotum with a brownish mesal stripe merging with cephalic and caudal marginal bands, divided by a paler median hairline and enclosing cephalad and caudad pairs of oval admesal paler spots; foveolae and adjoining rounded spots on dorsum buff. Dorsocephalic portions of meso- and metanotum mostly brownish. Epiproct brown, its proximolateral glandular areas nearly white; cerci ochraceous buff; paraprocts with brown edges and tip; sides and distal folds of subgenital plate dark brown. Legs ochraceous buff, femora darkening distad, femur III with brown scalariform pattern on basal part of outer face, tibia III with dorsal surface darker than remainder.

Head (Fig. 2, a): Fastigium very small, consisting of two low eminences, each subpyriform in dorsal aspect, with pointed cephalic ends and surfaces rising to narrowly rounded ridges separated by a narrow median sulcus, the ridges in side view highest behind midlength and there slightly apiculate, each bearing a single apical seta, crest concave-declivent to anterior end; breadth of fastigium about one-half interocular distance. Eyes completely pigmented, prominent, with nearly straight cephalic and arcuate caudal margin, breadth about two-thirds vertical diameter; interocular distance 1.35 and infraocular distance (to anterior mandibular condyle) 1.6 times vertical diameter of eye; proximal antennal segment slightly more than half as broad as interocular distance. Maxillary palpus four-fifths as long as femur I, its distal segment four-fifths as long as pronotum, 4th segment 0.6, 3rd 0.7 times as long as 5th.

Thorax: Pronotum in side view two-thirds as broad as long, its ventral margin rather strongly convex, sides deepest at caudal third; in dorsal view maximum breadth at caudal third, 1.1 times dorsal length.

Legs: Femur I 2.8 (2.7) times as long as pronotum; tibia I nearly one-tenth longer than femur; tarsus I 0.7 times as long as tibia, basitarsus I 1.1 times as long as pronotum. Femur II 0.9 times as long as femur I, tibia II of equal length. Femur III 4.4 (4.3) times as long as pronotum, 1.6 times as long as femur I, 5.7 (5.4) times as long as proximal breadth, its distal breadth one-fourth proximal breadth, slender distal portion about two-fifths of total length; tibia III 1.2 times as long as femur; tarsus III two-fifths as long as tibia; basitarsus as long as pronotum, 2nd and 4th segments subequal, half as long as basitarsus, claws two-fifths as long as 4th segment.

Leg armature: All femora unarmed; ventral carinae of tibia I with 5/4 cephalic, 5/5 caudal spurs, tibia II with 5 on each carina. Tibia III with 4/5 cephalic and 5/5 caudal spurs on distal three-fifths of

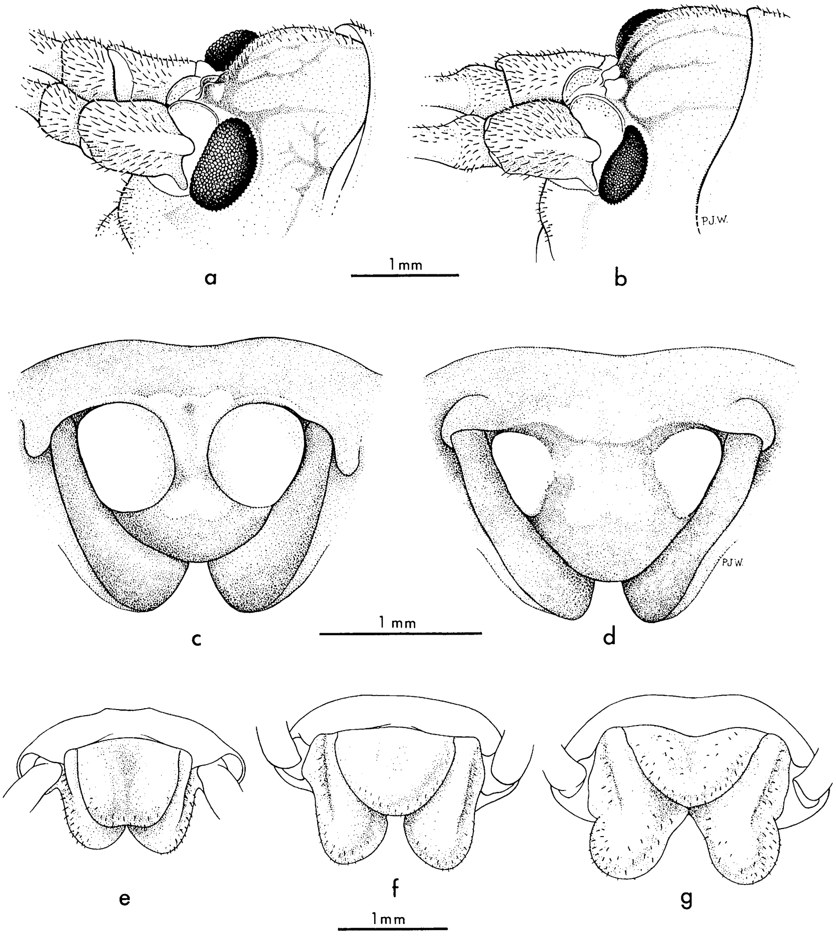

Fig. 2. Structural details of *Euhadenoecus* species. a,b—Oblique views of head: a—*Euhadenoecus puteanus* ♂, b—*E. adelphus*, both from Arrowwood Glade, Macon Co, N.C. c-g—Male epiprocts and paraprocts: c—*E. puteanus*, d—*E. adelphus*, same specimens as a and b; e—*E. fragilis*, Tawneys Cave, Giles Co, Va.; f—*E. insolitus*, Cedar Pole Cave, Jefferson Co, Ala.; g—*E. insolitus*, Bull Run Cave, Davidson Co, Tenn.

dorsal carinae, spurs about as long as tibial depth; predistal ventral spurs 2/2 (2/2) on cephalic, 0/0 (0/0) on caudal margins; dorsocephalic calcar half as long, dorsocaudal about three-fifths as long as basitarsus; spine formula of dorsal carinae, right and left, cephalic 30/34/16/10 = 90, 35/13/15/13/11 = 87 (70 and 77 in type), caudal 46/14/15/12/6 = 93, 45/9/17/11/6 = 88 (85 and 85 in type).

Terminal abdominal structures (Figs. 2, c; 5, a,b; Pl. II, a,b; Pl. III, a,b; Pl. IV, a): *Epiproct* subtriangular with rounded apex, four-fifths as long as broad, its pale proximolateral glandular areas rounded-quadrate, slightly elevated, with planate surfaces and narrow sclerotized inner edges separated by an hourglass-shaped space which, at narrowest point, is less than half the width of one of the pale areas. *Cerci* 1.2 times as long as pronotum. *Paraprocts* in side view with subtriangular base and parallel-sided distal portion, dorsal length about twice proximal breadth, dorsal and ventral margins narrowly rounded, weakly sclerotized, surface excavate between them, apex incurved and weakly decurved, flattened, adjacent ends obliquely truncate. *Subgenital plate* more than three times as broad as its mesal length, lateral thirds of distal margin set off as distinct plicae by obliquely transverse sulci, mesal ends of these folds obliquely truncate on either side of wide, shallowly subquadrate mesal emargination and bearing short, blunt socketted styles. *Phallus* with edge of mesal part of dorsal lobe somewhat sclerotized, forming a curved or bracket-shaped lamina with caudally directed median point (Fig. 5, a,b).

DESCRIPTION OF PLESIALLOTYPIC FEMALE:[1] Length of body exclusive of ovipositor ca. 14.3, of femur I 9.6 (10.0), of femur III 17.9 (17.0), of tibia III 21.2 (20.0), of antenna ca. 80 mm; proximal breadth of femur III 3.4 (3.0), distal breadth 0.80 (0.72), length of ovipositor 8.0 (7.3) mm.

Agrees with described male except as follows. Brown color pattern more distinct; fastigium more strongly brown-shaded on anterior margins and apices of ridges; brown lines of vertex connected by a transverse brownish blotch between eyes and caudad of fastigium; meso- and metanotum paler above and with more distinct median brownish stripe; supra-anal plate entirely brown.

Legs: Relatively shorter than in male; femur I 2.4 (2.5), basitarsus I 0.9 (1.1) times as long as pronotum; femur III 1.9 (1.7) times as long as femur I. Tibiae I and II with 5 spurs on each ventral carina; dorsal spurs of tibia III 5/5 (5/5) on cephalic, 5/4 (5/5) on caudal carinae; distoventral spurs as in male. Spine formulae of dorsal carinae of tibia III, right and left: cephalic 36/15/16/13/6 = 86, 39/12/14/15/5 = 85 (79 in allotype), caudal 43/14/14/12/2 = 85, 43/16/14/17 = 90 (81 in allotype).

Terminal abdominal structures: Epiproct with broadly parabolic distal margin, its proximolateral portions (corresponding to the glandular areas of the male) slightly elevated but not contrastingly pale and without dark sclerotized rim. Subgenital plate short, wide, with evenly convex margin. Ovipositor (Fig. 3, a-f; Pl. IV, c-e) 2.0 (1.8) times as long as pronotum, 0.45 (0.43) times as long as femur III; distal fourth of ventral valves with 8 teeth diminishing in size distad, the apical ones minute; the larger basal teeth rounded-triangular and slightly retrorse in side view, in ventral view incurvate, somewhat scoop-shaped,

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[1] Same data as plesiotypic male, in alcohol, UMMZ. Parenthesized figures apply to the allotype.

with concave inner faces and slightly projecting proximolateral oblique edges, the teeth slightly overlapping and separated by oblique, rounded ventral grooves.

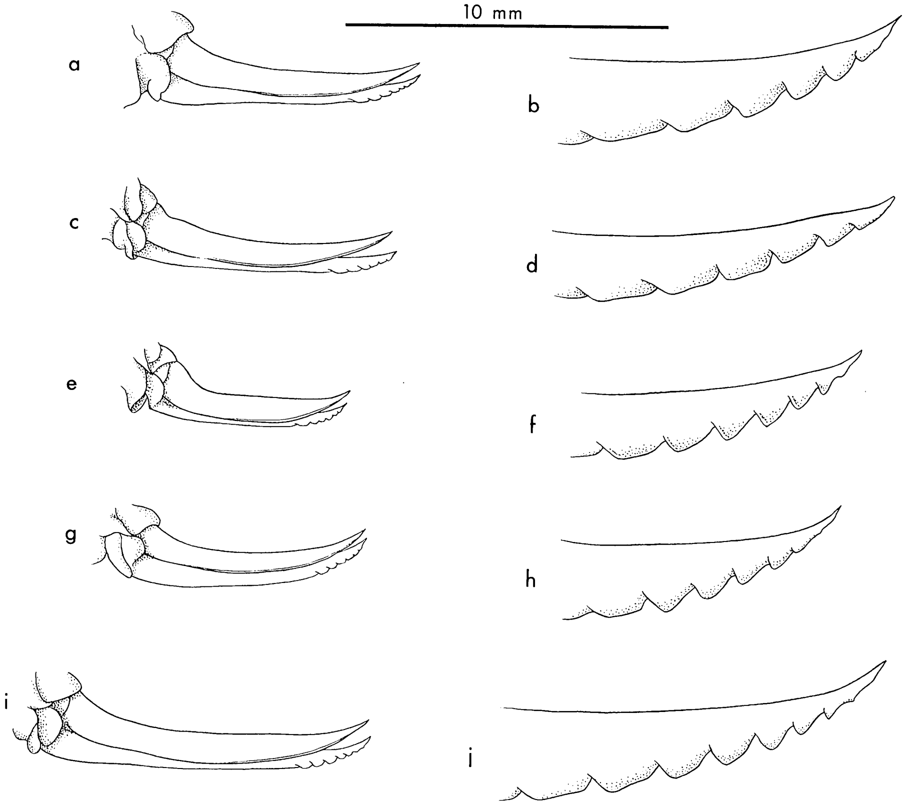

Fig. 3. Ovipositors of *Euhadenoecus* species. a,b–*Euhadenoecus puteanus,* Natural Bridge State Park, Powell Co, Ky.; c,d–*E. puteanus,* Middle Creek, Signal Mt, Hamilton Co, Tenn.; e,f–*E. puteanus* (depauperate high elevation form), Mt Sterling, elev 4900 ft, Haywood Co, N.C.; g,h–*E. insolitus,* Town Creek Cave, Marshall Co, Ala.; i,j–*E. fragilis,* Tawneys Cave, Giles Co, Va.

VARIATION. As previously mentioned, *Euhadenoecus puteanus* is the most widely distributed and most variable of the hadenoecine species, although it is remarkably constant in its principal diagnostic characters. The pale subquadrate or subcircular glandular areas on the sides of the male epiproct are distinct in all series except some of those from the highest elevations in the southern Appalachians, in which adults are unusually small and dark-colored and the males have these areas concolorous with the rest of the epiproct (Pl. II, b). Besides the individual variation in size and proportions found in local populations the species

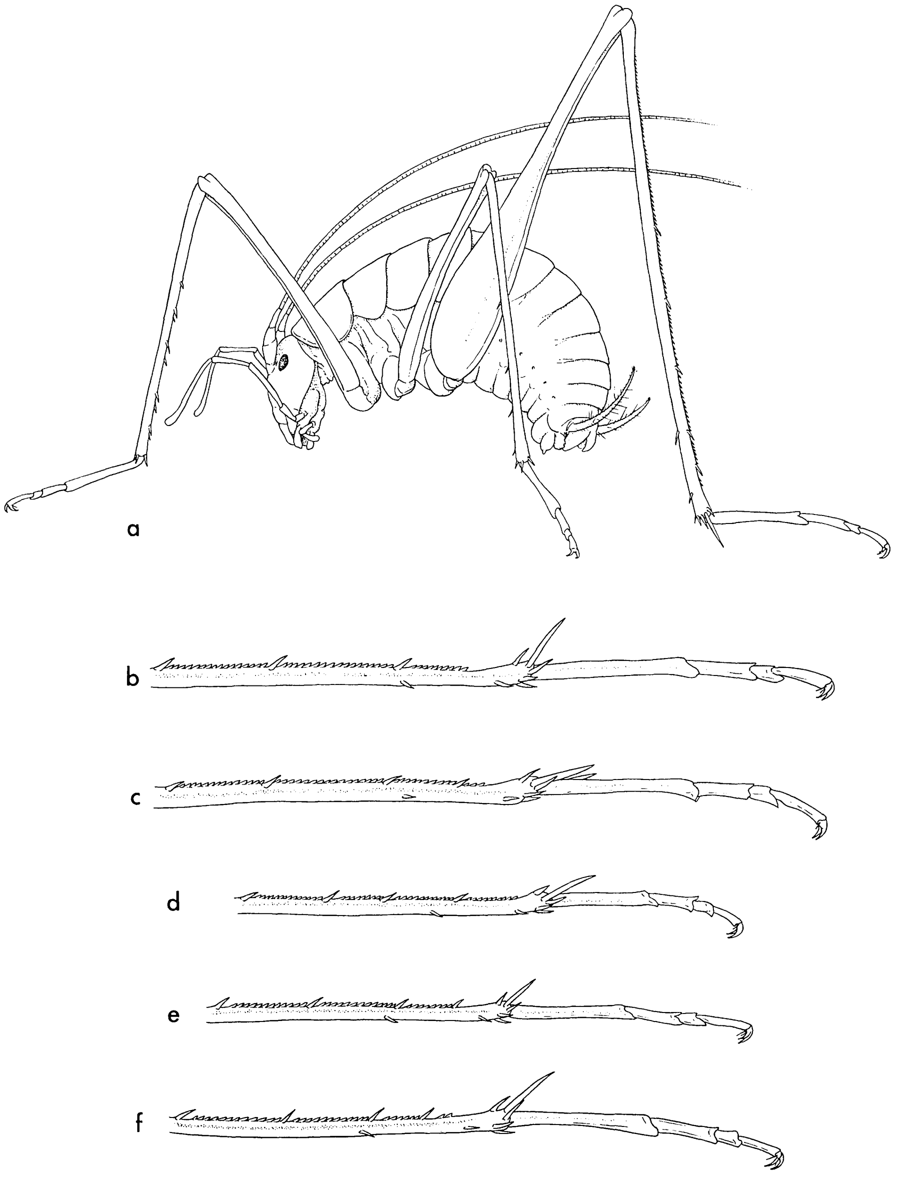

Fig. 4. *Euhadenoecus insolitus,* and Tibia III of *Euhadenoecus* species. a—*E. insolitus* ♂, side view, Town Creek Cave, Marshall Co, Ala.; b-f—Distal ends of tibia III: b—*puteanus* ♀, Natural Bridge State Park, Powell Co, Ky.; c—*puteanus* ♀, Middle Creek, Signal Mt, Hamilton Co, Tenn.; d—*puteanus* ♀ (depauperate high elevation form), Mt Sterling, elev 4900 ft, Haywood Co, N.C.; e—*fragilis* ♂, Tawneys Cave, Giles Co, Va.; f—*insolitus* ♂, Town Creek Cave, Marshall Co, Ala.

exhibits latitudinal, altitudinal and regional differences, not only in coloration but also in body proportions, the latter in part allometric effects of size differences. In Table 3 certain dimensions and proportions are given for samples from different parts of the range, and

TABLE 3

VARIATION IN SIZE (MM) AND PROPORTIONS IN *EUHADENOECUS PUTEANUS*

Region[1]	No. Spec.	Range	Mean	S.D.	Range	Mean	S.D.
			MALE				
		Length of Pronotum			Length of Femur I		
Northern Region	25	3.0- 3.7	3.24	0.17	9.0 -11.0	9.60	0.44
Appalachian Mts.	134	3.0- 4.2	3.54	0.22	8.7 -11.4	10.17	0.58
Alleghany Plateau	37	3.0- 3.9	3.46	0.20	9.3 -11.9	10.34	0.60
Cumberland Plateau	41	3.2- 4.3	3.85	0.23	9.7 -13.2	11.68	0.76
		Length of Femur III			Ratio Femur III/Pronotum		
Northern Region	25	14.7-17.2	15.34	0.54	4.34- 5.35	4.74	0.25
Appalachian Mts.	134	14.7-19.3	16.70	0.96	4.33- 5.32	4.69	0.22
Alleghany Plateau	37	15.0-18.7	16.62	0.84	4.39 - 5.35	4.82	0.22
Cumberland Plateau	41	15.0-21.7	19.04	1.26	4.49- 5.32	4.91	0.24
			FEMALE				
		Length of Pronotum			Length of Femur I		
Northern Region	45	3.0- 3.6	3.23	0.12	8.3 - 9.6	8.94	0.32
Appalachian Mts.	129	3.0- 4.3	3.60	0.21	8.4 -11.4	9.70	0.54
Alleghany Plateau	56	3.0- 3.9	3.58	0.19	8.6 -11.2	9.96	0.53
Cumberland Plateau	74	3.6- 4.6	3.99	0.22	9.7 -13.0	11.69	0.77
		Length of Femur III			Ratio Femur III/Pronotum		
Northern Region	45	14.0-16.6	15.24	0.60	4.35- 5.14	4.71	0.19
Appalachian Mts.	129	14.6-19.5	16.58	0.77	4.01- 5.26	4.62	0.21
Alleghany Plateau	56	14.7-18.3	16.72	0.86	4.29- 5.31	4.68	0.18
Cumberland Plateau	74	17.0-21.5	19.21	0.96	4.36- 5.54	4.76	0.24
		Length of Ovipositor					
Northern Region	45	6.2- 7.6	7.02	0.34			
Appalachian Mts.	129	6.4- 8.2	7.43	0.36			
Alleghany Plateau	56	6.7- 8.3	7.39	0.36			
Cumberland Plateau	74	6.9- 9.6	8.42	0.60			

[1] Localities are grouped under these regions as follows: *Northern,* those in southern New York, northwestern Pennsylvania and northeastern Ohio, mostly north of the glacial boundary; *Appalachians,* those in the Ridge and Valley Province in Virginia and West Virginia and the Unaka and Great Smoky Mountains in Tennessee, North Carolina and northeastern Georgia up to 4500 ft elevation; *Alleghany Plateau,* those in southwestern Pennsylvania and southeastern Ohio; and *Cumberland Plateau,* those in that province in eastern Kentucky, central Tennessee and northeastern Alabama.

in Fig. 8, in which the length of femur III in *puteanus* and *adelphus* is compared, the extent of variation in this dimension in certain local populations in the southern Appalachians is shown. The maxillary palpi also show variations in length relative to pronotal length that are correlated with those in relative leg length.

The four males and nine females seen from high elevations (4500-5000 ft) in the southern Appalachians are dark in color and very small, measuring as follows: length of pronotum, ♂ 2.9-3.3, mean 3.2, ♀ 3.0-3.6, mean 3.3; length of femur I, ♂ 7.9-8.4, mean 8.2, ♀ 7.6-8.6, mean 8.2; length of femur III, ♂ 13.3-15.0, mean 14.6, ♀ 13.3-15.2, mean 14.5; length of ovipostor 5.9-7.0, mean 6.5. The largest specimens of *puteanus,* with the longest legs relative to pronotal length, are from Fentress, Marion and Hamilton counties, Tennessee; in 21 males and 20 females from those localities the dimensions are: length of pronotum, ♂ 3.6-4.3, mean 3.9, S.D. 0.18, ♀ 3.7-4.6, mean 4.05, S.D. 0.25; length of femur I, ♂ 10.6-13.2, mean 12.20, S.D. 0.58, ♀ 10.7-13, mean 11.85, S.D. 0.56; length of femur III, ♂ 17.9-21.3, mean 19.81, S.D. 0.96, ♀ 19.0-21.5, mean 19.87, S.D. 0.63; femur III/pronotum, ♂ 4.74-5.42, mean 5.07, S.D. 0.19, ♀ 4.56-5.54, mean 4.92, S.D. 0.26; length of ovipositor 7.7-9.4, mean 8.59, S.D. 0.45. Coloration is darker at high elevations and in the northern part of the range, and becomes lighter at lower elevations and southward.

In side view the fastigial ridges vary from evenly arcuate to slightly umbonate or apiculate at or caudad of midlength, but their form is quite constant in local populations. The amount of darkening of the crests and anterior surfaces is also somewhat variable, but the apices are nearly always brownish, a condition rarely seen in *adelphus.* The pale glandular areas of the male epiproct are usually rounded-quadrate or subtrapezoidal in outline, varying to almost circular but never narrowly triangular or crescentic. Except in a few individuals from high elevations in the southern Appalachians they are always plainly evident and well-defined. The large basal ovipositor teeth in side view may be almost symmetrical or weakly retrorse, and sometimes have a short segment of the ventral edge nearly straight and oblique.

The number of denticles on the dorsal carinae of tibia III ranges from 70 to more than 100. It varies considerably in individuals of the same size from the same locality, but shows a definite correlation with tibial length. Other characters that are not correlated with size and that show about the same amount of variation in material from all regions include the following: length/breadth of eye, 1.5-1.8; interocular distance/length of eye 1.3-1.6; number of spurs on ventral carinae of tibiae I and II and on dorsal carinae of tibia III 4-7, with 5 as the strong mode in all; ventrocaudal margin of tibia III usually without, rarely with one predistal spur; number of ovipositor teeth 5-8, mode 7.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Throughout its range, as shown by collection dates, adults of *Euhadenoecus puteanus* begin to appear in late June and reach maximum abundance in late July, August and early September. In the north the latest records of adults are in early October, but in the south adults persist until at least early December. First and second instar nymphs have been trapped in August, September and November, and small juveniles in every month of the year except January. Medium-sized nymphs are numerous in trap

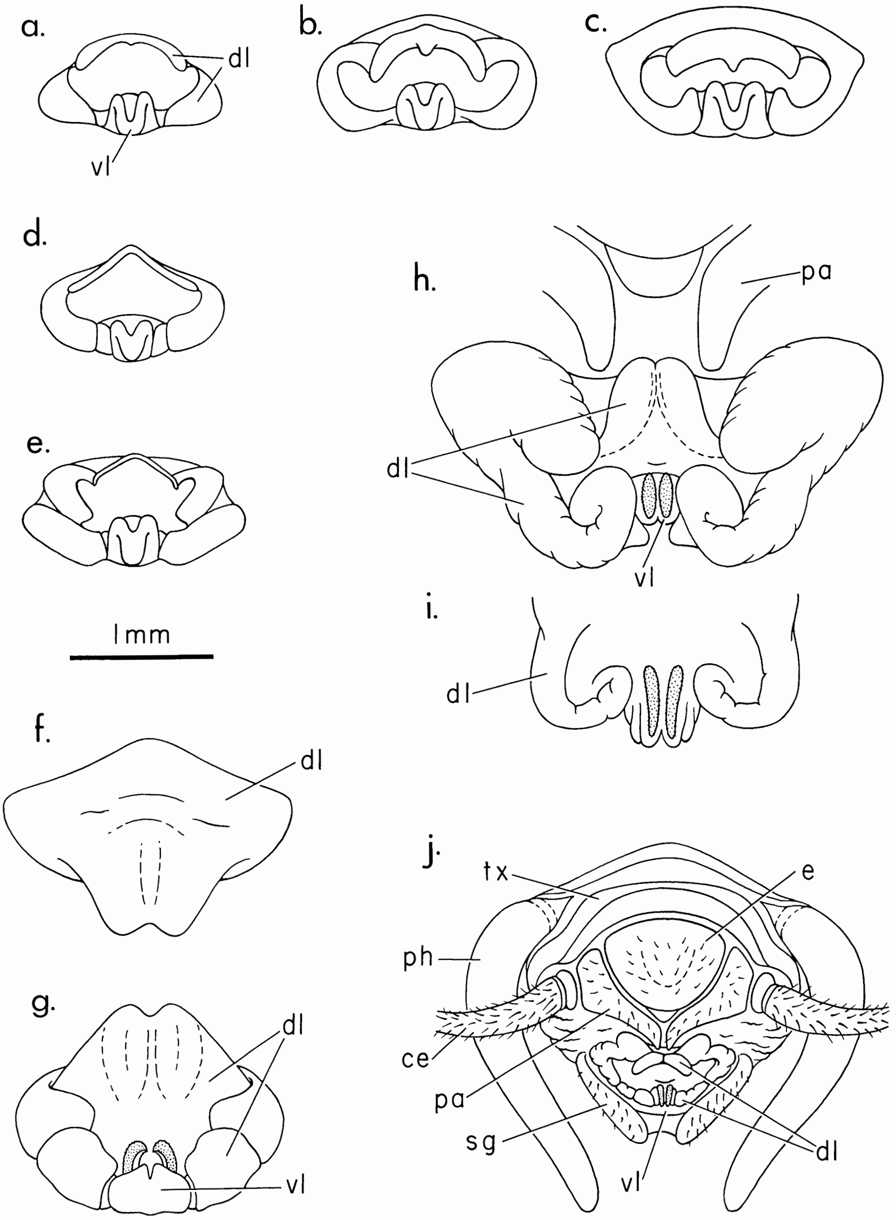

Fig. 5. Male terminalia of Hadenoecini. a-i—Partially extruded phallus, seen in distal aspect unless otherwise specified; a-e—*Euhadenoecus:* a—*puteanus,* Mountain Lake, Giles Co, Va.; b—*puteanus,* Arrowwood Glade, Macon Co, N.C.; c—*adelphus,* Highlands, Macon Co, N.C.; d—*fragilis,* Tawneys Cave, Giles Co, Va.; e—*insolitus,* Crystal Cave, Jefferson Co, Ala.; f-i—*Hadenoecus:* f—*subterraneus,* Pruitts Saltpeter Cave, Warren Co, Ky.; g—*subterraneus,* same specimen as f, ventrodistal aspect; h—*cumberlandicus,* Stab Cave, Pulaski Co, Ky.; i—*cumberlandicus,* another specimen from Stab Cave, inner face of ventral lobe; j—*subterraneus,* Mammoth Cave, Edmonson Co, Ky., distal view of end of abdomen, showing fully everted clasping organs. Symbols in figure: ce—cercus; dl—dorsal lobe; e—epiproct; pho—clasper and possible pheromone organ; sg—subgenital plate; t ix, t x—tergites IX and X; vl—ventral lobe.

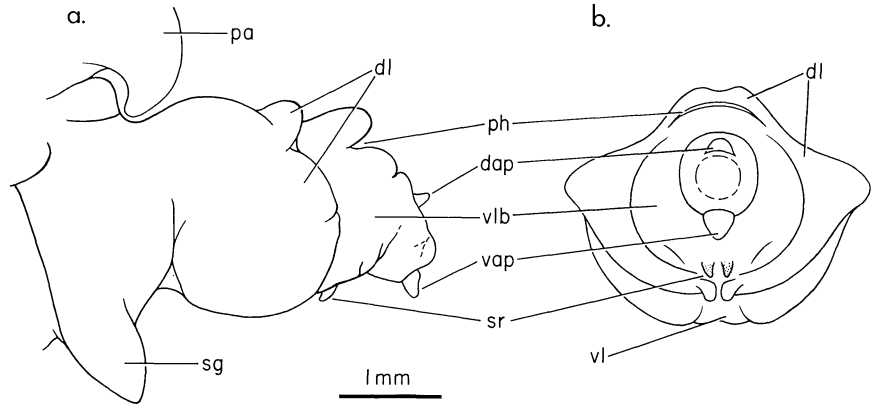

Fig. 6. Phallus of *Hadenoecus opilionoides*, fully extruded (Buffalo Cove, Fentress Co, Tenn.): a—side view; b—distal view. Symbols in figure: dap—dorsal apical papilla; dl—dorsal lobe; pa—paraproct; ph—phallotreme; sg—subgenital plate; sr—weakly sclerotized ridges or lobes; vap—ventral apical papilla; vl—ventral lobe; vlb—bulla of ventral lobe.

collections made between April and August, and large ones occur from early June to early October with a peak in July. Although collection data are not a reliable basis for estimating the duration of the life cycle, they suggest that in this species it extends over at least two years.

DISTRIBUTION. The range of *Euhadenoecus puteanus* is much more extensive than that of any other species of the Hadenoecini. It includes the entire Appalachian region and the greater part of the Interior Low Plateaus, from just north of the glacial boundary in northeastern Ohio and southern New York to northeastern Alabama and northern Georgia (map, Fig. 7). Limital northern records are Erie and Ashtabula counties, Ohio, and Olean and the Catskill Mountains in New York; the last and the vicinity of Philadelphia are northeasternmost records. The western limits of the range are in general coterminous with the western edges of the sandstone-capped Alleghany and Cumberland Plateaus in Ohio, Kentucky, Tennessee and northeastern Alabama. *E. puteanus* has not been recorded from the Piedmont south of Pennsylvania except in northern Georgia, and does not occur in the pine forests of the Southeastern and Southern Coastal Plains. There are, however, two outlying records from those regions—one from Monticello in southern Mississippi and the other from Billy's Island in the Okefenokee Swamp in southeastern Georgia. Both of these almost certainly represent relict populations that have survived since the Wisconsin Glacial in a region from which the species has all but disappeared. The altitudinal range of *E. puteanus* thus extends from a little over 100 ft in the Okefenokee Swamp to over 5000 ft in the Unakas and Great Smokies of North Carolina.

HABITAT. Field data on many collections of this species from most parts of its range show that it inhabits mesic or xeromesic, deciduous

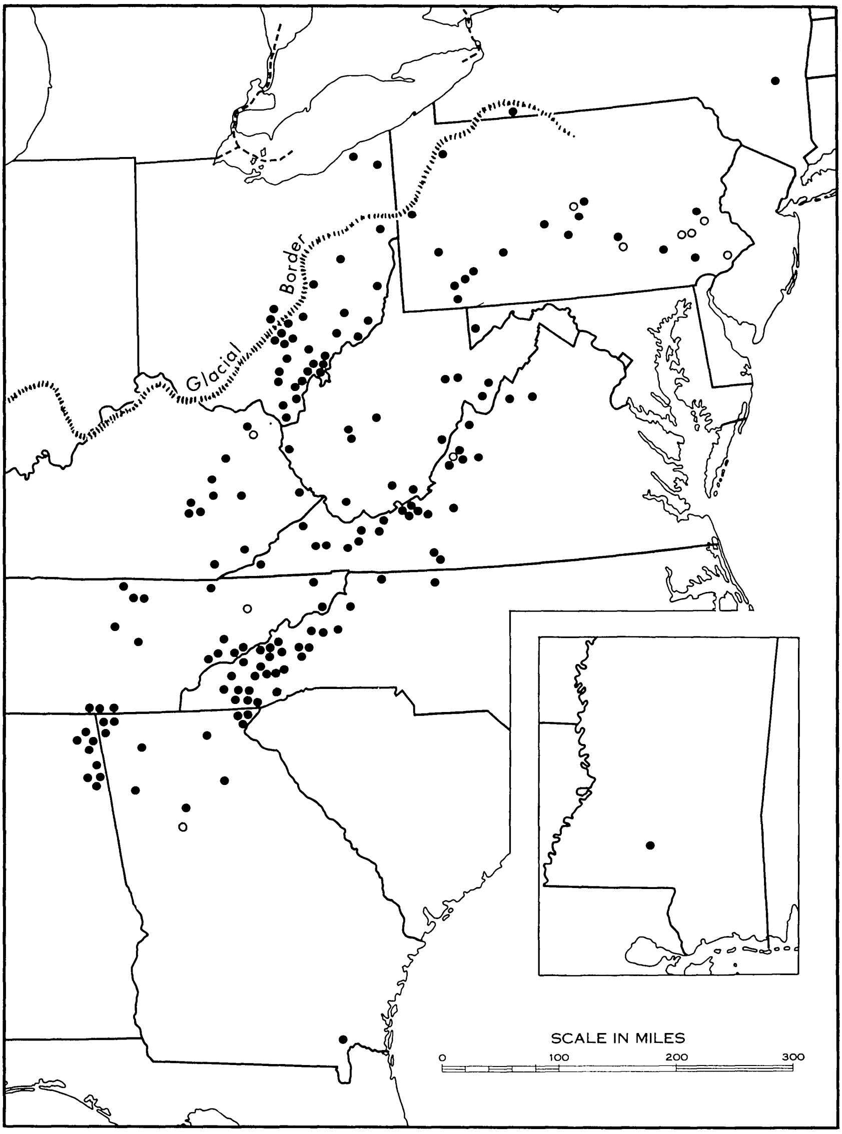

Fig. 7. Distribution of *Euhadenoecus puteanus.* Solid dots = specimens examined; open circles = records in literature.

or deciduous-coniferous forests on sites with arkosic, sandy or sandy loam soils, where forest debris or rock crevices afford protection during the day from sunlight and dessication. Forested talus slopes, the fissured bases of sandstone cliffs and "rock houses," and wooded ravines are especially favored situations, and wherever caves occur in such surroundings *puteanus* often congregates in their entrances and twilight zones; it never penetrates into the deep cave environment. The disjunct populations in the southern coastal plain probably inhabit hardwood forests; the specimens taken at Emory, Georgia were in a rough stone culvert over a permanent stream in rolling oak-maple-pine country, with an established colony of the adventive Asiatic rhaphidophorine *Tachycines asynamorus* Adel.

OTHER OBSERVATIONS. At night individuals of *E. puteanus* emerge from their diurnal hiding places and wander about on the forest floor, ascend rock faces, and climb to heights of three or four feet on tree trunks, herbs and shrubs. As shown by examination of gut contents they eat decaying vegetable material, fungi and insects. The insect material is usually too finely comminuted to be identifiable, but includes small beetles, ants, and fragments of weakly sclerotized integument that seem to be from soft insect larvae; its own exuviae may also be consumed. Like many other rhaphidophorids *E. puteanus* should probably be classed as a facultative predator, but by far the greater part of its food is certainly that of a scavenger. Individuals are attracted in numbers to trap jars baited with dilute molasses or malt, and to trails of oatmeal flakes. On one occasion, at Arrowwood Glade in Macon County, North Carolina, during a period of about two hours beginning shortly after nightfall more than 160 adults and many juveniles were collected along a half-mile oatmeal trail in woods bordering a small stream; here it was accompanied by almost equal numbers of *E. adelphus.*

The short, strong ovipositor of *E. puteanus,* with its large incurved teeth, seems adapted for penetration into leaf-mold or coarse-grained soils rather than fine silt or clay, and this may account for the apparent absence of the species from areas with clay soils, especially north of the glacial boundary. Many more adult females than males are represented in the collections examined, but whether this means that more females than males survive to that stage or merely that the former are more strongly attracted to the baits used cannot be stated.

SPECIMENS EXAMINED: 2,247–567♂, 839♀, 1,021 juveniles (all in UMMZ except as otherwise indicated), from the following localities:

NEW YORK: *Cattaraugus Co.:* Rock City, Olean [OSM] ; *Ulster Co.:* Chichester, Catskill Mts. PENNSYLVANIA: *Alleghany Co.:* Pittsburgh [CM] ; Schenley Park, Pittsburgh; *Berks Co.:* Stony Creek, in small cave [ANSP] ; Archer's Mine Shaft [ANSP] ; *Cambria Co.:* Johnstown; *Centre Co.:* Shalter Farm Cave [D] ; Woodward Cave (Stone 1953: 49; Davis 1970: 72) [D] ; *Chester Co.; Crawford Co.:* Burgess Park, Titusville; *Dauphin Co.:* Rockville [ANSP] ; *Fayette Co.:* Laurelville; Dulaney Cave (Stone 1932: 70; 1953: 88) [D] ; Barton Cave (Stone 1932: 68; 1953: 88) [D] ; *Huntingdon Co.:* Colerain State Park; *Lancaster Co.:* South Mts., 5 mi N. of Ephrata; *Lawrence Co.:* Slippery Rock Creek, Ellwood City; *Lehigh Co.:* Allentown (ANSP); *Mifflin Co.:* Aitken Cave (Stone 1932: 97; 1953: 113; Davis 1970: 52) [D] ; Rupert Cave (Stone 1932: 104; 1953: 121; Davis 1970: 61) [D] ; *Westmoreland Co.:* Mt. Pleasant; N of Laurelville. OHIO [all OSM unless otherwise indicated] : *Ashtabula Co.; Athens Co.:* Athens [OSM, OU, UMMZ] ; Coolville; *Belmont Co.:* Barton; *Columbiana Co.:* Elk Run Twp.; *Fairfield Co.:* Berne Twp.; Lancaster; Panther Cave, Sec. 10, Berne Twp.; Sugar Grove;

Gallia Co.: Carter Cave, nr Mudsock [UMMZ]; Double Cave, Rutland area [UMMZ]; Gallia; Saltpeter Cave, 1.5 mi from Centerpoint [UMMZ]; *Hocking Co.:* Ash Cave State Park [UMMZ]; Good Hope Twp., "Neotoma" [ANSP, OSM, UMMZ]; Laurel Twp.; Rock House; Saltpeter Cave; *Jackson Co.:* Indian Cave, Lake Catherine area [UMMZ]; Washington Twp.; *Lake Co.; Lawrence Co.:* Dean State Forest; Washington Twp.; *Meigs Co.:* Bennet Cave, 4 mi from Tupper's Plains [UMMZ]; Bunker Hill Cave (Lizey's Hole), 5 mi from Hemlock Grove [UMMZ]; Horse Cave, 6 mi from Chester [UMMZ]; Partlow Cave, 3.5 mi from Tupper's Plains [UMMZ]; Pencil Cave, 4 mi from Tupper's Plains [UMMZ]; Vineyard Cave [UMMZ]; Warnek Cave [UMMZ]; *Monroe Co.; Muskingum Co.:* Adams Mills, Muskingum Twp.; *Noble Co.:* Belle Valley; *Perry Co.:* Sayre; *Tuscarawa Co.; Vinton Co.:* McArthur, in sandstone cave; *Washington Co.:* Beverly, Newport Twp.; Waterford Twp. MARYLAND: *Garrett Co.:* Swallow Falls, nr Oakland. WEST VIRGINIA:[1] *Clay Co.* [CM]; *Kanawha Co.:* nr Charleston, in old mine tunnel; Hernshaw; *McDowell Co.:* Welch; *Monroe Co.:* Waiteville, 2 mi NW, 2600 ft; *Pendleton Co.:* Smoke Hole (Da: 244) [USNM]; Trout Cave (Cave at Trout, Trout Rock Cave; Da: 251) [D, ANSP]; *Pocahontas Co.:* Watoga State Park; *Randolph Co.:* Glady Cave (Da: 309) [USNM]; Simmons-Mingo Cave (E. S. Simmons Cave; Da: 312) [D]; *Summers Co.:* Bluestone State Park, 1600 ft; *Wayne Co.:* Cabwaylingo State Park. KENTUCKY: *Bath Co.:* Licking River at Menifee Co. line; *Bell Co.:* Pineville, 1150 ft; *Breathitt Co.:* Guage, 5 mi NE; *Carter Co.:* Carter Caves State Park (Bat, Cascade and Laurel caves, and forest) [ALA, ANSP, D, OU, ST, UMMZ]; *Harlan Co.:* Pine Mt. [ST]; *Jackson Co.:* Cole Cave [M]; Kerby Rock Shelter, Kerby [M]; Turkey Foot Cave, 15 mi NE of McKee [M]; *Lee Co.:* Oakdale; *Pike Co.:* Williamson, 1300 ft; *Powell Co.:* Natural Bridge State Park. VIRGINIA:[2] *Alleghany Co.:* Long Dale Furnace; Lowmoor Cave (D: 89, H: 43), 1 mi W of Lowmoor, 1150 ft [ALA]; *Bath Co.:* Alleghany Co. line; Flag Rock Pass, Warm Springs Mt., 2990-3500 ft [ANSP, UMMZ]; Hot Springs, 2400-2600 ft [ANSP, UMMZ]; *Bland Co.:* Big Walker Mt., 3950 ft; Wolf Creek, 1950-2600 ft; *Dickenson Co.:* Breaks Interstate Park, 1500 ft; *Giles Co.:* vicinity of Mountain Lake Biological Station (Pond Drain; Garden of the Gods, 3900 ft; Bear Cliff, 4000 ft; Bean Field Mt, 4200 ft; Bald Knob, 4360 ft); Glen Lyn, 1540 ft; New River Cave (D: 230; H: 97), nr Goodwins Ferry; *Highland Co.:* Van Devanters Cave (D: 263; H: 110) [USNM]; *Lee Co.:* Billeys Cave (= ? Baileys Cave, H: 115), nr Pennington Gap [H]; *Montgomery Co.:* nr Blacksburg, 2250 ft; *Page Co.:* Lewis Mt. Campground, 3380 ft; *Patrick Co.:* Fairy Stone Park, lake shore; *Roanoke Co.:* McVitty Cave (H: 200), nr Salem; *Rockbridge Co.:* Dollhouse Cave (D: 388) [USNM]; *Rockingham Co.:* in cave [H]; *Russell Co.:* Clinchfield [ST]; Seven Springs Cave (D: 442) [USNM]; *Smyth Co.:* Atwells Tunnel (D: 502); Stones Cave #2 (D: 505; H: 393); *Tazewell Co.:* Cassel Farm Cave (D: 528; H: 346). NORTH CAROLINA: *Alleghany Co.:* Sparta, 7 mi NE, 3200 ft; *Buncombe Co.:* Beech, 2500 ft; Craggy Mt., 3600 ft; Dula Springs, 2400-2500 ft; Hemphill, 5000 ft; High Hickory Mt, 1 mi S of Swannanoa, 3000 ft; Marshall, 4 mi S, 1800 ft; *Burke Co.:* Linville Caverns, 3.5 mi S of Linville Falls (Petrie 1942: 61), *Haywood Co.:* Balsam, 3 mi E, 4000-5000 ft [ST]; Balsam Gap Fish Hatchery, 3400 ft; Blue Ridge Parkway between Balsam Gap and Richland Balsam, 4800-5000 ft [ST]; Mt Pisgah, 5000 ft; Mount Sterling (town); Crestmont on Big Creek, 1700-2000 ft; slopes and summit of Mt Sterling, 3500-5000 ft; Sharptop Mt, 3000-4500 ft; Sunburst, 2800 ft [NCA]; Waynesville, 6 mi W, 3500 ft [OSM]; *Jackson Co.:* Balsam, 3400 ft [ST]; Sylva, Kings Mt., 2500-2800 ft; *Macon Co.:* Arrowwood Glade (Trout Rearing Station), 2300 ft (plesiotypic locality); Cliff Lake (Cliffside) Recreation Area, 4.4 mi NW of Highlands, 3000 ft; Franklin, 9 mi W, 2200 ft; Highlands, and 7 mi SE, both 3800 ft; road to Wayah Bald, Nantahala Mts, ca 4500 ft; Wayside Park Camp, 12 mi E of Franklin, 4000 ft; *Madison Co.:* Campbells Vegetable Cave; nr Marshall, 1700 ft; *Mitchell Co.:* Spruce Pine, 2700 ft; *Stokes Co.:* Hanging Rock State Park, 2250 ft; *Swain Co.:* Great Smoky Mts Nat'l Park [ST]; Cave in Indian Ridge, nr Judson [S. of Bushnell], ca 2000 ft; Newfound Gap and ascent, 3500 and 5000 ft [ASM]; *Transylvania Co.:* Bent Creek Gap, Pisgah Nat'l Forest; Lake Toxaway, 3200 ft; *Watauga Co.:* Blowing Rock; *Yancey Co.:* Bald Knob, E slope, 5000 ft. TENNESSEE: *Blount Co.:* Gregory Cave, Cades Cove (Barr 1961: 77), 1900 ft [ALA]; Tuckalechee Cave (Great Smoky Caverns), 1.5 mi S of Townsend in Tuckalechee Cove (Barr 1961: 82) [ALA, UMMZ]; *Carter Co.:* summit of Roan Mt, 5000 ft; *Claiborne Co.:* Yoakum Cave, 7 mi SW of Arthur; *Cumberland Co.:* Grassy Cove and

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[1] The references following names of caves, e.g. (Da: 244), refer to Davies (1965), in which the caves are located and described.

[2] Most of the caves listed are located and described in Douglas (1964) or Holsinger (1975), to which page references are given, e.g. (D: 388) or (H: 43), following the cave name.

slopes of Walden Ridge, 2070-2250 ft; Grassy Cove Saltpeter Cave [ALA, UMMZ]; *Fentress Co.:* Allardt, 1400-1600 ft; Buffalo Cove (Deer Gap Lookout, 1600 ft; small cave in bottom of cove, 1300 ft); *Greene Co.:* Afton Cave [B]; *Hamilton Co.:* Middle Creek on Signal Mt, 1000 ft; *Marion Co.:* Little Cedar Mountain Quarry Cave (Barr 1961: 303); Moonshine Cave, PU-1, 35°02'22" N, 85°42'22" W; Nickajack Cave, Shellmound (Barr 1961: 303); *Pickett Co.:* Bunkum Cave (Barr 1961: 363); *Putnam Co.:* Bridge Creek Cave (Creek Cave) (Barr 1961: 374) [ALA]; *Sevier Co.:* Bluff Mt, Chilhowee Mts, 7 mi SE of Seviersville, 3000 ft; Chimneys Camp, Great Smoky Mts Nat'l Park, 2700 ft [OSM]; Newfound Gap, 5000 ft [OSM]; *Sullivan Co.:* Morrill Cave (Barr 1961: 436) [B]. GEORGIA:[1] *Charlton Co.:* Billy's Island, Okefenokee Swamp, ca 100 ft elev. [ANSP, CU]; *Dade Co.:* Byers Cave, 1.5 mi SW of Rising Fawn [= ? Creek Bed Cave, ? Cricket Cave (HP)]; Cherokee Cave, 4.5 mi NE of Rising Fawn; Howards Waterfall Cave, 1.5 mi SW of Trenton (HP); Johnson Crook Cave, 4.5 mi NE of Rising Fawn, 800 ft (HP); Morrison Spring Cave, 2 mi E of Trenton (HP); Sittons Cave [= ? Saw Mill Cave (HP)]; *DeKalb Co.:* Emory; *Gordon Co.:* Roberts Cave (Ford Roberts Cave), Resaca (HP); *Jackson Co.:* Thompson's Mills, 5 mi W of Hoschton [ANSP]; *Lumpkin Co.:* Walnut; *Polk Co.:* White River Cave, Rockmart, 2 mi E of Lookout (HP) [B]; *Rabun Co.:* Clayton [NHW]; Dillard, 2200 ft [ANSP]; Mountain City, Rabun Mt, 3500-4000 ft; Raven Rocks Mt, 3000-3200 ft [ANSP]; *Walker Co.:* Bible Springs Cave, 2 mi NE of Lookout (HP). ALABAMA:[2] *Cherokee Co.:* Sharpshin Ridge, 2 mi W of Leesburg; *DeKalb Co.:* Cherokee Cave (AL 806); De Soto Park, nr Ft. Payne [ALA]; Manitou Caves (Fort Payne Caves) (AL 13) [ALA]; Section 26 Cave (AL 804); *Jackson Co.:* Coon Creek Cave (Saltpeter Cave) (AL 163) [ALA]; 7 mi N of Flat Rock, in rock cliffs [AU]; *Talladega Co.:* Cheaha State Park, nr Anniston [ALA]. MISSISSIPPI: *Lawrence Co.:* Monticello [paratype in ANSP; not seen].

References in Literature

Hadenoecus puteanus Scudder 1877: 37, cited above; Scudder 1894: 23 (in key; N.C., Miss.); Scudder 1899-1900: 81 (listed); Davis 1911: 217 (Clayton, Ga.); Caudell 1916: 659 (in key; Corning [Lehigh Co.], Pa.); Rehn & Hebard 1916: 269 (Sunburst, N.C.; Rabun Co., Thompson's Mills, Billy's Island, Ga.); Blatchley 1920: 608, 610 (redescribed, records); Karny 1930: 189 (Ga.); Chopard 1931: 398-9, Figs. 11, 15-18 (redescribed; Cascade Cave, [Carter Co.], Ky., Dixie Caverns, [Roanoke Co.], Va.); Hubbell in Hebard 1934: 222 (limital records; possibly [almost certainly not] in S. Ill.); Karny 1935: 393 (Ga.); Hubbell 1936: 7, 112, 149, 413, Pl. VII, Fig. 98 (ovipositor); Dearolf 1937a: 44 (Pa. caves); Dearolf 1937b: 45 (Pa. and Ga. caves; attracted by cheese and meat baits); Karny 1937: 260, Pl. VI, Fig. 9 (♂) (references; N.C., Ga., Miss., Philadelphia, Pa.); Hebard 1937-8: 98 (Pa. records, range); Brimley 1938: 21 (Crestmont, Mt Sterling, Spruce, N.C.); Semons 1939: 168, and 1943: 229 (*Gregarina hadenoeci* parasitic in midgut; Washington Co., Ohio); Dearolf 1941: 174 (in 7 Pa. caves); Hebard 1945: 95 (Hot Springs, Flag Rock Pass, Va.; on boulder sides and at bait on tree trunks); Judd 1948: 117, Figs. 28, 64 (proventriculus); Mohr 1953: 17, Fig. 4 (♀); Ander 1957: 91 (paraprocts, 10th tergum); Eades 1964: 77 (habitat); Holsinger 1964: 65 (Va. caves); Vandel 1965: 180 (exceptionally in caves); Leroy 1967: 664, 675, 676 (mentions); Holsinger & Peck 1971: 35 (11 caves in NW Georgia).

Hadenoecus subterraneus, not of Scudder 1861: Cope and Packard 1881: 882 (in part: Nickajack Cave, Tenn.); Packard 1888: 19 (same); Markovitch 1920: 91 (same); Ives 1927: 89 (same); Ives 1930: 116, 117 (Buttreys Cave [= Delaps Cave, Barr 1961: 242], Hamblen Co., Tenn.).

Hadenoecus cavernarum, not of Saussure 1862: Scudder 1894: 22 (in part: Nickajack Cave, Tenn.).

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[1] The indication (HP) following most of the cave names refers to Holsinger and Peck (1971: 26), in which the caves are located and described.

[2] The numbers following the cave names, e.g. AL 806, are those assigned by the Alabama Cave Survey; the caves are listed, located and described in Varnedoe (1971).

EUHADENOECUS ADELPHUS[1] Hubbell, n. sp. (Figs, 2, b,d; 5, c; 8 (graph); 9 (map); Pl. IV, b).

Type: Male, Granite City, on Macon-Jackson county line, North Carolina, elev. 3000-3200 ft, 15 Oct 1965 (T. H. Hubbell); *allotype* a female with the same data; both preserved in alcohol, in UMMZ.

This species is restricted to the southern Appalachians. It is sympatric throughout its range with the extremely similar *puteanus*, from which it is separable by the characters given in the key and, as shown in the accompanying graphs, by its larger size wherever the two species occur together, except at the highest elevations.

DESCRIPTION OF MALE TYPE:[2] Length of body ca. 16.5, of pronotum 4.3 (3.0-4.7), of femur I 13.3 (7.2-14.0), of femur III 21.7 (13.0-22.3), of tibia III 23.9 (15.3-26.0), of antenna ca 95 mm; proximal breadth of femur III 3.6 (2.4-3.6), distal breadth 0.86 mm.

General coloration as described for *puteanus* except as follows. Dorsum slightly paler, brownish borders of thoracic nota and abdominal tergites narrower, meso- and metanotum and basal abdominal tergites mostly pale above with faintly indicated median hairline and mere traces of brownish mesal longitudinal banding; fastigium entirely pale; epiproct brown, with proximolateral glandular areas and a triangular basal area pale; subgenital plate and penultimate sternite dilute brownish at sides, with a faintly indicated paler median stripe, styles pale.

Other features as described for *puteanus* except as follows. *Head* (Fig. 2, b): fastigial crests in side view more abruptly rounded apiculate, thence concave to anterior ends which are scarcely at all elevated. Maxillary palpus long, 0.74 times length of femur I, its distal segment 0.8 times pronotal length. *Legs:* length relative to pronotum, femur I 3.1 (2.4-3.3), femur III 5.1 (4.0-5.2); femur III 6.0 (5.9-6.7) times as long as proximal breadth, its slender distal portion long, ca. 0.4 (0.33-0.45) of total length, this averaging somewhat greater than in *puteanus*. Tibia I as long as femur I, tarsus I 0.66 times tibial length, basitarsus I 1.14 (1.12-1.8) times as long as pronotum. Ventral spurs of tibia I 5/5 on all carinae, of tibia II 5/4 on cephalic, 5/5 on caudal carinae. Tibia III with 6/5 spurs on dorsocephalic, 5/5 on dorsocaudal carinae, predistal ventral spurs 2/2 on cephalic, 0/0 on caudal margins; spine formulae of dorsal carinae, right and left, cephalic 40/13/15/13/9/0 = 90, 39/21/14/11/4 = 85, caudal 45/20/12/9/5 = 91, 46/18/15/13/3 = 95. *Terminal abdominal structures* (Figs. 2, d; 5, c; Pl. IV, b) as described in key, differing from those of *puteanus* in the size and form of the pale glandular areas of the epiproct, their wider separation, and the brown color of the intervening space.

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[1] Gr. *adelphos*, brother, twin.

[2] Figures in parentheses give the range of variation in the entire series studied.

DESCRIPTION OF FEMALE ALLOTYPE: Length of body ca. 15.5, of pronotum 3.9 (3.3-4.4), of femur I 10.2 (8.0-12.7), of femur III 18.6 (12.4-21.0), of tibia III 21.0 (13.9-24.3), of ovipositor 7.7 (6.4-9.3), of antenna ca. 84 mm; proximal breadth of femur III 3.4, minimum distal breadth 0.85 mm, length of slender distal portion ca. 6.9 mm.

Agrees with male type in coloration and other respects except as follows. Fastigium pale except for faint brownish shading on anterior part of lateral faces of ridges. *Legs:* relatively shorter and stouter than in male; femur I 2.6 (2.3-3.1), femur III 4.7 (4.0-5.2) times as long as pronotum, length of femur III 5.3 (5.1-6.0) times its proximal breadth, slender distal portion only about one-third total length. Tibia I 1.3 times as long as femur I, tarsus I 0.6 times as long as tibia, basitarsus I 0.9 times pronotal length. Ventral spurs of tibia I, cephalic 5/5, caudal 6/5; tibia II with 5 spurs on all ventral carinae. Dorsal spurs of tibia III, cephalic 5/6, caudal 5/5, predistal ventral spurs, cephalic 2/2, caudal 1/1; spine formula, right and left, cephalic 32/19/16/12/12 = 91, 43/13/10/11/11 = 88, caudal 48/13/11/13/14 = 99, 41/16/11/12/9 = 89. *Ovipositor* like that of *puteanus.*

VARIATION, AND COMPARISON WITH *PUTEANUS.* The pale glandular areas of the male epiproct vary in outline from subcrescentic with arcuate inner edges to narrowly triangular, but never approach the condition characteristic of *puteanus* either in form or in the width of the interval between them. In *adelphus* the fastigial ridges are usually somewhat more widely separated than in *puteanus*, and in side view usually more prominently umbonate with summits more abruptly rounded, the ridges more concave anteriorly and their anterior ends very low. In most series the fastigium is entirely pale, not shaded with brown as in *puteanus*, but some specimens have the lateral faces faintly tinged with brownish anteriorly, this usually not extending to the cephalic ends of the fastigial ridges. In *puteanus* the ridges are usually less prominently umbonate and more broadly rounded at the summit, less abruptly declivent anteriorly and their cephalic extensions more distinct; their anterior ends and sides are usually shaded with brown and a small pale ocellar spot is often present on the posterior lateral surface.

The proximal antennal segment in *puteanus* is usually dilute reddish brown above, shading gradually into the darker brown sides, while in *adelphus* the dorsal surface is usually paler and more sharply separated from the darker sides. In *puteanus* the meso- and metanotum and proximal abdominal tergites usually have a brownish median stripe and their margins are more broadly suffused with brown, so that the pale areas of the dorsum are smaller and interrupted, while in many series of *adelphus* the dorsum is largely pale, either without or with only faint traces of a median stripe and divided only by the darker bands along the caudal edges of the segments. The general coloration is, however, darker and more uniform in specimens of both species from high altitudes.

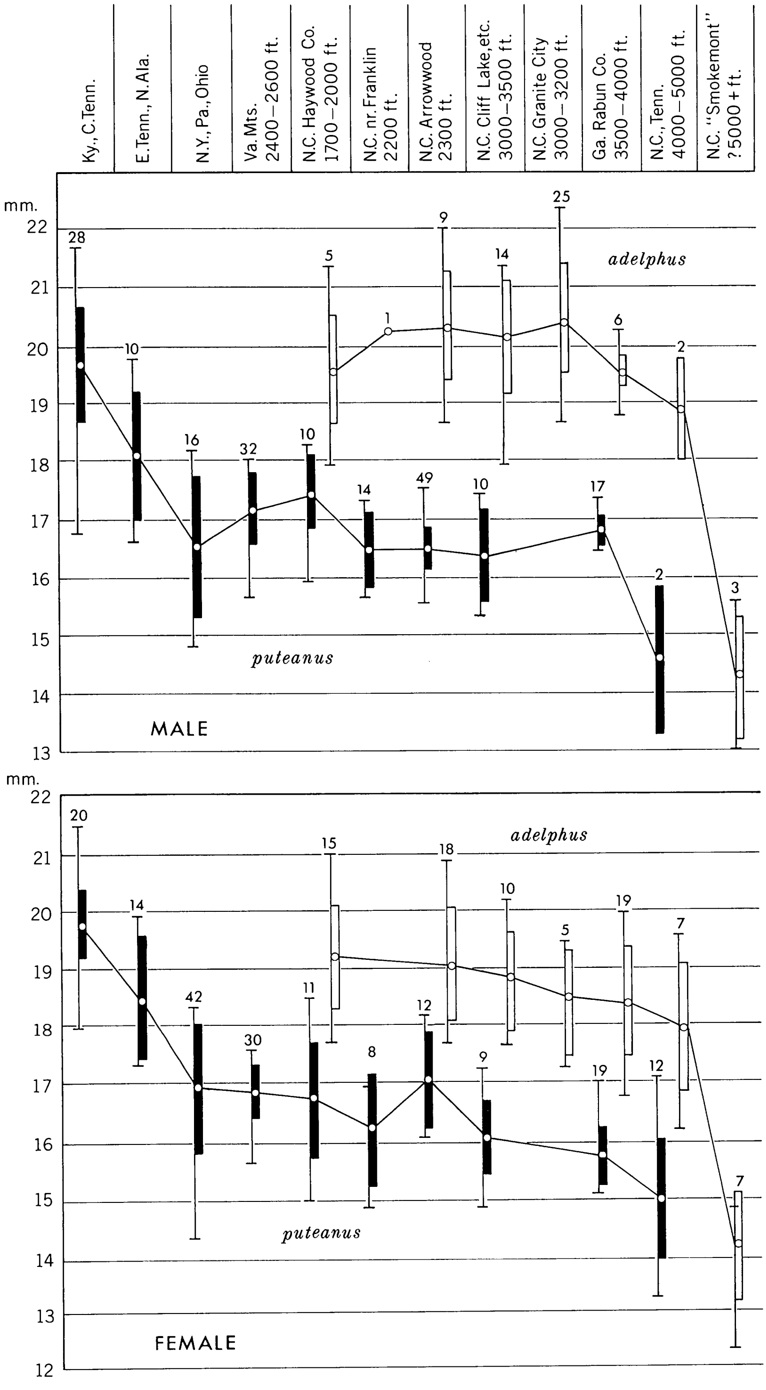

Fig. 8. Comparison of femur III lengths in *Euhadenoecus puteanus* and *E. adelphus*. Bar = one standard deviation on either side of mean.

Males of *puteanus* and *adelphus* can be distinguished immediately by the differences in the epiproct, but identification of females is more difficult and less certain. The initial sorting of that sex had to be made on the basis of the relatively subtle and somewhat variable differences in coloration and fastigial form. When this had been accomplished it became evident that specimens from most localities could be correctly identified by size alone, as is shown by the accompanying graphs (Fig. 8), in which size is expressed in terms of the length of femur III. These graphs show that wherever the two species occur together *adelphus* is consistently the larger, with very little overlap. The excellent agreement between the graphs for the two sexes indicated that most if not all the females were correctly assigned. Only at high elevations, where both species are depauperate and dark-colored, does the size inequality disappear, leaving only the male characters to be relied upon.

GENERAL OBSERVATIONS. The distinctness of *E. adelphus* from *E. puteanus* was not recognized until rather late in the course of this study, the differences between them having been attributed to individual variation in a single species. The clues that led to their being distinguished came from field observations of which the significance was not realized when they were made. On one occasion a series of over two hundred and sixty adults of "*puteanus*" was collected along oatmeal trails in a rocky stream valley and in outbuildings at Arrowwood Glade in Macon County, North Carolina. It was noted at the time that all those taken in a spring-house were of one sort, described in the field notes as being unusually large and long-legged. As later examination showed, all the spring-house males had narrow pale triangular areas on the sides of the epiproct instead of the usual broader ones. In the woods along the stream males of this kind were found along with others that were smaller and had broad pale areas on the supra-anal plate, and no intermediates were present. Again, a series was taken in 1965 at Granite City in Jackson County, N. C., mostly on the faces of the immense fissured boulders that strew the forested talus slopes; all were of what is now recognized as *adelphus*, and examination of collections previously made at this site by others revealed no specimens of *puteanus* type. These observations suggested that two species were represented in the southern Appalachians, and further study substantiated this conclusion.

DISTRIBUTION. The range of *Euhadenoecus adelphus* lies entirely within the southern Blue Ridge Province of the Appalachian Mountains in Tennessee, North Carolina and northeastern Georgia, where the species occurs at elevations of 1700-5000 ft in the Blue Ridge, Great Smokies, Unakas, and Nantahalas. Limital records are, on the north, Roan Mountain, Tennessee; on the east, Pineola in Avery County and the vicinity of Bat Cave in Henderson and Rutherford counties, North Carolina, and on the south, localities in Rabun County, Georgia (see map, Fig. 9). The western edge of its territory is formed by the mountain front overlooking the Ridge and Valley Province in Tennessee.

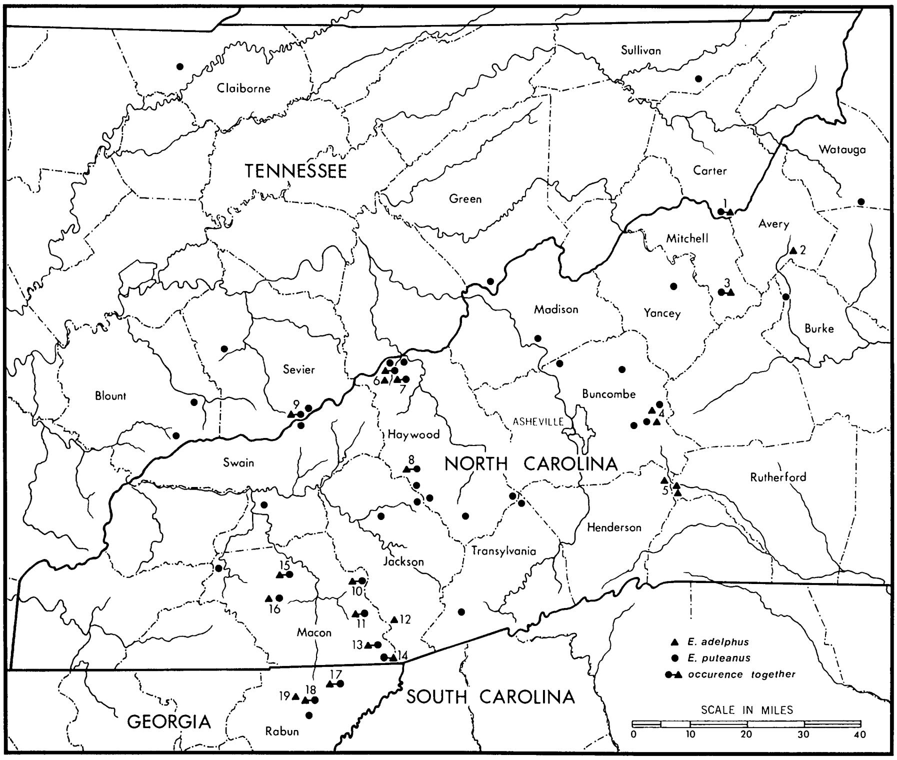

Fig. 9. Distribution of *Euhadenoecus adelphus* and *E. puteanus* in the southern Appalachians. Records of *E. adelphus:* 1–Roan Mountain; 2–Pineola; 3–Spruce Pine; 4–vicinity of Swannanoa; 5–vicinity of Bat Cave; 6–vicinity of Crestmont and Walnut Bottom; 7–Mt Sterling; 8–6 mi W of Waynesville; 9–Newfound Gap; 10–12 mi E of Franklin; 11–Cliff Lake Recreation Area; 12–Granite City; 13–Highlands; 14–7 mi SE of Highlands; 15–Arrowwood Glade; 16–8.9 mi W of Franklin; 17–Rabun Mountain; 18–vicinity of Mountain City; 19–Black Rock Mountain.

HABITAT. Field notes on 17 collections show that *adelphus* occurs in the same types of environment as does *puteanus*—in deciduous or deciduous-coniferous forests that range from mesic to xeromesic, and on mountainsides, talus slopes, at the bases of cliffs, in ravines and along the banks of mountain streams, nearly always where there are rock exposures. Within its range granite and metamorphic rocks prevail, but whether this has any bearing on the absence of *adelphus* from the Ridge and Valley Province, where the ridges are mostly sandstone and *puteanus* is generally distributed, cannot be stated. The two species have been found in association at 13 localities (see map); at nine others only *adelphus* was encountered, and at 25 localities within the range of *adelphus* only *puteanus* was found. Neither species occurred at a number of places in North Carolina where collections were made in deciduous forests on clay soil. Like *puteanus, adelphus* has been taken during the day in shallow caves and cave entrances, in outhouses, and in spring boxes, always in forested surroundings.

SPECIMENS EXAMINED: 391-106♂, 150♀ (type, allotype and paratypes) and 135 juveniles, as follows:

TENNESSEE: *Carter Co.:* Roan Mt summit, 5000 ft, 9 Aug 1922 (H) 1♂, 1♀; *Sevier Co.:* Newfound Gap, ca 5000 ft, Sept 1932 (R. Dury) 1♀ [OSM]. NORTH CAROLINA: *Avery Co.:* Pineola, ca 3500 ft, late July 1945 (D. L. Wray) 1♀ [NCA]; Pineola Fish Hatchery, ca 3500 ft, 3 Sept 1952 (H, C) 5 small juvs; *Buncombe Co.:* High Hickory Mt, 1 mi S of Swannanoa, 2500-3000 ft, 3 Aug-2 Sept 1933 (Ba) 2♂, 3♀; Swannanoa, 3000-4000 ft, 2 Sept 1933 (C. F. Walker) 1♂, 3♀ [OSM]; *Haywood Co.:* Crestmont, on Big Creek, 1700-4500 ft, 23-28 July 1922 (H) 1♂, 10♀; Mt Sterling, slopes, 1900-3000 ft, May, Sept., Oct. 1938 (J) 4♂, 19 juvs [ALA]; Walnut Bottom, ca 3000 ft, 24 June 1938 (J) 1♂, 4 juvs [ALA]; Waynesville, 6 mi W 3500 ft, 6♂, 4♀ [OSM]; *Henderson Co.:* Bat Cave (town), 1400-1500 ft, 8 July 1962 (A) 3♀, 6 juvs; 25 Aug 1971 (L) 1♂, 1♀; *Jackson Co.:* Granite City, at Macon Co. line, ca 2.5 mi E of Highlands, 3000-3200 ft, 3 Sept 1952 (Fr) 16♂, 7♀; 27 Aug 1953 (Pl, Be) 3♂, 2♀ [ST]; 15 Oct 1965 (H) 4♂, 10♀ (including types), 28 juvs; *Macon Co.:* Arrowwood Glade (Trout Rearing Station), 2300 ft, 5 Sept 1952 (H, C) 42♂, 56♀; Cliff Lake Recreation Area, 4.4 mi NW of Highlands, ca 3000 ft, 7 Sept 1952 (H, C) 1♂, 7♀; Franklin, 8.9 mi W, 4000 ft (Fr) 1♂; Highlands, ca 3800 ft, 1 July 1947 (Fr) 10♂, 1♀, 14 juvs; 27 Aug 1953 (Pa, Be) 1♂, 1♀ [ST]; 15 Oct 1957 (C. J. Durden) 1♂, 1♀, 1 juv [CNC]; 7 mi SE, ca 3500 ft, 25 Aug 1950 (Fr) 1♂; Wayside Park, 12 mi E of Franklin, 4000 ft, 5 juvs; *Mitchell Co.:* Spruce Pine, ca 2700 ft, July 1917 (S. G. Gordon) 1♂, 3♀, 3 juvs. [ANSP]; *Rutherford Co.:* below the Bat Caves, nr Henderson Co. line, 1 mi ESE of Bat Cave (town), 1450-1700 ft, 9 Apr 1963 (A) 2 juvs; Blue Rock Mt, Bat Cave, 1500 ft (in shallow cave), 24 Mar, 1964 (C. & P. Allen) 1♀; *Swaine Co.:* [above] Smokemont (Ramey) 3♂, 7♀, juvs. [ALA]. GEORGIA: *Rabun Co.:* Summit Black Rock Mt, 3 mi W of Mountain City, 3500-4000 ft, 28 Aug 1953 (F. N. Young) 1♀; Mountain City, 1.3 mi W, 27-28 June 1956 (T. J. Cohn, P. Kannowski) 1♀, 4 juvs; Rabun Mt, 3500-4000 ft, 15 Oct 1965 (H) 6♂, 20♀, 34 juvs.

EUHADENOECUS FRAGILIS Hubbell, n. sp. (Figs. 2, e; 3, i,j; 4, e; 5, d; 10, 11 (maps); Pl. II, c; Pl. III, c).

Type: Male, Tawneys Cave, Giles Co., Virginia, 24 July 1946 (T. H. Hubbell); *allotype* a female with same data; both preserved in alcohol, in UMMZ.

This species is abundant in caves of the Appalachian Ridge and Valley Province from Bath County, Virginia and Greenbrier County, West Virginia to southeastern Kentucky and northeastern Tennessee. It is most similar to *E. insolitus*, from which it is distinguished by the characters given in the key. The ranges of the two species are widely separated. Both differ from the epigeic members of *Euhadenoecus* in their more delicate build, more slender legs, and paler coloration—modifications associated with their cavernicolous existence.

DESCRIPTION OF MALE TYPE:[1] Length of body ca. 13.8, of pronotum 3.0 (2.7-3.3), of femur I 11.0 (9.0-11.7), of femur III 17.5 (15.0-17.8), of tibia III 20.5 (17.0-21.6), of antenna ca. 95 mm; proximal breadth of femur III 2.1 (1.9-2.3), its distal breadth 0.65 mm.

General coloration of dorsum and legs dilute ochraceous buff; margins of pronotum, caudal edges of meso- and metanotum and abdominal tergites, and a medio-longitudinal dorsal stripe on metanotum and abdomen very faintly darker; cerci and glandular areas on sides of epiproct whitish.

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[1] Parenthesized measurements give the range of variation in the entire series studied.

Head: Fastigium very small, like that of *puteanus,* its ridges highest caudad and sloping evenly to anterior ends, brownish and with a few minute setae. Eyes completely pigmented, slightly prominent, narrow, 1.7 (to 1.9) times as tall as broad; interocular distance 1.6 (1.5-1.8), infraocular distance (to mandibular condyle) 1.7 (1.5-1.8) times height of eye. Maxillary palpus three-fourths (to four-fifths) as long as femur I, its distal segment as long as pronotum.

Thorax: Like that of *puteanus,* except ventral angles of pronotum a little more broadly rounded.

Legs: Relatively longer and more slender than in *puteanus.* Femur I 3.5 (3.4-3.6), femur III 5.6 (5.3-5.9) times as long as pronotum, femur III 7.9 (7.2-8.8) times as long as its proximal breadth; all femora unarmed. Tibia I 1.08 (1.04-1.11) times as long as femur I, tarsus I 0.65 times tibial length, basitarsus I 1.33 (1.2-1.4) times as long as pronotum. Spurs of tibia I, ventrocephalic 5/5, ventrocaudal 6/6; both ventral carinae of tibia II with 5/5 (3-6, mode 5) on both legs. Tibia III (Fig. 4, e) with 6/6 spurs on dorsocephalic carinae, with 5/5 on dorsocaudal (5-8 on both margins, with mode 6 on cephalic, 5-6 on caudal carinae); predistal ventral spurs on cephalic margin 2/2 (nearly invariable), on caudal margin 2/1 (usually 1/1). Spine formulae of dorsal carinae, right and left: cephalic 29/12/14/11/6/3 = 75, 26/13/13/14/7/2 = 75; caudal 37/16/15/11/10 = 89, 33/15/13/12/14 = 87. Dorsocephalic calcar 0.40 (0.36-0.42), dorsocaudal 0.43 (0.39-0.46) times as long as basitarsus III.

Terminal abdominal structures (Figs. 2, e; 5, d; Pl. II, c; Pl. III, c): *Phallus,* as in *insolitus,* with rim of dorsal lobe narrowly sclerotized, its straight sides meeting in a dorsal angulation; remaining structures differing from those of *insolitus* as described in key. In addition the dorsal carina of the paraprocts has its proximal end narrowly furcate, enclosing a short, distally narrowing membranous area which in most individuals appears as a small whitish spot similar to the adjacent whitish glandular areas of the epiproct.

DESCRIPTION OF FEMALE ALLOTYPE: Length of body ca. 15.7, of pronotum 3.3 (3.0-3.5), of femur I 10.2 (9.6-12.6), of femur III 16.7 (15.8-19.2), of tibia III 19.7 (18.8-22.9), of ovipositor 7.7 (7.2-8.9), of antenna ca 95 mm; proximal breadth of femur III 2.3, its subdistal breadth 0.67 mm.

Agrees with male type except as noted. *Legs* relatively shorter and less slender; femur I 3.1 (to 3.6), femur III 5.1 (to 5.6) times as long as pronotum, femur III 7.3 (6.9-8.3) times as long as its proximal breadth; basitarsus I 1.17 (1.13-1.30) times as long as pronotum. Tibia I with 5/5 ventrocephalic, 6/6 ventrocaudal spurs; tibia II with 6/5 ventrocephalic, 5/6 ventrocaudal spurs, variation on both tibiae as in male. Tibia III with 6/5 dorsocephalic, 5/6 dorsocaudal, 2/2 predistal ventrocephalic, 1/1 ventrocaudal spurs, variation as in male; spine formula of dorsal carinae, right and left, cephalic 29/14/13/15/6/3 = 80, 29/18/15/13/12 = 87, caudal 41/20/10/10/10 = 91, 36/9/10/13/11/8 = 87. *Subgenital plate* 2.0 mm broad, 0.9 mm long, its margin paraboloid with weak apical notch. *Ovipositor* (Fig. 3, i,j), 2.3 (2.1-2.9) times as long as pronotum, 0.75 (0.70-0.88) times as long as femur I, 0.46 (0.43-0.56) times as long as femur III; distal fourth of ventral valves with 6 (to 8) rounded, slightly retrorse teeth.

VARIATION. In addition to the variation in size, proportions and leg armature noted above, the following individual and regional differences have been observed. The dorsum may be almost entirely pale, or may be faintly cross-banded by having the hind margins of the tergites dilute brownish, and there may be a fairly well-defined median stripe on the hind part of the thorax and base of the abdomen. The dorsal spines of tibia III range in number from 52 to 95, with the mode about 75 in males, 80 in females. In the Virginia series the female subgenital plate averages slightly longer and more paraboloid than in those from West Virginia, in which it is broader and more evenly arcuate distad, and in the former dried specimens usually show a small apical notch rarely seen in the latter.

DISTRIBUTION AND HABITS. As previously stated, *Euhadenoecus fragilis* occupies caves in the Appalachian Ridge and Valley Province (see maps, Figs. 10, 11). Divides between the major river systems do not constitute barriers to its dispersal. In the New River drainage it inhabits caves in the valleys of the Greenbrier River and Indian Creek in West Virginia and those of Sinking Creek and Wolf Creek in Virginia. Northward in the latter state it reaches the headwater areas of the James and Roanoke rivers, and southwestward it is present in areas drained by the Kentucky, Cumberland, Powell and Holston rivers. This probably means that the species is not restricted to large caves, but can exist wherever there are rock crevices and talus cavities in which it can take shelter, making it possible for it to move between major cave systems. *E. fragilis* has, in fact, been found away from the immediate vicinity of known caves—once at the base of cliffs near Hot Springs in Bath County, and again at two places on the opposite side of Sinking Creek from Tawney's Cave in Giles County, Virginia, where it was taken at molasses bait painted on tree-trunks and in malt traps set among large rocks.

Nevertheless the species has the pale coloration and attenuate legs associated with cavernicolous life, and is evidently well adapted to the cave environment. In numerous caves it has been collected in the region of total darkness, far beyond the twilight zone, and in Tawney's Cave, the type locality, it is present throughout the cave though most abundant in the entrance chamber. It is probably on its way to becoming an obligate trogloxene like the members of the genus *Hadenoecus*,

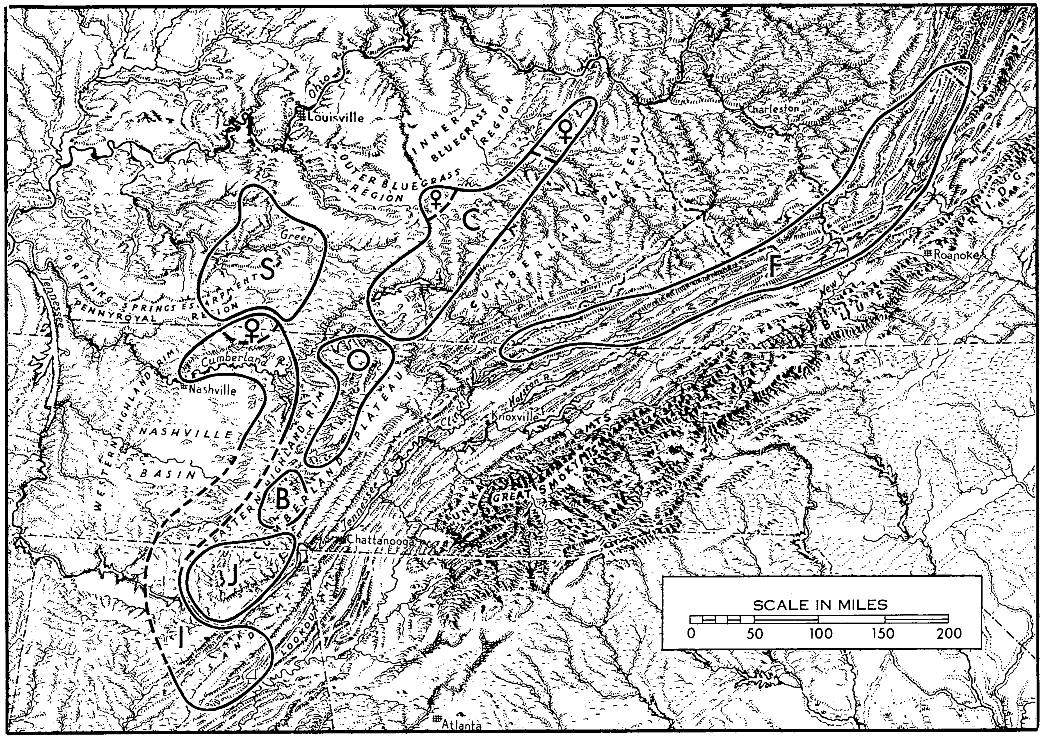

Fig. 10. Distribution of the cavernicolous species of *Euhadenoecus* and *Hadenoecus*. F—*Euhadenoecus fragilis;* I—*Euhadenoecus insolitus* (parthenogenetic populations in area marked ♀); C—*Hadenoecus cumberlandicus* (parthenogenetic populations in areas marked ♀); S—*Hadenoecus subterraneus;* O—*Hadenoecus opilionoides;* B—*Hadenoecus barri;* J—*Hadenoecus jonesi.* (Shown on "Landform Map" by Erwin Raisz).

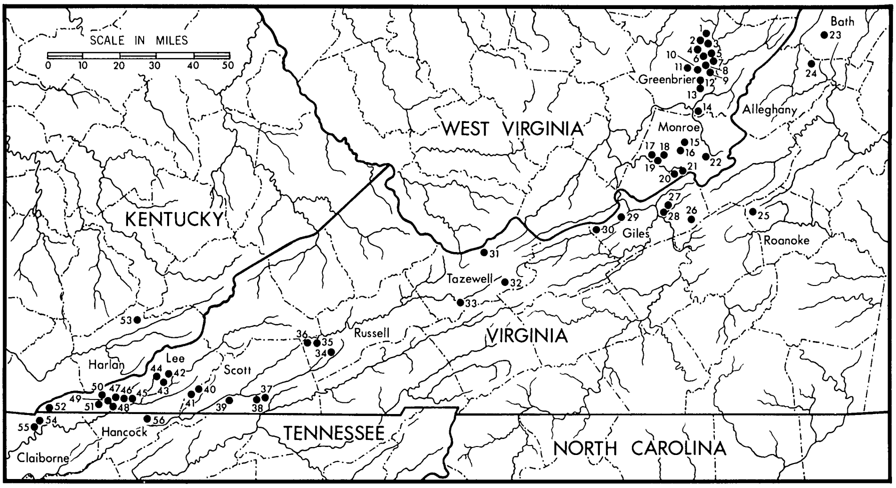

Fig. 11. Distribution of caves with populations of *Euhadenoecus fragilis.* Names of numbered caves are as follows: 1—Reinhold Cave; 2—Rapps Cave; 3—Buckeye Creek Cave; 4—Hinkles Unus Cave; 5—Higginbotham Caves; 6—Coffman Cave; 7—The Hole; 8—Arbuckle Cave; 9—Benedict Cave; 10—Ludington Cave; 11—McClung Cave; 12—Grapevine Cave; 13—Court Street Cave; 14—Indian Cave; 15—Union Cave; 16—Steeles Cave; 17—Greenville Saltpeter Cave; 18—Laurel Creek Cave; 19—Cross Road Cave; 20—Rock Camp Cave; 21—McClung-Zenith Cave; 22—Patton Cave; 23—Hot Springs; 24—Wares Cave; 25—Millers Cove Cave; 26—Tawneys Cave (type locality); 27—Smokehole Cave; 28—Links Cave; 29—Ballards Cave; 30—Starnes Cave; 31—Wagoners Cave; 32—Cassell Farm Cave; 33—Glenwood Church Cave; 34—Seven Springs Cave; 35—Banners Corner Cave; 36—Indian Cave; 37—Coley Cave #1; 38—Coley Cave #2; 39—Speers Ferry Cave; 40—Blowing Hole Cave; 41—Hortons Cave; 42—Gilley Cave; 43—Pennington Gap caves; 44—Cattle Cave; 45—Unthanks Cave; 46—Gibson-Fraser Cave; 47—Thompson Cedar Cave; 48—Smiths Milk Cave; 49—Sweet Potato Cave; 50—Spangler Cave; 51—Young-Fugate Cave; 52—Indian Cave; 53—Saw Mill Hollow Cave; 54—English Cave; 55—Bug Hole Cave #1; 56—Newmans Ridge cave, approximate location.

and like them is known to emerge from the caves at night to forage. Judging from the shortness of the ovipositor and its relatively strong teeth *E. fragilis* probably oviposits in sandy soil rather than in the mud of cave floors.

SPECIMENS EXAMINED: 780—161 ♂, 234 ♀ (type, allotype and paratypes) and 385 juveniles, as follows:

VIRGINIA:[1] *Alleghany Co.:* Wares Cave (D: 85; H: 45), 21 July 1962 (Ho) 1♂; *Bath Co.:* Hot Springs, 2400-2600 ft, 20 Aug 1916 (He) 1♂, 1♀ [ANSP]; *Giles Co.:* Ballards Cave (D: 227; H: 87), 29 June 1974 (Ho) 3 juvs; Links Cave (D: 238; H: 95), 10 July 1973 (Me) 3 juvs; Smokehole Cave on Sinking Creek (D: 242), 29 July 1962 (Ho) 2♂, 1♀, 1 juv [H]; Starnes Cave (D: 223), 19 May 1974 (Ho) 3 juvs [H]; Tawneys Cave on Sinking Creek (D: 244; H: 103; NSS Guidebook 1971: 91, 101), 10 July and 9 Aug 1935 (H. H. Hobbs, Be) 13♂, 23♀; 8-21 Aug 1945 (H) 6♂, 6♀, 91 juvs; 24-30 June 1946 (J. S. Rogers, W) 2♂, 4♀, 2 juvs; 24 July 1946 (H) 4♂, 5♀ (including types), 20 juvs; 24 June 1959 (D. C. Eades) 1♂, 6♀, 19 juvs; 3 Aug 1959 (R. Emmons) 2♂, 1♀; 25 July 1973 (Me) 1♂, 7♀; Limestone cliffs and talus across Sinking Creek from Tawneys Cave, 9-21 Aug 1945 (H) 4♂, 5♀, 10 juvs; O. B. Williams Cave, 10 July 1973 (Me) 7♂, 6♀, 1 juv; *Lee Co.:*[2] Cattle Cave (D: 298; H: 121), 31 July 1974 (Ho, C) 1♂,

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[1] Nearly all of the caves here listed are located and described by Douglas (1964) or Holsinger (1975), to which page references are given, e.g. (D: 85) or (H: 45), following the names.

[2] T. Barr observed what was undoubtedly *fragilis* in Ewing (=Jones) Saltpeter Cave, Lee Co., 5 July 1957).

4♀, 1 juv [H]; Cliff Cave (H: 124), 24 Nov. 1966 (D. Pinley, N) 1♂, 5♀ [H]; Ely Cave near Pennington Gap (Shaler 1885; D: 294), Aug 1875 (W. Faxon) 8♂, 10♀, 11 juvs [ANSP]; Gibson-Frasier Cave (D: 312; H: 158), 30 July 1967 (Ho) 2♀, 4 juvs [H]; Gilley Cave (D: 291; H: 138), 1 mi S of Pennington Gap, 26 June 1963 (Ho) 1 juv; Indian Cave in Lewis Hollow, Cumberland Gap Nat'l Park (D: 319; H: 144), 19 Aug 1962 (Ho) 2♂ [H]; Kinzer Hollow Cave (D: 312; H: 148), 1 Aug 1967 (Ho) 1♀, 2 juvs [H]; Molly Wagle Cave, 1.2 mi SW of Jonesville (H: 155), 8 Apr 1974 (Ho) 1♂, 6 juvs [H]; Pennington Gap, in 2 small caves, 25 June 1879, 1♂, 1♀ [USNM]; Roadside Cave #1 (H: 159), 31 July 1974 (Ho, C), 4♂, 3♀ [H]; Smiths Milk Cave (H: 164), 6 mi SE of Rose Hill near Powell River, 17 Aug 1962 (Ho, C) 2♂, 1 juv [H]; 31 July 1974 (Ho) 2♂, 6♀ [H]; Spangler Cave (D: 312; H: 165), 8 Apr 1974 (Ho) 2 juvs [H]; Sweet Potato Cave (D: 310), 8 Apr 1974 (Ho) 3♀, 3 juvs [H]; Thompson Cedar Cave (D: 310; H: 169), 9 Apr 1974 (Ho, Di) 2♂, 1♀, 1 juv [H]; Unthanks Cave (D: 320; H: 175), 9 Apr 1974 (Ho, Di) 7 juvs [H]; Young-Fugate Cave (D: 320; H: 175), 25 June 1963 (Ho) 1♂, 1♀ [H]; *Roanoke Co:* Millers Cove Cave (D: 364, H: 200), 8 mi NW of Salem [not seen, record from Ho; H]; *Russell Co.:* Banners Corner Cave (D: 439; H: 229), 29 Feb 1963 (P) 1♂; Indian Cave (D: 428; H: 245), 29 Aug 1974 (Ho, C) 2♂, 5♀, 1 juv [H]; Seven Springs Cave (D: 442), 13 July 1961 (Ho) 1♂ [H]; *Scott Co.:* Blowing Hole Cave (D: 448), 10 mi W of Clinchport, 22 Apr 1962 (Ho) 2♂, 2 juvs [H]; Coley Caves #1,2 (D: 459; H: 275), 3 June 1967 (Ho) 6 juvs [H]; Hortons Cave (H: 289), 10 mi W of Clinchport, 16 Aug 1962 (Ho) 1♂ [H]; Speers Ferry Cave (H: 313), 8 July 1963 (A) 2 juvs; 27 Mar 1964 (C. & P. Allen) 2♂, 2 juvs; *Tazewell Co.:* Cassell Farm Cave (D: 528; H: 346), 3 July 1937 (D) 1♂ [ANSP]; 12 Apr 1963 (Ho) 3 juvs [H]; Glenwood Church Cave (D: 520; H: 352), 5 Apr 1961 (R. E. Graham) 1♂, 1♀, 4 juvs; Lawson Cave (H: 358), 3 July 1937 (D) 2♂, 2 juvs [D. ANSP]; Spider Cave (H: 362), 6 mi S of Pounding Hill, 27 July 1974 (Ho, C) 5♂, 2♀ [H]; Wagoners Cave (D: 514; H: 364), 19 Aug 1967 (Ho, C) 10 juvs. WEST VIRGINIA:[1] *Greenbrier Co.:* Arbuckle Cave (Da: 75), 1 Oct. 1932 (R) 3♂, 3 juvs [USNM, UMMZ]; 4 July 1937 (D) 3♀, 4 juvs [ANSP]; 22 Sept 1950 (J) 1♂, 14♀, 11 juvs [ALA]; 11 Apr 1957 (D. F. Black, B) 6♂, 1♀, 2 juvs [B]; Benedict Cave, 1.5 mi SE of Maxwelton (Ru) 2♂, 4 juvs [WVAC]; Buckeye Creek Cave (Da: 79), 18 Aug 1963 (Ho) 1♂ [H]; Coffman Cave (Da: 81), 24 June 1932 (R) 1♀ [USNM]; 9 May 1964 (Ho) 3♂, 5♀, 3 juvs [H]; Court Street Cave (Da: 84), 12 July 1969 (M, Ca) 3♂, 2♀; Grapevine Cave (Da: 91), 28 Aug 1967 (Ho) 2♂, 2 juvs [H]; Higginbothams Caves (Da: 95-98), 4 July 1937 (D) 2♂, 7♀, 5 juvs [D, ANSP]; 12 July 1969 (M, Ca) 1♂, 3♀; 10 July 1973 (Me) 3♂, 15♀, 4 juvs; Hinkles Unus Cave (Da: 99), 17-18 Aug 1963 (Ho) 1♀, 4 juvs [H]; Indian Cave, ca 3 mi S of Ronceverte (Ru) 1♂ [WVAC]; Ludington Cave (Da: 106), 12 May 1962 (Ho) 1♂ [H]; McClung Cave (Da: 107) 1 Oct 1932 (R) 2♂, 1♀, 1 juv [USNM]; 8 July 1961 (Ho) 1♂, 1♀ [USNM]; 10 July 1973 (Me) 1♂, 4♀, 1 juv; Rapps Cave (Da: 124), Oct 1932 (R) 1♂ [USNM]; 13 May 1962 (Ho) 3♂, 2 juvs [H]; Reynold Cave (Reinhold Cave?, Da: 126), 26 Aug 1967 (C. Maus, Ho) 3♂, 1♀, 2 juvs [H]; Snedegar-Crookshank Cave System (Da: 290 and Suppl: 57), 23 Nov 1962 (Ho) 1♂, 1♀, 2 juvs [H]; The Hole, ca 1 mi SE of Frankford (Lewis Hole?, Da: 105), (Ru) 1♂, 1♀, 6 juvs [WVAC]; *Mercer Co.:* Ingleside Cave (Da: 157), 21 Sept 1950 (J, V) 4♀, 5 juvs [ALA]; *Monroe Co.:* Cross Road Cave (Da: 171), 1 Sept 1967 (Ho) 1♂, 1♀, 2 juvs [H]; Greenville Saltpeter Cave (Da: 175), 26 Apr 1932 (R) 6 juvs; 21 Sept 1950 (J, V) 1♂, 11♀, 19 juvs [ASM]; Hunt Cave (Da: Suppl: 34), (Ru) 1♀, 3 juvs [WVAC]; Laurel Creek Cave (Da: 183), 22 Sept 1950 (J, V) 3♀, 4 juvs [ALA]; McClung-Zenith Cave (Da: 191), 31 Aug 1967 (Ho) 1♂, 3♀, 2 juvs [H]; Patton Cave (Da: 194), 28 June 1974 (Ho) 2♂ [H]; Rock Camp Cave (Da: 197), 1 July 1968 (B, Ca) 1♂, 1♀, 2 juvs [B]; Steeles Cave (Da: 198), 4 July 1937 (D) 3♂, 9♀, 9 juvs [ANSP]; Union Cave (NSS Bull.19: 32), 27 Apr 1932 (R) 1♂, 2♀, 4 juvs [USNM, UMMZ]; *Pocahontas Co.:* Blue Springs Cave (Da: 260), 2 Sept 1967 (L. Baroody, Ho) 1♂, 4 juvs [H]; Hughes Creek Cave (Da: 273), 18 May 1974 (Ho, C, Di) 5 juvs [H]; Overholt Blowing Cave (Da: 278), 2 Sept 1932 (R) 2♀, 2 juvs; Overholt Saltpeter Cave (Da: 281), 22 Sept 1932 (R) 1♀, 2 juvs; Steam Cave (Da: Suppl: 58), 2 July 1963 (Ho) 2 juvs [H]; *Randolph Co.:* Simmons-Mingo Cave (Da: 312), 28 Aug 1931 (R) 4♀. KENTUCKY: *Harlan Co.:* Cave in Pine Mountain, 700 m elev, 19 July 1946 (W. L. & C. K. Necker) 20♂, 10♀, 4 juvs [FMNH, UMMZ]; Saw Mill Hollow Cave, near town of Pine Mountain, 18 Apr 1975 (J. P. Rogers) 1♂, 3 juvs [B]. TENNESSEE: *Claiborne Co.:* Bug Hole Cave #1, 1 mi WSW of Arthur, 2 Aug 1964 (Ho) 1♂, 2♀, 4 juvs [H]; English Cave, in Harrogate, 3 mi S of Cumberland Gap, 2 July 1937 (D) 1 juv [D]; *Hancock Co.:* Newmans Ridge Cave, 17 Aug 1963 (L. G. K. Carr) 2♀; Sinks Cave, 18 Aug 1963 (L. G. K. Carr) 1♂, 1♀, 1 juv (Both caves near Sneedsville).

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[1] Most of the caves listed are located and described in Davies (1965), page references to which, e.g. (Da: 75), follow the cave names.

References in Literature

Rhaphidophora sp.: Hubbard 1880: 34 (caves near Pennington Gap, Lee Co., Va.).

Hadenoecus cavernarum, not of Saussure 1862: Scudder 1894: 22-3 (Ely Cave and ? Turners Caves, Lee Co., Va.).

Hadenoecus subterraneus, not of Scudder 1861: Fowler 1941: 45 (Cochrans Cave [probably Clyde Cochran Sink Cave], Pocahontas Co., W. Va.).

Hadenoecus sp.: Tucker 1963: 199; 1965: 51 (Dead Horse Cave, Mercer Co., W. Va. [probably *fragilis,* possibly *puteanus*]; Holsinger 1971: 18 (caves of the Greater Blacksburg area); Holsinger, Baroody & Culver 1976: 40-1 (W.Va. caves; troglophile; populations usually smaller than those of *Hadenoecus subterraneus* in Ky. caves).

Hadenoecus n. sp.: Holsinger 1964: 65 (caves of Virginia and West Virginia; found to great distances from entrances; better adapted to subterranean life than *puteanus*).

Cave-crickets: Fischer 1945: 70 (abundant in Smoke Hole Cave, Giles Co., Va., in steeply inclined passage leading to stream, a drop of about 120 ft); Sollens 1963: 16 (in Cricket Cave, Greenbrier Co., W. Va.).

EUHADENOECUS INSOLITUS[1] Hubbell, n. sp. (Figs. 2, f,g; 3, g,h; 4, a,f; 5, e; 10, 17, 18 (maps); Pl. II, d; Pl. III, d).

Type: Male, McCluney Caverns, Jefferson Co., Alabama, 16 Sept. 1965 (S. Peck); *allotype* a female with the same data; both preserved in alcohol, in UMMZ.

This species occupies caves in northeastern Alabama, central Tennessee and adjoining south-central Kentucky, in territory that lies to the west and south of that occupied by species of *Hadenoecus.* It is very similar to *fragilis,* from which it differs in the form of the male epiproct and paraprocts as described in the key, and by having legs that average less slender and shorter relative to the pronotal length (Table 2 and Fig. 4, a). In at least some of the caves in the northernmost part of its range the species is parthenogenetic.

DESCRIPTION OF MALE TYPE:[2] Length of body ca. 13, of pronotum 3.9 (3.2-4.6), femur I 11.4 (10-16.2), of femur III 20.0 (16.5-25.2), of tibia III 22.5 (19.7-32.0), of antenna ca. 90 mm; proximal breadth of femur III 3.1 (2.3-3.2), distal breadth 0.80 mm. (Size averaging slightly larger than in *fragilis;* see Table 2.) Dorsum, femora and basal parts of tibiae dilute ochraceous buff with scarcely a trace of darker markings, rest of body paler.

Head: Fastigium verticis very small, in side view somewhat shorter and higher than in *fragilis,* with strongly rounded apices at midlength of ridges, apices faintly brownish. Eyes as in *fragilis;* interocular distance 1.6 (to 1.4), infraocular distance (to anterior mandibular condyle) 1.6 (1.4-1.8) times as long as length of eye. Maxillary palpus 0.9 (to 0.7) times as long as femur I, its distal segment 0.9 (to 1.05) times as long as pronotum.

Thorax: Like those of *puteanus* and *fragilis,* except ventral margin more oblique in side view and ventrocephalic and ventrocaudal angles

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[1] L. *insolitus,* strange, unusual.

[2] Figures in parentheses give the range of variation in the series studied.

more broadly rounded; broadest and deepest at caudal fourth, breadth 1.1, depth 0.67 times dorsal length.

Legs: Longer relative to pronotal length than in *puteanus,* shorter and less slender than in *fragilis.* Femur I 3.0 (2.6-3.6), femur III 5.2 (4.6-5.6) times as long as pronotum, femur III 6.4 (6.1-8.0) times as long as maximum breadth; all femora unarmed. Tibia I 1.1 (1.0-1.2) times as long as femur I; tarsus I 0.72 (0.68-0.75) times as long as tibia, its basitarsus 1.24 (1.1-1.5) times as long as pronotum; armed with 5/6 ventral spurs on cephalic, 5/5 on caudal carinae (on both range 4-7, mode strongly 5). Tibia III with 6/7 dorsocephalic, 5/6 dorsocaudal spurs (4-7, mode 6 on both margins; number of dorsocaudal spurs varying geographically as noted below); ventral face, in addition to the ventral calcars, with 2/2 (rarely 3) predistal spurs on cephalic margin and 0/0 on caudal margin. Spine formulae of dorsal carinae of tibia III, right and left: cephalic 40/17/14/9/0/0 = 80, 38/17/10/8/5/6/0 = 84; caudal 43/13/14/8/5 = 83, 46/14/8/12/8/0 = 88. Dorsocephalic calcar 0.43 (0.39-0.47), dorsocaudal 0.50 (0.45-0.53) times as long as basitarsus III. Tarsus III 0.37 (0.34-0.41) times as long as tibia III, basitarsus 1.11 (0.97-1.32) times as long as pronotum.

Terminal abdominal structures (Figs. 2, f,g; 5, e; Pl. II, d; Pl. III, d): Cerci pale, 1.5 (to 1.2) times as long as pronotum. Epiproct and paraprocts differing from those of *fragilis* as described in key and in description of latter species. Paraprocts of type entirely pale, with apices strongly tumid and divaricate, as is typical of Alabama and most Tennessee material (see discussion of variation below).

DESCRIPTION OF FEMALE ALLOTYPE: Length of body ca 17, of pronotum 4.0 (3.1-4.2), of femur I 12.0 (10.2-12.4), of femur III 19.9 (16.1-20.0), of tibia III 23.7 (20.4-25.3), of ovipositor 9.2 (7.7-10.6) mm; proximal breadth of femur III 3.2 (2.1-3.3), subdistal breadth 0.86 mm.

Almost indistinguishable from female of *fragilis* except for larger average size and relatively shorter, less slender legs. Agrees with male except as noted. *Legs:* Femur I 3.0 (2.8-3.6), femur III 5.0 (to 5.5), basitarsus I 1.19 (1.17-1.48), basitarsus III 1.09 (1.07-1.34) times as long as pronotum, femur III 6.4 (6.1-7.7) times as long as maximum breadth. Tibia III with 5/6 spurs on cephalic and 5/5 on caudal carinae; spine formulae of dorsal carinae, right and left: cephalic 37/18/11/9/8 = 83, 37/15/15/10/1/0 = 78; caudal 42/15/9/12/6 = 84, 48/11/9/13/5 = 86. *Subgenital plate* 2.2 mm broad, 1.1 mm long, distal margin paraboloid, apex rounded subtruncate. *Ovipositor* (Fig. 3, g,h) 2.3 (2.1-2.9) times as long as pronotum, 0.76 (0.72-0.88) times as long as femur I, 0.46 (0.44-0.58) times as long as femur III, distal third of ventral margin of ventral valves with 7 (6-8, mode strongly 7) rounded, slightly retrorse teeth like those of *fragilis.*

VARIATION. The dorsal coloration in most series is like that of the types, almost uniform dilute ochraceous buff, but specimens from some Tennessee caves are somewhat darker, dilute ochraceous tawny or Prout's brown. None, however, have the faint pattern of brownish bands and pronotal markings sometimes present in *fragilis*. The denticles on the dorsal carinae of tibia III number 62 to 104 with a mode of about 84 in both sexes—about the same as in *fragilis*. In most series the number of dorsal spurs on that tibia ranges from 5 to 7, mode 6, but in the parthenogenic females from two Kentucky caves there is a tendency toward reduction in their number and irregularity in their spacing, the range being 3 to 6, mode 5, and 3 or 4 common. The male paraprocts have pale, strongly divaricate apices in all the Alabama series and most of those from Tennessee, but in those from Indian Grave Point, Tenpenny and Bull Run caves in northern Tennessee the tips are rounded, subattingent and often slightly darkened. In the Alabama series the glandular areas at the sides of the male supra-anal plate are usually rather distinct and moderately large, but in those from northern Tennessee these areas are generally small and inconspicuous and sometimes scarcely distinguishable.

DISTRIBUTION. This species occupies caves in the Highland Rim sections of southernmost Kentucky, northcentral Tennessee and northeastern Alabama (maps, Figs. 10, 17, 18). The ranges of *E. insolitus* and *E. fragilis* are separated by the full width of the Cumberland and Pennyroyal plateaus, which are occupied exclusively by the species of *Hadenoecus*. In Alabama, where much collecting has been done, *insolitus* with a single exception has been found only in caves south of the Tennessee River, where *H. jonesi* is not present. North of the river, so far as known, only the latter species now occurs. In 1938, however, W. B. Jones collected a small series of *insolitus* in Jackson Cave on the north bank of the Tennessee in Marshall County, a cave later submerged following the construction of the Guntersville Dam. The species is also known from 14 caves north and east of the Nashville Basin and on both sides of the Cumberland River in Tennessee and Kentucky. The considerable gap between these and the Alabama records may be attributable to lack of collecting in the intervening region, but no hadenoecines were found by L. E. Matthews and associates in five caves in the Highland Rim sections of Bedford, Coffee and Moore counties, Tennessee, where they were sought.

PARTHENOGENETIC POPULATIONS. In the three northernmost caves in which *E. insolitus* has been found only females are present. Barr collected 14 females and no males in Cole Cave, Barren Co., Kentucky and saw no males among the many individuals observed. The series at hand from Grandmother Cave in Allen Co., Kentucky, contains 64 females and no males, and Lamb and Willey (1975) reported that 345 females and no males were collected there. They also recorded 44 females and no males from Aunt Beck Simmons Cave in Macon Co., Tennessee. It is noteworthy that the last-named cave is only about three miles distant from Anne White Cave in Macon County and about eight miles from Mason Cave in Sumner County, Tennessee, in both of which sexual populations occur. This situation is remarkably similar to that in *H. cumberlandicus;* in both species only a few populations in the northernmost parts of their respective ranges are parthenogenetic.

SPECIMENS EXAMINED: 408—77♂, 118♀ (type, allotype and paratypes) and 213 juveniles, as follows:

Sexual Populations

TENNESSEE:[1] *Cannon Co.:* Tenpenny Cave (B: 103), 9 Aug 1965 (P, F) 2♂, 2♀, 11 juvs; *Davidson Co.:* Bull Run Cave (B: 145), 22 June 1957 (B) 1♂, 2 juvs [B] ; 4 Aug 1968 (B) 7♂, 5 juv ♀ [B] ; *DeKalb Co.:* Avant Cave (Lindsey Williams Cave) (B: 156), 17 Oct 1948 (J) 9♂, 9♀, 2 juvs [ALA] ; Cathcart Cave (=? Cripps Mill Cave, B: 159), 17 Oct 1948 (J) 4♀ [ALA] ; Indian Grave Point Cave (B: 165), 19 Apr 1975 (Ma) 3♂, 3♀; *Jackson Co.:* Carter Cave (B: 272), 21 Sept 1968 (Co) 1♂, 1♀, 3 juvs; Pilot Knob Cave, 36° 28′ 00″ N, 85° 43′ 08″ W, 6 Sept 1975 (Ma) 3♂, 4♀; *Macon Co.:* Ann White Cave (B: 293), 6 Jan 1966 (B) 1♂, 3 juvs [B] ; *Putnam Co.:*[2] Ament Cave, PU-1, 36° 08′ 42″ N, 85° 29′ 24″ W (Ne) 1 juv ♂; *Smith Co.:*[3] Neil Fisher Cave (Rip Van Winkle Cave) (B: 423), 18 Oct 1948 (J) 4♂, 9♀, 4 juvs [ALA] ; Petty Bluff Cave #1, 36° 17′ 50″ N, 86° 00′ 00″ W, 14 Sept 1975 (Ma) 4♂, 2♀; *Sumner Co.:* Mason Cave (B: 442), 25 Mar 1949 (J) 1♂, 1♀, 5 juvs [ALA] ; *Trousdale Co.:* Alan Duncan Cave #1, 36° 20′ 58″ N, 86° 07′ 49″ W, 29 Nov 1975 (Ma) 3♂, 3♀; *Wilson Co.:* Hayes Cave (B: 525), 25 Mar 1949 (J) 2 juvs [ALA]. ALABAMA:[4] *DeKalb Co.:* Bartlett Cave (AL 251), 12 Aug 1955 (J) 1♂ [ALA] ; *Jefferson Co.:* Cedar Pole Cave (AL 705), 10 Sept 1965 (P) 6♂; McCluney Cave (Crystal Cave, Alabama Caverns) (AL 17), 18 Sept 1937 (J) 2♂, 54 juvs [ALA] ; 12 July 1951 (J, V) 5♂, 5♀, 34 juvs [ALA] ; 16 Sept 1965 (P) 8♂, 6♀ (including the types), 2 juvs; *Marshall Co.:* Jackson Cave (Fort Deposit Cave; now submerged) (AL 33), 11 June 1938 (J) 2♀, 3 juvs [ALA] ; Terrill Cave #1 (AL 32), 11 June 1938 (J) 2♂, 2♀, 26 juvs [ALA] ; 2 Sept 1968 (P) 3♂, 12 juvs; Town Creek Cave (AL 40), 8 Jan 1939 (J) 11♂, 18♀, 13 juvs [ALA, UMMZ] ; *St. Clair Co.:* McGlendon Cave (AL 56), 27 Sept 1937 (J) 7 juvs [ALA].

Parthenogenetic Populations

KENTUCKY: Locality? [presumed parthenogenetic] (K. Knight) 1♀ [INHS] ; *Allen Co.:* Grandmother Cave, 1.3 mi SSE of Petroleum, 25 Sept 1949 (J, V) 36♀, 5 juv ♀ [ALA] ; 21 July 1963 (B) 5♀, 18 juv ♀; 2 Oct 1972 (L) [345♀, no males seen or collected] ; *Barren Co.:* Cole Cave, 2 Dec 1966 (N, B, M) 5♀, 9 juv ♀ (no males seen or collected). TENNESSEE: *Macon Co.:* Aunt Beck Simmons Cave (B: 294) [record from Lamb and Wiley (1975: 721—44♀, no males seen or collected)].

References in Literature

Hadenoecus puteanus, not of Scudder 1877: Barr (1961: 40) (Central Basin, Tenn.).

Hadenoecus sp. *B:* Lamb and Willey (1975: 721-2) (parthenogenetic in Grandmother Cave, Ky., and Aunt Beck Simmons Cave, Tenn.; bisexual in Ann White Cave, Tenn.).

Hadenoecus insolitus Hubbell MS: Lamb (unpublished thesis, University of Illinois, Chicago, 1975) (Chromosomes; cytology of embryogenesis).

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[1] The citations following most of the cave names, e.g. (B: 103), are page references to Barr (1961), in which the caves are described and located.

[2] In field notes T. C. Barr recorded the presence of *Ceuthophilus* and *Hadenoecus* sp. (almost certainly *insolitus*) on 20 July 1957 in Jared Hollow Cave, 3.4 mi NE of Chestnut Mound, Putnam County; this cave is in Ordovician limestone at the Central Basin level.

[3] On 5 Jan 1957 T. C. Barr observed a few *Hadenoecus* (almost certainly *insolitus*) in Piper Cave (B: 424) in Smith County.

[4] The references following the cave names, e.g. AL 251, are the Alabama Cave Survey numbers, under which the caves are listed and described by Varnedoe (1973).

HADENOECUS Scudder

Hadenoecus Scudder 1862: 439; *Hadenoecus* pars: Scudder 1869: 47; Walker 1869: 200; 1871: 22; Bolivar 1880: 71, 72; Brunner 1888: 257, 310; Scudder 1894: 20, 22; Kirby 1906: 135; Caudell 1916: 656, 659; Blatchley 1920: 607, 608; Karny 1929a: 168, map 6; 1929b: 58; Chopard 1931: 390-94, figs.; Karny 1934: 70, 71; Hubbell 1936: 29, 30; Karny 1937: 258, 260; Ander 1939: 19 et passim; Beier 1955: 245; Leroy 1967: 664 et passim.

Type species: *Rhaphidophora subterranea* Scudder, by monotypy.

Hadenoecus includes five species, all cavernicoles, pale in color and without distinct markings. They have the aspect of *Dolichopoda*, with extremely long, slender legs, antennae and maxillary palpi. The type species, *subterraneus*, is restricted to the caves of the Pennyroyal Plateau in south-central Kentucky, of which Mammoth Cave is the best known. The other four species, all new, occur in sequence from north to south along the western edge of the Cumberland Plateau and adjoining parts of the Eastern Highland Rim—*cumberlandicus* in eastern Kentucky, *opilionoides* in north central and *barri* in central Tennessee, and *jonesi* in southernmost Tennessee and northeastern Alabama north of the Tennessee River.

GENERAL FEATURES: Size larger than in *Euhadenoecus*, length of femur I rarely less than 13 mm, of femur III rarely less than 20 mm, of ovipositor rarely less than 11 mm. Appendages longer relative to pronotal length than in *Euhadenoecus* (see Table 2). Femora II and III usually with a minute caudogenicular spinule. Denticles of dorsal carinae of tibia III (Fig. 12, b-d) less crowded and overlapping than in *Euhadenoecus*, those at base of series very small and well separated, their size increasing and both size and spacing more irregular distad; denticles usually absent from one or more of the predistal inter-spur intervals; predistal ventral spurs of tibia III 1-6, usually 2 or more on cephalic margin, 1-5, usually 1 or 2 on caudal margin.

MALE CHARACTERS. A pair of slit-like openings with sclerotized lips in membrane between 9th and 10th abdominal tergites, cephalad of cercal bases, from which are extruded during copulation a pair of long, tubular, translucent *eversible organs* (Pl. I; Fig. 5, j), that curve around to enclose the end of the female's abdomen just in front of the cercal bases.[1] *Epiproct* without proximo-lateral membranous glandular areas.

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[1] From his observations on copulation in *H. subterraneus* and *H. cumberlandicus* Norton reports that these organs function as claspers (see Part III). Similar membranous, glandular, but shorter and pyriform organs, protruded from between the 1st and 2nd abdominal tergites in *Tachycines*, and from between the 5th, 6th and 7th in *Troglophilus*, are identified as pheromone attractant glands by Chopard (1938) and Leroy (1967). The corresponding structures in *Hadenoecus* have been given the same interpretation by those authors, by me, and as long ago as 1891 by Garman and 1895 by Packard.

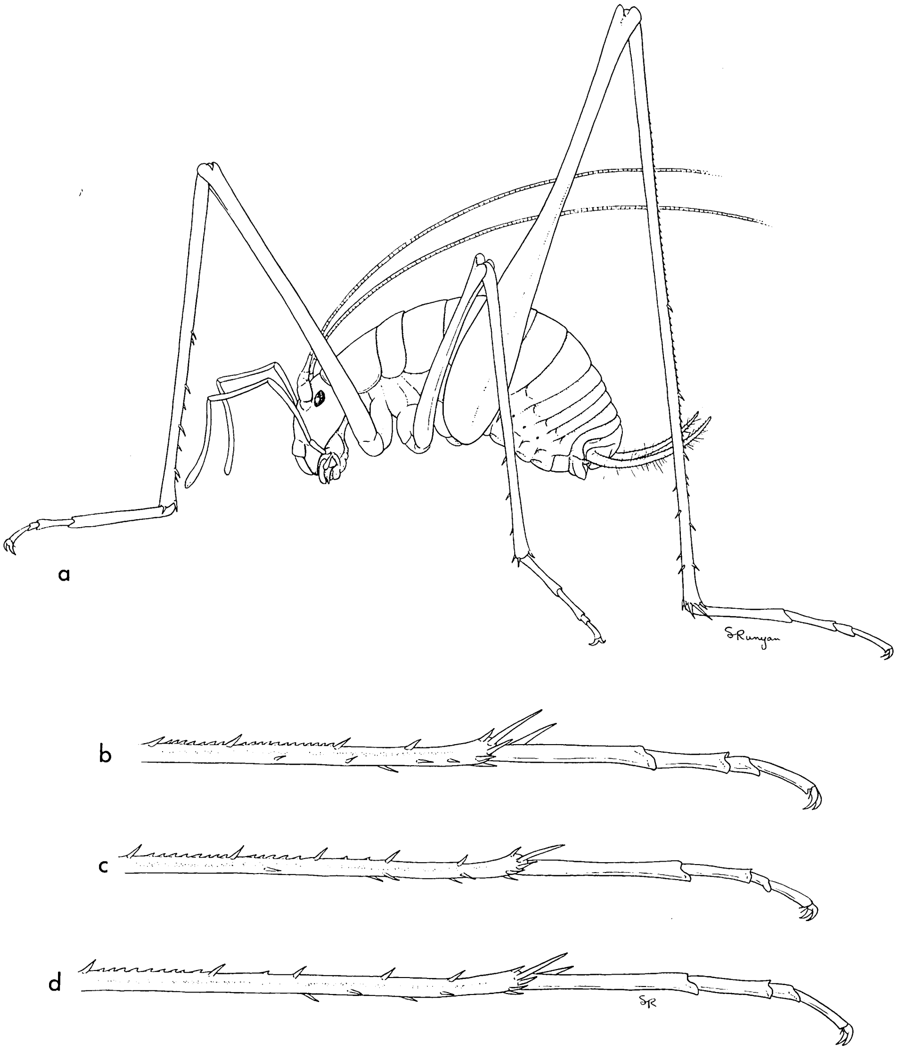

Fig. 12. *Hadenoecus o. opilionoides* and tibia III of *Hadenoecus* species. a–*H. o. opilionoides* ♂, paratopotype, side view, from small cave in Buffalo Cove, Fentress Co, Tenn. b-d–distal ends of tibia III: b–*subterraneus* ♂, New Discovery Cave, Edmonson Co, Ky.; c–*jonesi* ♂, Gary Self Pit (Cave Stand Cave), Jackson Co, Ala.; d–*o. opilionoides* ♂, small cave in Buffalo Cove, Fentress Co, Tenn.

Paraprocts variously modified as described in key and species treatments, furnishing the best specific characters for the male sex. *Phallus* with dorsal lobe less sclerotized than in *Euhadenoecus*; as usually seen, in only partially evaginated condition and distal aspect (Fig. 5, h,i—*subterraneus*; j—*cumberlandicus*), the margins of the infolded dorsal lobe nearly surround the transverse invagination containing the phallotreme, with the dorsal lip somewhat projecting and more or less bilobate; only a narrow ventral part of the rim of the invagination is formed of the ventral lobe, and this is more or less cleft and bears on its inner face a pair of small approximated admesal ridges, weakly sclerotized, brownish, with projecting ends and microscopically denticulate surfaces. When fully evaginated (Fig. 6, a,b—*opilionoides*) the phallus is short, thick, lobulate, with its phallobase formed mostly of the dorsal lobe, the phallotreme a transverse slit on the distodorsal surface, and the ventral lobe forming a rounded-conical distal bulla that bears two short, blunt-conical papillae, one above and one below the apex. So far as has been observed the form of the phallus is very similar throughout the genus. *Subgenital plate* as described in key, its subconical distal lobes not set off from rest of plate by distinct sulci; *styles* very small, short-conical, partly fused to tips of lobes.

FEMALE CHARACTERS. *Ovipositor* (Fig. 14, a-f; Pl. IV, f-h) relatively longer than in *Euhadenoecus* (see Table 2); the larger proximal teeth of ventral valves much longer than deep, with straight ventral edges, separated by small shallow grooves, all except the distal ones with a delicate hairlike point projecting distad from their distoventral angles. *Subgenital plate* (Fig. 13, a-j) specialized, its ventral surface with an intramarginal sclerite of species-specific form as described in key, this providing the most reliable means for identification of this sex. *Spermatheca* an elongate, thick, slightly leftward-curved pouch, attached to the tip of which is a narrower terminal diverticulum bent back along the left side of the pouch, this apparently representing the left lobe shifted to a distal position.

COMMENTS. The species of *Hadenoecus* are more advanced in a number of respects than are those of *Euhadenoecus*—notably in the more modified paraprocts, more reduced styles and development of eversible tubular "clasping" organs in the male, and in the specialized ovipositor and subgenital plate and the peculiarly modified spermatheca of the female.

The more evident similarities and differences among the species of this genus, partly described in the key and in more detail in the specific treatments, may be summarized as follows. Males of *cumberlandicus* and *subterraneus* are very similar, both having distally narrowed and ventrally produced paraprocts unlike those of the other species, but the form of the produced dorsal lip of the dorsal phallic lobe is slightly different in the two (Fig. 5, f,h); females of these species, however,

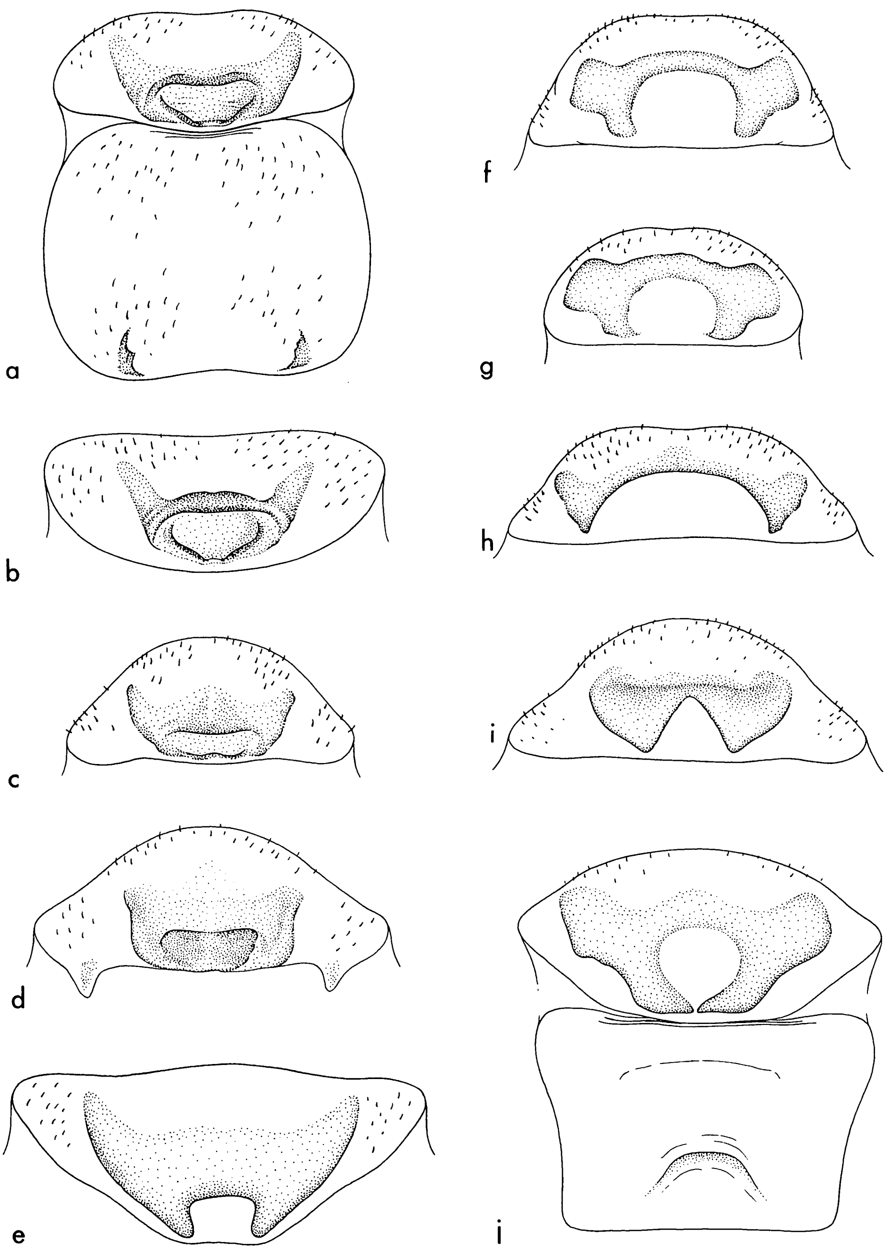

Fig. 13. Female subgenital plates of *Hadenoecus* species, X 22-25. a–*subterraneus* (with 7th sternite), New Discovery Cave, Edmonson Co., Ky.; b–*subterraneus*, same locality as last; c–*subterraneus*, southwestern phase, McGinnis Cave, Warren Co, Ky.; d–same as last, Friendship Cave, Warren Co, Ky.; e–*cumberlandicus*, Dykes Cave, Pulaski Co, Ky.; f–*o. opilionoides*, small cave in Buffalo Cove, Fentress Co, Tenn.; g–same as last, another specimen; h–*opilionoides australis*, Blue Spring Cave, White Co, Tenn.; i–*barri*, Cumberland Cavern, Warren Co, Tenn.; j–*jonesi* (with 7th sternite), Limrock Blowing Cave, Jackson Co, Ala.

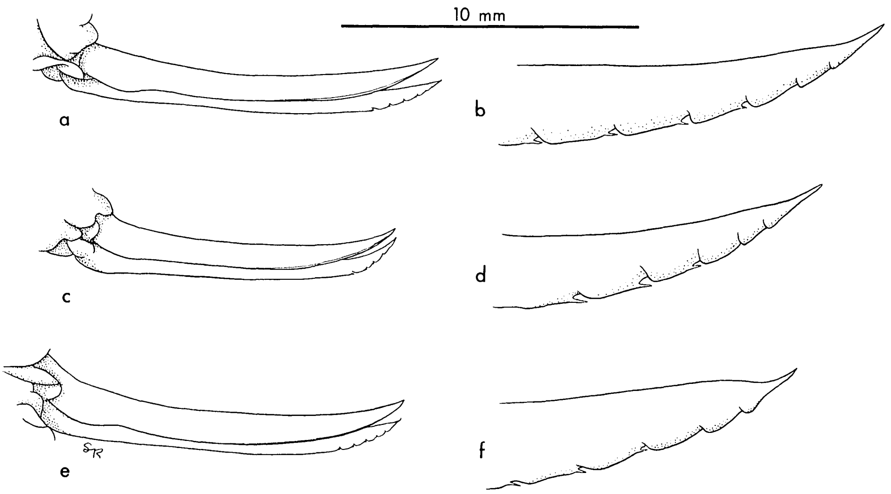

Fig. 14. Ovipositors of *Hadenoecus* species. a, b—*subterraneus*, New Discovery Cave, Edmonson Co, Ky.; c, d—*jonesi*, Gary Self Pit (Cave Stand Cave), Jackson Co, Ala.; e, f—*o. opilionoides*, small cave in Buffalo Cove, Fentress Co, Tenn.

differ strikingly from each other and from the other species in the form of the subgenital plate sclerite. These two species have relatively shorter legs and stouter hind femora than the others, as shown in Table 2, and also have a larger number of denticles on the dorsal carinae of tibia III—from 60 to 92, with a mode of about 70. In the others the denticle number varies between 37 and 68, and the mode lies between 50 and 60, depending on the species. In *opilionoides*, *barri* and *jonesi*, also, the number of distal interspur intervals without denticles averages larger than in *subterraneus* and *cumberlandicus*, in which it is usually one, sometimes two; in the other species there are most often two unarmed spaces, but about one-third of all the individuals examined have three such spaces on at least one carina of one leg.

Since the five species of *Hadenoecus* here distinguished are not only very similar morphologically but have narrowly separated allopatric or parapatric ranges, the possibility that they may be only subspecifically distinct must be considered. This appears highly unlikely on the following grounds. In no instance has any indication of intergradation in male or female characters been found in specimens collected in areas where the ranges of pairs of species are most nearly contiguous. Furthermore, a single electrophoretic study made by Norton on the isozyme systems of the two most similar species, *H. cumberlandicus* and *H. subterraneus*, demonstrated a constant difference between the two in samples from different parts of their respective ranges with regard to tetrazolium oxidase (TO); as shown in Plate 5, TO-1 seems to be diagnostic of the first, TO-2 of the second. Until or unless evidence of intergradation among these taxa is found all five should be considered distinct species; together they constitute a superspecies in the classic and orthodox sense of that concept.

HADENOECUS SUBTERRANEUS (Scudder) (Figs. 5, f,g,j; 12, b; 13, a-d; 14, a, b; 10, 15 (maps); Pl. I; Pl. II, e; Pl. III, e; Pl. IV, f-h).

1861. *Rhaphidophora subterranea* Scudder, Proc. Boston Soc. Nat. Hist., 8: 8-9 (Mammoth and adjoining White's Cave, Kentucky).

Type: Female (pinned, lacking fore and middle legs), bearing labels "Mammoth Cave, Ky. A. Hyatt; *Rhaphidophora subterranea* Scudd.; MCZ Type 773; S. H. Scudder Coll.," in ANSP ex MCZ; *plesiotype* a female, Mammoth Cave, Ky., above Frozen Niagara, 18-19 June 1973 (R. M. Norton), here designated; *plesiallotype* a male, Mammoth Cave, Ky, Marion Avenue, 17 Sept. 1973 (R. M. Norton), here designated; both latter preserved in alcohol, in UMMZ.

This species, the type of the genus, is by far the best known North American cave-cricket. It is abundant in Mammoth and other caves of the Pennyroyal Plateau in south-central Kentucky, and in recent years a number of studies have been published on its life history, behavior and ecological role in the cave biocoenosis. It is easily distinguished from the other species of the genus by the characters given in the key and summarized under the generic description.

DESCRIPTION OF PLESIOTYPIC FEMALE:[1] Length of body exclusive of ovipositor ca. 17.5, of pronotum 4.0 (3.2-4.4), of femur I 14.2 (11.0-15.6), of femur III 22.4 (17.5-24.6), of tibia III 28.3 (21.8-32.0), of antenna ca. 95 mm; proximal breadth of femur III 2.9 (2.5-3.3), distal breadth 0.85 mm; length of ovipositor 12.2 (9.4-14.2) mm.

Coloration pale; dorsum of head, thorax and base of abdomen pale ochraceous buff, pronotum with edges and discal markings slightly darker reddish brown, hind margins of mesonotum and metanotum and dorsocephalic portions of abdominal segments I-III also slightly brownish; femora and proximal three-fourths of tibiae orange buff, femur III with very faint brownish scalariform markings on basal portion of outer face; vertex without dark lines; greater part of head, mouthparts, ends of tibiae, tarsi and venter pale; antennae and cerci dilute orange-brown; tergite VIII with very narrow brown sclerotization along anterior edge, tergite IX with similar sclerotization widest ventrolaterad; sternite VII with a pair of small dark irregularly Y-shaped sclerotizations at its anterolateral angles; ovipositor reddish brown.

Head: Vertex abruptly declivent, terminated by a very small fastigium consisting of two low, bluntly rounded tubercles, these slightly compressed and divaricate with bases attingent along midline, pale,

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[1] Figures in parentheses give the range of variation in the series studied.

without ocellar spots, their apices faintly tinged with brown. Eyes small, black except for upper angle, rounded-triangular with convex caudal and weakly concave cephalic margins, moderately prominent, highest near anterior edge, vertical diameter 1.7 (1.4-1.8) times breadth, interocular distance 1.35 (1.15-1.50), infraocular distance (to anterior mandibular condyle) 1.76 (1.63-1.91) times length of eye; proximal antennal segment slightly more than half as broad as interocular distance, three-fourths as broad as length of eye. Maxillary palpus very long and slender, 0.9 (0.8-0.9) times as long as femur I, its fifth (distal) segment 1.17 (1.07-1.38) times as long as pronotum, slightly upcurved, with apical sensory area occupying its knobbed tip and extending briefly onto ventral surface, 4th segment 0.64, 3rd segment 0.76 times as long as 5th.

Thorax: Pronotum almost semicylindrical, very weakly sellate; fore and hind margins in dorsal aspect gently convex, side margins more strongly so, greatest breadth at caudal third, 1.2 (to 1.4) times mesal length; in side view shallow, height slightly more than half dorsal length, ventrocephalic angle rather abruptly rounded, ventral margin oblique and nearly straight in anterior two-thirds, thence rounding broadly into caudal margin; cephalic and lateral edges narrowly, caudal edge not marginate; foveolae of disc very weakly impressed. Metanotum with hind margin gently convex dorsad, gently concave laterad, its ventrocaudal angles rounded and slightly produced; mesonotum with hind margin broadly convex, ventrocaudal angles not produced; neither marginate.

Legs: Fore and middle legs very long and slender; femur I 3.5 (3.2-4.0) times as long as pronotum; tibia I 1.11 (1.0-1.15) times as long as femur I; tarsus I compressed, 0.82 (to 0.67) times as long as tibia, basitarsus I 1.6 (1.3-1.7) times as long as pronotum, longer than remaining segments taken together, 2nd and 4th segments subequal, 3rd very short, claws strongly curved, aciculate, about one-half as long as 4th segment. Femur II 0.94 (0.90-1.00) times as long as femur I, tibia II 1.06 (1.0-1.17) times as long as femur, tarsus II slightly shorter than tarsus I. Femur III 5.6 (5.2-6.5) times as long as prototum, 1.6 (1.4-1.7) times as long as femur I, 7.7 (6.7-8.3, mean 7.5) times as long as basal breadth, distal three-fifths slender, least breadth less than one-third that of base. Tibia III 1.26 (1.18-1.33) times as long as femur; tarsus III like tarsus I but shorter and more compressed, 0.39 (0.37-0.41) times as long as tibia; basitarsus III 1.32 (1.14-1.39) times as long as pronotum, 2nd segment distinctly longer than 4th, about one-half as long as basitarsus, claws 0.4 (to 0.33) times as long as 4th segment.

Leg armature: Caudogenicular lobes of femora II and III with minute spinule (often absent on femur III, rarely on femur II). Tibia I armed on ventral carinae with 5/7 (5-8) cephalic, 5/5 (5-7) caudal spurs (mode 6 on both); tibia II with 5/6 (5-7, mode 6) on cephalic, 5/6 (5-7, mode 5) on caudal carinae. Tibia III with 6/5 dorsocephalic, 6/6 dorsocaudal spurs (5-8 on each, mode 7), intervals between spurs decreasing distad, spurs of two sides not opposite; spurs short (subdistal cephalic spur 1.2 (to 0.8) times as long as tibial depth), straight except for slightly hooked tip, dorsally bicarinate, glabrous; ventral surface of tibia with 5/3 (1-6, mode 4-5) spurs on distal half of cephalic margin, caudal margin with 2/2 (1-4, mode 2) spurs. Dorsal denticles of tibia III very small proximad, size increasing to about 4th interspur interval, spacing wider and more irregular distad; spine formulae, right and left: cephalic 46/15/10/12/0/0 = 83, 43/13/10/16/0 = 82, caudal 50/14/9/10/2/0 = 85, 38/9/14/8/7/0 = 76 (highly variable); ventral calcars short, spiniform, intermediates slightly longer, both pairs subequal, dorsals long, slender, hooked at tip, externally pubescent, caudal longer than cephalic, 0.35 (to 0.50) times as long as basitarsus III.

Ovipositor (Fig. 14, a,b; Pl. IV, f-g): Long, proximal four-fifths nearly straight and of subequal breadth, distal fifth of dorsal valves slightly upcurved and narrowing to very acute tips; inner valves only a little shorter than dorsals; ventral valves 3.0 (2.7-3.7) times as long as pronotum, 0.9 (0.8-1.0) times as long as femur I, 0.54 (0.51-0.65) times as long as femur III, ventral margin with 6 (5-8, mode 6) subdistal teeth, these shallow, flat-edged, diminishing in size distad, each terminating in an oblique ventral groove that forms a small marginal notch and a sharp but not out-flared proximal edge on tooth, the four proximal notches each with a minute, translucent hairlike process projecting distad from its proximal angle, tip of valve a slender translucent point.

Subgenital plate (Fig. 13, a,b): Width about three times length, distal margin broadly arcuate with faint mesal emargination, submembranous, distal and lateral areas minutely and sparsely setose; sclerite subtrapezoidal with concave distal edge, narrowing distolateral arms almost reaching sides of distal margin of plate, side margins convergent proximad and proximal arms incurvate with their mesal ends connected by a short sclerotized bar; mesoproximal pouch deeply impressed, its floor sclerotized and transversely ridged, bordered by elevated sclerotized rims, the distal a transverse ridge with recurvate ends, the lateral rims formed of the raised inner edges of the proximal arms, highest proximolaterad, their lower distal ends disappearing under the curved ends of the distal ridge; anterior wall of pouch overhanging, lateral walls subvertical; in ventral view outline of pouch broadly ovate, in side view edges of pit high distad and proximad, lower between. (Varying as described below).

Seventh sternite (Fig. 13, a) with a pair of small brownish or blackish sclerotizations near proximolateral angles, these irregularly crescentic or triangular, their mesal angles not connected by a narrow sclerotization along the margin of the sternite such as is present in some of the other species; surface transversely convex, not tumid or forming a ridge mesoproximad, distad with distant, rather large brownish setae in middle portion.

DESCRIPTION OF PLESIALLOTYPIC MALE: Lenth of body ca. 13.4, of pronotum 3.9 (2.9-4.0), of femur I 14.2 (10.7-16.2), of femur III 22.2 (17.2-24.5), of tibia III 29.3 (22.8-31.8), of antenna ca. 95 mm; proximal breadth of femur III 2.9 (2.3-3.3), least distal breadth 0.83 mm.

Agrees with described female except as noted. Coloration a little more intensive; margins of thoracic nota and abdominal tergites slightly darker, giving the dorsum a faintly transverse-banded appearance. *Legs:* Femur I 3.6 (3.2-4.1) times as long as pronotum; tibia I 1.06 (1.0-1.13) times as long as femur I; femur III 5.8 (5.4-6.5) times as long as pronotum, 1.6 (1.5-1.7) times as long as femur I, length 7.7 (6.8-9.0, mean 7.7) times as long as basal breadth; tibia III 1.32 (1.11-1.35) times as long as femur III. Armature of all tibiae nearly as in described female; spine formulae of dorsal carinae of tibia III, right and left: cephalic 25/11/14/11/11/0/0 = 72, 23/14/13/11/11/1/0 = 73, caudal 21/16/16/8/10/0/0 = 71, 32/15/13/8/13/0/0 = 81; subdistal ventral spurs of tibia III, cephalic 5/4 (2-6, mode 4), caudal 2/2 (1-5, mode 2).

Terminal abdominal structures (Fig. 5, f,g,j; Pl. II, e; Pl. III, e): Hind margin of 9th tergite gently emarginate at sides before the transverse slit-like openings of the extrusible tubular clasping organs; proximal edge of 10th tergite very narrowly sclerotized and brownish, this widest just mesad of openings of extrusible organs (sclerotization often weak or absent). *Epiproct* about two-thirds as long as broad, with parabolically rounded outline, surface convex laterad and distad and with shallow, hourglass-shaped mesoproximal impression. *Paraprocts* in side view subtriangular, with strongly decurved apices which in both lateral and distal aspect are narrow, with subacute ventral tips that project below remainder of ventral margin; outer face with a short, subhorizontal rounded ridge extending distad from near base of cercus but not reaching dorsal margin; ventral margin with a short lunate membranous area just proximad of tip; inner edges of decurved apices in rear view straight and in resting position attingent. *Cerci* slender, evenly tapering to acute apices, 6.2 mm. long, 1.6 (1.4-1.8) times as long as pronotum. *Evaginable "clasping" organs* (described from other specimens; Fig. 5, j) when fully extruded elongate tubular, about 5.0 mm. long and 0.5 mm. in diameter, slightly tapering and blunt-tipped, white, projecting from slits between the 9th and 10th tergites cephalad and slightly mesad of the cercal bases, flexible but in preserved specimens usually bowed downward and more or less strongly incurvate. *Phallus* (partially evaginated, Fig. 5, f,g) having mesal lip of dorsal lobe subtriangularly produced with shallowly bilobate flattened apex, lateral portions curling around ends of transverse opening as membranous, more or less wrinkled and lobate folds with narrowly convex edges, their mesal ends attached to sides of narrow median ventral lobe; latter with a narrow mesodistal cleft and its dorsal surface bearing a pair of short sclerotized ridges with microscopically dentate surfaces and vertically compressed distal ends; distal portion of fully evaginated phallus as described for *opilionoides* in generic description.

VARIATION: Individuals of *H. subterraneus* vary considerably in size and proportions, and the means of the principal dimensions differ somewhat in the populations of different caves, as indicated in the above descriptions and shown in Tables 2 and 4. Egg-predation by carabid beetles as a cause of increased ovipositor length is discussed by Norton in Part III.

The dorsal armature of tibia III is more variable in the Hadenoecini than in most Rhaphidophoridae, and greater in *Hadenoecus* than in *Euhadenoecus*. In *H. subterraneus* the number of spurs on the dorsal carinae is most often 7, and in individuals with this number the spine formula (similar on both carinae in both sexes) shows the following range, without any marked mode for the inter-spur intervals: 16-50/8-18/6-18/5-16/0-14/0-2; total 60-97, mean 74 (about the same as in *cumberlandicus* and considerably more than the means in the other species of *Hadenoecus*). When the carina has 7 spurs the distal inter-spur interval has 0, rarely 1 or 2 denticles; when 8 spurs are present the distal interval has 0 and the subdistal 0 or rarely 1 to 3.

GEOGRAPHIC VARIATION. In all populations sampled from caves in the main body of the range of *H. subterraneus*, extending from Edmonson, Barren and Hart counties north to Meade County, the female subgenital plate has essentially the form described for the plesiotype (Fig. 13, a,b). There is some variation in degree of elevation and sclerotization of the rim and of the depth, sclerotization and transverse ridging of the basal excavation of the sclerite, but even when least sclerotized the appearance is that of a shallow ovate pit with a darker raised edge.

In specimens from caves in Allen, Warren and Logan counties, southwest of the Mammoth Cave region, the sclerite, though basically the same in structure, has a different appearance (Fig. 13, c,d). The impressed area is much shallower and its rim only slightly raised, so that it cannot be described as pouched, and its edges do not form a well-defined dark outline; often it is only weakly impressed and bounded only distad by a low ridge. In some individuals from Friendship Cave the sclerite is flat, subquadrate in outline with short distolateral arms and mesodistal point, and is uniformly sclerotized except for darker proximal admesal areas. In the series from Steep Hollow Cave the sclerite shows all gradations from the Mammoth Cave form to the other. It seems probable that the southwestern populations should be treated as a subspecies, but in the absence of other distinguishing characteristics assignment of that status is deferred awaiting more information.

[*Note, added in proof:* T. C. Barr, Jr., has just written me that he has found *Neaphaenops*, the beetle that eats *H. subterraneus* eggs, to comprise four taxonomic entities—a subspecies *N. t. tellkampfii* in the Mammoth Cave region, two other subspecies occurring further north, and a southwestern population with distinctive characters that may be another subspecies

TABLE 4

VARIATION IN SIZE (MM) AND PROPORTIONS IN *HADENOECUS SUBTERRANEUS*

	No. Spec.	Max.	Min.	Mean	S.D.	Max.	Min.	Mean	S.D.
		MALE							
		Length of Pronotum				Length of Femur I			
All Caves	120	4.02	2.86	3.56	0.26	16.2	10.7	13.26	1.06
Wonderland Cave	10	4.05	3.80	3.93	0.08	15.7	13.7	14.72	0.72
Mammoth Cave System	24	3.87	3.29	3.59	0.22	14.7	12.3	13.50	0.68
McGinnis Cave	13	3.72	3.25	3.56	0.12	13.6	12.2	12.91	0.37
Dismal Creek Cave	7	3.43	2.80	3.14	0.18	13.0	11.2	12.00	0.56
		Length of Femur III				Length of Tibia III			
All Caves	120	24.5	17.2	20.8	1.53	31.8	22.8	26.2	1.98
Wonderland Cave	10	24.0	21.3	22.8	0.89	29.9	27.0	26.5	1.09
Mammoth Cave System	24	23.0	19.4	21.4	1.10	29.3	23.5	26.5	1.88
McGinnis Cave	13	21.5	19.3	20.4	0.59	26.0	23.6	25.4	0.72
Dismal Creek Cave	7	20.5	18.5	19.0	0.69	24.6	22.8	23.7	0.66
		FEMALE							
		Length of Pronotum				Length of Femur I			
All Caves	158	4.42	3.17	3.68	0.24	15.6	11.0	13.29	0.93
Wonderland Cave	12	4.40	3.84	4.11	0.15	15.6	13.3	14.73	0.65
Mammoth Cave System	42	4.15	3.30	3.77	0.17	15.5	13.2	13.97	0.58
McGinnis Cave	18	3.86	3.58	3.70	0.09	13.6	12.4	13.04	0.44
Dismal Creek Cave	19	3.72	3.29	3.45	0.10	14.0	12.0	12.75	0.71
		Length of Femur III				Length of Tibia III			
All Caves	158	24.6	17.5	21.40	1.75	32.0	21.8	26.94	2.14
Wonderland Cave	12	24.6	20.4	23.17	1.30	32.0	26.6	29.50	1.62
Mammoth Cave System	42	24.2	20.9	22.41	0.90	31.0	26.0	28.20	1.36
McGinnis Cave	18	22.6	19.9	20.78	0.72	27.9	24.6	25.91	1.06
Dismal Creek Cave	19	21.2	18.7	19.86	0.71	25.7	23.9	24.50	0.70
		Length of Ovipositor				L. Ovip./L. Pron.			
All Caves	158	14.2	9.4	11.84	0.99	3.75	2.66	3.22	0.22
Wonderland Cave	12	14.2	12.2	13.05	0.45	3.42	2.93	3.17	0.15
Mammoth Cave System	42	13.9	11.4	12.48	0.64	3.75	3.03	3.30	0.17
McGinnis Cave	18	11.6	9.9	10.85	0.48	3.16	2.66	2.93	0.13
Dismal Creek Cave	19	12.7	10.0	11.80	0.75	3.55	2.85	3.23	0.19

of *tellkampfii*, a semispecies, or even a full species. This last occupies caves in the Barren River drainage and has approximately the same range as southwestern *H. subterraneus*; it occurs as far east as Howell Cave in northwestern Allen County, only 4.6 miles from Buchanon Cave, also in Allen County 0.8 miles W. of Gainesville, in which *N. t. tellkampfii* is present. Specimens of *H. subterraneus* just received from Barr, collected in Buchanon Cave and in Lynn

Cave, 1 mile SW of Settle, Allen County, have the typical southwestern type of subgenital plate sclerite; these caves are farther east and closer to typical *subterraneus* territory than is Steep Hollow Cave in which, as was noted above, intergradation occurs. The situation obviously requires further investigation, but it looks as if populations of both the beetle and *H. subterraneus* had been isolated and diverged in the Green and Barren river drainages and are now coming into renewed contact, with secondary intergradation occurring between the cave-cricket populations in some places.]

DISTRIBUTION AND FAUNAL ASSOCIATIONS. The range of *Hadenoecus subterraneus* is shown in relation to those of other species of the genus in Fig. 10, and mapped in detail in Fig. 15. The species is confined to the Pennyroyal Plateau in south-central Kentucky. Within this region Barr (1967) has distinguished faunal districts characterized by having rather different assemblages of cave animals. One of these assemblages constitutes the Mammoth Cave fauna, of which *H. subterraneus* is a characteristic, abundant and ecologically important member. The species also extends into the southern part of the Breckenridge faunal district, and its deviant southwestern populations occur in the eastern part of the Hopkinsville faunal district. The Mammoth Cave fauna extends eastward up the Green River valley along a tongue of St. Louis limestone, and Dr. Barr writes that in this area there is a very close correlation between the presence of *H. subterraneus* and its predator *Neaphaenops* and that of the cave crayfish *Orconectes pellucidus*. The boundary separating the ranges of *H. subterraneus* and *H. cumberlandicus* is the interfluve between, on the west, the drainage basins of the Barren and Green rivers and, on the east, the valleys of the Cumberland River and of the headwaters of the Kentucky River.

ECOLOGY, BEHAVIOR AND LIFE HISTORY. In part III of this paper Norton has summarized the results of various studies that have been made on these topics by himself and others.

SPECIMENS EXAMINED:[1] 1,519–219♂, 389♀, 911 juveniles, from the following localities:

Mammoth Cave Phase

KENTUCKY: *Barren Co.: (Vicinity of Cave City):* Cave City Cave [ALA], Bat Cave [D], Blood Cave [D], Downers (= Johnsons) Cave [ALA], Cave under Gardners Knob [ANSP], Turner Cave [ALA], Wonderland Cave ca. 2 mi WNW of Cave City [ALA]; *(Vicinity of Park City* = old Glasgow Junction): Caves nr Glasgow Junction [ANSP, MINN], Mail Robbers Cave

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[1] Nearly all the specimens collected before 1900 by Sanborn, Putnam, Packard and others have been seen, including those recorded by Packard in his 1888 monograph; originally in the MCZ, most of these are now in the ANSP. A great amount of more recently collected material has also been studied. Many of the older records are from caves originally thought to be separate, but now recognized as parts of the major cave systems of the Pennyroyal Plateau, under which they are here grouped as far as this could be done from available information, in part furnished by T. C. Barr, Jr. and L. Hubricht. Some have not been identified with certainty.

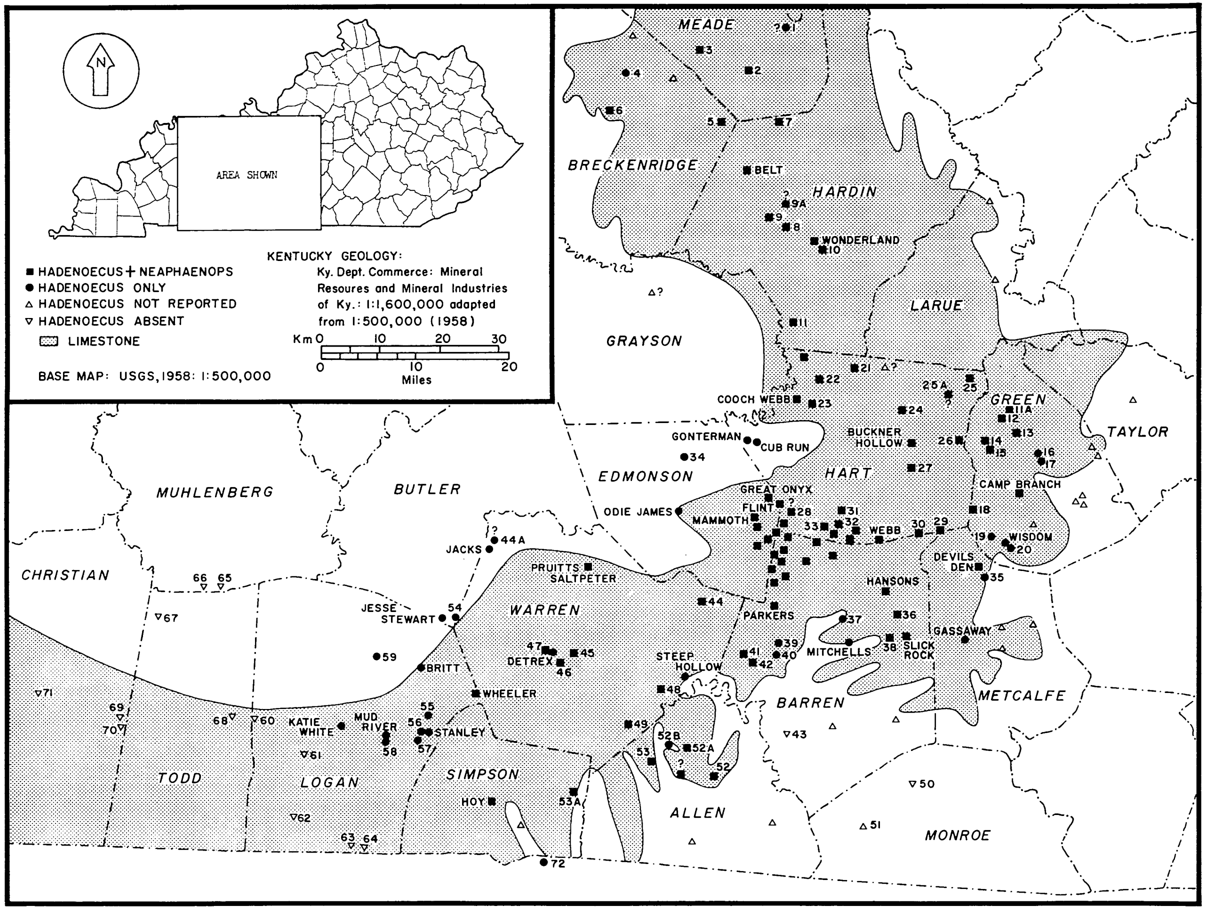
AREA SHOWN
N
■ HADENOECUS + NEAPHAENOPS
● HADENOECUS ONLY
△ HADENOECUS NOT REPORTED
▽ HADENOECUS ABSENT
▨ LIMESTONE
BASE MAP: USGS, 1958: 1:500,000
KENTUCKY GEOLOGY:
Ky. Dept. Commerce: Mineral Resoures and Mineral Industries of Ky.: 1:1,600,000 adapted from 1:500,000 (1958)
Km 0 10 20 30
0 10 20
Miles
MEADE
BRECKENRIDGE
HARDIN
LARUE
GRAYSON
GREEN
TAYLOR
EDMONSON
HART
BUTLER
MUHLENBERG
CHRISTIAN
WARREN
BARREN
METCALFE
TODD
LOGAN
SIMPSON
ALLEN
MONROE
BELT
WONDERLAND
COOCH WEBB
GONTERMAN
CUB RUN
BUCKNER HOLLOW
CAMP BRANCH
GREAT ONYX
FLINT
MAMMOTH
ODIE JAMES
WEBB
WISDOM
DEVILS DEN
HANSONS
PARKERS
GASSAWAY
MITCHELLS
SLICK ROCK
STEEP HOLLOW
PRUITTS SALTPETER
JACKS
JESSE STEWART
BRITT
WHEELER
DETREX
KATIE WHITE
MUD RIVER
STANLEY
HOY

Fig. 15. The distribution of caves with populations of *Hadenoecus subterraneus* and of its predator, *Neaphaenops tellkampfii*, in western Kentucky (map prepared by Norton). (*Hadenoecus* can spread overland and consequently has a slightly greater range than *Neaphaenops*, which is chiefly limited to subterranean dispersion). Names of numbered caves are as follows: KENTUCKY: *Meade Co.:* 1–Rock Haven; 2–Sig Shacklett; 3–Scotts; *Breckenridge Co.*: 4–Penitentiary; 5–Thornhill; 6-Norton Valley; *Hardin Co.*: 7–Saltpeter; 8–Patterson; 9–Wilmoth; 9A–Roaring Spring; 10–Turkey Hollow; 11–Bland; *Green Co.*: 11A-Tater; 12–Brush Creek; 13–Milby; 14–Aetna; 15–Scott; 16–Creason; 17–Pitman Creek; 18–Saltpeter; 19–Three Room; 20–Greasy Creek; *Hart Co.*: 21–Lone Star Saltpeter; 22–Riders Mill; 23–Puckett; 24–Barnes Smith; 25–Turner; 25A–Close; 26–Crump; 27–Bald Knob; 28–Northtown; 29–Three Springs; 30–Bert Burd Sink; 31–Mammoth Onyx; 32–Hogan; 33–Ronalds; *Edmonson Co.*: 34–Dismal Creek; *Metcalfe Co.*: 35–Fancher; *Barren Co.*: 36–Brown; 37–Geralds; 38–Neals Chapel; 39–Beckton; 40–Edmuns (=Bryant Edmuns, Edmunds); 41–Buck Creek; 42–Crawhorn (=Price Jewell); 43–Cole; *Warren Co.*: 44–Crump; 44A-Thomas; 45–Bypass; 46–Horseshoe and Lost River; 47–McGinnis; 48–Moats; 49–Friendship; *Monroe Co.*: 50–Cedar Hill; 51–Holland; *Allen Co.*: 52–Buchanon; 52A–Howell; 52B–Lynn; 53–Bear; *Butler Co.*: 54–Orange Cemetary; *Logan Co.*: 55–Robertson; 56–Carter; 57–Metlock; 58–Gorham; 59–Chandler; 60–Potato; 61–Cave Spring; 62–Collier Saltpeter; 63–Holman; 64–Cook; *Muhlenberg Co.*: 65–John Jenkins; 66–Lovell; *Todd Co.*: 67–Poe Hill; 68–Haddon; *Christian Co.*: 69–House; 70–Cave Spring; 71–Chandler. TENNESSEE: *Sumner Co.*: 72–Whiteoak.

[ANSP], Poynters Cave [ANSP], Wetzels Cave [ANSP], Diamond Caverns (Diamond Cave #2) ca. 2 mi NNE of Park City [ANSP, CU, UMMZ], Onyx Cave 2 mi N of Park City, Short Cave 1.5 mi N of Park City [ANSP], Sugar Bowl Cave 3 mi NW of Park City [ANSP]; (*Other caves*): Mitchell Cave, at Glasgow Jailhouse in town of Glasgow; Brown Cave, 3.5 mi ESE of Coral Hill [B]; Franklin Cave on Barren River [B, UKY]; Cascade Cave [ANSP, D]; Sanders Spring Cave [ANSP, D]; Edmunds Cave, 0.95 mi SW of Beckton at head of Greens Creek [B].

Edmonson Co.: Mammoth Cave Nat'l Park: (*Northwest corner of Park*): Bee Spring [ANSP], Dismal Creek Cave [ANSP], Ganter Cave [ANSP, D], John and Fred Fields Cave on E. bank of Dismal Creek [ANSP]; (*Flint Ridge*): Cathedral Cave (Nicholas 1962) [D, UMMZ], Colossal Cave [OSU, UKY], Great Onyx Cave [ANSP], Great Salts (Salts) Cave [ANSP]; (*Mammoth Cave Ridge*): Mammoth Cave and many specific locations within the cave [AMNH, ANSP, CM, CNC, D, FMNH, INHS, ISU, K, MHNG, MINN, NHW, OSU, OU, UK, UKY, UMMZ, WSU]; Dixon Cave [ANSP], Frozen Niagara Entrance, Historic Entrance, New Discovery Entrance; (*Jim Lee Ridge,* spur of Mammoth Cave Ridge): White (Whites) Cave [ANSP, D]; *Joppa Ridge:* Cedar Sinks Cave [ANSP, D], Cedar Springs Cave (both in Cedar Sinks-Turnhole system: Barr 1967: 149), Long Cave (Grand Avenue Cave) [ANSP, D], Proctor Cave [ANSP]; *Other caves:* Haunted Cave [ANSP], Yothers Cave [ANSP], cave near Baker's Furnace [ANSP].

Green Co.: Greasy Creek Cave; Tater Cave, 1.3 mi S of Bloyd's Crossing; *Hardin Co.:* Belt Cave, 3.5 mi NW of Howe Valley; Wonderland Caverns, 1.5 mi SE of old Stephensburg; *Hart Co.:* Buckner Hollow Cave, 7 mi ENE of Munfordville on Green River; Cartmill Cave [INHS] and Hidden River (Horse) Cave, both nr town of Horse Cave; Mammoth Onyx Cave [D, UMMZ]; Cooch Webb Cave, ca 3 mi N of Macon; Ice Cave, ca 1.5 mi SE of Northtown [ANSP]; Ronalds (Reynolds) Cave, 2.6 mi N of Cave City[1] [ALA]; *Meade Co.:* Sig Shacklett Cave, halfway between Garrett and Big Spring [K]; *Metcalfe Co.:* Devils Den Cave, halfway between Center and Sulphur Well; Gassaway Cave, ca 2 mi E of Wisdom.

Transitional to Southwestern Phase

Warren Co.: Steep Hollow Cave, 1.0 mi SW of Three Forks, 21 June 1972 (N) 3♀; Jan and 18 Jan 1973 (N) 40♀ (this series varying from typical *subterraneus* through intermediate conditions to the atypic southwestern phase).

Southwestern Phase

Warren Co.: Pruitts Saltpeter Cave (N) 3♂, 2♀; (Vicinity of Bowling Green): Danger Cave, 1 mi E, 27 June 1973 (O. & H. Kukal, P) 1♂, 2♀; Detrex Cave, 2.5 mi SW, 27 June 1973 (O. & H. Kukal, P) 2♂, 14♀, 7 juvs; Lost River Cave, Bowling Green, 14 Sept 1946 (P. Brodkorb) 1♂, 1♀; McGinnis Cave, 2 mi SW, 26 Sept 1949 (J, V) 13♂, 18♀ [ALA]; (Vicinity of Scottsville): Friendship Cave, 1 mi W of Allen Springs, 25 Sept 1949 (J, V) 1♂, 1♀, 2 juvs [ALA].

Logan Co.: Mud River Cave, 4 mi E of Russellville, 5 Sept 1972 (N) 8♀; Britt Cave, 19 July 1972 (N) 2♂, 2♀, 4 juvs; Chandler Cave, 16 July 1972 (N) 3♂, 1♀, 1 juv; Stanley Cave, 16 July 1972 (N) 1♂, 4♀.

Allen Co.: Buchanon Cave, 0.8 mi W of Gainesville, 25 Feb. 1978 (B) 1♂, 3♀, 1 juv.; Lynn Cave, 1.0 mi SW of Settle on Sulphur Creek, 11 Mar. 1978 (B), 12♂, 6♀, 3 juv.

TENNESSEE: *Sumner Co.:* Whiteoak Cave (Barr 1961: 443) [specimens not seen; record from Barr].

References in Literature[2]

Phalangopsis sp. nr. *longipes* Serville: Thompson 1844: 112 (first notice of presence in Mammoth Cave).

Rhaphidophora subterranea Scudder 1861: 8-9 (Mammoth and White's Caves, Ky.; description and notes).

Hadenoecus subterraneus Scudder 1862: 439-40 (type of genus); Scudder 1868: 40; Walker 1869: 201; Packard 1871: 745-6, fig. 126 (notes); Cope 1872: 167 (Ky. caves; not in Wyandotte Cave, Ind.); Glover 1872: pl. 8, fig. 6; Hubbard 1880: 37 (notes); Brunner 1888: 310, pl. 8, fig. 34; Packard 1888: 8, 10-12, 24, 69, 83, 116, 131, text fig. 16, pl. 18, fig 3 (in part: many caves in Mammoth Cave region, [not] Carter Caves, Ky.; occurrence and behavior, eyes and brain, parasitic fungus); Packard 1889: 198-9 (epipharynx and taste organs); Garman 1891: 105, fig., and Packard 1895: 126 (protrusible abdominal attractant glands of male); Garman

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[1] So located by Barr in letter; label gives 4 mi SW of Cave City, which would place it in Barren Co.

[2] Exclusive of bare citations and casual references. When no locality is given Mammoth Cave, Kentucky is understood.

1894: 27 (notes); Call 1897: 390 (fungus *Isaria (Sporotrichum) densa* on dead *Hadenoecus*); Kirby 1906: 135, and Caudell 1907: 290 (*H. cavernarum* Saussure a synonym); Banta 1907: 53 (not in Indiana caves); Caudell 1916: 659 (in key); McIndoo 1917: 64 (alluring glands of male); Blatchley 1920: 608, fig. 204 (descr., habits, distr.); Ives 1927: 89 (in part: Mammoth Cave); Karny 1930: 189; Chopard 1931: 394-7, figs. 1-10, 12-14 (detailed descr., variation; in part: Mammoth and Horse Caves, Ky.); Giovannoli in Bailey 1933: 606-7, fig. 86 (notes); Wolf 1934-8, vol. 2 (cave records), vol. 3: 158-9 (in part: not Ind., Tenn., Va. caves and Carter Caves, Ky.); Dearolf 1937b: 44-46, photo ♀; Karny 1937: 261 (in part: not Tenn., Va.); Chopard 1938: 70, 75, 149 (biol.); Ander 1939: 8 *et passim* (morphology); Dearolf 1953 (in part: caves of Mammoth Cave region); Nicholas 1955: 104, fig. ♀; Ander 1957: 91 (terminal abdominal structures); Park & Barr 1961: 144 (guano producer); Nicholas 1962a: iii, iv, 55-70, figs. 11-13, graph; 1962b: 102 (Cathedral Cave, Ky.; general biol. and ecol; behavior, nocturnal migrations); Barr 1963a: 158, and 1963b: 11 (trogloxene, facultative troglophile; with its guano, a primary food source in Ky. caves); Reichle 1963: 98, and Park & Reichle 1963: 126-7; 1964: 79 (ecol., behavior, circadian activity rhythm); Barr 1964a: 78-9; Barr 1964b: 322, cover photo (♀) (biol, egg predation by beetle *Neaphaenops*); Nicholas 1964: 62-3, and Mohr 1964a: 827, 834, color ill., 1964b: cover photo (nocturnal migrations); Reichle, Palmer & Park 1965: 55-7 (circadian activity rhythm); Vandel 1965: 178 *et passim* (biol.); Mohr & Poulson 1966: 28 *et passim*, figs. (biol.); Barr 1967a: 476, 477, 481, and 1967b: 155, 169 (in part: caves of Pennyroyal Plateau, [not] Cumberland Plateau, Ky.; biol.); Leroy 1967: 664, 669, 676, 683, 685 (review of biol. from lit.); Barr 1968: 51, 52, 65 (biol.); Poulson & Culver 1969: 155 (Flint Ridge cave system, Ky.; occurrence, population density); Barr & Kuehne 1971: 57 *et passim*, fig. 4 (review of biol.); Richards 1971b: 137, 1972: 28 (troglophile, not trogloxene); Poulson 1972: 55-9 (guano as food for other cave organisms); Barr 1973: 30 (biol.); Freeman et al. 1973: 121-2 (Lee Cave, Ky.; site requirements for oviposition); Nicholas 1974: B5/1-7, figs. 1-3 (behavior, longevity); Kane et al. 1975: 45 *et passim* (seasonal pattern of oviposition; incubation and hatching of eggs; predation by *Neaphaenops*); Norton et al., 1975: 55 *et passim* (egg and nymph predation by *Neaphaenops*).

Rhaphidophora cavernarum Saussure 1862: 492 (Mammoth Cave, Ky.); synonym.

Hadenoecus cavernarum (Sauss.) Scudder 1869: 408 (*subterraneus* Scudd. erroneously synonymized); I. Bolivar 1880: 71-2; Riley 1884: 184-5, fig. 260; Blatchley 1893: 153 (erroneously states that Cope 1872 recorded it from Wyandotte Cave, Ind.); Scudder 1894: 22-3, and 1899-1900: 80 (in part—only Ky. records); Rehn 1901: 337 (Mammoth Cave; variation); Kirby 1906: 135, and Caudell 1907: 290, 1916: 659 (*cavernarum* synonymized).

Erroneous records: Besides those cited under other species of *Hadenoecus*, the following: Walker 1871: 22 ("West coast of America" = *Tropidischia xanthostoma* Sc.); Simon 1973: 31-9 (Golden, Colo. = *Ceuthophilus utahensis* Thos., det. Hubbell 1974).

HADENOECUS CUMBERLANDICUS Hubbell and Norton, n. sp. (Figs. 5, h,i; 13, e; 10, 16 (maps).

Type: Female, Milk Cave, 1 mi E of Mill Springs, Wayne Co., Kentucky, 20 Sept. 1951 (W. B. Jones, J. M. Valentine); *allotype* a male with the same data; both preserved in alcohol, in UMMZ.

This species is almost indistinguishable from *H. subterraneus* except by the very different form of the ventral sclerite of the female subgenital plate, which is quite invariable and never approaches that characteristic of any of the other species. It is the only species of *Hadenoecus* present in eastern Kentucky, where it occupies caves along the western edge of the Cumberland Plateau and in adjoining parts of the Bluegrass Region, in the drainage basins of the Ohio, Licking, Kentucky and Cumberland rivers. In the southwest, as previously noted, its range is separated from that of *subterraneus* by the divide between the Cumberland River basin and the headwaters of the Green and Barren rivers, and at approximately the Tennessee line it gives place to *opilionoides*. Its northernmost populations, in Carter and Menifee Counties, are parthenogenetic.

DESCRIPTION OF FEMALE TYPE:[1] Length of body ca. 17.5, of pronotum 4.3 (3.4-4.7), of femur I 16.2 (12.9-16.6), of femur III 24.9 (20.3-26.6), of tibia III 31.9 (25.3-34.2), of ovipositor 13.2 (11.2-16.7), of antenna ca. 110 mm.

Very similar to females of *subterraneus*, differing as noted below. Coloration as described for that species but darker markings less distinct. Head and thorax like those of *subterraneus*; maxillary palpus 0.82 (to 0.96) times as long as femur I, its distal segment 1.10 (to 1.30) times as long as pronotum. *Legs* proportioned as in *subterraneus*; tibia I with 6/7 ventrocephalic and 7/7 ventrocaudal spurs; tibia II with 7/6 ventrocephalic and 5/6 ventrocaudal spurs (carinae of both legs with 5-7, usually 5-6 spurs); femur III 7.6 (to 9.5, mean 8.2) times as long as basal breadth, caudal genicular lobe with a minute spine (sometimes absent). Tibia III 1.28 (1.16-1.39, mean 1.26) times as long as femur III, cephalic and caudal dorsal carinae each with 6 spurs (5-8, mode 7 on both), subdistal ventral spurs 5/5 (2-6, usually 4 or 5) on cephalic and 3/3 (1-3, usually 2) on caudal margins; spine formulae of dorsal carinae, right and left: cephalic 38/13/10/10/0/0 = 71, 36/11/12/10/1/0 = 70, caudal 40/9/10/4/0/0 = 63, 43/11/9/7/0/0 = 70.

Terminal abdominal structures: Ovipositor like that of *subterraneus*, 3.0 (2.9-3.6, mean 3.3) times as long as pronotum, 0.8 (to 1.1, mean .91) times as long as femur I, 0.53 (0.50-0.65, mean 0.57) times as long as femur III, teeth of ventral valves 7 (5-8, mode 6). *Subgenital plate sclerite* (Fig. 13, e) subtrapezoidal, its distal margin concave and distolateral angles prolonged as in typical *subterraneus* (sometimes also with short admesal projections), sides convergent caudad, proximolateral arms narrowly triangular with narrowly rounded tips extending to base of plate, separated by a subquadrate mesoproximal membranous area distinctly broader than long, with straight, weakly convergent (to parallel) sides and nearly straight distal margin, its rim a little more heavily sclerotized than rest of sclerite but not at all elevated. *Seventh sternite* with proximal edge not sclerotized, without (or with mere traces of) the small dark proximolateral sclerotizations usually distinct in *subterraneus*, its surface evenly convex and very minutely and sparsely setose.

DESCRIPTION OF MALE ALLOTYPE: Similar in all respects to males of *subterraneus* and like female type except as noted. Length of body ca. 20, of pronotum 4.3 (3.3-4.6), of femur I 16.0 (11.7-16.5), of femur III 24.7 (18.0-25.5), of tibia III 31.8 (22.0-32.8), of antenna ca. 120 mm. *Legs:* Ventral spurs of tibia I 5/5 on cephalic, 6/6 on caudal carinae, of tibia II 7/6 on cephalic, 5/7 on caudal carinae (5-8, usually 5 or 6 on each carina of both legs); femur III 7.8 (6.6-8.5, mean 7.7) times as

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[1] Figures in parentheses give the range of variation in the entire series.

long as basal breadth. Tibia III 1.29 (1.14-1.40, mean 1.27) times as long as femur III; spurs of dorsocephalic carinae 7/6, of dorsocaudal carinae 6/6 (5-8, mode 7 on both), subdistal ventral spurs 4/5 (3-6, mode 4) on cephalic, 3/3 (mode 2) on caudal margins. Spine formulae of dorsal carinae of tibia III: cephalic 35/10/13/8/9/0/0 = 75, 39/12/12/8/0/0 = 71, caudal 37/16/8/4/0/0/0 = 65, 38/15/8/3/0/0/0 = 64. *Terminal abdominal structures* very similar to those of *subterraneus*, but mesal projection of dorsal lobe of phallus (Fig. 5, h,i) shorter, broader, less tapering, its lobes wider, thicker, and with more broadly arcuate margins.

VARIATION. *H. cumberlandicus* shows about the same range of variability in body proportions as does *subterraneus*. Southern material (from Russell, Pulaski, Wayne and McCreary counties) averages slightly larger than the mean of *subterraneus* and than parthenogenetic females from Carter County at the northern end of the species range, as shown in Table 5.

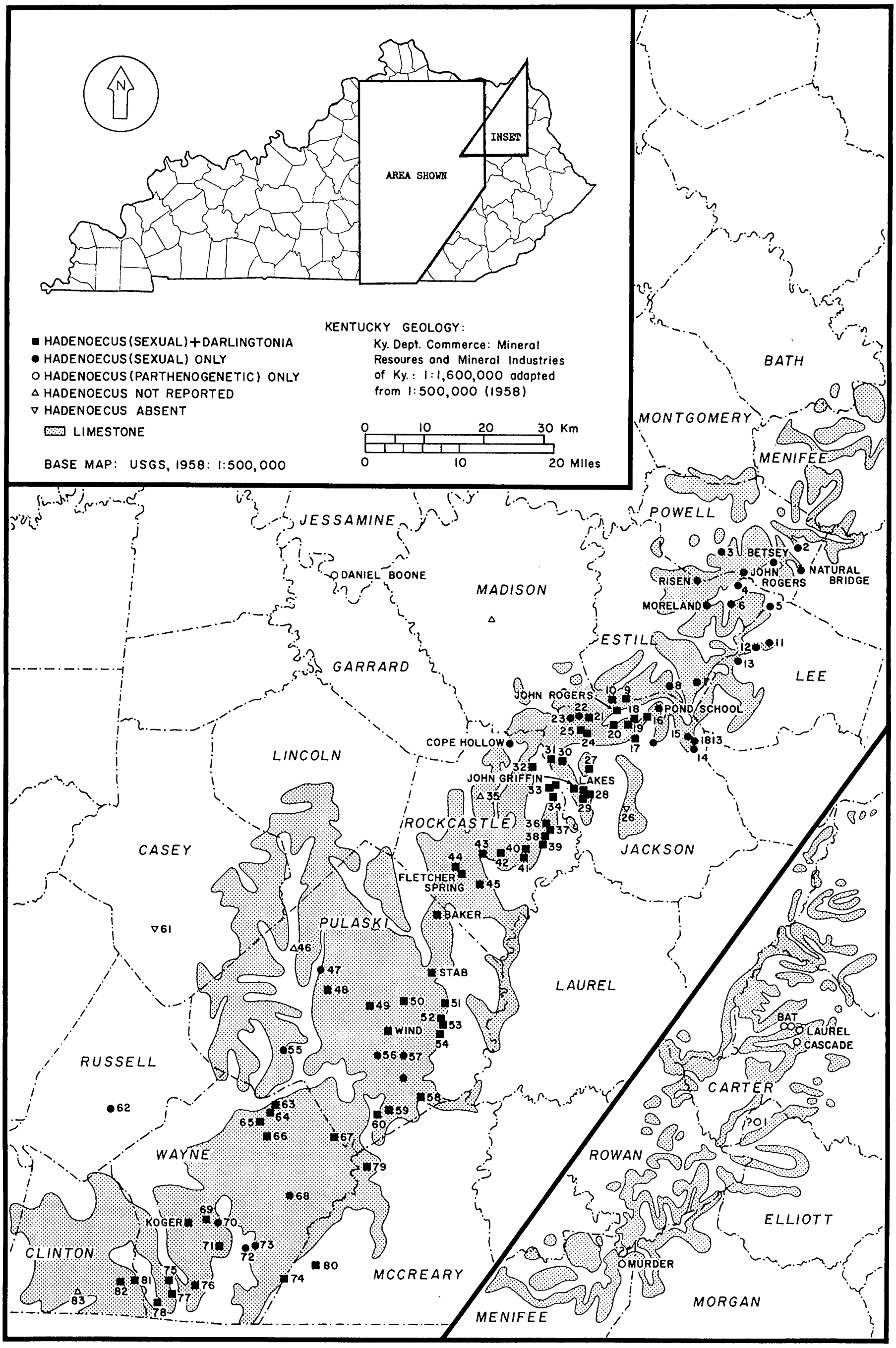
TABLE 5

DIMENSIONS OF *H. CUMBERLANDICUS* AND *H. SUBTERRANEUS*

	cumberlandicus (southern sexual) 91 ♂, 53 ♀		*cumberlandicus* (Carter Co. parthenogenetic) 35 ♀		*subterraneus* (whole range) 125 ♂, 136 ♀	
MALE	Mean	S.D.	Mean	S.D.	Mean	S.D.
Length of pronotum	4.02	0.10			3.56	0.26
Length of femur I	14.7	0.94			13.3	1.06
Length of femur III	23.3	1.41			20.8	1.53
Length of tibia III	29.5	1.92			26.2	1.98
FEMALE						
Length of pronotum	4.14	0.20	3.61	0.23	3.68	0.24
Length of femur I	14.9	0.84	14.1	0.70	13.3	0.93
Length of femur III	23.8	1.45	22.0	0.84	21.4	1.75
Length of tibia III	30.1	2.26	27.1	1.11	26.9	2.14
Length of ovipositor	13.5	0.89	12.9	0.85	11.8	0.99

Variation in the number of spurs and spines on the tibiae is nearly the same as that encountered in *subterraneus*, except that a larger proportion of individuals have no spines on the dorsal carinae of tibia III in the distal three spur-intervals.

SEXUAL AND PARTHENOGENETIC POPULATIONS. Throughout most of the range of *Hadenoecus cumberlandicus* (maps, Figs. 10, 16) only sexual populations are present, but all-female ones occur in a few caves at the northernmost and northwesternmost edges of the species' territory. No males are among the 108 specimens seen from caves in Carter Caves


N
INSET
AREA SHOWN
■ HADENOECUS (SEXUAL) + DARLINGTONIA
● HADENOECUS (SEXUAL) ONLY
○ HADENOECUS (PARTHENOGENETIC) ONLY
△ HADENOECUS NOT REPORTED
▽ HADENOECUS ABSENT
▨ LIMESTONE
BASE MAP: USGS, 1958: 1:500,000
KENTUCKY GEOLOGY:
Ky. Dept. Commerce: Mineral Resoures and Mineral Industries of Ky.: 1:1,600,000 adapted from 1:500,000 (1958)
0 10 20 30 Km
0 10 20 Miles
BATH
MONTGOMERY
MENIFEE
POWELL
JESSAMINE
DANIEL BOONE
MADISON
GARRARD
ESTILL
LEE
BETSEY
NATURAL BRIDGE
JOHN ROGERS
RISEN
MORELAND
POND SCHOOL
COPE HOLLOW
JOHN GRIFFIN
LAKES
LINCOLN
ROCKCASTLE
JACKSON
CASEY
FLETCHER SPRING
BAKER
PULASKI
STAB
WIND
LAUREL
RUSSELL
WAYNE
KOGER
CLINTON
MCCREARY
BAT
LAUREL
CASCADE
CARTER
ROWAN
ELLIOTT
MURDER
MORGAN
MENIFEE

State Park in Carter County,[1] and Lamb and Willey (1975) reported none among the 117 specimens they collected there, and observed none in the caves. Those authors also state that no males were included among the 131 specimens collected in Murder Cave in Menifee County, and Norton informs me that only females are present in Daniel Boone Cave in Jessamine County. Females from the parthenogenetic populations do not differ morphologically from those of the sexual ones, except for their slightly smaller average size and somewhat shorter ovipositors relative to leg length. This situation is discussed in Part II, and a hypothesis is there proposed to explain the origin and maintenance of the all-female populations on the northern edge of the range.

ECOLOGY, BEHAVIOR AND LIFE HISTORY. These topics are dealt with by Norton in Part III of this study.

Fig. 16. The distribution of caves with populations of *Hadenoecus cumberlandicus* and of its predator, *Darlingtonea kentuckensis*, in eastern Kentucky (map prepared by Norton). (*Hadenoecus* can spread overland and consequently has a slightly greater range than *Darlingtonea*, which is chiefly limited to subterranean dispersion). Names of numbered caves are as follows: *Elliott Co.:* 1–Clay Fork; *Powell Co.:* 2–Cave Branch; 3–Nowland; *Estill Co.:* 4–Prairie Hall; 5–Crack; 6–Peter; 7–Crybaby; 8–Sparks Saltpeter; 9–Happy Top; 10–Clifford Pearson; *Lee Co.:* 11–Ash; 12–Cave Hollow; 13–Spruce Pine; *Jackson Co.:* 14–Spring; 15–Wind; 16–Lainhard #1; 17–Viney Bottoms; 18–Big Hollow; 19–Hiksey; 20–Morning Hole; 21–Blowing Spring; 22–Clemons; 23–Smilax; 24–Rises; 25–Sinks; 26–Coles; 27–Mud; 28–Swimming Hole; 29–Horse Lick Creek; 30–John Henry; 31–Bowman Saltpeter; *Rockcastle Co.:* 32–Climax; 33–Crooked Creek (2); 34–Smokehole; 35–Greenhill; 36–Mullins Spring; 37–Great Saltpeter; 38–Ice; 39–Teamers; 40–Cinder; 41–Sinks; 42–Pine Hill; 43–Duvalt; 44–Fletcher Spring Pit; 45–Marlow; *Pulaski Co.:* 46–Dumpling; 47–Andes; 48–Girdler; 49–Richardson; 50–Piney Grove; 51–Pourover; 52–Whetstone; 53–Saltpeter; 54–Dykes; 55–Burton; 56–Old Kentucky; 57–Coral; 58–Hydens; 59–Sloans Valley; 60–Tater; *Casey Co.:* 61–Indian; *Russell Co.:* 62–Millers; *Wayne Co.:* 63–Cooper; 64–Hogg (= Hog); 65–Milk; 66–Lasher Steele; 67–Keith; 68–Clark Spring; 69–Hurt; 70–Sumpter; 71–Elmer Hurt; 72–Blue Hole Hollow; 73–Johnson Fork; 74–Lonesome; 75–Jesse; 76–Triple S; 77–Wind; 78–Blowing; *McCreary Co.:* 79–Eureka; 80–Steele Hollow; *Clinton Co.:* 81–Will (= Columbus Flowers); 82–Copperas Saltpeter; 83–Shipley.

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[1] Packard (1888: 16, 17) recorded *Hadenoecus subterraneus* from the Carter Caves (Bat, Zwingle's and X caves). Examination of the specimens upon which these records are based (in ANSP ex MCZ) and others labelled "VanMeter's Meat Cave," another of the Carter Caves, shows that both males and females are represented, but the females are all typical *subterraneus* and the collections are certainly mislabelled. At the time they were supposedly made Packard was doing much work in the Mammoth Cave area, from which these specimens undoubtedly came.

SPECIMENS EXAMINED: 623—173♂, 239♀ (including type, allotype and paratypes, the latter exclusive of parthenogenetic females), and 211 juveniles, as follows:

Sexual Populations

KENTUCKY: *Jackson Co.:* John Griffin Cave, 2 Mar 1968 (M) 4♂, 23♀; John Rogers Cave, 17 Sept 1966 (J. Reddell, W. Andrews) 1 juv; 17 Mar 1968 (M) 3♂, 15♀; 9 Jan 1975 (N) 5♂; Lakes Cave, 2 Mar 1968 (M) 1♂, 12♀; *McCreary Co.:* Steele Hollow Cave, 2 mi S of Griffin, 26 Sept 1964 (B, N) 1♂, 1♀ [B]; *Powell Co.:* Betsey Cave, 4 mi SSE of Bowen (O. Krekeler, J. Rittman) 1 juv ♂ [K]; Natural Bridge Cave, Natural Bridge State Park, 27 Aug 1956 (D. C. Eades, J. Liu) 7♂, 8♀, 15 juvs [Lamb & Willey, 1975: 721 reported 79♂, 61♀ from this cave]; *Pulaski Co.:* Baker Cave, 2 Mar 1968 (M) 4♂, 27♀; Cumberland Cave, 6 mi E of Burnside, 14 Apr 1939 (Fr) 4 juv ♂, 3 juv ♀; Diamond Cave, 3.5 mi NW of Somerset, 6 Nov 1949 (J, V) 6♂, 5♀, 6 juvs [ALA]; Dykes Cave, 10 mi E of Somerset, 10 Nov 1949 (J, V) 2♂, 3♀, 11 juvs [ALA]; Mill Creek (Hargis) Cave, 11 mi SE of Somerset, 10 Nov 1949 (J, V) 12♂, 6♀, 3 juvs [ALA]; Richardson Cave, 2.5 mi E of Somerset, 29 Nov 1949 (J, V) 11♂, 10♀, 2 juvs [ALA]; Sloans Valley (Cassidy) Cave, 6 mi E of Burnside (now flooded), 7 Nov 1949 (J, V) 7♂, 1♀, 6 juvs [ALA]; 7 Apr 1963 (A) 5♂, 3♀, 2 juvs; Stab Cave, at Stab, 14 Sept 1973 (N) 4♂; Taylor Cave (probably = Stab Cave), at Stab, 10 Nov 1949 (J, V) 12♂, 11♀, 2 juvs [ALA]; Wind Cave, ca. 4.5 mi E of Somerset, 29 Nov 1974 (L) 9♂, 11♀ (2 with spermatophores), 6 juvs [Lamb, UMMZ]; 7 Jan 1975 (N) 4♂; *Rockcastle Co.:* Fletcher Spring Cave, 8 Jan 1975 (N) 5♂; Cave nr Mt. Vernon (Pine Hill Cave?), Aug 1961 (L. Carr) 2♀; Millers Pit #1, 10 Nov 1972 (T. Siebert) 1♂ [Siebert]; *Russell Co.:* Millers Cave, 3 mi S of Jamestown, 31 July 1964 (B, P) 1♀, 3 juvs [B]; *Wayne Co.:* Cooper Cave, 3 mi E of Mill Springs, 20 Sept 1951 (J, V) 7♂, 7♀, 5 juvs [ALA]; Hogg Cave, 1 mi E of Mill Springs, 7 Nov 1951 (J, V) 11♂, 14♀, 4 juvs [ALA]; across river from Jones Cave, 12-13 June 1925 (C. L. Hubbs) 12♂, 7♀, 11 juvs; Koger Cave, 7 Jan 1975 (N) 4♂; Lasker Steele Cave, 3 mi SE of Monticello, 21 Sept 1951 (J, V) 10♂, 10♀, 7 juvs [ALA]; Luke Hines Cave, 0.5 mi E of Mill Springs, 22 Dec 1955 (G. Kinney, L. Cross) 6♂, 3 juvs; Milk Cave, 1 mi SE of Mill Springs, 20 Sept 1951 (J, V) 8♂, 10♀ (including type and allotype), 9 juvs [UMMZ, ALA]; Peter Cave, 5 mi SW of Mill Springs, 20 Sept 1951 (J, V) 7♂, 6♀, 6 juvs [ALA]; Wind Cave, 4 mi NW of Slick Ford, 21 Sept 1951 (J, V) 2♀, 3 juvs [ALA].

Parthenogenetic Populations

KENTUCKY: *Carter Co.:* Carter Caves State Park: Bat Cave, 14 Aug 1874 (S) 3 juv ♀ [ANSP]; (15 May 1874) (Pa) 3♀, 9 juv ♀ [ANSP]; 22 Jan 1944 (W. C. Stehr) 1♀, 9 juv ♀ [OU]; 4 Nov 1950 (P. J. Spangler) 1 juv ♀; no date (B) 1♀, 2 juv ♀ [B]; 23 Nov 1973 (R. C. Willey, L) 1 juv ♀ [Lamb & Willey, 1975: 721, report 171♀s, no ♂s from this cave]; Burchells Cave (S) 2♀ [ANSP]; Laurel Cave, 10 July 1973 (A. Mesa, H) 1♀, 4 juv ♀; Cave in front of hotel (Pa) 10 juv ♀ [ANSP]; Caves unspecified, 1 Sept 1946 (J. & R. Bailey) 2 juv ♀; 16 Aug (W. Trailer) 2 juv ♀; 19 Nov 1949 (P. J. Spangler) 2 juv ♀; 26 Aug 1956 (D. C. Eades, J. Liu) 25♀, 24 juv ♀; *Jessamine Co.:* Daniel Boone Cave, 8 Nov 1949 (J, V) 4 juv ♀ [ALA]; 15 Aug 1963 (B) 5 juv ♀ [B] (population of this cave certainly parthenogenetic—Norton); *Menifee Co.:* Murder Cave, ca. 7.8 mi NNW of Ezel, May-Dec 1972 (R. B. Willey, L) 10♀ [Lamb & Willey (1975: 721) report 131♀, no ♂s collected here, no ♂s seen].

References in Literature

Hadenoecus subterraneus of authors, not of Scudder 1861: Records from Carter Caves, Ky., by Packard 1888: 16, 70, Bolivar & Jeannel 1931: 311, and Wolf 1934-38: vol. 2 (cave records), vol. 3: 158-9. Barr 1967b: 169 (in part: along W edge of Cumberland Plateau in eastern Kentucky); Rebman 1972: cover ill. (good photo of ♂, Muellen Springs Cave, Rockcastle Co., Ky.).

Hadenoecus cavernarum of authors, not of Saussure 1862: Records from Carter Caves, Ky., by Scudder 1894: 22-3.

Hadenoecus sp. A: Lamb & Wiley 1975: 721-2 (sexual population in Natural Bridge Cave, Powell Co., Ky.; parthenogenetic populations in Bat Cave, Carter Co., and Murder Cave, Menifee Co., Ky.).

HADENOECUS OPILIONOIDES Hubbell, n. sp. (Figs. 6; 12, a,d; 13, f,g; 14, e,f; 10, 17 (maps); Pl. II, g; Pl. III, g).

Type: Female, Small cave in Buffalo Cove, Fentress Co., Tenn, 27 Aug 1962 (T. H. & S. P. Hubbell); *allotype* a male with the same data; both preserved in alcohol, in UMMZ.

This species, confined to the western edge of the Cumberland Plateau and adjacent portions of the Highland Rim in northern Tennessee, differs from the others of the genus in the form of the male paraprocts and the sclerite of the female subgenital plate, as described in the key. In body proportions and leg armature it most closely resembles *barri*; in both species the average length of femur I relative to pronotal length and of femur III relative to basal breadth is greater than in *subterraneus* and *cumberlandicus* and less than in *jonesi.* The average number of denticles on the dorsal carinae of tibia III is about 75 in *subterraneus*, 65 in *cumberlandicus*, and 50 in *opilionoides, barri* and *jonesi*; in the last four, also, there is a higher proportion of individuals having three distal interspur intervals without denticles, although the mode is two (mode one in *subterraneus*).

DESCRIPTION OF FEMALE TYPE:[1] Length of body ca. 14.5, of pronotum 4.0 (3.7-4.4), of femur I 15.9 (14.3-16.5), of femur III 23.6 (21.2-26.0), of tibia III 29.9 (27.4-30.0), of ovipositor 13.9 (12.0-15.5), of antenna 121 mm.

Very similar to females of *subterraneus*, differing as noted below. Dorsum dilute ochraceous orange, almost without darker markings; fastigium, face, palpi, venter and distal portions of tibiae and tarsi paler, very dilute warm buff; ovipositor ochraceous orange. *Head* and *thorax* as described for *subterraneus. Legs:* femur I 3.95 (3.6-4.1) times as long as pronotum, tibia I 1.06 (1.0-1.15) times femur I, ventral carinae of tibia I and II each with 5 spurs (4-6, mode 5); minute spine on caudogenicular lobe of femur II (often absent); femur III 5.9 (5.0-6.2) times as long as pronotum, 9.2 (7.8-9.4, mean 8.6) times as long as basal breadth, caudal genicular lobe unarmed (often with minute spinule); tibia III 1.27 (1.22-1.37) times as long as femur III, spurs of dorsal carinae, cephalic 6/6, caudal 7/7 (5-8, mode 7 on both carinae), subdistal ventral spurs 2/2 (2-4, mode 2) on cephalic, 2/2 (1-2, mode 2) on caudal margins; spine formulae of dorsal carinae, right and left: cephalic 35/14/12/3/0/0 = 64, 37/14/8/2/0/0 = 61, caudal 25/12/9/6/1/0/0 = 53, 29/14/10/8/1/0/0 = 62.

Terminal abdominal structures; Ovipositor (Fig. 14, e,f) like that of *subterraneus*, 3.5 (3.2-3.7) times as long as pronotum, 0.9 (0.8-0.95)

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[1] Figures in parentheses give the range of variation in the entire series studied, including the subspecies *H. o. australis* described below.

times as long as femur I, 0.6 (0.55-0.62) times as long as femur III, teeth of ventral valves 6 (5-6, mode 6). *Subgenital plate* (Fig. 13, f,g) with gently convex, faintly bilobate distal edge, margins widely membranous; ventral sclerite a curved subplanate bar of moderate and subequal width, its middle portion gently arcuate distad, sides more strongly incurved, their ends briefly obliquely truncate along proximal edge of plate, with subacute inner angles, sides of bar before ends explanate as a pair of subquadrate lateral wings; membranous mesoproximal area semielliptic, with convex distal margin and more strongly rounded, slightly incurvate sides, about twice as broad as long and widely open; margins of sclerite bordering this space a little more heavily sclerotized than remainder but not forming a raised rim. *Seventh sternite* with a very narrow, weakly sclerotized edging along proximal border, its ends slightly widened; surface of sternite evenly convex, not tumid proximad, minutely, evenly and sparsely setose.

DESCRIPTION OF MALE ALLOTYPE: Length of body ca. 14.5, of pronotum 4.0 (3.5-4.2), of femur I 16.2 (14.0-17.0), of femur III 23.7 (20.3-25.8), of tibia III 30.6 (26.8-33.5), of antenna ca. 105 mm (paratopotype, Fig. 12, a).

Agrees with female type except as noted. *Legs:* femur I 4.25 (3.8-4.4, mean 4.1) times as long as pronotum; femur III 6.4 (5.7-6.7, mean 6.2) times as long as pronotum, 8.8 (8.3-9.8, mean 8.9) times as long as proximal breadth; tibia III 1.35 (1.23-1.40) times as long as femur III, spurs of dorsal carinae, cephalic 8/7, caudal 7/7 (6-8, mode 7 on both carinae), subdistal ventral spurs 3/2 (2-3, mode 2) on cephalic margins, 2/2 (1-3, mode 2) on caudal margins; spine formulae of dorsal carinae, right and left, cephalic 27/10/5/0/0/0 = 42, 19/9/10/4/0/0 = 42; caudal 21/8/10/5/2/0/0 = 46, 21/11/9/3/0/0/0 = 44.

Terminal abdominal structures (Pl. II, g; Pl. III, g; extruded phallus, Fig. 6): Cercus 1.5 (to 1.8) times as long as pronotum. *Paraprocts* in side view rather broad, their dorsal and ventral margins gently convergent distad in proximal half, thence subparallel, both gently decurved; apical breadth very slightly less than proximal; distal end obliquely subtruncate, its edge forming a distinct angle with dorsal margin; ventral margin bordered by a low ridge extending distad from cercal base and merging into convex outer face of apex; distal end narrowly margined with membrane along lower edge; in dorsal aspect paraprocts incurved distad, their straight distal margins attingent end to end; apices in distal aspect distinctly decurved, with mesal edges attingent except at the narrowly rounded ventral tips.

VARIATION. In addition to the geographic variation described below, on the basis of which two subspecies of *opilionoides* are distinguished, there is a considerable amount of variability in size, proportions and leg armature that is about the same in all populations. The range of variation in measurements and in spur-counts given in the above descriptions applies to the entire species. In the whole series, also, the number of denticles on the dorsal carinae of tibia III ranges from 34 to 64, with a mean of about 50, and the number of denticle-free distal inter-spur intervals varies from 1 to 4, with 2 most common and 3 almost as frequent.

The condition of the female subgenital plate sclerite and the male paraprocts present in the types of *opilionoides* and described above is characteristic of material from the northern part of the range of the species, in Clay, Fentress and Pickett counties, Tennessee. Farther south in that state, in Overton, Putnam, Van Buren and White counties, all the populations agree in having a somewhat different condition of those structures that is quite constant. The differences are greater than those that exist between the typical and southwestern populations of *subterraneus,* and unlike the situation in that species, intergradation between the northern and southern forms has not been observed, although it is presumed to occur in the narrow zone between them. For these reasons the northern and southern populations are considered subspecifically distinct, and the latter is described below.

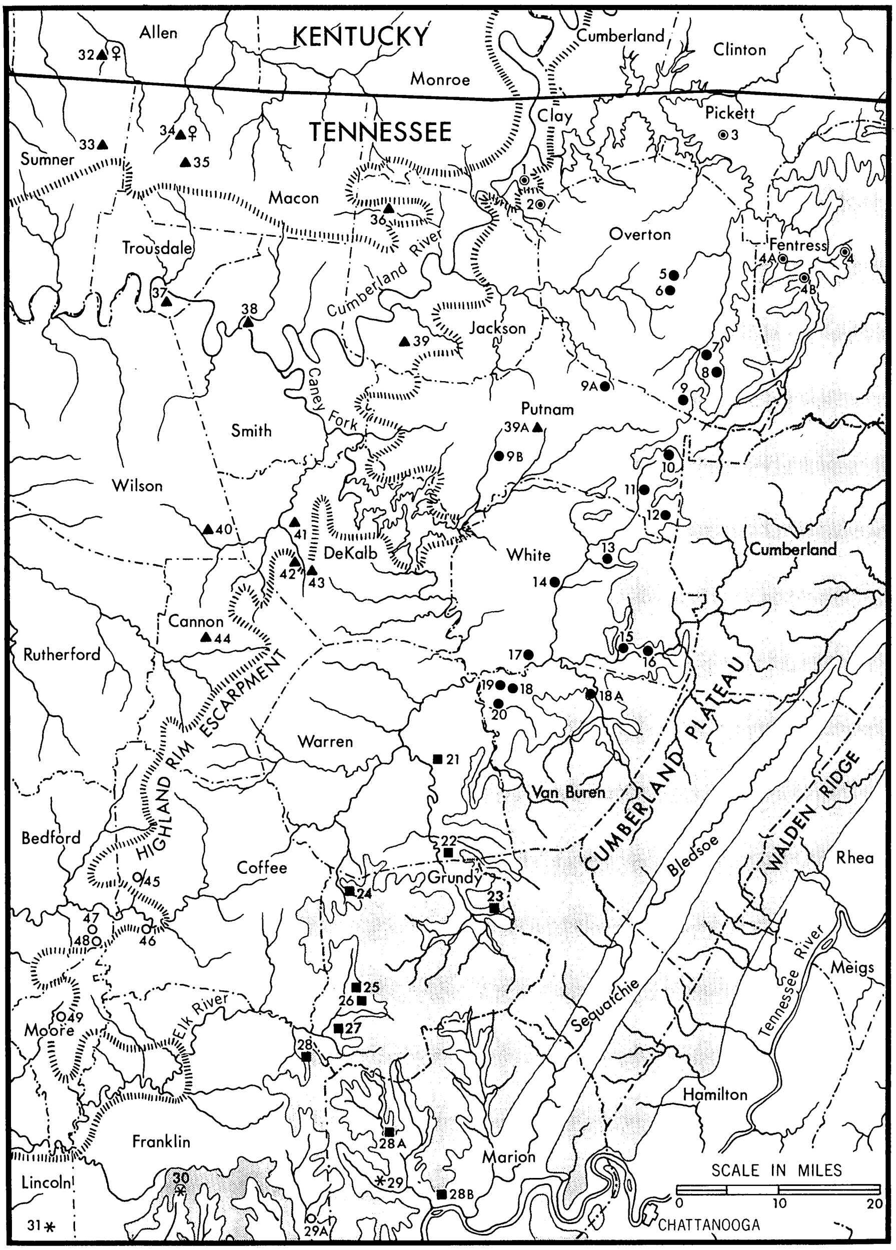
HADENOECUS OPILIONOIDES AUSTRALIS Hubbell, ssp. nov. (Figs. 13, h; 10, 17 (maps)).

Type: Female, Indian Cave, White Co., Tennessee, 17 Aug. 1975 (L. & M. Matthews, L. Adams, M. Biache); *allotype* a male with the same data; both preserved in alcohol, in UMMZ.

Distinguished from *o. opilionoides* as follows: *Female subgenital plate sclerite* (Fig. 13, h) narrower, less strongly curved, its lateral expansions situated nearer the ends of the bar and forming with them broad, subacute triangular sclerotizations that are not (or scarcely) incurvate; membranous area within the curve of the sclerite more transverse, about twice as wide as long, semielliptic, widest along proximal edge of subgenital plate. *Male paraprocts* with their distal ends more membranous and tumid on outer face, attingent only dorsad, divaricate ventrad and their ventral angles broadly rounded.

Dimensions of types: Length of body, ♀ 17.9, ♂ 17.5 m; length of pronotum, ♀ 4.29, ♂ 3.72 mm; length of femur I, ♀ 17.2, ♂ 15.7 mm; length of femur III, ♀ 26.0, ♂ 23.6 mm; length of tibia III, ♀ 32.9, ♂ 30.0 mm; length of ovipositor, ♀ 15.3 mm (ovipositor with 7 teeth). Spine formula of dorsal carinae of tibia III, right and left: ♀ cephalic 40/7/6/8/4/0/0 = 65, 38/13/7/7/0/0 = 65, caudal 44/8/10/6/3/0/0 = 71, 49/9/6/3/0/0 = 67; ♂ cephalic 32/10/6/5/0/0 = 53, 27/15/10/8/0/0 = 60, caudal 37/10/6/4/0/0 = 57, 40/10/6/3/0/0 = 59. Subdistal ventral spurs of tibia III, right and left: ♀ cephalic 3/2, caudal 2/2; ♂ cephalic 2/3, caudal 1/1.

Variation in size, proportions and leg armature is about the same in *H. o. australis* as in the typical subspecies and is included in that given


KENTUCKY
TENNESSEE
Allen
Monroe
Cumberland
Clinton
Clay
Pickett
Sumner
Macon
Overton
Fentress
Trousdale
Jackson
Putnam
Smith
Wilson
DeKalb
White
Cumberland
Cannon
Rutherford
Warren
Van Buren
Bedford
Coffee
Grundy
Bledsoe
Rhea
Meigs
Moore
Franklin
Marion
Hamilton
Lincoln
Cumberland River
Caney Fork
Elk River
Sequatchie
Tennessee River
HIGHLAND RIM ESCARPMENT
CUMBERLAND PLATEAU
WALDEN RIDGE
CHATTANOOGA
SCALE IN MILES
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20
1
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4A
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for the species as a whole. The female subgenital plate sclerite varies slightly in curvature, in the wideth of the band connecting the broadened ends, and in the exact shape of the latter in the populations of different caves. There are also minor variations in the form of the paraproct apices and the degree of their divarication.

DISTRIBUTION. The range of *H. opilionoides* extends along the western edge of the Cumberland Plateau and the adjacent Highland Rim in northern and central Tennessee (maps, Figs. 10, 17). On the north the valley of the Cumberland River separates it from that of *subterraneus* and from the main body of the range of *cumberlandicus.* The latter species, however, occurs south of the Cumberland River in southernmost Kentucky, where the interfluve between the Wolf and Cumberland drainages appears to mark the boundary between it and *opilionoides.* The caves from which the last-named is known are situated in the valleys of creeks flowing into the Cumberland and Obey rivers and the northern and eastern headwaters of Caney Fork, itself a tributary of the Cumberland. No evident barrier separates the ranges of *o. opilionoides* and *o. australis.* The latter and *H. barri* occur in caves separated by only a few miles; *barri* occupies the southern headwater areas of Caney Fork and also territory drained by tributaries of the Elk River, which flows into the Tennessee. Thus the ranges of *cumberlandicus, opilionoides* and *barri* are not separated by major divides or any other apparent barrier, making it difficult to account for the differentiation and strictly allopatric distribution of these species. Possible explanations for this situation are discussed in Part II.

SPECIMENS EXAMINED: 423–98♂, 122♀ (including the types and paratypes of both subspecies), and 203 juveniles, as follows:

Fig. 17. The known distribution of populations of *Hadenoecus opilionoides, H. barri* and, in part, of *H. jonesi* and *Euhadenoecus insolitus.* Names of numbered caves are as follows: *Hadenoecus o. opilionoides* (circled dot): 1–Bailey; 2–Tom Daley; 3–Bunkum; 4–Caves in Buffalo Cove; 4A–Strawberry Sink; 4B–East Fork Saltpeter. *Hadenoecus o. australis* (solid circle): 5–Wash Lee; 6–Copeland Saltpeter; 7–Three Forks; 8–Falling Springs; 9–Neeley; 9A–Talent Hollow; 9B–TTU Cave; 10–Verble Hollow Falls; 11–Johnson; 12–Bridge Creek; 13–Blue Spring; 14–Ward; 15–Lost Creek; 16–Virgin Falls; 17–Indian; 18–Big Bone; 18A–Cliffside; 19–McElroy; 20–Laurel Creek. *Hadenoecus barri* (square): 21–Cumberland Caverns; 22–Hubbards; 23–Caves in Savage Gulf; 24–Hubbards Saltpeter; 25–Nunelly; 26–Payne Saltpeter; 27–Wonder; 28–Dry; 28A–Logging Camp; 28B–Kimball. *Hadenoecus jonesi* (star): 29–Honeycutt; 30–Caroline Cove; 31–Elora Spring. *Euhadenoecus insolitus* (Triangle; ♀ = parthenogenetic populations): 32–Grandmother; 33–Mason; 34–Aunt Beck Simmons; 35–Ann White; 36–Pilot Knob; 37–Alan Duncan # 1; 38–Petty Bluff; 39–Carter; 39A–Ament; 40–Hayes; 41–Avant; 42–Indian Grave Point; 43–Cripps Mill; 44–Tenpenny. *Caves in which no Hadenoecini were found* (open circle): 29A–Crownover Saltpeter; 45–Riley Creek; 46–Crumpton; 47–Bishop; 48–Ray; 49–Dance. [West of the areas shown on this map Barr found no Hadenoecini in the following caves: Bromley, Lawrence Co.; Benderman, Maury Co.; Inman, Perry Co., and De Priest Branch, Hickman Co.].

Hadenoecus o. opilionoides

TENNESSEE:[1] *Clay Co.:* Bailey Cave (B: 122), 19 Oct 1948 (J, V) 2♂, 3♀, 4 juvs [ALA]; *Fentress Co.:* Small cave on east face of Buffalo Cove (Now destroyed by quarry), 11 Aug 1922 (H) 1♂; Small cave in north end of Buffalo Cove, ca 5 mi SW of Jamestown, elev 1300 ft 27 Aug 1962 (T. H. & S. P. Hubbell) 42♂, 43♀ (including types of *o. opilionoides*), 59 juvs; Buffalo Cove, in rock crevices around mouth of small spring, 11 July 1973 (A. Mesa, H) 1♀, 18 juvs; East Fork Saltpeter Cave, FE-58, 36° 21′ 05″ N, 85° 01′ 45″ W, elev 860 ft (Ne) 3 juvs; Strawberry Sink Cave, FE-56, 36° 21′ 52″ N, 85° 04′ 10″ W, elev 1210 ft (Ne) 4 juvs; *Pickett Co.:* Bunkum Cave (B: 363), 17 Sept 1950 (J, V) 1♂, 3♀, 9 juvs [ALA].

Hadenoecus o. australis

TENNESSEE: *Overton Co.:* "Ealey Cave" (=? Neeley Cave, B: 346), 22 Mar 1949 (J) 4♂, 4♀, 5 juvs [ALA]; Falling Springs Cave (Falling Water Cave) (B: 344), 23 Sept 1949 (J, V) 2♂, 4♀, 17 juvs [ALA]; 22 Mar 1949 (J) 1♂, 3 juvs [ALA]; Gigur Cave, Oct 1948 (J) 3♂, 1♀, 1 juv [ALA]; [Copeland] Saltpeter Cave (B: 342), (J) 3♂, 3♀, 1 juv [ALA]; Three Forks Cave (B: 351), 22 Mar 1949 (J, V) 1♂, 3♀, 2 juvs [ALA]; Wash Lee Cave (B: 351), 5 Apr 1935 (C. L. Hubbs) 1♂, 1♀, 1 juv; *Putnam Co.:* [Bridge] Creek Cave (B: 374), 31 Mar 1949 (J, V) 2♂, 8♀, 17 juvs [ALA]; Johnson Cave (B: 380), 20 Oct 1948 (J, V) 4 juvs [ALA]; 26 Mar 1949 (J, V) 2♂, 8♀, 17 juvs [ALA]; 12 Apr 1975 (Ma) 2♂, 1♀, 4 juvs; Talent Hollow Cave, PU-130, 36° 12′ 36″ N, 85° 22′ 52″ W, elev 1080 ft (Ne) 1♀, 2 juvs; TTU Cave, PU-121, 36° 06′ 50″ N, 85° 32′ 58″ W, elev 1000 ft (Ne) 1♂, 1♀, 4 juvs; Verble Hollow Falls Cave (Upper Verble Hollow Cave), 36° 07′ 15″ N, 85° 16′ 13″ W, 19 Apr 1975 (Ma) 2♂, 1♀, 2 juvs; *Van Buren Co.:* Big Bone Cave (B: 451), (Ne) 3♂, 1♀, 1 juv; [Big] Bone Cave East (B: 451), 12 Apr 1975 (J. Hodson) 3♂, 2♀; Cliffside Cave, VB-122, 35° 45′ 26″ N, 85° 23′ 22″ W, elev 1120 ft (Ne) 1♀, 3 juvs; Laurel Creek Cave, 35° 42′ 36″ N, 85° 28′ 47″ W, 25 May 1975 (J. Hodson) 3♂, 1♀, 2 juvs; McElroy Cave (B: 464), 25 Mar 1949 (J, V) 4♂, 6♀, 5 juvs [ALA]; 27 Jan 1970 (T. G. Marsh et al.) 1♀; *White Co.:*[2] Blue Spring Cave (Bob Hill Cave) (B: 505), 25 Mar 1949 (J, V) 4♂, 6♀ 5 juvs [ALA]; Indian Cave (B: 508), 17 Aug 1975 (Ma) 4♂, 3♀ (including the types of *o. australis*); Lost Creek Cave (B: 608), 12 Oct 1975 (Ma) 3♂, 2♀; (Ne) 1♀, 2 juvs; Virgin Falls Cave, 35° 50′ 22″ N, 85° 19′ 52′ W, 11 Oct 1975 (Ma) 2♂, 2♀, 1 juv; Ward Cave (B: 517), 17 July 1969 (M, Ca) 1♀, 2 juvs.

Reference in Literature

Hadenoecus subterraneus, not of Scudder 1861: Barr 1961: 39-41 (in part: Cumberland Plateau and Highland Rim, Tennessee).

HADENOECUS BARRI[3] Hubbell, n. sp. (Figs. 13, i; 10, 17 (maps)).

Type: Female, Cumberland Caverns, Warren Co., Tennessee, Aug 28, 1962 (T. H. & S. P. Hubbell); *allotype* a male with same data; both in alcohol, UMMZ.

This species differs from the very similar *opilionoides,* which it replaces in south-central Tennessee, in the distinctive form of the female subgenital plate sclerite and by having the apices of the male paraprocts narrower, more heavily sclerotized, and not conspicuously swollen laterad.

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[1] Most of the Tennessee caves listed are described and located by Barr (1961), page references to which, e.g. (B: 122), follow the cave names.

[2] *Hadenoecus* sp. (almost certainly *o. australis*) was recorded in field notes by T. C. Barr, Jr. as present on 19 Feb 1961 in Ike Leary Cave on Walker Mountain and in Slatton Cave, both in this county. In the second of these caves the millipede *Ameractis satis* Causey was very abundant in a low crawlway at the back, probably feeding on the *Hadenoecus* guano.

[3] Named for Dr. Thomas C. Barr, Jr., who has aided us in this study and whose work has contributed so importantly to a knowledge of the cave faunas of eastern North America and the systematics and ecology of some of their constituents.

DESCRIPTION OF FEMALE TYPE:[1] Length of body ca. 25, of pronotum 4.4 (to 3.5), of femur I 17.5 (to 14.2), of femur III 25.0 (to 21.5), of tibia III 32.8 (27.8-33.6), of ovipositor 15.0 (to 11.9), of antenna ca. 115 mm.

Coloration and other features as described for *opilionoides* except as noted. *Legs:* Femur I 3.94 (3.6-4.2) times as long as pronotum; tibia I 1.1 (to 1.0) times as long as femur I, ventral carinae with 6/5 cephalic, 5/5 caudal spurs (mode 5 on both), tibia II with 4/5 cephalic, 5/5 caudal spurs (mode 5 on both); femur III 5.6 (5.4-6.1) times as long as pronotum, 8.8 (7.7-9.4) times as long as basal breadth; tibia III 1.3 (1.2-1.4) times as long as femur; dorsal spurs (cephalic) 6/7 (4-7, mode 6-7), (caudal) 7/7 (6-7, mode 7); predistal ventral spurs, cephalic 3/2 (2-4, mode 2), caudal 2/1 (1-2, mode 2); spine formulae of dorsal carinae: (cephalic) 38/14/6/4/0/0 = 62, 42/14/6/5/0/0/0 = 67, (caudal) 41/14/3/5/1/0/0 = 61, 32/9/10/6/2/0/0 = 59.

Terminal abdominal structures: Ovipositor like that of *subterraneus,* 3.4 (3.0-3.7) times as long as pronotum, 0.9 (0.8-0.95) times as long as femur I, 0.6 (0.5-0.65) times as long as femur III, teeth of ventral valves 7 (5-7, mode 6). *Subgenital plate* (Fig. 13, i) with broadly paraboloid margin that is weakly emarginate mesad; its sclerite consisting of two broad subtriangular lateral wings connected distad by a short narrow bridge; distal edge of sclerite bracket-shaped, distolateral angles rounded, a narrow brownish band of heavier sclerotization extending nearly the full width of sclerite just inside its distal margin; membranous area between lateral wings subtriangular with nearly straight sides and narrowly rounded distal angle; proximal ends of wings not reaching proximal edge of plate, subacute (to rounded). *Sternite VII* with anterior margin very narrowly sclerotized, surface slightly bulged or with a small weakly sclerotized conical point mesoproximad but not forming an elevated ridge, setae sparse, all minute.

DESCRIPTION OF MALE ALLOTYPE: Length of body ca. 22, of pronotum 4.2 (to 3.4), of femur I 16.3 (to 13.2) of femur III 24.3 (20.2-25.3), of tibia III 31.5 (26.7-32.6), of antenna ca. 105 mm. Coloration, proportions and leg armature as in female, except femur III relatively longer and more slender, 5.9 (5.6-7.1) times as long as pronotum and 9.4 (to 8.0) times as long as basal breadth. Spine formulae of dorsal carinae of tibia III, right and left: cephalic 39/12/7/3/0/0 = 61, 28/16/6/3/0/0 = 53, caudal 29/10/9/6/3/0/0 = 57, 40/11/8/4/0/0 = 63.

Terminal abdominal structures: As described for *opilionoides* except as follows. Paraprocts in side view with dorsal and ventral margins weakly convergent in proximal half, subparallel in distal half, their apices obliquely subtruncate, outer faces of distal portions convex but not swollen; in distal aspect apical margins straight and attingent, their ventral tips narrowly rounded, not divaricate.

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[1] Figures in parentheses give the range of variation in the paratypic series.

VARIATION. Range in size, proportions and leg armature similar to that in *opilionoides;* minute caudogenicular spinules present on femur III in about half of all individuals; dorsal spurs of tibia III 4-8, mode 6-7 on both carinae; denticles of dorsal carinae 33-72, mean about 55; number of denticle-free distal inter-spur intervals 1-4, mode 2, about one-third of all individuals with 3 on at least one carina. No geographic variation has been observed.

DISTRIBUTION. *Hadenoecus barri* occupies caves along the western edge of the Cumberland Plateau and adjacent part of the Eastern Highland Rim in southcentral Tennessee (maps, Figs. 10, 17). Its range lies between those of *opilionoides* to the north and *jonesi* to the south, and includes the southern headwater areas of Caney Fork, the easternmost ones of the Elk River, and overlaps with that of *jonesi* in the valley of Battle Creek in Marion County, Tennessee. As was noted earlier, no evident barrier separates *barri* from *o. australis,* but with the exception just noted the ranges of *barri* and *jonesi* in general lie on opposite sides of the sandstone-capped plateau remnants that form the interfluve between the upper Elk River and the Alabama portion of the Tennessee valley. The species appears to be absent from the western part of the Eastern Highland Rim in southern Tennessee. L. D. Matthews and three companions made a special search for it in Bishop and Ray caves in Bedford County, in Crumpton and Riley Creek Caves in Coffee County, and in Dance Cave in Moore County, but found no Hadenoecini in them.

SPECIMENS EXAMINED: 154—37♂, 46♀ (including type, allotype and paratypes), and 71 juveniles, as follows:

TENNESSEE:[1] *Franklin Co.:* Dry Cave (B: 192), 23 Aug 1975 (Ma) 3♂, 3♀; *Grundy Co.:* Hubbards Saltpeter Cave, Hubbards Cove (B: 228), 22 June 1955 (B) 1♂, 1 juv [B]; Nunelly Cave, 8 mi SW of Altamont, 25 Nov 1955 (B) 1♀, 1 juv [B]; Payne Saltpeter Cave, Paynes Cove (B: 229), 28 Mar 1955 (B) 2 juvs [B]; Cave in Savage Gulf, 8 mi ENE of Altamont, 12 Oct 1955 (C. L. McCary) 1♂ [B]; Wonder Cave, nr Monteagle (B: 234), 30 June 1937 (D) 1♂, 1♀, 1 juv; 16 Oct 1941 (J) 6 juvs [ALA]; Oct 1945 (R. L. Usinger) 1♂, 1♀ [CAS]; 16 Apr 1946 (C. D. Michener) 1♂, 7 juvs [AMNH]; July 1949, 2♀ [ST]; 31 Aug 1962 (T. H. & S. P. Hubbell) 6♂, 14♀ (including type and allotype), 22 juvs; 17 Aug 1975 (Ma) 4♂, 2♀; Hubbards Cave (B: 484), 16 Oct 1948 (J) 3♂, 7♀, 4 juvs [ALA]; Irving College (probably in Hubbards Cave), 31 June 1949 (B) 1♂, 2 juvs [B]; *Marion Co.:* Kimball Cave, MN-61, 35° 03′ 04″ N, 85° 40′ 05″ W, elev 680 ft (Ne) 1♀, 2 juv ♂; Logging Camp Cave, MN-19, 35° 08′ 51″ N, 85° 46′ 56″ W, elev 860 ft (Ne) 3 juvs.

Reference in Literature

Hadenoecus subterraneus, not of Scudder 1861: Barr 1961: 39-41, fig. 13 (photo of ♂). (In part: Eastern Highland Rim, Tennessee).

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[1] Most of the Tennessee caves listed are described and located by Barr (1961), page references to which, e.g. (B: 192), follow the cave names.

HADENOECUS JONESI[1] Hubbell, n. sp. (Figs. 12, c; 13, j; 14, c,d; 10, 17, 18 (maps); Pl. II, f; Pl. III, f).

Type: Female, Limrock Blowing Cave, Jackson, Co., Alabama, 29 Dec 1965 (S. Peck); *allotype* a male with the same data; both in alcohol, in UMMZ.

This species closely resembles the other members of *Hadenoecus,* but can be distinguished from them by the characters given in the key and by having proportionately longer and more slender legs (see Table II) and longer antennae. In the extreme attenuation and length of its appendages it is the most highly modified for cave existence of North American rhaphidophorids. It is the only species of the genus present in Alabama and southernmost Tennessee.

DESCRIPTION OF FEMALE TYPE:[2] Length of body ca. 17, of pronotum 3.9 (3.4-4.3), of femur I 17.2 (14.9-17.9), of femur III 26.5 (to 21.0), of tibia III 31.6 (27.5-34.9), of ovipositor 13.0 (to 10.0), of antenna ca. 132 mm.

Coloration of dorsum, femora and proximal parts of tibiae dilute ochraceous buff, dorsum almost without darker shadings; venter, face mouthparts and distal parts of legs paler. *Legs:* Femur I 4.5 (4.2-4.8) times as long as pronotum; tibia I 1.12 (1.04-1.17) times as long as femur, ventral spurs 6/6 (5-7, mode 6) on cephalic, 5/5 (4-6, mode 5) on caudal margin, tarsus I 0.77 times tibial length, basitarsus I 2.0 (1.6-2.2) times as long as pronotum. Femur II slightly shorter than femur I, with minute caudogenicular spinule (sometimes absent); tibia II 1.1 (to 1.4) times as long as femur, ventral spurs 6/5 (5-7, mode 5) on cephalic, 4/5 (3-6, mode 5) on caudal margin. Femur III 6.9 (6.0-7.3, mean 6.5) times as long as pronotum, 1.5 (1.4-1.6) times as long as femur I, 10.9 (to 8.9, mean 9.7) times as long as basal breadth, with minute caudogenicular spinule (sometimes absent). Tibia III 1.19 (1.17-1.32) times as long as femur, dorsal spurs 7/7 (5-7, mode 6) on cephalic, 8/8 (5-8, mode 7) on caudal carinae; predistal ventral spurs of cephalic margins 2/2 (2-4, mode 2), of caudal margins 1/1 (0-2, mode 1); spine formulae of dorsal carinae, right and left: cephalic 41/10/4/6/0/0/0 = 61, 35/10/6/6/0/0/0 = 57, caudal 23/11/9/4/1/1/0/0 = 49, 31/10/10/3/1/0/0/0 = 55.

Terminal abdominal structures: Ovipositor (Fig 14, c,d) like that of *subterraneus,* 3.4 (2.9-3.5) times as long as pronotum, 0.76 (to 0.69) times as long as femur I, 0.49 (0.43-0.53) times as long as femur III, teeth of ventral valves 5 (to 7, mode 5-6). *Subgenital plate* (Fig. 13, j) with distal margin broadly convex, more sharply rounded at sides and faintly emarginate mesad; its ventral sclerite consisting of a broad distal bar with bisinuate distal margin and wide wings projecting toward

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[1] Named for the late Dr. Walter B. Jones, a leader in the development of North American speleology, who himself collected much of the material used in this study.

[2] Figures in parentheses give the range of variation in the paratypic series.

distolateral angles of plate, and a pair of broad, proximally convergent arms extending to basal margin of plate and there obliquely truncate, their acute mesal ends attingent; these arms completely enclosing a pyriform membranous mesoproximal area broadest distad and about as long as broad. *Sternite VII* (Fig. 13, j) unlike that of any other species in having a low, short, transverse, moderately sclerotized ridge one-quarter as wide as sternite and at about its midlength, its crest narrowly rounded, its anterior face sloping, planate and with sides convergent to truncate crest, base subpyramidal and caudal face slightly overhanging; anterior edge of sternite with a narrow sclerotized rim not enlarged at ends.

DESCRIPTION OF MALE ALLOTYPE: Length of body ca. 14.5, of pronotum 3.7 (3.2-4.0), of femur I 16.7 (14.3-17.0), of femur III 24.9 (21.0-26.6), of tibia III 31.9 (26.3-34.2), of antenna ca. 100 mm. Coloration, proportions and leg armature as in female; femur III 9.7 (9.1-10.4) times as long as basal breadth. Spine formulae of dorsal carinae of tibia III, right and left: cephalic 29/8/10/4/3/0/0 = 54, 38/14/7/3/0/0 = 62, caudal 36/14/9/4/0/0 = 63, 33/9/13/1/0/0 = 59. *Terminal abdominal structures* (Pl. II, f; Pl. III, f): As described for *subterraneus* except as follows. *Paraprocts* in side view broad relative to length, subtrapezoidal, dorsal margin gently convex in basal half, thence more strongly and evenly downcurved to ventral tip; outer face with an oblique ridge extending from near cercal base to dorsal edge near beginning of strong distal decurvature of latter, this ridge separating a more heavily sclerotized, weakly impressed dorsoproximal portion of surface from a less sclerotized, broadly lunate distal area with planate or slightly concave surface and membranous ventral margin; in distal aspect dorsal edges convex-convergent, becoming straight and subattingent toward tips, latter scarcely projecting ventrad of straight lower edges of paraprocts.

VARIATION. Range in size, proportions and leg armature similar to that in *opilionoides* and *barri;* denticles of dorsal carinae of tibia III 37-68, mode about 50; number of denticle-free distal intervals 2-4, mode 2, about one-quarter of all individuals with 3 on at least one carina. No geographic variation has been observed.

DISTRIBUTION. This species is known from 46 caves in northeastern Alabama and adjoining Tennessee, all in the Cumberland Plateau and Highland Rim regions north of the loop of the Tennessee River (maps, Figs. 10, 17, 18). In Alabama it occurs, so far as known, only in Jackson, Madison and northern Marshall counties. The two northwesternmost records, from Elora Spring Cave in Lincoln County and Caroline Cove Cave in Franklin County, Tennessee, are just south of the divide between the Elk River drainage (along the headwaters of which *barri* occurs) and the Tennessee River drainage; the northeasternmost record is from Honeycutt Cave in Marion County, Tennessee.

SPECIMENS EXAMINED: 1,060—171♂, 153♀ (type, allotype and paratypes), and 736 juveniles, as follows:

ALABAMA:[1] *Jackson Co.:* Boxes Cave (AL 536), 20 Mar 1966 (P) 1 juv; Devils Stair Steps Cave (AL 80), 11 June 1940 (J) 4♂, 5♀, 7 juvs [ALA]; Doug Green Cave (AL 601), 14 Mar 1966 (P) 2♀, 8 juvs; Engle Double Pit (AL 266), 29 July 1940 (J) 6♂, 2♀, 15 juvs [ALA]; Fern Cave (AL 597), 14 June 1967 (J. Fish, T. R. Evans) 4♂, 1♀, 8 juvs; Gary Self Pit (AL 290), 4 June 1940 (J) 12♂, 3♀, 27 juvs [ALA]; 20 Apr 1967 (D. Askias) 1 juv [AU]; Gross Skeleton Cave (AL 224), 13 Aug 1967 (P, F) 4♂, 1♀, 1 juv; Hambrick Cave (AL 90), 2 Jan 1942 (J) 2 juvs [ALA]; Horseshoe Cave (AL 222), 30 June 1967 (P, F) 5♂, 1♀, 2 juvs; Keel Cave (AL 79), 11 June 1940 (J) 11♂, 18♀, 6 juvs [ALA]; Kennamer Cave (and Orgy Entrance) (AL 490), 9 Dec 1963 (L. McLennan) 2♂, 1♀, 6 juvs; 15 Mar 1966 (P) 1♂, 4♀, 3 juvs; Limrock Blowing Cave (AL 311), 29 Dec 1965 (P) 6♂, 2♀ (including types), 34 juvs; 14 Sept 1968 (P) 3♂, 4♀, 1 juv; McFarland Cave (AL 65), 29 Feb 1940 (J) 4♂, 6♀, 26 juvs [ALA]; 11 June 1940 (J) 1♂, 1♀, 2 juvs [ALA]; 14 Apr 1965 (J. E. Cooper, M. L. Riser) 1 juv; McFarland Spring Cave (AL 67), 29 Feb 1940 (J) 3 juvs [ALA]; 11 June 1940 (J) 1♂, 1♀, 2 juvs [ALA]; Montague Cave (AL 379), 10 Aug 1960 (J) 3♂, 3♀, 2 juvs [ALA]; Out Cave, 9 mi SW of Scottsboro (P, F) 1♂; Paint Rock Cave (AL 185), 6 Sept 1965 (P) 3♂, 5♀, 3 juvs; Paint Rock Valley, in dry spring, 25 Nov 1963 (L. McLennan) 5♂, 3♀, 3 juvs [AU]; Pig Pen Cave (AL 519), 28 July 1967 (P, F) 6♂, 4♀, 6 juvs; Ridley Cave, Russell Cave Nat'l Mon. (AL 170), 10 Aug 1967 (P, F) 2♂, 2♀; Rousseau Cave (AL 81), 29 July 1965 (P) 1 juv; Saltpeter Cave (AL 74), 17 June 1939 (J) 1 juv [ALA]; 9 June 1940 (J) 7♂, 3♀, 15 juvs [ALA]; Saltriver Cave (AL 221), 7 July 1967 (P, F) 2♂, 3♀, 3 juvs; Schiffman Cave (AL 174), 27 Jan 1967 (P) 2♂, 3♀, 2 juvs; 23 Aug-1 Sept 1968 (P) 4♂, 2♀, 3 juvs; Talley Ditch Cave (AL 248), 11 Aug 1967 (P, F) 2♂; Tony Sinks Cave (Cox Cave) (AL 78), 11 June 1940 (J) 2♂, 9♀, 20 juvs [ALA]; Williams Saltpeter Cave (AL 590), 5 Aug 1967 (P, F) 2♂, 3♀, 3 juvs; *Madison Co.:* Aladdin Cave (AL 26), (J) 1♂, 5♀, 5 juvs [ALA]; 17 June 1968 (J) 1♂, 13 juvs [ALA]; Cold Spring Cave (AL 120), 22-30 Aug 1968 (P) 8♂, 2♀, 31 juvs; Grayson Spring Cave (AL 122), 31 Aug 1968 (P) 2♀; Hering Cave (Cave Spring Cave) (AL 6), 26 Apr 1939 (J) 3♂, 7♀, 11 juvs [ALA]; 26 Sept 1939 (J) 10 juvs [ALA]; 30 Dec 1965 (J. Cooper, P) 1♂, 2 juvs; Hutton Cave (AL 91), 3 Jan 1942 (J) 2 juvs [ALA]; Scott Cave (AL 58), 7 Oct 1939 (J) 8♂, 10♀, 2 juvs [ALA]; 13 Mar 1966 (P) 1♂, 5♀, 4 juvs; 15 Sept 1968 (P) 1♀; *Marshall Co.:* Bishop Cave (AL 43), 12 Jan 1939 (J) 8♂, 9♀, 15 juvs [ALA]; 14 Aug 1967 (P, F) 1♂, 2♀, 3 juvs; Cathedral Caverns (Bat Cave) (AL 165), 17 Sept 1952 (J) 5♂, 5♀, 11 juvs [ALA]; 20 Dec 1965 (P) 3 juvs; Dunham Cave (AL 329), 17 Mar 1966 (P) 2♀, 1 juv; 14 Aug 1967 (P) 3♂, 1♀, 3 juvs; Guffey Cave (AL 317), 11 Feb 1961 (J) 7♂, 4♀, 1 juv [ALA]; Hambrick Cave (AL 44), 11 Jan 1939 (J) 6♂, 6♀, 20 juvs [ALA]; Honeycomb Cave (AL 36), 11 Jan 1939 (J) 6♂, 5♀, 50 juvs [ALA]; Kellers Cave (AL 326), 26 June 1967 (P, F) 1♂, 3 juvs; Kirkland Cave (AL 400), 16 Mar 1966 (P) 1 juv; McHardin Cave (AL 35), 12 Jan 1939 (J) 1♀, 10 juvs [ALA]; Merrill Cave (AL 186), 16 Mar 1966 (P) 1 juv; 26 June 1967 (P, F) 1♂, 3 juvs; 10 July 1967 (P, F) 2♂, 9 juvs; Walnut Cave (AL 321), 22 Apr 1966 (P) 4♂, 2♀.

TENNESSEE: *Franklin Co.:* Caroline Cove Cave, 5.5 mi SE of Belvidere, 11 July 1967 (P, F) 3♂, 5 juvs; *Lincoln Co.:* Elora Spring Cave, 0.5 mi S of Elora, 9 July 1967 (P, F) 2♀; *Marion Co.:* Honeycutt Cave, 8 mi N of Pittsburg, 28 Aug 1968 (P) 1 juv.

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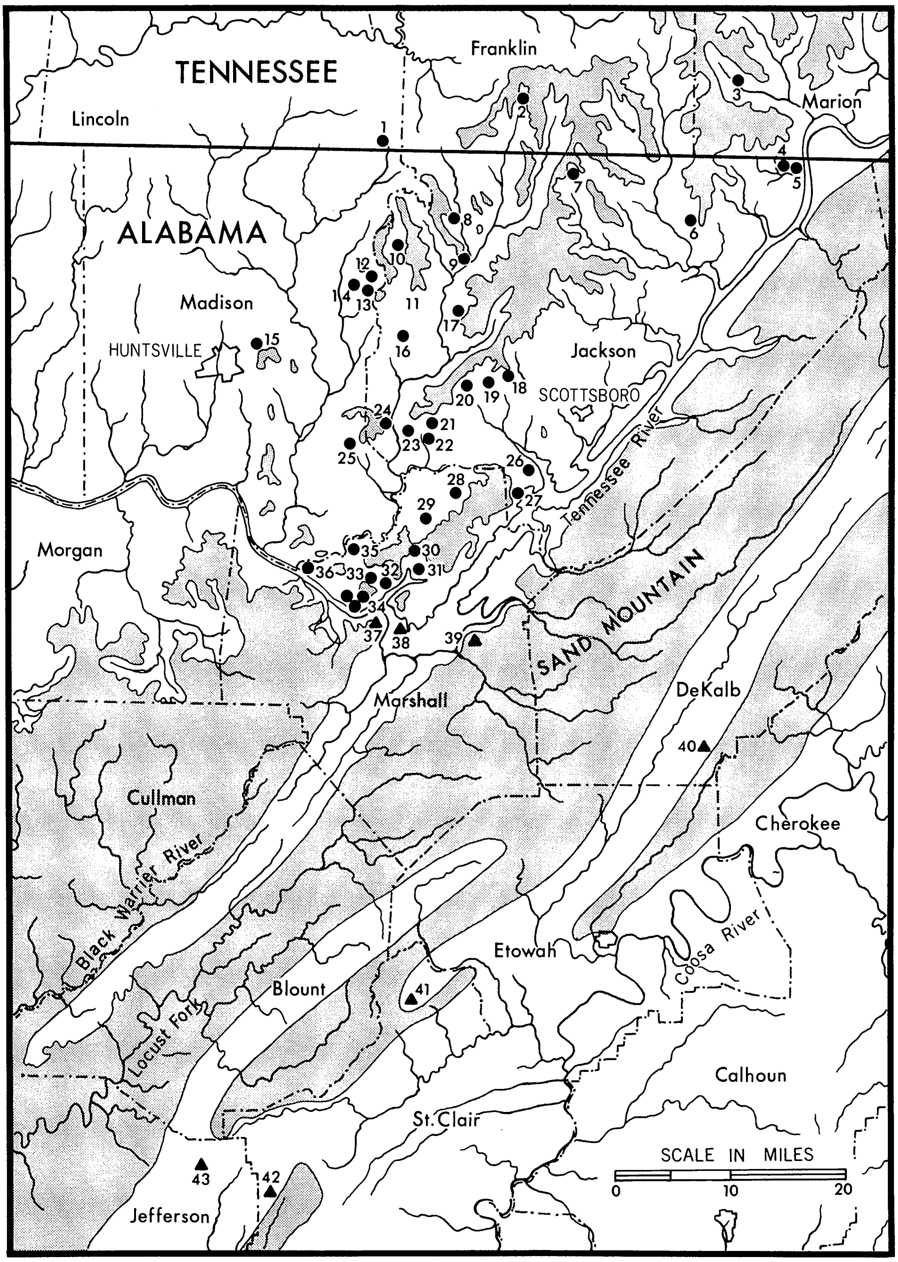
[1] Caves listed and described by Varnedoe (1973) under Alabama Cave Survey numbers cited, e.g. (AL 536).


TENNESSEE
Franklin
Lincoln
Marion
ALABAMA
Madison
HUNTSVILLE
Jackson
SCOTTSBORO
Tennessee River
Morgan
SAND MOUNTAIN
Marshall
DeKalb
Cullman
Cherokee
Black Warrior River
Etowah
Coosa River
Blount
Locust Fork
Calhoun
St. Clair
Jefferson
SCALE IN MILES
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PART II. THE PHYLETIC AND ZOOGEOGRAPHIC HISTORY OF THE RHAPHIDOPHORIDAE WITH SPECIAL REFERENCE TO THE HADENOECINI

by Theodore H. Hubbell

Any attempt to reconstruct the history of the Hadenoecini and their relatives has to be based on indirect evidence, since the entire fossil record of the family Rhaphidophoridae consists of three species of the genus *Prorhaphidophora* described from the Lower Oligocene Baltic amber of East Prussia by Chopard (1936a, b). But a probable phylogeny of the family can be constructed from morphological data (Fig. 1), and this can be correlated with current knowledge of the past distribution of land and sea, climates and vegetation,[1] taking into account the geographic relations of the rhaphidophorid taxa. By so doing it is possible to deduce with considerable confidence the time of origin of the Rhaphidophoridae and the circumstances under which its subfamilies and tribes evolved. The overall geographic pattern of the taxa of this family resembles those of certain other animal groups the history of which is documented by fossil records; the similarity of their histories to that ascribed to the Rhaphidophoridae is supportive of the latter. The following discussion deals principally with the Dolichopodinae and Hadenoecini.

RELATIONSHIPS AND EARLY HISTORY OF THE RHAPHIDOPHORIDAE. Phylogenetic studies of the Ensifera have with few exceptions been based primarily on the wing-venation of fossil and recent alate forms, leaving the relationships of the totally apterous Rhaphidophoridae to be assessed on other grounds. Most authors have followed Karny (1921 et seq.) in assuming that the rhaphidophorids are closely related to the gryllacridids, and have either, like Karny, treated them as a subfamily of Gryllacrididae, or, more recently, have regarded them as

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[1] Useful works dealing with these topics include Schwarzbach (1963), Axelrod and Raven (1972), McKenna (1972), Raven and Axelrod (1974), Cracraft (1973, 1974) and Savage (1973). They contain bibliographies and summaries of much of the voluminous literature of the past two decades on plate tectonics, paleoclimatology and paleobotany and their bearing on zoogeographic problems.

Fig. 18. The known distribution of populations of *Hadenoecus jonesi* and of a part of those of *Euhadenoecus insolitus*. Names of numbered caves are as follows: *Hadenoecus jonesi* (dot): 1–Elora Spring; 2–Caroline Cove; 3–Honeycutt; 4–Ridley; 5–Montague; 6–Talley Ditch; 7–Salt River; 8–Horsehoe; 9–Doug Green; 10–Hambrick; 11–a group of eight caves; McFarland, McFarland Spring, Saltpeter, Tony Sinks, Keel, Devils Staircase, Engle Double Pit, Gary Self Pit (Cave Stand); 12–Aladdin; 13–Hutton; 14–Scott; 15–Cold Spring; 16–Rousseau; 17–Williams Saltpeter; 18–Boxes; 19–Limrock Blowing; 20–Schiffman; 21–Pigpen; 22–Kennamer (and Orgy entrance); 23–Fern; 24–Paint Rock; 25–Hering; 26–Out; 27–Gross Skeleton; 28–Cathedral Caverns; 29–Guffey; 30–Kirkland; 31–Dunham; 32–Walnut; 33–Bishop; 34–a group of three caves: McHardin, Honeycomb, Hambrick; 35–Kellers; 36–Merrill. *Euhadenoecus insolitus* (triangle): 37–Terrill # 1; 38–Jackson (now submerged); 39–Town Creek; 40–Bartlett; 41–McGlendon; 42–Cedar Pole; 43–McCluney.

constituting a family of the superfamily Gryllacridoidea. In 1939, however, Ander conclusively demonstrated that the Rhaphidophoridae are much more primitive than the Gryllacrididae and cannot be very closely related to the latter. In Ander's phylogeny the Tettigonioidea and Grylloidea diverge from near the base of the stem of the Ensifera, with Rhaphidophoridae forming the earliest branch of the tettigonioid line, followed in succession by the Schizodactylidae, Gryllacrididae, Stenopelmatidae, Prophalangopsidae (= Haglidae), and Tettigoniidae. Blackith and Blackith (1968) derived the Gryllacrididae (including the Rhaphidophoridae) from the tettigonioid line after the separation of the Grylloidea, but other authors, including Karny (l.c.), Zeuner (1935), and Sharov (1971), have treated them as an early branch from the grylloid stem, and Beier (1955) and Ragge (1955) considered the superfamily Gryllacridoidea to have branched off from the ensiferan stem prior to the separation of the tettigonioid and grylloid lineages.

Regardless of these differences of opinion about the relationship of the Rhaphidophoridae to other Ensifera, there can be no doubt of the great antiquity of the family. This is evidenced both by its primitive morphology and its geographic distribution. The most striking specialization of the group, complete loss of wings, must have been acquired by its earliest ancestors, and since the very beginning rhaphidophorids must have travelled only on foot over continuous land. Except for a few species that have been spread by human agency there is nothing to suggest that accidental transport has played any part in the dispersal of these insects. Today the members of this family are almost wholly confined to the north and south temperate zones, with the primitive Macropathinae present in Australia, New Zealand, and southernmost South America and Africa, and the remaining more advanced subfamilies in North America, Eurasia and, presumably as the result of relatively recent invasion, the East Indian tropics.

Both Karny and Ander, early converts to the Wegenerian theory of continental drift, long ago saw in this distributional pattern proof that the Rhaphidophoridae arose in the southern hemisphere during the latest Paleozoic or earliest Mesozoic, before the breakup of Gondwanaland, and that the ancestors of the Laurasian groups reached that landmass when it and Gondwanaland were still united into the supercontinent Pangaea. The time of origin of the Rhaphidophoridae has been variously estimated as Upper Carboniferous (Ragge 1955), Permian (Ander 1939), Triassic (Beier 1955) or Jurassic (Sharov 1971), depending on the hypothesized sequence of phyletic branchings and the known ages of the fossil Ensifera assumed to be their closest relatives. It cannot have been later than early Jurassic, since by the end of that period Africa had separated from Antarctica and Laurasia from Gondwanaland, interrupting the dispersal routes which the rhaphidophorids must have followed. To allow sufficient time for the spread of the Macropathinae to all parts of Gondwanaland and of another stock to

Laurasia, and for the accompanying adaptive changes that this would have required, a Permian or Triassic origin seems most likely.

Two possibilities as to where the Rhaphidophoridae arose are suggested by their distribution. The first and most probable is the one proposed by Karny and Ander, that this occurred in the temperate zone of Gondwanaland, in the separated parts of which the primitive Macropathinae survive in rich variety today, and that an offshoot from the macropathine stock reached Laurasia and was the progenitor of all the advanced northern hemisphere subfamilies. This hypothetical immigrant ancestor must have been adapted to tropical environments, since it had to cross the equator and become established in Laurasia, most of which was tropical or subtropical throughout the early Mesozoic. The second alternative is that the earliest rhaphidophorids lived in the tropics of Pangaea and thence spread north and south; but this would not explain why the primitive forms are circum-Antarctic and the more advanced groups all in the northern hemisphere. Either hypothesis requires the assumption that during the early Mesozoic primitive rhaphidophorids inhabited the tropical zone, from which they later disappeared. The few modern species present in the Asiatic and East Indian tropics all belong to advanced genera of the advanced tribe Rhaphidophorini and, as stated, above, are presumed to have invaded those regions in relatively recent (Tertiary) times.

MESOZOIC DIFFERENTIATION OF THE LAURASIAN SUBFAMILIES. The broad outlines of the geotectonic and paleoclimatic history of the earth in post-Paleozoic time are now well established, although there remain many uncertainties about its details and the precise timing of some events. Throughout the early Mesozoic Laurasia, still joined to Gondwanaland, lay much nearer the equator than now and entirely within the tropical and subtropical zones. A broad but interrupted arid belt bordered its tropical portion, and in its more humid northern regions there were coal-swamps and forests of conifers, gingkos, cycadophytes and tree-ferns, while tropical savannas and rain-forests existed in the south. Rhaphidophorids must have occupied the forested regions, but we know nothing of them.

By the beginning of the Cretaceous Laurasia had separated from Gondwanaland and was drifting into higher latitudes, so that eventually its northern margins became warm-temperate. Angiosperms, first appearing in the south, spread northward during the Lower Cretaceous and largely replaced the older types of vegetation. In Upper Cretaceous and early Tertiary times much of northern Laurasia was covered by deciduous or mixed forests of modern aspect, in which were present birch, ash, maple, oak, walnut, tulip, sycamore, magnolia and sweetgum, along with conifers and other survivors from the earlier floras. All the less specialized northern hemisphere rhaphidophorids now live in similar forests, and it is therefore reasonable to suppose that they have descended from ancestors that evolved in these northern warm-temperate Upper Cretaceous forests. The distribution of the modern subfamilies is compatible with this hypothesis, as is the presence of fossil species of the advanced subfamily Rhaphidophorinae in the Lower Oligocene Baltic amber. For the reasons discussed below it seems almost certain that the evolution of the modern subfamilies occurred in the late Mesozoic and Paleocene.

Throughout most of the Upper Cretaceous two epeiric seas divided Laurasia into separate land-masses. One sea extended across North America in the Cordilleran trough and Great Plains region from the Arctic Ocean to the Gulf portion of the expanding Atlantic. The other, comprising the Turgai Straits and Obik Sea, stretched across Eurasia from the Arctic to Tethys in the Ural region. To the east of the Ural seaway lay Angaria, consisting of northern and northeastern Asia (to which India and southeastern Asia were not yet joined), and Angaria was probably connected to western North America through Beringia, since the Arctic and northern Pacific marine faunas of this time were quite distinct. Europe, Greenland and northeastern America formed a single continuous landmass, the North Atlantic continent (Euramerica); separation of Greenland from America by the Labrador Sea was incomplete. By the end of the Upper Cretaceous the epeiric seas had withdrawn, and although the connection between Europe and North America persisted, at least in the far north, through the Paleocene and early Eocene, it was finally interrupted by the northward opening of the Atlantic that separated Greenland from Spitzbergen and Norway by middle Eocene (Lutetian) time.

The present center of distribution of the Rhaphidophorinae is Angaria, from which the lines of dispersal of its tribes radiate. The tribe Rhaphidophorini occupies central and eastern Asia and has spread thence into southeastern Asia and through the East Indies as far as New Guinea. The Troglophilini are in Asia Minor and the northern borders of the Mediterranean region. The Gammarotettigini, the only Rhaphidophorinae in North America, are confined to the Pacific slope and presumably evolved from an ancestral stock that crossed the Beringian bridge in late Cretaceous or early Tertiary times. The Tropidischiinae, now surviving as a single relict species on the Pacific Coast of North America, may also have originated in Angaria and reached the New World via Beringia. But in view of the primitiveness of *Tropidischia* and its frequent association with *Sequoia* forests it is also possible that the tropidischiine stock developed prior to the division of Laurasia and had a wide distribution coextensive with that of *Sequoia* along the northern borders of that landmass.

According to the phylogeny proposed above the Ceuthophilinae branched off from near the base of the Laurasian stem. This early separation and the fact that the subfamily is strictly North American suggest that its ancestral stock reached that continent prior to the formation of the Upper Cretaceous seaway, perhaps by late Triassic or early Jurassic time and by a more southerly route than was subsequently available. The reason for such a supposition is that two of the tribes descended from that stock, the Pristoceuthophilini and Argyrtini, developed in and are confined to territory that lay west of that barrier, while the third, Ceuthophilini, arose east of the seaway but after its disappearance spread westward into the montane forests and, with fossorial adaptations, into the dry grasslands and deserts.

THE DOLICHOPODINAE. This subfamily, an early branch from the rhaphidophorine stem in the phyletic scheme derived herein, is represented today by the Hadenoecini in eastern North America and by the Dolichopodini in southern Europe and the Near East. Such a distribution is most easily explained on the assumption that the ancestral stock of this group evolved in the isolated North Atlantic continent during the Upper Cretaceous, and that its differentiation into two descendent tribes resulted from the mid-Eocene separation of Europe and North America. Vandel (1967: 277) cited *Hadenoecus* and *Dolichopoda* among the vicarious cavernicolous genera to which he assigned such an origin. The possibility of east-west migration via a North Atlantic route is amply attested by fossil evidence in many mammal genera, evidence that, according to McKenna (1972), proves that transfer of faunas via an unbroken far northern land route between Europe and North America continued from Upper Cretaceous times until the end of the Sparnacian stage in middle Eocene, some 50 to 60 million years ago. According to that author Norway was connected to eastern North America by way of Spitzbergen and Greenland, and his conclusion does not appear to conflict with those of the latest studies of the Tertiary movements of Greenland relative to Norway, Spitzbergen and North America (Talwani and Endholm, 1977; Kristoffersen and Talwani, 1977).

The modern Dolichopodini, all cavernicoles, inhabit the northern borders of the Mediterranean sea, Asia Minor and the Aegean archipelago. But on the assumption that their ancestors, like the more primitive of the existing hadenoecines, lived in temperate-zone forests, they must have originally been restricted to the far north, because most of Europe was tropical to subtropical until late in the Tertiary. Its central part, also, was largely submerged during the Eocene and Oligocene, but land existed across what is now the northern Mediterranean. The western extension of this land (the Tyrrhenid) reached from the Pyrenees through Italy, and its eastern part (the Aegeid) from Greece to the Caspian and Aral basins. The Alpine-Carpathian chain was created by thrusting from the south that began in the Oligocene and culminated in the Pliocene. From mid-Miocene onwards a progressive cooling of climate occurred, ending with the Pleistocene glaciations. This was accompanied by a southward shift of the temperate forests, which would have permitted the sylvicolous northern Dolichopodini (and presumably also the descendants of *Prorhaphidophora*) to spread into the by now emergent central parts of Europe and eventually to its southern borders.

No rhaphidophorids survived the Pleistocene glaciations north of the Alpine-Carpathian barrier. South of it, however, in the remnants of the Tyrrhenid and northern Aegeid lands, which were partially submerged and fragmented during the Pleistocene, there is a rich cavernicolous fauna that includes the many localized species of *Dolichopoda*, the only existing genus of Dolichopodini. Jeannel (1944), reasoning principally from the relationships among the cave beetles, concluded that the faunal migration into the northern Aegeid and Tyrrhenid lands was post-Miocene and came from the region north of the Caspian Sea, and that it had been prevented from reaching the southern Aegeid and northern Africa by the sea that occupied the trans-Aegean trench. Baccetti (1961) and Leroy (1967) explained the distribution of the Dolichopodini in much the same terms, and Sbordoni et al. (1976) postulated that the entry of ancestral *Dolichopoda* into caves began in the Pliocene. The caves evidently protected their inhabitants not only against the rigors of the ice ages but also against the aridity of the Mediterranean climate that supervened during the interglacials and in post-glacial time. Isolation of the cave systems, both on the mainland and especially on the Mediterranean islands, resulted in prolific speciation among the cavernicoles, including *Dolichopoda*.

THE HADENOECINI. According to the hypothesis presented above, Dolichopodinae existed in the northern parts of the North Atlantic continent in the Upper Cretaceous, and the ancestors of the Hadenoecini were isolated from their European relatives in the middle Eocene. The Cordilleran sea had withdrawn from North America by the end of the Cretaceous, and the northern part of the continent was covered by a temperate Arcto-Tertiary forest that graded southward into the warm-temperate to subtropical forests that existed over most of what is now the United States.[1] As in Europe, the southward shift of the temperate forest that accompanied the general Tertiary cooling of climates must have carried with it ancestral hadenoecines. It is reasonable to suppose that by Pliocene times a species of *Euhadenoecus*, the progenitor of the modern species of that genus and those of *Hadenoecus*, had evolved and occupied much of the present range of the group as well as territory to the north that was later covered by the Pleistocene ice sheets. There are no Hadenoecini in the central and western parts of North America, and since with few exceptions the existing species occur in rocky situations and caves in dissected plateaus and mountains, it seems probable

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[1] The changes in the climate and vegetation of North America that occurred during the Tertiary are described in the previously cited publications by Axelrod, Raven, Cracraft and Savage, and also by Dorf (1959), Hibbard (1960) and Schwarzbach (1963) among others. As Dorf notes, usage of climatic terms is often imprecise; thus the present climate of the southeastern United States would be classed as subtropical by most climatologists, but as warm-temperate by most botanists.

that the interior lowlands have always constituted a barrier to their westward spread. The Appalachians, elevated at the end of the Paleozoic, have been profoundly eroded, and are generally supposed to have been peneplaned during the Cretaceous and since then intermittently upwarped, dissected and partially peneplaned. But according to a recent interpretation, summarized by Hack (1969), their erosion was accompanied by isostatic uplift, so that they persisted throughout the Cenozoic as a chain of low ridges and massifs, highest in the north and south, that would have formed a corridor along which northern animals and plants could penetrate into the warmer southeastern region.

PHYLOGENY OF THE HADENOECINI. Today this tribe is represented by two genera—the more primitive *Euhadenoecus*, with two epigeic and two cavernicolous species, and the more highly modified *Hadenoecus*, with five species, all cavernicoles. The probable phylogeny of these taxa is diagrammed in Figure 19 on the basis of their morphological characters; the indicated timing of events is conjectural.

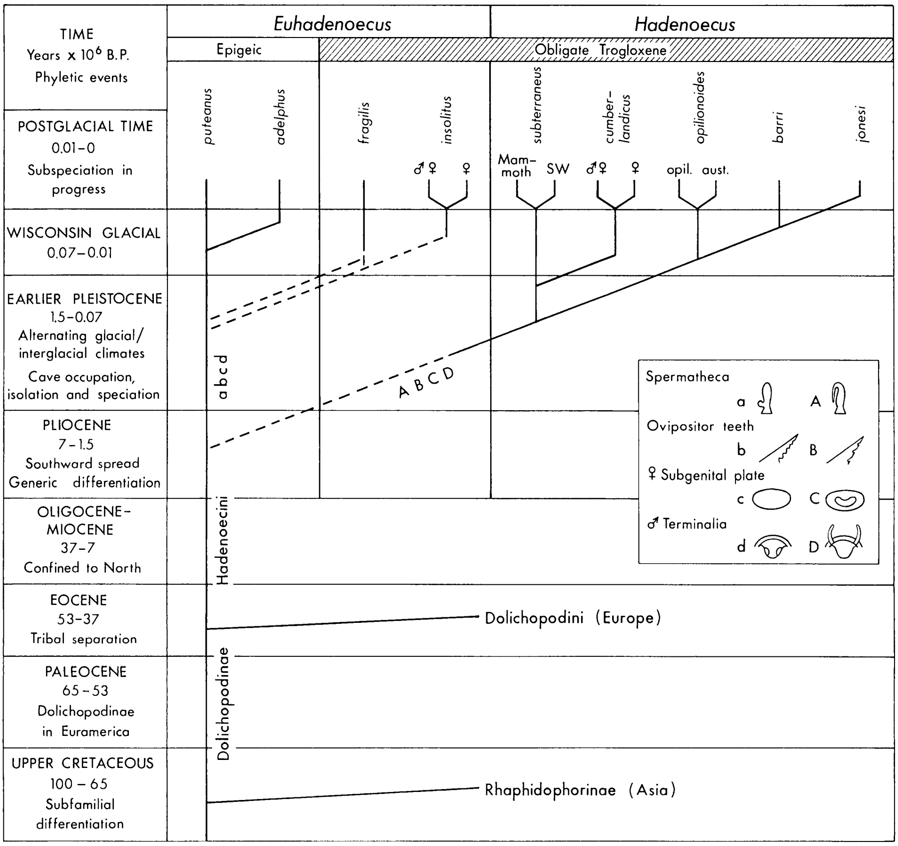

Fig. 19. Hypothetical phylogeny of the Hadenoecini.

The common ancestor of *Euhadenoecus* and *Hadenoecus* must have been very much like *E. puteanus*, the most primitive and most widespread of the existing species. It would have resembled *puteanus* in being sylvicolous and saxophilous, intolerant of dessication, active at night and seclusive during the day, and a facultative troglophile. Its females must have had a basally furcate spermatheca with reduced left arm, a simple subgenital plate, and a short ovipositor with coarse teeth; its males must have possessed well-developed styles, and in them pheromone organs may or may not have been present as glandular areas on the sides of the supra-anal plate. These characters would place it in the genus *Euhadenoecus*. The species *puteanus* and *adelphus* are its little modified descendants, and *fragilis* and *insolitus* cavernicolous offshoots from the *puteanus* line.

It is evident that somewhere in the Interior Low Plateau region and almost certainly before the end of the Pliocene there developed a second species, derived from the *puteanus* stock, which was the ancestor of *Hadenoecus*. Its females had a longer and differently armed ovipositor adapted for egg-laying in soft mud, a specialized subgenital plate with intramarginal sclerite, and a spermatheca in which the left arm was reduced to an apical recurvate appendage. In the males the styles had become partially fused with the subgenital plate, and a pair of eversible tubular organs, used to clasp the female and perhaps also having a pheromone function, had been developed between the ninth and tenth abdominal tergites. Along with these changes went increased size, reduced spination of tibia III, elongation of the appendages, and some loss of pigmentation. The last two features are common adaptations to cave life, suggesting that this *Hadenoecus* ancestor was already an obligatory trogloxene or on the way to becoming one. How early it branched off from the *puteanus* lineage is uncertain, but considering the extent of its modifications and the fact that before the end of the Pleistocene it had given rise to five species, it seems possible that it evolved as early as mid-Pliocene.

The following reconstruction of the subsequent history of the Hadenoecini is based on morphological evidence and the distributional pattern of the species. It attempts to explain the following phenomena: (1) the sympatry between *E. puteanus* and *E. adelphus* in the southern Appalachians; (2) the strict allopatry of all the cavernicolous species of both genera; (3) the exclusive occupancy by the species of *Hadenoecus* of a core area in the limestone regions of the Interior Low Plateaus, and the occurrence of the two cavernicolous species of *Euhadenoecus* on opposite sides of this area; (4) peculiarities in the distribution of *E. insolitus*; and (5) the existence in two distantly related species, *E. insolitus* and *H. cumberlandicus*, of parthenogenetic populations in the northernmost parts of their ranges. Before taking up these problems it is necessary to consider the mode of dispersal of these insects, the nature of the barriers to their spread, and effects of the fluctuating climates of the Pleistocene as the primary cause of the formation of the existing species.

DISPERSAL AND BARRIERS. Being wingless, hadenoecines can spread only through areas in which their habitats are continuous or nearly so. For the sylvicolous species the only apparent limiting factors are the extent of suitable forest, temperature and humidity tolerances, and the requirements for oviposition. For the cavernicoles the requirements are more restrictive.

The species of *Hadenoecus* not only penetrate the furthest recesses of extensive cave systems but also occupy many isolated caves within their territories, so that both subterranean and epigeic dispersal must be possible. Spread on the surface could only have occurred at times when more or less continuous temperate mesic forest occupied the limestone regions. As is well known, these insects emerge from their caves on warm nights to forage, and according to Nicholas (1962a) as many as one-third of the individuals inhabiting a particular cave may on a given night be wandering about outside. Some must occasionally get lost, and although most of these would perish, a few might survive for a time in the forest and a still smaller number ultimately chance upon a cave, perhaps very small, in which they could reproduce. For an obligatory trogloxene such "sweepstakes" dispersal, with many starters and few winners, would be most likely to populate all the caves in a region where caves are numerous and closely spaced, as they are in the thick flat-bedded limestones of the Interior Low Plateaus. Evidence that such epigeic spread does occur in the species of *Hadenoecus* includes the finding of individuals of *H. opilionoides* among rocks around the mouth of a small spring in a forested hollow on the floor of Buffalo Cove, Tennessee, at some distance from the nearest known cave.

In the Appalachian Ridge and Valley province limestone exposures tend to be linear and separated by ridges of non-calcareous rocks; the cave systems extend along the strike of the beds, are seldom extensive, and are on the whole much more isolated than are those of the interior plateaus. Under these conditions it would appear much more difficult for an obligatory trogloxene to spread from cave to cave in this region than in the other. Yet *Euhadenoecus fragilis* occupies many or most of the caves in an area extending from northern Virginia and West Virginia to eastern Kentucky and northeastern Tennessee. This suggests that *fragilis* may be less strictly cavernicolous and more capable of epigeic dispersal than are the species of *Hadenoecus*, as does the fact that on three occasions this species has been taken on forested slopes away from the vicinity of known caves, once at the base of cliffs near the summit of a ridge.

The ranges of the cave species of Hadenoecini are often bounded in part by obvious physical barriers. Belts of non-calcareous rocks without caves intervene between the territories occupied by *H. subterraneus*, *H. cumberlandicus* and *E. fragilis* and define the eastern limits of the ranges of the Tennessee species of *Hadenoecus*. The valley of a large river may also constitute a barrier separating species, even though there may be caves close to the banks of the river on both sides. Thus *subterraneus* and *opilionoides* are on opposite sides of the Cumberland, *jonesi* has its southern limit at the Tennessee, across which only *insolitus* occurs, and no member of the *Hadenoecus* stock has been able to invade the cave systems that lie north of the Ohio during the time since the last ice-sheet withdrew.

In other instances, however, no evident extrinsic barrier separates the ranges of closely related *Hadenoecus* species that occupy adjacent or almost contiguous but non-overlapping territories. *Hadenoecus opilionoides, H. barri* and *H. jonesi* succeed one another from north to south along the west side of the Cumberland Plateau in Tennessee and northern Alabama, but the boundaries of their ranges do not conform to the surface drainage pattern, and it seems unlikely that they reflect subsurface discontinuities between major cave systems.

Barr (1962) has described a parallel situation among the species of the *robustus* group of the carabid beetle genus *Pseudanophthalmus* that inhabit caves in this same part of Tennessee. Three of these troglobitic species are closely related and allopatric and occupy the same areas as do *opilionoides* and *barri*, but have ranges not congruent with those of the two cave-crickets, although like them they are not separated by any apparent extrinsic barriers. A similar situation has been described by Hobbs and Barr (1972) with respect to the cave crayfishes *Orconectes i. inermis* and *O. pellucidus*, the ranges of which abut without overlap in Hart County, Kentucky.

In his 1962 paper Barr suggested that the distribution of the species of the *robustus* group of *Pseudanophthalmus* is probably decided by selective factors rather than by inability of the species to penetrate beyond the area in which it occurs. One possibility is competitive exclusion; it may be that in the restrictive cave environment prior occupancy by a species occupying a particular niche gives it sufficient advantage to preclude the entry and establishment of another that occupies the same niche. In the case of *Hadenoecus*, however, competition for limited food resources could not be a critical factor, for these insects have access to abundant supplies outside the caves. A second and more plausible hypothesis to explain the close apposition, sharp delimitation, and absence of overlap in ranges observed in the above instances was outlined in a recent letter received from Dr. Barr. It is, that where two of the related species populations come into contact inviable hybrids are produced, and that selection makes the hybrid zone very narrow, so that it is unlikely to be encountered in casual sampling. Barr writes that "in various superspecies of the genus *Pseudanophthalmus* I have been unable to find anything other than an 'either-or' situation: the range of one species ends and that of the next begins within a distance of 3-5 miles (with no intervening caves known), and the adjacent populations show no morphological evidence of introgression." Although the distribution of the cave-crickets is known in less detail, there is good reason to believe that the same description would apply to their ranges and populations.

PLEISTOCENE ISOLATION AND SPECIATION IN THE HADENOECINI. It used to be thought that during the Pleistocene glacial stages climate and vegetation were little affected much beyond the limits of the ice, but there is now ample paleobotanical evidence to show that there was a displacement of the climatic zones southward at those times. Boreal forests descended to lower latitudes and lower elevations, supplanting or fragmenting temperate deciduous forests over much of the Interior Low Plateaus, Appalachians and upper Piedmont, and extending south on the Coastal Plain into Virginia and northern North Carolina (Martin 1958, Whitehead 1965). During the glacials temperate forests existed in southern Georgia and the Gulf Coast region. Reverse shifts occurred during the interglacials, and the climatic fluctuations were accompanied by changes in sea-level.

In most animal groups, especially those possessed of high mobility, little speciation occurred in eastern North America as a result of the Pleistocene alternations of climate. Under special circumstances, however, in particular areas and in groups characterized by low vagility, extensive Pleistocene speciation did occur as the result of some form of insular isolation. Thus during the interglacials much of Florida and parts of the adjacent Coastal Plain were inundated by the sea, leaving islands on which populations of flightless or sedentary insects and other animals were isolated and underwent differentiation (Hubbell 1954, 1956, 1961; Howden 1969). Some of these isolates evolved into distinct species with very limited ranges; other persisted as well-marked subspecies connected by narrow zones of secondary intergradation after genetic contact between the populations was restored.

A somewhat comparable situation existed during the Pleistocene in the limestone regions of eastern North America. Here many facultative troglophiles were able to survive in the refugia provided by caves, in which temperatures were cool and equable and humidity was high, during those times when the outer world was either too cold or too warm and dry for their epigeic existence. The resultant isolation led to speciation and often to the development of troglobites, as has been described by many authors including Vandel (1965), Leroy (1967) and Barr (1960, 1968, 1969). Vandel classified cavernicoles, exclusive of recent immigrants and aquatic forms, into two groups: *glacial relicts*, of boreal or montane origin and intolerant of high temperatures and aridity, and *thermophile relicts*, remnants of a tropical fauna dating back to the early Tertiary and intolerant of low temperatures. He noted that examples of both may occur in the same cave. The cavernicolous Hadenoecini, members of a group which by hypothesis arose in the temperate zone, do not fit either of Vandel's categories, although like his thermophiles they cannot exist in cold environments.

Peck (1973), in his excellent study of the carabid beetles of the genus *Ptomaphagus*, subgenus *Adelops*, described (and diagrammed in his figure 216) his concept of the movements and speciation of *Adelops* populations in the southeastern United States in response to Pleistocene climatic changes. He used fluctuating climates as a mechanism to introduce preadapted montane (boreal) ancestors to cave areas and caves during the glacials and to isolate them there during the interglacials. The result was the formation of troglobitic species that seem to have undergone range adjustments by overland dispersal during the Wisconsin Glacial. Peck attempted to relate the speciational events in the *hirtus* and *loedingi* groups of *Adelops* to the classical divisions of the continental North American Pleistocene as far back as the Yarmouth Interglacial (175-125 thousand years b.p.). But, as he himself pointed out, his interpretation is simplistic and controversial, perhaps making too rapid the speciational events. There is, moreover, increasing evidence that the climatic history of the Pleistocene was more complicated than has been supposed, and that it included at least nine episodes of lowered temperature and glacial advance during its last half million years (Hays, Imbrie and Shackleton 1976).

For the Hadenoecini a model the reverse of that proposed by Peck would have operated, with dispersal occurring before the onset of glaciation and during the interglacials, and isolation in caves during the cold periods. It seems reasonable to assume that the most recent differentiations among the cavernicoles of this group occurred during the Wisconsin Glacial, and that some modification of local populations has taken place in post-glacial time. But in view of the uncertainties involved no attempt is here made to ascribe speciational events to specific stages of the Pleistocene.

THE SYMPATRY OF *EUHADENOECUS PUTEANUS* AND *E. ADELPHUS*. The first of these two sylvicolous species ranges from the Catskill Mountains and northeastern Ohio south through the Alleghany and Cumberland Plateaus and the Appalachians to northern Georgia and Alabama, with outlying colonies in southeastern Georgia and southern Mississippi. During the Pleistocene interglacials it presumably occupied much of its present territory, but during the glacials its range must have contracted in the north and expanded to the south, as boreal forests spread over the plateau and mountain regions and temperate forests moved onto the southern Coastal Plain. The southern relict colonies are proof that such southward spread did occur during the Wisconsin Glacial.

The very closely allied *E. adelphus* must have developed from a *puteanus* population isolated somewhere in the southern Appalachians or adjoining Piedmont during the Wisconsin or, less probably, the preceding glacial stage. When *puteanus* reestablished contact with it the ancestral *adelphus* population had already diverged to the point where it had become reproductively isolated; no evidence of intergradation between them has been observed. As the climate ameliorated the two were able to move together into higher elevations. The fact that in some localities only one or the other of the species appears to be present, while in others they occur together in approximately equal numbers (map, Fig. 8), suggests that they may differ slightly in their ecological requirements or in their susceptibility to predation under different circumstances. They are certainly not resource-limited, and probably do not directly compete with one another.

THE ZOOGEOGRAPHY OF THE CAVE SPECIES. A satisfactory reconstruction of the distributional history of the cavernicolous Hadenoecini must account for (1) the presence of the more primitive *E. fragilis* and *E. insolitus* on opposite sides of the range of *Hadenoecus*, and (2) the occurrence of *insolitus* both north and south of the Tennessee River while *Hadenoecus* is limited to the region north of it. The history of the river itself is relevant to these problems. In 1894 Hayes and Campbell presented evidence that the Tennessee once flowed to the Gulf of Mexico via the Coosa-Alabama valley, and that at some time, presumably in the early Pleistocene, its upper portion was captured by a tributary of the Sequatchie River and diverted to its present course westward to the Mississippi. Hayes subsequently named the earlier stream the Appalachian River. Although this concept has since then been argued pro and con by numerous authors, the biological evidence that this or some equivalent capture did occur is overwhelming (Ross 1971). The possible bearing of this change in course of the Tennessee River on the zoogeography of the Hadenoecini is discussed below.

Three alternative hypotheses to explain the distribution of the cave species have been considered, none of which is wholly satisfactory. The first two assume that *fragilis* and *insolitus* had a common ancestor (FI), the third that they arose independently from the *puteanus* stock.

(1) The ancestral species FI arose early in the Pleistocene at a time when the *Hadenoecus* stock was confined to the Kentucky cave regions. Judging from the paucity of its cavernicolous modifications compared with those of *Hadenoecus* it seems highly improbable that its origin antedated the separation of that genus. During early interglacials FI or its little changed descendants attained a wide distribution that included much of the Appalachian Ridge and Valley Province and the Interior Low Plateaus west of the Appalachian River and south of the Cumberland River in Tennessee and northern Alabama. Such spread would have been facilitated if FI was merely troglophilous and less dependant upon caves than its descendants became. Subsequently the more completely cave-adapted *Hadenoecus* stock, with which FI could not compete as a cavernicole, moved south and displaced the FI populations from the caves along the west side of the Cumberland Plateau. Its southward expansion was stopped by the Tennessee River in northern Alabama, which, by the time *Hadenoecus* reached it, had been diverted

into its present westward course. The incursion of *Hadenoecus* separated the northeastern from the southwestern FI populations, resulting in their speciation into *fragilis* and *insolitus*. The latter was left in possession of the territory south of the Tennessee in Alabama and north of that river in the Highland Rim along the margins of the Central Basin. The population of *insolitus* that survived until recently in Jackson Cave on the north bank of the Tennessee records the former presence of the species in territory otherwise exclusively occupied by *Hadenoecus jonesi*. During a pre-Wisconsin glacial stage the *Hadenoecus* stock was divided into a northern species SC, ancestral to *subterraneus* and *cumberlandicus*, and a southern one OBJ, ancestral to *opilionoides, barri* and *jonesi*, and isolation during the Wisconsin resulted in the formation of the existing species of *Hadenoecus*.

Although this hypothesis accounts quite well for the distributional pattern of the cave species it is open to serious objections. It leaves unexplained why the older and more completely cave-adapted *Hadenoecus* stock should have remained confined to the Kentucky cave regions while the FI stock spread widely, and why such a broad interval now separates the *fragilis* and *insolitus* ranges. It also implies a very slow rate of evolutionary change in the FI stock compared with that in *Hadenoecus*, as evidenced both by the relatively slight divergence in morphological characters between *fragilis* and *insolitus* and the failure of the latter to speciate following the separation of its northern and southern populations by the diversion of the Tennessee River.

(2) If, as the morphological data suggest, separation of the *Hadenoecus* ancestor from the *puteanus* stock occurred considerably earlier than the formation of the hypothesized FI ancestor, the course of events might have been as follows. *Hadenoecus* populations had occupied all of the present range of the genus by mid-Pleistocene times, but after the diversion of the Tennessee River. Isolation during pre-Wisconsin glacials separated the SC and OBJ ancestors, and formation of the existing species of the genus occurred during the Wisconsin Glacial, as in the preceding hypothesis. In *Euhadenoecus* the FI ancestor evolved from *puteanus* somewhere within the range of its descendants, presumably during the penultimate glacial, spread during the succeeding interglacial around the periphery of the territory preempted by *Hadenoecus*, and during the Wisconsin Glacial was separated into the two populations that became *fragilis* and *insolitus*.

The following considerations weaken this hypothesis. First, there is nothing to indicate that FI ever actually occurred east of the range of *Hadenoecus* in the gap between the present ranges of *fragilis* and *insolitus*. If it did so, and if it was an obligatory trogloxene, it probably occupied caves along the east front of the Cumberland Plateau in Tennessee, where they are few and widely separated. Migration from one to another would have been difficult and genetic continuity between the end populations would have been tenuous; but this objection might not hold if FI was sylvicolous and only a facultative troglophile. If, as is here supposed, FI originated after the diversion of the Tennessee, ancestral *insolitus* must have crossed that river, either twice, to the east and west of the Cumberland Plateau, or once if the crossing occurred before ancestral *jonesi* had completed its occupation of Alabama north of the Tennessee. The second alternative would explain the presence of a relict colony of *insolitus* in Jackson Cave in *jonesi* territory.

(3) The third hypothesis is the same as the second insofar as *Hadenoecus* is concerned, but it assumes that in *Euhadenoecus* the cavernicolous *fragilis* and *insolitus* arose independently, both from *puteanus*, and that this occurred late in the Pleistocene. The resemblances between them would have to be attributed not to an immediate common ancestry, but to parallel adaptive modifications in the cave environment, and to retention of many *puteanus* characteristics. Although this explanation is in some respects the simplest of the three and evades some of the objections that can be made to the others, it fails to account for the occurrence of *insolitus* both north and south of the Tennessee River and its presence in Jackson Cave. The unlikelihood that two such similar species should have arisen independently on opposite sides of the range of *Hadenoecus* and from widely separated populations of the presumptive ancestor, and that the many close similarities between them (epiproct, paraprocts, dorsal phallic lobe) that would ordinarily be accepted as evidence of common ancestry have to be dismissed as parallelisms under this hypothesis, make it the least plausible of the three.

In summary, none of the explanations outlined above seems able fully to account for the distribution of the cave species. The first is in a sense the most "elegant," embodying the classical concept of W. D. Matthews, according to which "more advanced" and presumably better adapted forms evolve in the evolutionary center of the range of a group and thence spread outwards, supplanting more primitive ones the survivors of which persist on the peripheries. But on balance the probabilities seem more to favor the second.

PARTHENOGENETIC POPULATIONS. Lamb (1975) and Lamb and Willey (1975) reported the occurrence of all-female populations of *Hadenoecus cumberlandicus* (as *Hadenoecus* sp. A) and of *Euhadenoecus insolitus* (as *Hadenoecus* sp. B) in some of the northernmost caves inhabited by each of those species (mapped in Figs. 10, 16 and 17, and listed in the specific treatments). These are the first parthenogenetic populations known among North American Saltatoria.[1] Lamb found the sexual populations of both species to have a karyotype of ♀ 34 autosomes + XX, ♂ 34 autosomes + neo-XY, but noted that the structure and behavior of the neo-X and neo-Y chromosomes differ in the two

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[1] The European *Troglophilus cavicola* is the only other rhaphidophorid in which parthenogenetic and sexual populations are known to occur (Baccetti 1961).

species. In both *cumberlandicus* and *insolitus* the all-female populations have a karyotype of 34 autosomes + XX. The mechanism by which diploidy is maintained in them has not yet been determined.

The situation in these two cave-crickets exemplifies the phenomenon first described by Vandel (1928) and named by him geographic parthenogenesis. Although it is relatively rare, instances of it are known in many groups of insects and in amphibians and reptiles, to cite only terrestrial animals (Suomalainen 1950; Ghiselin 1974; Cuellar 1977; Glesener and Tilman 1978). Frequently the parthenogenetic populations are polyploid and believed or known to be of hybrid origin, but in other cases they are diploid, as in the hadenoecines. Although a diploid population may arise through hybridization, such an origin for those of *H. cumberlandicus* and *E. insolitus* is highly unlikely, because they exist at the margins of the ranges of the sexual populations farthest away from the areas where occur the only other species with which hybridization would be possible. In these two species the parthenogenetic populations have almost certainly developed from sexual ones by suppression of meiosis or by automyxis.

In the light of recent contributions to the theory of the genetic basis of natural selection, it has come to be realized that it is not the existence of parthenogenetic populations that needs explanation, but rather why it is that the vast majority of higher organisms are diploid and sexual.[1] Among recent works dealing with this problem are those by Maynard Smith (1971a, b), Ghiselin (1974), Hamilton (1975), Williams (1975) and Cuellar (1977). Williams, in particular, has stressed the apparent paradox that this preponderance of sexuality exists in spite of its genetic cost in meiosis, which puts a sexual population at a 50% disadvantage compared with an asexual or parthenogenetic one. The explanation of the ubiquity of sexuality must be that it confers short-term benefits to the individual in terms of maximizing its reproduction, and the problem is to determine the nature of those benefits and the circumstances under which they will accrue.

Since sexuality ensures a high degree of genotypic and phenotypic variability in the offspring, it is logical to relate it to environmental unpredictability, because it will increase the chances of survival of some progeny under a variety of circumstances. Williams showed how sexual reproduction would be favored in high-fecundity species colonizing unpredictable habitats in each generation, but still argued that it might be non-adaptive in low-fecundity organisms. Hamilton called attention to the biological components of environmental uncertainty as a cause of sexuality. Ghiselin, who dealt principally with the geographic relations of asexual and parthenogenetic populations to their sexual relatives, noted, as did Suomalainen, that they tend to occur at higher

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[1] Although male-female populations are often spoken of as bisexual and all-female ones as unisexual, those terms are so generally used to distinguish monoecious from dioecious individuals that it seems better to refer to populations as being sexual or parthenogenetic.

latitudes and altitudes, in xeric as opposed to mesic conditions, and in disturbed rather than in undisturbed habitats. There is also a tendency for them to occur on islands or in island-like situations, while mainland populations remain sexual. Ghiselin did not discuss these tendencies in the context of uncertainty, but attributed them to increased intraspecific competition for limited resources under what are assumed to be more constant conditions, favoring a system that produces individuals that switch resources. Cuellar, attempting to elucidate the evolutionary ecology of parthenogenesis in the light of what is known of it in all parthenogenetic animals, gives three reasons for believing that parthenogenetic populations can evolve only in isolation from the generating sexual ones. These are (1) that hybridization by males of the sexual population would impede clone establishment; (2) that competition with the sexuals would impede clone expansion; and (3) that it is observed that parthenogenesis evolves either at the periphery of the range of the parent sexual population, or if within the range then in areas periodically devoid of the sexual form. He cites evidence suggesting that parthenogenetic forms, in spite of their higher intrinsic rate of increase, cannot compete with the sexual form, and can exist only in special and limited habitats where that form does not exist. He does not, however, go into the reasons why this should be so.

The whole subject of geographic parthenogenesis in terrestrial animals, considered in relationship to sexuality and the components of environmental uncertainty, is reviewed by Glesener and Tilman (1978).[1] They point out that Ghiselin's and Williams' ideas are logically very similar. They reject Ghiselin's hypothesis as to the causes of the observed trends, and note that Williams' models are also inappropriate for the situations Ghiselin discussed. But they do accept some of Williams' ideas, particularly when the life history conditions he imposes are met, but in that case Ghiselin's model would probably apply as well. They agree with Hamilton on the importance of the biological components of environmental uncertainty in maintaining sexuality, but go beyond him in proposing the hypothesis that sex itself is not only one of these components, but perhaps the most important of them, because its influence is so all-pervasive. In the authors' own words, they suggest that "once evolved, sex in one individual or species leads to the persistence of sex in a community of interacting individuals by increasing the uncertainty of the direction and intensity of selection imposed by these interactions." This hypothesis seems adequate to account for the ubiquity of sex and the inability of parthenogenetic populations to compete successfully with their sexual relatives.

The caves occupied by the parthenogenetic populations of *H. cumberlandicus* and *E. insolitus* differ from those inhabited by the sexual populations of those species only in their peripheral location. Although

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[1] To whom I am indebted for permission to refer to their work prior to its publication. The preceding survey is based largely upon it.

they lie along the northern edges of the ranges, they are not in colder climates or at higher elevations, and the environments they provide are essentially identical with those of caves in the main body of the range—equable, humid, undisturbed, and highly predictable except with respect to biological components. For the scavenging cave-crickets food is not a limiting resource, being accessible in practically unlimited amounts outside the cave mouths.

The following hypothesis is advanced to explain the existence and distribution of parthenogenetic populations in these two species. It assumes that a very small proportion of their virgin females produce viable young, which are always female and diploid. Such occasional parthenogenesis has been observed in most groups of insects, including numerous species of Saltatoria; its occurrence in the Hadenoecini would provide a basis for the formation of parthenogenetic populations from sexual ones. A single wandering female, unfertilized but capable of producing some parthenogenetic eggs, could, if it reached a previously unoccupied cave, found there an all-female colony in which selection for increased production of such eggs would occur. Since by hypothesis the founding female would have outdistanced its predators and competitors, and since the cave environment is uniform and highly predictable except for biotic factors, lack of variation in the resulting parthenogenetic population would not prevent it from being highly successful so long as it remained isolated.

As was pointed out above, uninhabited caves must be colonized by "sweepstakes" dispersal, in which the chances for success are very small for any individual and overwhelmingly against the simultaneous arrival of both sexes. They are greater for an unfertilized female than for a fertilized one, for the former can begin its wanderings while still a nymph while the latter must mature and mate before setting out, since opportunities for mating would be very rare away from the home cave. In discussing a similar situation in the the instance of the isopod *Trichoniscus elisabethae*, White (1954) observed that the most likely explanation of the peripheral distribution of the parthenogenetic forms is that they "have found it easier to expand their ranges just because every individual was capable of founding a local colony of the species, and because there was no reproductive wastage, however small or scattered the population."

According to this hypothesis the sexual populations in the main body of the range are maintained as such by their interaction with predators (and perhaps with competitors, if such exist) that are themselves sexual and hence a source of environmental unpredictability. For *Hadenoecus cumberlandicus* the most important predator by far is *Darlingtonea kentuckensis* Valentine, a trechine carabid beetle that feeds on the eggs and first-instar nymphs (Marsh 1969; Norton et al. 1975). It is present in the great majority of the *Hadenoecus* caves except on the northern periphery of the range of the cave-cricket, and excluding the caves where the parthenogenetic populations occur (see map, Fig. 16). As Norton shows in Part III, this predator exerts a strong selective influence on ovipositor length of *H. cumberlandicus*, and presumably does so also on less obvious characteristics of the species involving behavior. The cave-cricket and the beetle, furthermore, are merely components (though major ones) of communities of interacting species of terrestrial cavernicoles, all sexual, that vary somewhat in composition from cave to cave. The hypothesis assumes that wherever *H. cumberlandicus* exists in association with *Darlingtonea* (and perhaps other interacting sexual species) sexuality will be favored over parthenogenesis. One would expect, then, to encounter parthenogenetic populations only where the cave-cricket is expanding into unoccupied territory, and that such populations would persist only until they were overtaken by *Darlingtonea* (and other interacting species) and by sexual *cumberlandicus* adapted to coexist with sexual predators and competitors. A parthenogenetic population would itself send out colonizers. Those moving outward into vacant territory would found new parthenogenetic colonies, themselves destined eventually to be replaced by sexual populations, while parthenogenetic females moving into areas already occupied by sexual populations would in those areas be at a competitive disadvantage. For these reasons parthenogenetic populations would always be peripheral and more or less ephemeral; only when their founders succeeded in crossing a barrier temporarily impassable to the principal interacting species could they endure for any length of time.

One objection that might be raised to this hypothesis is that the predator *Darlingtonea* seems to be absent from about one-third of the caves in the main range of *H. cumberlandicus* that nevertheless have sexual populations. These instances are probably to be explained by the caves having been colonized by fertilized females, by gene-flow from surrounding sexual populations, by the undetected presence of the predator, or by a combination of these.

The distribution of the parthenogenetic and sexual populations of *Euhadenoecus insolitus* (map, Fig. 17) is similar to and presumably explainable in the same terms as that of *H. cumberlandicus*, but with different predators and associates playing corresponding roles. By hypothesis both species are expanding into unoccupied territory along the northern borders of their ranges. In the instance of *cumberlandicus* such a vacancy could have resulted from elimination of the more northern populations of that species during the latest glacial episode, as is believed to have occurred in Europe in the case of *Trichoniscus* and various species of insects. But this explanation can scarcely apply to *insolitus*, the parthenogenetic populations of which appear to be pushing into territory in which *H. subterraneus* survived the Pleistocene and flourishes today. Perhaps the northward spread of this species is the result of a relatively recent overpassing of a former physical barrier somewhere to the south (the Cumberland valley?), and something similar might have happened in the instance of *cumberlandicus*. The apparent absence of parthenogenetic populations in *H. subterraneus* may be owing to the fact that it has run out of frontiers and that its sexual populations have caught up with and eliminated any (hypothetical) earlier parthenogenetic pioneer colonies.

PART III. THE BIOLOGY OF *HADENOECUS SUBTERRANEUS* AND *H. CUMBERLANDICUS*

by Russell M. Norton

This account of the ecology, life history, and behavior of *Hadenoecus subterraneus* and *H. cumberlandicus* in part summarizes previously published information but is principally a report on observations and experiments made by the author in several seasons of field work in the karst regions of Kentucky. The Kentucky karsts are developed on two broad but discontinuous regional exposures of the same Mississippian limestone: the Pennyroyal Plateau in the western portion of the state and the edge of the Cumberland Plateau in the east. Both plateaus have large numbers of caves containing species of the rhaphidophorid cricket genus *Hadenoecus*, the members of which are cave-limited in their distribution. Although these crickets are obligate cavernicoles, adults and later instar nymphs leave the cave on warm moist nights to feed. They often roost as large aggregates on the cave ceiling during the day, use the deep cave areas for oviposition, and pass their early life entirely within the cave. These crickets are often the most abundant terrestrial macrofauna in the cave, and their guano, eggs and carcasses are of great importance to the terrestrial cave community. In Mammoth Cave, over one-half of the 25 species of terrestrial troglobites (i.e., obligatory cavernicoles confined to the subterranean environment) are associated with *Hadenoecus* guano, or predaceous on the eggs and nymphs of *Hadenoecus*, or predaceous on animals themselves associated with the guano (for a detailed discussion of the Mammoth Cave biota see Barr, 1968).

These cave-crickets usually occur with a cave-limited carabid beetle (Coleoptera) that specializes as a predator on the eggs and nymphs of the crickets. In the Pennyroyal Plateau of western Kentucky the cricket is *Hadenoecus subterraneus* and its predator is *Neaphaenops tellkampfii* (Erichson) (Fig. 15); in the Cumberland Plateau of eastern Kentucky the cricket is *Hadenoecus cumberlandicus* and its predator is *Darlingtonea kentuckensis* Valentine (Fig. 16). The predators are members of closely related monotypic genera of the tribe Trechini (Carabidae).

The two *Hadenoecus* species live under practically the same environmental conditions: constant darkness, high humidity, stable temperature, the presence of a single very important trechine beetle predator, and the availability of ample food supplies outside the cave. In addition, the details of their overwintering, copulation, oviposition, and foraging behaviors are very similar, as are their evolutionary responses to selective pressures. The observations contained in this section, although made principally on *H. subterraneus*, may therefore be applied in a general way to both species.

FOOD AND FEEDING. *Hadenoecus* leaves the cave on sufficiently warm, moist nights. Even in mid-winter, relatively warm nights will bring these crickets above ground in very large numbers (Norton, unpublished; Barr and Kuehne, 1971). *Hadenoecus* feeds opportunistically and omnivorously as a scavenger. In caves surrounded by blackberry patches, the crickets gorge on the ripe fruit; in caves surrounded by cow pastures, they eat their fill of bovine feces. They have been known to nibble the ears of hibernating bats and are supposed to have partially eaten Floyd Collins' ears after his death in Sand Cave. They are strongly attracted to molasses, peanut butter, and other baits.

Although Park believed the crickets to be predaceous because of the numerous arthropodan fragments in the guts (Park and Reichle, 1963; Reichle, Palmer and Park, 1965), they lack any raptorial adaptations and show no evidence of predaceous behavior. Because adult *Neaphaenops* beetles eat *Hadenoecus* eggs and nymphs, predation by *Hadenoecus* on *Neaphaenops* would presumably be highly advantageous to the cave cricket, adults of which appear large and strong enough to kill the relatively small (ca. 7mm) beetle. But although the crickets quickly find and eat *Neaphaenops* experimentally killed by heat with no external injury, direct observation gave no indication that they hunt live *Neaphaenops*. An important result of over 300 gut content analyses of *H. subterraneus* from Mammoth and Whites Caves was the finding that only 1.3% of the recognizable arthropodan fragments were from *Hadenoecus* and *Neaphaenops*, the two most abundant members of the terrestrial macrofauna in these caves (Park, Reichle and Suter: unpublished diagrams). Although *Hadenoecus* do eat moribund or otherwise defenseless invertebrates, they seem not to be predaceous in the usual sense of habitually seeking and capturing prey. In other rhaphidophorid groups some or many of the species are facultative predators; both *Tachycines* and *Troglophilus* are said to obtain much of their food by active predation.

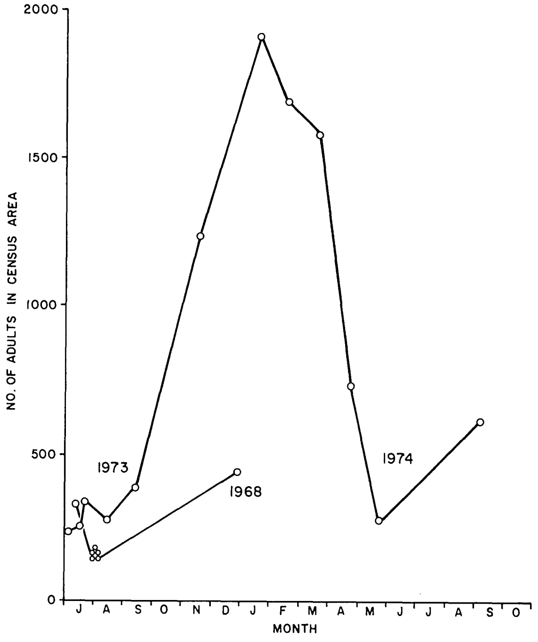

Fig. 20. Graph based on visual census of adult *Hadenoecus subterraneus* in a segment of Marion Avenue, Mammoth Cave. Marion Avenue is utilized by the cave-cricket both for over-wintering and for oviposition, and fluctuations in numbers of adults are therefore mainly owing to immigration and emigration.

Hadenoecus individuals clearly find the vast preponderance of their food outside the cave. In the study by Reichle, Palmer and Park (1965) mentioned above, at least 90% of the recognizable food fragments were from outside and only 1.3% apparently from inside the cave. While the percentages must vary greatly with locale and season, in this study plant material constituted 13% of the recognizable fragments and 85% came from arthropods. Since chitinous materials resist the digestive process, the proportion of arthropods in the food intake is likely to be overestimated from the recognizable gut content fragments, and the importance and role of animal protein in the diet of *Hadenoecus* therefore needs further clarification.

Although *Hadenoecus* may be found inside the cave at enormous distances from the nearest (human) entrance, it is incorrect to conclude that they are able to obtain adequate food or to complete their life history in the deep cave. During much of the winter the crickets are unable to feed outside the cave and seek refuge in its deeper, more climatically stable portions, where there is a marked increase in the number of late instar nymphs and adults (Fig. 20). The greatest concentration of individuals resulting from this winter influx occurs around the area of domepits and crevices bordering the margins of the impervious sandstone caprock. These domepits and crevices are easily accessible to *Hadenoecus* and sometimes to larger animals, such as the cave rat, *Neotoma*. Overwintering *Hadenoecus* exhibit markedly lower fecundity near entrances than in the deep cave (Table 6). This is an indication that although the deep cave is used for oviposition, when a female is not gravid it tends to roost near the entrance, awaiting an opportunity to feed outside.

TABLE 6

FECUNDITY OF ENTRANCE- AND INTERIOR-ROOSTING ADULT FEMALES OF *HADENOECUS SUBTERRANEUS*

	Entrance				Interior			
Cave	Eggs[a]	Gravid[b]	Total[c]	Location[d]	Eggs	Gravid	Total	Location
Great Onyx								
July 1972[e]	2.10	15	20	0-18	5.55	16	20	18-135
Jan. 1973[f]	5.30	17	20	0-18	7.00	10	10	90-110
Parkers								
8 Jan. 1973	3.60	16	20	0-10	7.60	20	20	53
Total Gravid	4.56	48			7.24	46		
	s = 3.54				s = 5.59			
t = 2.76, df = 76.9: P < 0.005 Student's t-Test (Owen, 1962)								
Total Including Nongravid								
	3.67		60		6.66		50	
	s = 3.64				s = 5.71			
t = 3.20, df = 81.4: P < 0.005 Student's t-Test (Owen, 1962)								

[a] Mean number of eggs 3 mm or more in length in ovaries per gravid female.
[b] Number of adult females in sample with eggs 3 mm or more in length in ovaries.
[c] Number of adult females in sample.
[d] Approximate distance in meters from current human entrance.
[e] Entrance sample 24 July, interior sample 28 July.
[f] Entrance sample 4 January, interior sample 22 January.

The vast majority of the individuals that leave the cave at night to feed seem to find their way back before morning to the cave or to cool, moist solutional crevices (karren, subsoil karren, grikes) associated with karsted limestone. An occasional individual *Hadenoecus* may be forced to seek refuge outside during the day, and as previously noted some must have survived occasional wanderings to considerable distances from their original subterranean abodes. My own observations during the early evening hours of peak activity in all seasons have shown, however, that it is difficult to find *Hadenoecus* more than 70 meters from the limestone. It is sometimes possible to determine the existence of subsurface spaces in limestone dolinas (sinks) surrounded by sandstone by observing *Hadenoecus* returning to the entrance after foraging outside in the early evening.

DAILY ACTIVITY RHYTHMS. Two recent studies seem to show the existence of diurnal activity rhythms in the rhaphidophorids. Reichle, Palmer and Park (1965) investigated the spontaneous locomotor behavior of *Hadenoecus subterraneus* continuously for 23 days under laboratory conditions, in complete darkness and at a constant temperature of 17°C. They used five crickets per 8×8×7 cm actograph, accumulated 2,200 "cricket hours" of data on their activity, and plotted the overall mean relative activity vs. time in bihourly periods. The resulting graph seems to show a definite nocturnal activity rhythm. Although the experiments were run in a simple laboratory incubator, it seems unlikely that human disturbance influenced the activity pattern, which decreases after 2 AM and has a moderate increase at 8 AM. These authors found that as mean activity increases, the mean standard deviation in activity also increases, producting a resultant "nocturnal rhythm in mean bihourly standard deviations." Perhaps this rhythm in standard deviation is the result of the mathematical relation between the magnitude of the mean and the standard deviation(mean × constant is proportional to standard deviation × constant). No test of statistical significance, such as autocorrelation or Fourier analysis, was performed, but the data seem convincing. Reichle et al. interpret the activity rhythm as a means of insuring that the nocturnal feeding migration is properly timed; they suggest hunger and daylight as modulators of the basic rhythm, although its underlying mechanism is unknown.

Simon (1973) studied activity rhythms of *"Hadenoecus subterraneus"* (*Ceuthophilus utahensis* Thomas, det. T. H. Hubbell) at Bergen Park, Colorado, in an inactive mine tunnel used as a geophysical observatory of the Colorado School of Mines. She used 12-30 individuals per actograph in three replicate experiments, and concurrently recorded earth tides. The autocorrelations of the cricket activity data seem to show virtually nothing. The Fourier transformations appear to show convincing daily rhythms. Unfortunately levels of statistical significance are given for neither the autocorrelations nor the Fourier analyses. The cross correlation between cricket activity and earth tides can be attributed to there being a diurnal component in both rhythms. Examination of the figures has convinced me that there is no basis for Simon's claim of a "shift" at "27.042 days" in the cross correlation between the cricket activity and earth tide data. Although the title of the paper would seem to imply more, the only conclusion reached is that both rhythms are approximately diurnal.

MATING. Nicholas (1962a) has given a cursory and somewhat misleading account of mating in *Hadenoecus subterraneus*, and Barr (1967b, Fig. 19, Pl. 55) has published a photograph of a copulating pair of that species. A similar photograph, a little clearer in detail, is reproduced here as Plate I.

Mating behavior appears to be essentially identical in *Hadenoecus subterraneus* and *H. cumberlandicus*. Males seem to be drawn toward females that are ready to mate, probably by an olfactory attractant; several males are often seen at the same time in attendance upon a single female. Physical contact is first made with the elongate antennae, after some interplay with which the female finally mounts the male from behind. So far as has been observed the male's paired dorsolateral exsertile organs, located cephalad of the cercal bases, are not extruded prior to this stage, so that it seems unlikely that they function as pheromone organs, a conclusion also supported by the fact that males seek out the female instead of the reverse. But they are protruded when the female mounts, and act as claspers, enclosing the end of the female's abdomen (Plate I, inset). Once in position these fleshy organs exert a grip often sufficient to hold the pair together as they move away from a disturbance, and occasionally it is possible to preserve a male and female *in copula* with the organs in place. Copulation may continue for a long time before the phallus is eventually everted to place the spermatophore in position. The remarkably long duration of copulation, correlated with absence of spermatophylax as noted below, can perhaps be explained as the result of almost complete lack of serious disturbances during the act and the consequent lack of selective pressure to shorten it.

The spermatophore of *Hadenoecus cumberlandicus* is indistinguishable from that of *H. subterraneus*. It is rather large, about 4-5 mm long and 2 mm in breadth and depth. Its rear portion is ovate; its dorsal surface, applied to and evidently molded by the base of the ovipositor, has a triangular concavity anteriorly and a pair of thin lateral flanges appressed to the sides of the ovipositor. The anterior end is a short, wide, thin-walled tubular neck that fits closely into the dilated opening of the spermathecal duct, exposed in the roof of the gonopore chamber by depression of the female subgenital plate. The walls of the spermatophore are tough and translucent, and there is no spermatophylax. (Nicholas noted that the male exudes a white, syrupy fluid when affixing the spermatophore, which he assumed to be spermatophylax, but it does not form the gummy masses attached to the spermatophore that constitute true spermatophylax, and probably serves merely to help hold the spermatophore in place.) The spermatophore of *Hadenoecus*, like the smaller one of *Dolichopoda*, contains a single ampulla or sperm chamber that is partly divided by a low ridge on its floor and rear wall. According to Boldyrev (1915) absence of spermatophylax in *Dolichopoda* and various other tettigonioids is correlated with prolonged copulation that prevents premature removal of the spermatophore by the female; in species having spermatophylax the same result is attained by the time required for the female to chew off the spermatophylax before the spermatophore can be extracted with the mandibles. In *Dolichopoda* the copulatory posture is maintained for one or two hours after transfer of the spermatophore, and Nicholas reported that *Hadenoecus* pairs frequently remain in copula for several hours. My own field observations have confirmed the fact that copulation in *Hadenoecus* is prolonged and that the functioning of the male eversible organs as claspers is extremely important in holding the partners together.

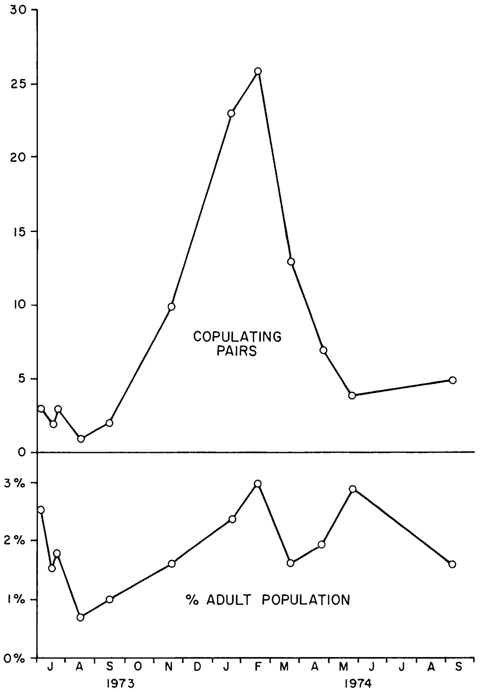

Fig. 21. Graph based on visual census of copulating *Hadenoecus subterraneus* in a segment of Marion Avenue, Mammoth Cave. Both copulation frequency and the number of crickets in copula reach a maximum in late winter, just prior to the maximum in oviposition associated with the resumption of epigean feeding in early spring.

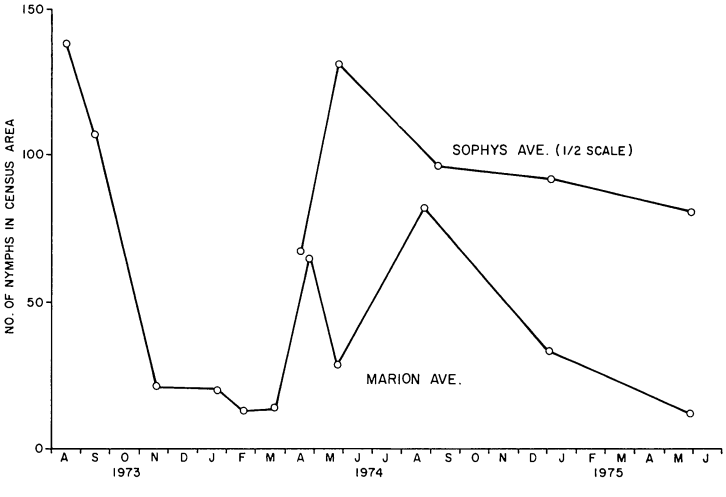

Fig. 22. Graph based on visual census of first-instar nymphs of *Hadenoecus subterraneus* in defined areas of Mammoth Cave. The census data are consistent with the timing of the late winter-early spring maximum in oviposition.

There is a gradual increase in the frequency of copulation to a midwinter peak (Fig. 21), followed by an abrupt decrease associated with a pulse in oviposition (Kane, Norton and Poulson, 1975, Fig. 4), and with the spring egress of crickets as epigean feeding outside the cave is resumed. These data substantiate and extend the impressions about copulation described by Barr (1967b).

OVIPOSITION. Barr (*l.c.*) stated that oviposition of *Hadenoecus* occurs on silted ledges or in silt floors of passages above flood level. It is true that these crickets show a clear preference for loose sand and silt as a substrate for oviposition, but they will oviposit in rotting leaves, wet mud, or anywhere else when they have no alternative. The crickets test the substrate by inserting their ovipositors at an angle normal to the surface. If an egg is not laid the ovipositor is withdrawn, leaving a small puncture hole that *Neaphaenops* avoids digging near (Norton, in prep.).

If an egg is laid, the cricket uses the serrated tip of its ovipositor to rake the substrate toward the hole. In substrate with typical clay and moisture content this often produces a roughly conical mound about 6-7 mm high by 15 mm in diameter directly over the egg. Radiating lines left by the raking process partially surround the mound to a distance of about 3 cm in a 90°-120° arc. In a substrate that is loose and less moist the mound may be more nearly 1 mm in diameter and almost imperceptible. Occasionally a recognizable mound may be entirely lacking, and only the arc or area of ovipositor raking marks is visible. Eggs appear always to be laid singly, although occasionally the same or another individual may deposit another egg within a few millimeters of a previously laid one.

The marked seasonality associated with the influx of *Hadenoecus* into deep cave areas, and the pulsed nature of the oviposition just prior to the spring egress, are the two important determinants of the seasonality exhibited by much of the terrestrial biota of the cave community in upper level passages.

EGGS. *Hadenoecus* eggs are roughly 4 mm long at maturity and weigh approximately 5 mg, although there is statistically significant variation in weight with season and location. Females carrying up to 37 mature eggs have been taken just before the spring peak in oviposition. This peak occurs during the three-month period from February to April, and accounts for over half the annual egg input after predation (Kane, Norton and Poulson, 1975, Fig. 4). The eggs generally hatch in twelve weeks, although some, probably smaller eggs with less yolk or possibly unfertilized eggs developing parthenogenetically in a normally sexual population, may take up to six months to hatch.

NYMPHS. The main hatch of nymphs occurs in summer (Fig. 22). The first instar is an unsclerotized, non-feeding stage which molts in approximately five weeks. Nymphs from eggs that have taken an abnormally long time to hatch also take an abnormally long time to molt and have a drastically lowered probability of survival. The second instar feeds, and seems to molt in approximately ten weeks. Although the distribution of hind femur lengths appears to differentiate the first four instars fairly clearly, later instars are less easily separable. The larger nymphs, however, can be sexed by differences in the developing terminalia, and a plot of their hind femur lengths made separately for each sex suggests that the total number of instars, including the adult, is approximately eight. The number is known to be somewhat variable in other rhaphidophorids and probably is so in *Hadenoecus*. The nymphs usually begin to leave the cave at night to feed when they reach the fifth instar.

ADULTS. Following the final molt, the ovipositor of the female becomes fully sclerotized in about one day. Her subgenital plate, however, takes about one month to attain its fully sclerotized condition, and prior to that time she carries no mature eggs.[1] The maximum observed longevity, determined by marking studies, is about eight months (Norton) to eleven months (Nicholas, 1974). As already mentioned, there is an enormous influx of adults into the deep cave areas during the winter months (Fig. 20), and during the late winter and early spring, just before the resumption of epigean feeding, there is a marked increase in copulation (Fig. 21) and in oviposition.

Seasonal differences in adult body size of *Hadenoecus* are shown in Tables 7 and 8. Although the magnitudes of the seasonal differences are not always significant in themselves, there is a statistically significant tendency for adults sampled in summer to be slightly larger than those sampled in winter. When only statistically significant differences in size are considered, the tendency still remains. Predated populations seem to exhibit statistically greater seasonal stability in body size than do nonpredated populations. This may be owing to reduced nymphal competition in predated populations, which may stabilize size distributions.

Because of the apparent seasonal differences in body size, it would be possible to bias the results slightly toward more statistically significant size differences between predated and nonpredated populations by sampling the predated populations in summer and the nonpredated populations in winter. For the ovipositor lengths reported in this study (Tables 9 and 10) only two nonpredated populations of each species were sampled in winter. Both of the winter-sampled nonpredated *cumberlandicus* populations were parthenogenetic ones that could not be sampled in summer because there were not enough crickets in accessible areas of the caves. All of the predated *cumberlandicus* populations compared with these were also sampled in winter.

PREDATION. Using paired predator exclosure and control plots, Norton, Kane and Poulson (1975) were able to determine that over 90%

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[1] This is true for *H. subterraneus*, but possibly not for *H. cumberlandicus*.

TABLE 7

MEAN ADULT OVIPOSITOR AND HIND TIBIA LENGTHS FOR PREDATED AND NONPREDATED POPULATIONS OF *HADENOECUS*[1]

	OVIPOSITOR					HIND TIBIA				
	Summer[a] 1972 Mean in mm.	N	January 1973 Mean in mm.	N	P[b]	Summer[a] 1972 Mean in mm.	N	January 1973 Mean in mm.	N	P[b]
Hadenoecus subterraneus:										
Parkers	13.70	12	12.97	20	***	27.41	14	26.67	40	***
Mammoth	13.13	20	12.96	10	NS	28.10	20	27.83	29	NS
Great Onyx	12.93	21	13.26	10	NS	27.36	10	27.21	10	NS
Cub Run	12.36	14	11.60	10	***	27.53	9	26.56	22	**
Jacks	11.76	15	11.51	10	NS	26.66	10	26.33	22	NS
Stewart	11.63	20	11.72	10	NS	25.05	28	24.98	18	NS
Steep Hollow	11.60	13	11.56	27	NS	26.99	26	26.78	52	* -0.23
Hadenoecus cumberlandicus:										
Stab	14.66	15	14.56	17	NS	30.00	31	30.09	33	NS
J. Rogers[c]	14.23	9	13.79	21	NS	29.38	17	29.29	40	NS
J. Rogers[d]	13.99	10	13.42	21	**	29.08	8	27.71	21	NS
Cope	13.73	12	13.36	19	**	28.84	10	28.63	37	NS
Moreland	13.61	18	13.27	11	**	29.07	35	28.56	19	* -0.15
1813	13.51	12	12.96	19	**	29.52	23	29.20	37	**
Natural Bridge	13.32	5	14.10	14	**	27.53	4	29.49	11	***
Murder	13.20	1	12.33	9	NS	29.98	2	26.44	15	**

[a] 21 July-24 August

[b] Mann-Whitney (Wilcoxon) Two-Sample Statistic (two-tailed; Owen, 1962).

[c] Jackson County.

[d] Powell County.

* P-minimum $\leqslant 0.05$

** P-minimum $\leqslant 0.05$, P-maximum $\leqslant 0.10$

*** P-maximum $\leqslant 0.05$

NS Not statistically significant

[1] Italicized cave names indicate predated populations.

TABLE 8

SEASONAL DIFFERENCES IN ADULT BODY SIZE OF *HADENOECUS*

SUMMER vs. WINTER:

All differences: (Summer $>$ Winter) = 25, (Summer $<$ Winter) = 5
P $<$ 0.01 (two-tailed) Sign Test (Owen, 1962). H_0: Summer = Winter.

Significant[a] differences by population: (Summer $>$ Winter) = 9, (Summer $<$ Winter) = 1
P = 0.05-0.10 (two-tailed) Sign Test (Owen, 1962). H_0: Summer = Winter.

PREDATED vs. NONPREDATED:

	Significant[a]	Nonsignificant[a]
Predated	1	4
Nonpredated	8[b]	2

P = 0.05[b] (two-tailed) hypergeometric (Owen, 1962). H_0: identical distributions.

[a] Seasonal differences are scored as significant if either or both ovipositor length and tibia length have a (two-tailed) P-minimum of 0.05 or less.

[b] P = 0.10 if Steep Hollow is scored as nonsignificant.

TABLE 9

MEAN ADULT OVIPOSITOR LENGTHS FOR PREDATED AND NONPREDATED POPULATIONS OF *HADENOECUS SUBTERRANEUS*

CAVE[a]	MEAN in mm	N	CAVE	MEAN in mm	N
Parkers	13.70	12	*Hanson*	12.06	10
Flint Ridge (Columbia Ave.)[b]	13.17	5	Detrex	11.82	10
Mammoth (Marion Ave.)[c]	13.07	30	Jacks	11.81	14
Mammoth (Radio Room)[c]	13.07	10	Jesse Stewart	11.69	19
Great Onyx (rear)[b,d]	13.04	31	Katie White	11.67	16
Webb	12.89	19	Steep Hollow	11.56	27
Great Onyx Front)[d]	12.88	73	Odie James	11.49	14
Cooch Webb	12.83	11	*Slick Rock*	11.39	15
Wonderland	12.75	5	Mitchell	11.37	5
Buckner Hollow	12.42	11	Mud River	11.36	8
Belt	12.38	13	*Wheeler*	11.34	5
Cub Run	12.36	14	Britt	11.25	2
Camp Branch	12.35	8	Stanley	11.18	4
Pruitts Saltpeter	12.21	11	*Devils Den*	11.18	2
Gonterman	12.20	4	*Hoy*	11.16	10
Wisdom	12.11	7	Gassaway	11.14	4

Mann-Whitney (Wilcoxon) Two-Sample Statistic U = 51, N = 30 (16 predated,[e] 14 nonpredated), $P < 0.02$ (two-tailed).

[a] Predated populations italicized.

[b] Populations separated by 0.5 km.

[c] Populations separated by 2.2 km.

[d] Populations separated by 1.2 km of dry cave passage that constitutes a physiological barrier.

[e] Mammoth and Great Onyx populations counted once each.

of the *Hadenoecus* eggs laid in loose silt are destroyed by *Neaphaenops*. In other situations a smaller percentage is predated by the beetle, seemingly because of increased moisture content in clay-rich substrate. First-instar nymphs of *Hadenoecus* appear to make up about one-third of the diet of adult *Neaphaenops*, although an occasional later instar nymph is also eaten. Of the predated first-instar nymphs about one-third appeared to have been captured during emergence, and since active first-instar nymphs are able to persist in three-dimensional confinement with *Neaphaenops* until ecdysis, it seems likely that most of those eaten are taken during eclosion or ecdysis. Healthy nymphs may, however, sometimes be caught in situations where they are unable to escape by jumping.

EFFECTS OF PREDATION BY *NEAPHAENOPS* AND *DARLINGTONEA* ON *HADENOECUS* MORPHOLOGY. Early in the course of the present study it was observed that populations of *Hadenoecus* in caves where a beetle predaceous on their eggs is present seemed to have longer ovipositors than did those populations where that predator is absent. Comparison of ovipositor lengths in samples from predated and nonpredated populations (Tables 9 and 10) demonstrated this to be true. The statistics

TABLE 10

MEAN ADULT OVIPOSITOR LENGTHS FOR PREDATED AND NONPREDATED POPULATIONS OF *HADENOECUS CUMBERLANDICUS*

CAVE[a]	MEAN in mm	N
Fletcher Spring	16.68	18
Baker	15.79	17
Wind	15.24	20
Griffin[b]	14.77	18
Lakes[b]	14.66	21
Stab	14.61	32
Betsey	14.12	19
J. Rogers (Jackson Co.)	13.92	30
Natural Bridge[c]	13.89	19
Koger	13.88	12
J. Rogers (Powell Co.)[c]	13.60	31
Cope Hollow[c]	13.50	31
Moreland[c]	13.48	29
Daniel Boone[d]	13.41	15
Pond School	13.38	13
1813[c]	13.18	31
Risen	13.02	5
Murder[d]	12.33	9
Bat[d]	11.75	13

Mann-Whitney (Wilcoxon) Two-Sample Statistic U = 3, N = 19 (8 predated, 11 nonpredated), $P < 0.001$ (two-tailed)

[a] Predated populations italicized

[b] Separated by 0.5 km

[c] Statistically significant seasonal differences observed.

[d] Parthenogenetic population.

are, for *Hadenoecus subterraneus:* predated populations n=16, nonpredated populations n=14, $P < 0.002$, Mann-Whitney [=Wilcoxon], two-tailed; for *H. cumberlandicus:* predated populations n=5, nonpredated populations n=6, P=0.004, Mann-Whitney [=Wilcoxon], two-tailed. The exceptions invariably occur in predated populations located at the margins of the predator's range and which are surrounded by and presumably interbreed with nonpredated ones.

There is, however, a potential allometric problem. Most nonpredated *Hadenoecus* populations occur at the edges of the ranges in the case of both species. These peripheral populations tend to have smaller bodies and shorter ovipositors and shorter hind tibiae than do those in the central parts of the species' distributions (see maps, Figs. 15 and 16), where the overall body size is generally larger and only predated populations occur. In order to eliminate the possibility that the longer ovipositor in predated populations is solely the result of larger overall body size, some non-biased basis of comparison is required. Ideally, nonpredated populations from the center of the range would be compared with predated populations, also from the center; but unfortunately the former do not exist. A comparison of predated populations

TABLE 11

CORRELATION BETWEEN MEAN LENGTH OF HIND TIBIA AND MEAN LENGTH OF DORSAL ASPECT OF PRONOTUM IN *HADENOECUS SUBTERRANEUS*[a]

		Tibia		Pronotum	
Cave	N	Rank	Mean in mm	Rank	Mean in mm
Mammoth	16	1	28.79	2	3.77
Ice	6	2	27.48	3	3.68
McGinnis	31	3	25.69	4	3.64
Belt	11	4	25.36	8	3.33
Wonderland	12	5[b]	24.50	1	4.11
Mitchell	2	6[b]	24.50	7	3.40
Dismal Creek	9	7	24.58	5	3.48
Gassaway	2	8	22.65	6	3.44

Kendall's Rank Correlation Coefficient (Owen, 1962) $k=19$, $P < 0.09$ (one tail).

[a] Means calculated from measurements by T. H. Hubbell.

[b] Tie broken with supplemental measurements of both populations by R. M. Norton.

TABLE 12

CORRELATION BETWEEN MEAN LENGTH OF HIND TIBIA AND MEAN OVIPOSITOR LENGTH IN *HADENOECUS SUBTERRANEUS*

	N	k§	<k>	<s>	P (one-tail)*
Predated	16	79	60	11.1	<0.044
Nonpredated	13	66	39	8.2	<0.001
Both	29	286	203	26.7	0.001

§Kendall's Rank Correlation Coefficient (Owen, 1962).

* Normal approximation.

with nonpredated ones, both from the margins of the predator's range, is not likely to be significant, because gene exchange there is likely to be high and predation rates are likely to be low. The second supposition is borne out by the fact that, in some populations so located and known to be predated, no predators were seen on several of the visits made to their caves.

One approach to this problem is to examine ovipositor lengths of individual crickets of comparable body size from both predated and nonpredated populations. The length of the hind (metathoracic) tibia was used as a measure of overall size, since that is the longest single sclerotized structure of the body of a *Hadenoecus* and therefore most likely to show significant measurable differences. Hind tibia length in *H. subterraneus* is correlated both with the dorsal length of the pronotum (Table 11) and length of ovipositor (Table 12 and Fig. 23). Because nonpredated populations tend to be marginal in distribution and to have smaller body size, it might be hypothesized that crickets from predated populations have longer ovipositors. When only

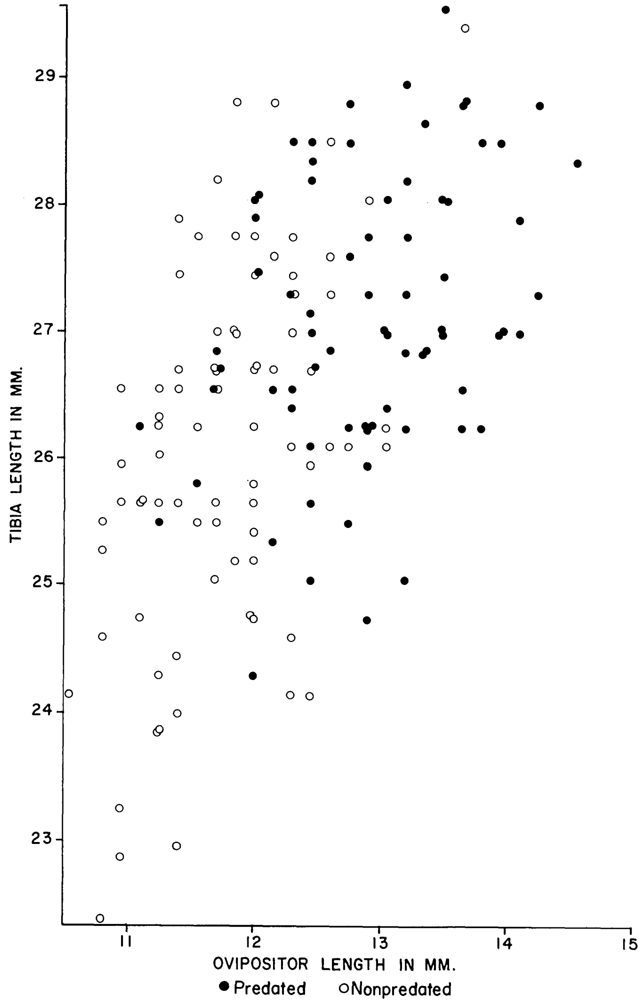

Fig. 23. Hind tibia and ovipositor lengths of individual adult *Hadenoecus subterraneus* from predated populations (64) and nonpredated populations (36). When individuals of comparable body size are compared, those from nonpredated populations tend to have shorter ovipositors than those from predated populations (P=0.013).

H. subterraneus with hind tibia lengths of 26.25 mm or more are considered (Fig. 23), there are 64 individuals from predated populations and 36 from nonpredated ones. Since the tibial length could be measured only to 0.15 mm there are many ties in the data. The hypothesis that individuals of this species of comparable body size from predated and nonpredated populations have equivalent tibia lengths is given its strictest test when ties are broken so that individuals from nonpredated populations appear to have shorter tibia lengths. The probability that individuals from nonpredated populations are smaller

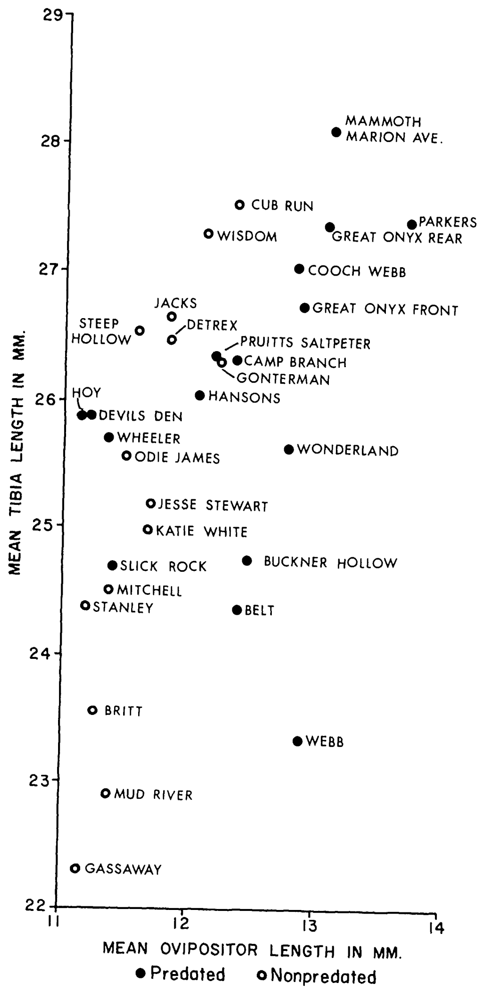

Fig. 24. Mean adult ovipositor length versus mean adult hind tibia length in predated and nonpredated populations of *Hadenoecus subterraneus*. Except for a few predated populations located at the edge of the predator's range, the means tend to occur in two separate areas of the graph.

than those from predated populations in this tibia-length range is P=0.17 (Mann-Whitney [=Wilcoxon], two-tailed); therefore the hypothesis that the crickets of comparable body-size have equivalent tibia lengths is accepted.

The hypothesis that *H. subterraneus* of comparable body size (see above) from predated and nonpredated populations have equivalent ovipositor lengths is given its strictest test when ties are broken so that individuals from nonpredated populations appear to have longer ovipositors. Under this condition the probability that crickets

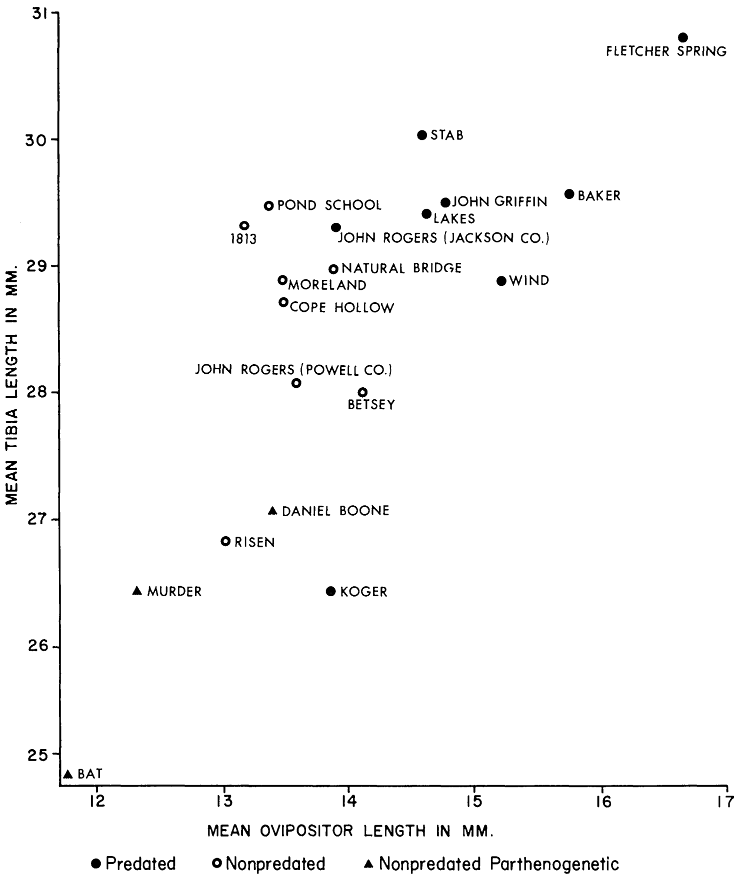

Fig. 25. Mean adult ovipositor length versus mean adult hind tibia length in predated and nonpredated populations of *Hadenoecus cumberlandicus*. The means tend to occur in two separate areas of the graph.

from nonpredated populations have ovipositor lengths equivalent to those from predated ones is P=0.0013 (Mann-Whitney [=Wilcoxon], two-tailed), so this hypothesis is clearly to be rejected. The conclusion is that (at the 0.9987 confidence level) crickets of comparable size have shorter ovipositors in nonpredated populations than in predated ones.

A second basis for comparison of the effect of body size on ovipositor length is to examine mean ovipositor length with respect to mean tibia length for both predated and nonpredated populations (Figs. 24 and 25). The means for predated and nonpredated populations tend to occur in two separate areas of the plots, and in both species of crickets a line could be constructed between the areas that would separate nearly all the nonpredated from the majority of the predated populations. The appropriate statistical treatment for data of this type is discriminant analysis, which classifies each individual population as "predated" or "nonpredated" on the basis of its similarity to the remaining predated and nonpredated population means. The discriminant analysis of the *Hadenoecus* data was run on the Yale IBM 360 computer, using the standard BMDP7M stepwise discriminant analysis program (Dixon, 1975). When ovipositor length alone is used as the basis for classifying populations as "predated" or "nonpredated," *Hadenoecus subterraneus* populations are classified correctly in 76.7% of the instances, *H. cumberlandicus* populations in 83.3%. A most important result of the analysis is that the addition of tibia length as a second variable of classification makes absolutely no difference in the outcome. This is interpreted as meaning that the allometric effect of body size on ovipositor length is very minor as compared to the effect of predation. The inference drawn from this result is that, in *Hadenoecus* populations exposed to egg predation by the beetles, selection has been effective in increasing ovipositor length by increasing the chance of survival of more deeply buried eggs. This conclusion has been partially borne out in field experiments (Norton, in prep.) which have shown that *Neaphaenops* destroys a smaller than usual proportion of eggs that have been artificially buried 2 mm deeper than normal.

When the discriminant analysis is run with *Hadenoecus* populations classified into four groups, on the basis of whether predated or nonpredated and whether adjacent or nonadjacent to the margin of the predator's range, the addition of tibia length as a second variable slightly improves the discrimination, but only in nonpredated populations at the margins of the predator's range in the case of *H. subterraneus*, and in nonpredated sexual populations of *H. cumberlandicus*. In both species, predated populations at the margins of the predator's range have the lowest percentage of correct classification. This is presumably a result of interbreeding with nonpredated populations. Support for this hypothesis is provided by the fact that in *H. subterraneus* only four predated populations are always misclassified: Hoy, Devils Den, Wheeler and Slick Rock. These are all located at the edge of the *Neaphaenops* range and are surrounded by nonpredated populations.

THE ROLE OF *HADENOECUS* IN THE TERRESTRIAL CAVE COMMUNITY. As was noted in the introduction to Part III, a large proportion of the terrestrial troglobites that occur in the same caves as *Hadenoecus* consists of species that are dependent upon these crickets for their existence. This relationship has been discussed by numerous authors, including Nicholas (1962a), Park and Reichle (1963), Reichle (1963), Reichle, Palmer and Park (1965), Barr (1967a, b), Barr and Kuehne (1971), and Kane, Norton and Poulson (1975). The observations recorded in the literature are here briefly summarized. In all caves occupied by species of *Hadenoecus* the eggs, carcasses and guano of these insects constitute a major food resource. The guano accumulates in a thin layer (up to 5-10 mm deep) beneath the roosts of large aggregations of the crickets, and in smaller amounts under more isolated roosting spots. Since the food of the crickets is for the most part obtained outside the cave, guano production is largely limited to the periods during which epigean feeding occurs.

The animal communities based on the crickets, their feces and their eggs differ in the number and identity of their component species in different parts of the Interior Low Plateaus, where Barr (1967) distinguishes several distinctive faunas. Within a faunal area there are also differences in the species composition from one cave to another. The food web in the terrestrial community of White Cave, Kentucky, was discussed and diagrammed by Barr and Kuehne (1971, Fig. 5). Nearly the entire animal life of this cave is dependent upon *Hadenoecus subterraneus* and, to a lesser extent, on a few pieces of rotten wood near the end of the cave. The fauna consists in part of saprophiles feeding on the partially decomposed cricket guano; these include two species of snails, an isopod, two millipedes, two collembolans, a campodeid and a catopid beetle. As usual *Neaphaenops* is the chief predator of *Hadenoecus*, attacking its eggs and first-instar nymphs, but the cave spider, *Meta menardi* Latreille, also preys on larger nymphs and adults of the cricket. The other predators in this cave feed chiefly on the saprophiles; they include an opilionid, two pseudoscorpions and four trechine carabid beetles.

During its excursions from the cave *Hadenoecus* encounters other insect, arachnid and vertebrate predators, among which toads and salamanders may be important. It is sometimes one of the principal food items in the diet of the cave salamander, *Eurycea lucifuga* Rafinesque, which frequents cave entrances and the neighboring cliffs. *Hadenoecus* is also parasitized by a gordiid worm, and possibly by a tachinid fly; and a parasitic fungus, "*Isaria densa*" (probably *Cordiceps* sp.), has been recorded as a cause of its death (Call, 1897).

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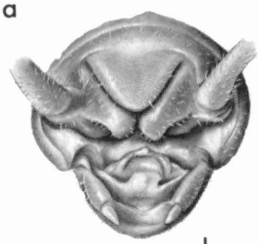
PLATE II

Male terminalia of Hadenoecini in distodorsal aspect

a–*Euhadenoecus puteanus*, Natural Bridge State Park, Powell Co., Ky.;
b–*E. puteanus* (depauperate high altitude form), Mt. Sterling, Haywood Co., N.C. (the epiphallus-like structure is the dorsal phallic lobe);
c–*E. fragilis*, Tawneys Cave, Giles Co., Va.;
d–*E. insolitus*, Town Creek Cave, Marshall Co., Ala.;
e–*Hadenoecus subterraneus*, Mammoth Cave, Edmonson Co., Ky.;
f–*H. jonesi*, Hambrick Cave, Jackson Co., Ala;
g–*H. o. opilionoides*, small cave in Buffalo Cove, Fentress Co., Tenn.

a



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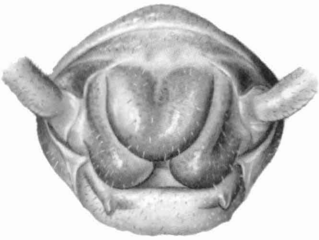

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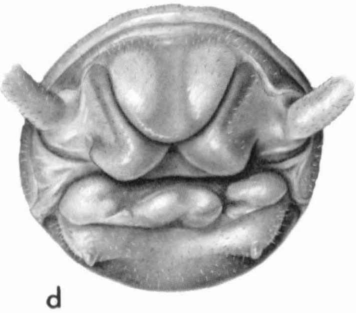

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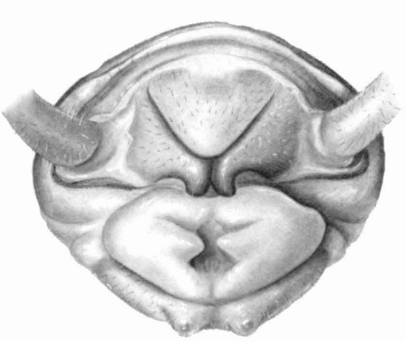

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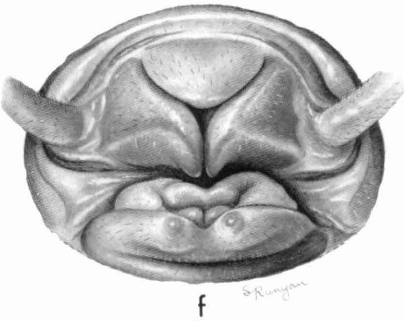

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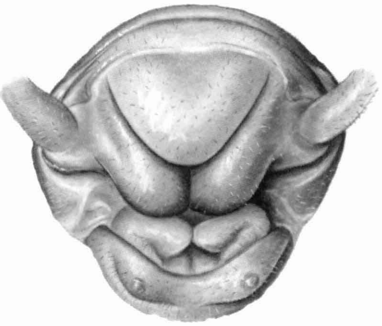
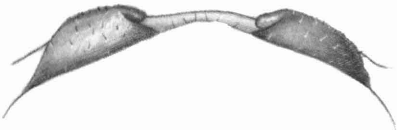


g

PLATE III

Male subgenital plates of Hadenoecini in ventrodistal aspect

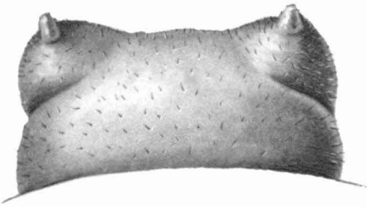
a—*Euhadenoecus puteanus*, Natural Bridge State Park, Powell Co., Ky.;
b—*E. puteanus* (depauperate high altitude form), Mt. Sterling, Haywood Co., N.C.;
c—*E. fragilis*, Tawneys Cave, Giles Co., Va.;
d—*E. insolitus*, Town Creek Cave, Marshall Co., Ala.;
e—*Hadenoecus subterraneus*, Mammoth Cave, Edmonson Co., Ky.;
f—*H. jonesi*, Hambrick Cave, Jackson Co., Ala.;
g—*H. o. opilionoides*, small cave in Buffalo Cove, Fentress Co., Tenn.

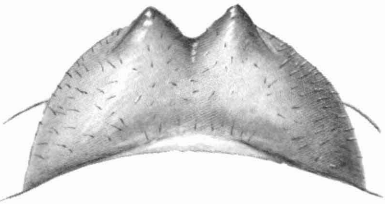


a

b

c





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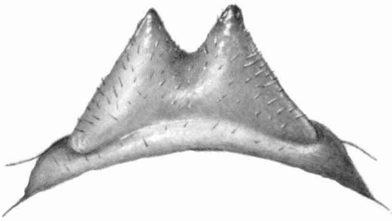

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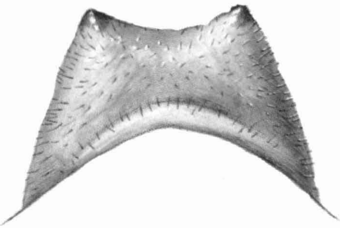


PLATE IV

Scanning electron micrographs of structures of Hadenoecini
(Micrographs by Dr. H. K. Townes)

Male epiprocts:
  a—*Euhadenoecus puteanus*,Cascade Cave, Carter Co., N.C.;
  b—*Euhadenoecus adelphus*, Swannanoa, Buncombe Co., N.C.
Ovipositors: Left, *Euhadenoecus puteanus*, Pine Mountain, Harlan Co., Ky.:
  c—ventral view X ca. 30;
  d—side view X ca. 40;
  e—teeth X ca. 70;
Right, *Hadenoecus subterraneus,* Mammoth Cave, Edmonson Co., Ky.:
  f—ventral view X ca. 30;
  g—teeth X ca. 65;
  h—teeth X ca. 70.

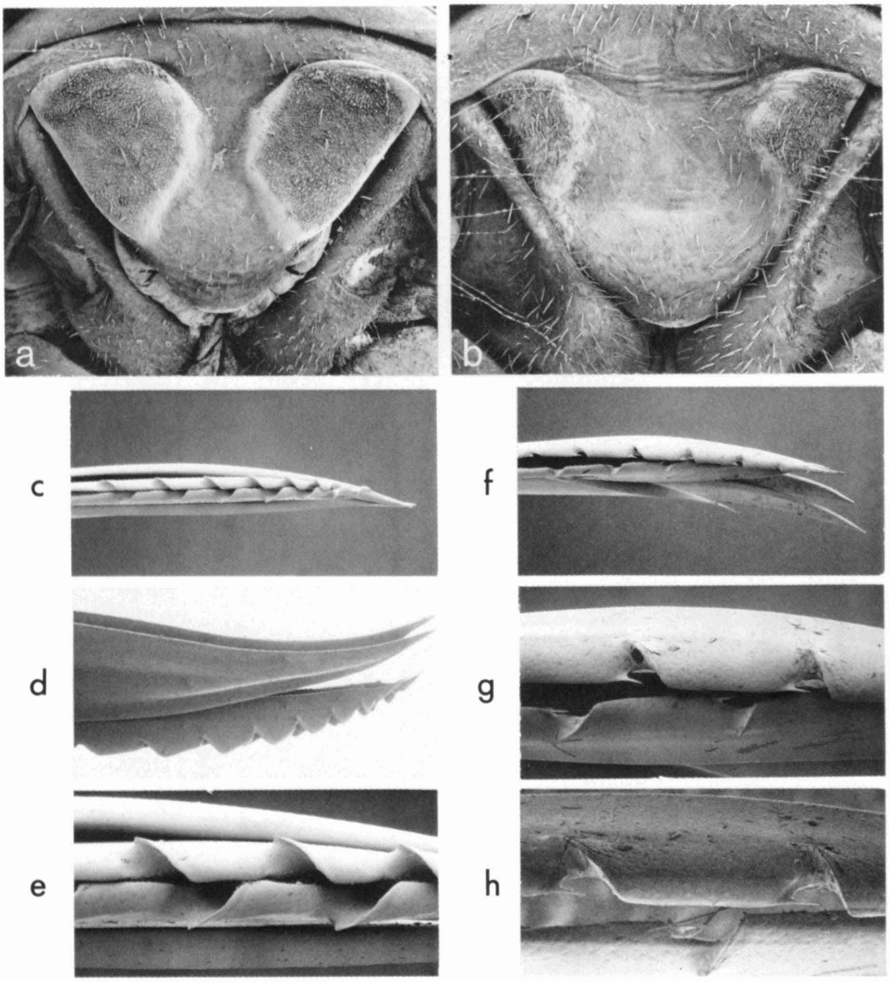
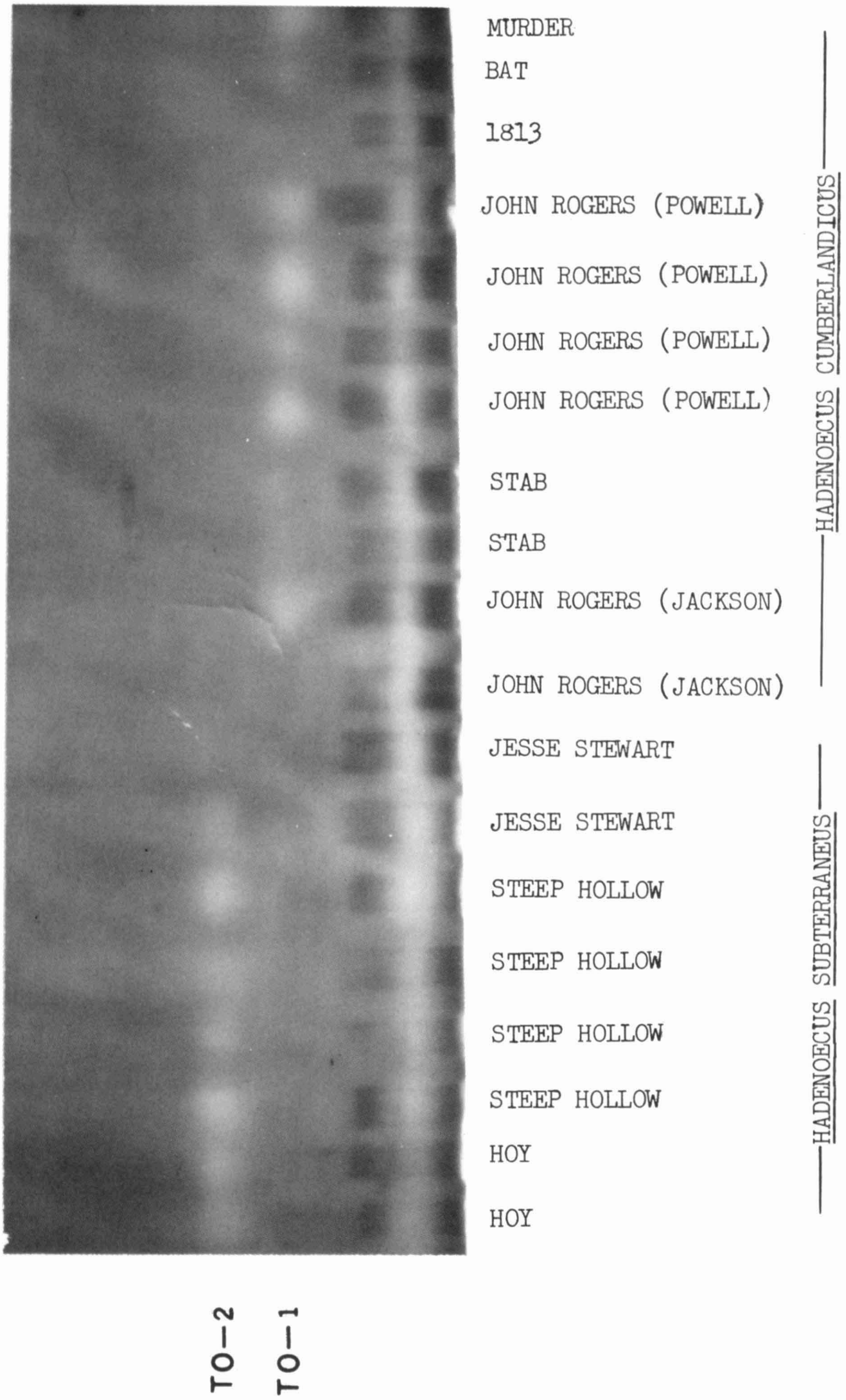

a
b
c
f
d
g
e
h

PLATE V

Electrophoretic starch gel stained for Tetrazolium Oxidase, from samples of *Hadenoecus cumberlandicus* and *H. subterraneus*

Judging from this single sample, this negatively staining isozyme system seems to be diagnostic for these two species; only TO-1 is found in *H. cumberlandicus* and only TO-2 in *H. subterraneus.*


MURDER
BAT
1813
JOHN ROGERS (POWELL)
JOHN ROGERS (POWELL)
JOHN ROGERS (POWELL)
JOHN ROGERS (POWELL)
STAB
STAB
JOHN ROGERS (JACKSON)
JOHN ROGERS (JACKSON)
JESSE STEWART
JESSE STEWART
STEEP HOLLOW
STEEP HOLLOW
STEEP HOLLOW
STEEP HOLLOW
HOY
HOY
HADENOECUS CUMBERLANDICUS
HADENOECUS SUBTERRANEUS
TO—2
TO—1