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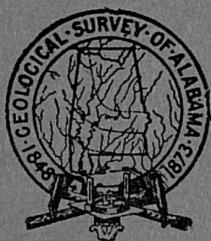
Cavernicolous Pselaphid Beetles of Alabama And Tennessee,  
with Observations on the Taxonomy of the Family<sup>1</sup>

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by

ORLANDO PARK

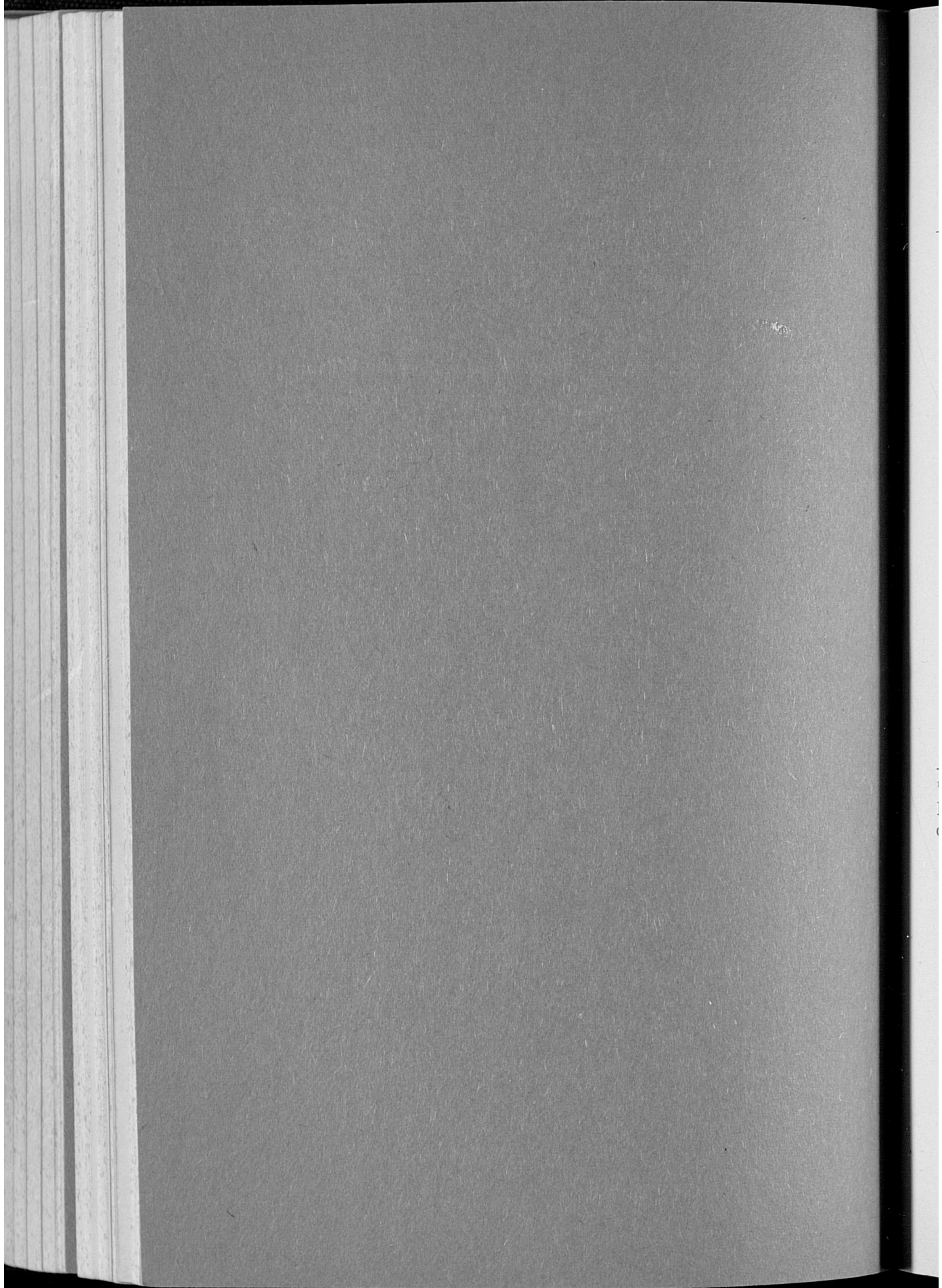
Northwestern University

<sup>1</sup>This study has been facilitated by a grant from the Graduate School of Northwestern University to defray expenses incurred in preparing certain of the illustrations.



UNIVERSITY, ALABAMA

OCTOBER 15, 1951



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OCTOBER 15, 1951

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1951

LETTER OF TRANSMITTAL

University, Alabama

April 30, 1951

Honorable Gordon Persons  
Governor of Alabama  
Montgomery, Alabama

Sir:

I have the honor to transmit herewith the transcript of a report on "Cavernicolous Pselaphid Beetles of Alabama and Tennessee, with Observations on the Taxonomy of the Family", by Orlando Park. It is requested that this be printed as Muesum Paper 31 of the Geological Survey of Alabama.

Respectfully,

WALTER B. JONES,

State Geologist

## TABLE OF CONTENTS

Introduction .....	5
Key to Genera .....	7
Tribe Batrisini	
<i>Batrisodes</i> .....	8
Global key to subgenera .....	11
Key to American cavernicolous species .....	14
<i>spelaeus</i> n. sp. ....	16
<i>quisnamus</i> n. sp. ....	20
<i>jeanneli</i> n. sp. ....	21
<i>trogloodytes</i> n. sp. ....	23
<i>cavernosus</i> n. sp. ....	25
<i>jonesi</i> n. sp. ....	27
<i>subterraneus</i> n. sp. ....	30
<i>valentinei</i> n. sp. ....	32
<i>specus</i> n. sp. ....	35
Key to American cavernicolous species based on aedeagus .....	38
<i>Arianops</i> .....	40
Key to subgenera and species of North America .....	40
<i>cavernensis</i> n. sp. ....	41
Tribe Bythinini	
<i>Bythinopsis</i> .....	43
<i>jonesi</i> n. sp. ....	43
<i>Machaerites</i> .....	45
Global key to subgenera and species .....	45
<i>Speleochus</i> n. subgen. ....	46
<i>stygicus</i> n. sp. ....	47
<i>ferus</i> n. sp. ....	49
Tribe Speleobamini new tribe	
<i>Speleobama</i> new genus .....	52
<i>vana</i> n. sp. ....	53
Tribe Tmesiphorini	
<i>Tmesiphorus costalis</i> Leconte .....	55
Key to the Tribes of the Western Hemisphere .....	56
General discussion of American Cavernicolous Pselaphidae .....	68
Abstract .....	85
Literature Cited .....	86

## INTRODUCTION

It is seldom the good fortune of a specialist in a group of organisms to be given the opportunity to work over an entirely new fauna in his special field of study. It is still more unusual if this opportunity is presented within a geographic area already relatively well known in that particular group of organisms.

Such a paradoxical situation is the occasion for this paper. From a global point of view, Pselaphidae of North America are known relatively much better than the large and diverse tropical faunas of the world, but up to the present no true cavernicolous pselaphids have been described from the whole of the Nearctic Region. This is even more surprising since the Palaearctic Region, especially the southern European areas, has a large and complex fauna of cavernicolous Pselaphidae, recently enlarged through the discoveries of Jeannel (1950).

Since 1931 Dr. Walter B. Jones, State Geologist of Alabama, and his associates, have collected 315 pselaphids from 58 caves in 19 counties of Alabama and Tennessee. Several years ago, at the request of Dr. J. Manson Valentine, the author undertook the study of this material.

Subsequent analysis demonstrated that these cavernicolous pselaphids represented a new fauna in North America, previously alluded to by Loding (1945, p. 42) and Park (1947, p. 109). The 315 specimens represented four tribes: Batrisini, Bythinini, Tmesiphorini, and Speleobamini, the last of which was a new tribe of unusual taxonomic import since it combined diagnostic features of the brachysceline and macrosceline divisions of Pselaphinae. There were six genera, one of which, *Speleobama*, was new to science, and 15 species. Of these latter, 14 were cavernicoles in the strict sense and were all new species, whereas the fifteenth belonged to a widespread and vagile species, described many years ago, and apparently is a recent entrant into the cave habitat from an evolutionary viewpoint.

Of especial note were the full geological and ecological data that accompanied the insects. These data are of material assistance in a general discussion of American cave pselaphids presented later.

The new tribe is integrated with recent work in a key to the tribes of Pselaphidae of the Western Hemisphere.

Type specimens and half of the paratypes are deposited with Dr. Jones; half of the paratypes are retained by the author.

The author thanks Dr. Jones and Dr. Valentine for their many kindnesses throughout the protracted period of this study.



**KEY TO GENERA**

The function of the following artificial key is to discriminate the six genera of pselaphids known to inhabit caves in Alabama and Tennessee. It will not serve any other purpose.

- 1. Eyes absent..... 4
- Eyes vestigial or well-developed, but always present and conspicuous..... 2
- 2. (1) Abdomen with distinct lateral margins on the first two or three segments..... 3
- Abdomen without margins

**Batrisodes**

- 3. (2) Maxillary palpi with second segment studded with small tubercles

**Bythinopsis**

Maxillary palpi with second segment not so studded, but bearing laterally a setiform appendage

**Tmesiphorus**

- 4. (1) Abdomen with distinct lateral margins on the first two or three segments..... 5
- Abdomen without margins; position of eye occupied by short spine

**Arianops**

- 5. (4) Head with a conspicuous ruff of long setae, formed by setae directed posteriorly from occiput and setae directed anteriorly from cervicum

**Speleobama**, new genus

Head lacking any such feature

**Machaerites**

**Batrisodes** (Reitter, 1881)

Before describing the numerous new species of this genus collected from caves in the area under examination a discussion of the genus is essential in view of recent research that has complicated the taxonomy from a global viewpoint.

*Batrisodes* was erected by Reitter (1881) to contain the Palaearctic species. Later, Raffray (1904) extended the genus to embrace Nearctic, Ethiopian, Oriental and Australian species as well. Raffray followed this position in his later work (1908, 1911, 1923-24). Furthermore, local studies did not alter this general organization, e. g. Casey, 1908; Reitter, 1909; Bowman, 1934.

The epigean species of *Batrisodes* of America, east of the Rocky Mountains were monographed by Park (1947). In this paper the genus was considered in the Raffrayan sense, and included a discussion of the comparative external anatomy, keys to species, diagnoses of known species, ecology, and a discussion of the genus as a whole from a zoogeographic and evolutionary viewpoint. The following year (Park, 1948), *Batrisodes*, in the Raffrayan sense, was discussed by zoogeographic regions in a global checklist.

This was the general situation in 1948. The reason for this brief survey is that the recent taxonomic work of Jeannel (1949) on African species, and of Jeannel (1950) on European species inevitably affects the taxonomy of the North American fauna.

Jeannel (1949, pp. 133-135) erected a new genus, *Batristerus*, to contain the species of *Batrisodes* of the Ethiopian, Oriental and Australian Regions, and consequently restricted *Batrisodes*, in the more limited sense, to the Palaearctic and Nearctic Regions.

First, Jeannel finds that the species of *Batristerus* have only the sides of the first tergite equipped with an entire lateral carina, whereas the second and third tergites lack an entire marginal carina; in *Batrisodes*, as limited, the sides of the first three tergites have an entire marginal carina.

Second, in addition to this small abdominal character, Jeannel finds that the aedeagus of *Batristerus* has an enclosed basal capsule, internal musculature and well developed styles; in *Batrisodes*, as limited, the aedeagus is reduced to a sclerotized frame, without internal musculature, and without styles.

Jeannel (1950, pp. 351-358), working over the French species in particular but with general implications for the European fauna, divided the genus *Batrisodes*, as limited, into two subgenera: *Batrisodes*, s. str., in which the metatibiae lack the apical spurs, and in which the face is wide, rugose and not medianly excavated; and *Batrisodinus*, in which the metatibiae have apical spurs, and the face is deeply excavated between the antennae.

The characterization of *Batrisodes* by Jeannel will not hold for all of the American species. The distribution of marginal carinae follows the same pattern as given for the European species, but the American species have two types of aedeagi. The great majority of the American species (Groups III to IX, inclusive, of Park, 1947) do have the aedeagus as described by Jeannel for the European species, but Group I of Park, 1947 has a radically different aedeagus. It is very similar to that of *Batristerus*, e. g., there is an enclosed basal bulb, internal musculature is developed, and two styles are not only present but very diversified, and one is a movable process.

Now this Group I, with the complicated aedeagus, is the only American group that lacks metatibial spurs. Therefore it can not belong to either European subgenus, and a new subgenus, *Batriasymmodes*, with *monstrosus* (LeConte, 1850, p. 95) as its type is erected.

*Batriasymmodes* is restricted to the deciduous forest biome of eastern North America, so far as known, and contains six species (Park, 1947) plus four new species collected from caves of Alabama and Tennessee. This subgenus has the abdominal margins of *Batrisodes*, in the restricted sense of Jeannel, but has an aedeagus similar to *Batristerus*. Since these several considerations reduce the gap between *Batrisodes* and *Batristerus* to the question whether or not the second and third tergites have or do

not have an entire marginal carina, it is the opinion of the author that the carinal feature is of subgeneric rank, and he feels that the genus *Batrisodes* should be restored to the sense of Raffray, 1904. If this is a too conservative view, then there will have to be quite a few genera instead of subgenera.

In the next place, the characterization of the subgenus *Batrisodinus* (Jeannel, 1950) will not hold for the American species, since a great many of the latter do not have the face excavated and many others do, and added to this are numerous other features of equal rank, e. g., excavation of the face between antennal cavities is a secondary sex character of males in American species, and the possession of abnormal mesotarsi in many males is just as important (Park, 1947).

It is obvious that the structure of the aedeagus is of primary importance, and that secondary sex characters are of secondary importance in a long range, phylogenetic view of this complicated assemblage of species.

The author has been cognizant of this aedeageal structural divergence for quite a few years, as the following quotation will demonstrate: "Within the large genus *Batrisodes* a reliable key can be made to species, based on the aedeagus. In the first place, no *Batrisodes* has a primitive aedeagus. This is a genus where reduction of parts is strikingly developed. Overlaid upon this superficial simplicity is a developing asymmetry. Thus *Batrisodes furcatus* and *riparius* are bilaterally symmetrical while *globosus*, *denticollis* and *schaumi* are progressively asymmetrical. The species of this genus studied so far culminate in the aberrant *monstrosus*. In this latter species the asymmetry is extreme and an accessory piece is developed. The aedeagus of *monstrosus* is so far removed that it should serve to divide the genus into two subgenera" (Park, 1942, pp. 16-17).

The cavernicolous members of *Batrisodes* to be described subsequently include members of Groups I (*monstrosus* group), V, and IX so that some adjustment of the broader problem is necessary at this time.

The author was astonished to find that the aedeagus had not been used in pselaphid taxonomy, and in the 1942 study cited



## Metatibiae lacking apical spurs

BATRISODES Jeannel, 1950, pp. 351-352, *s. str.*Type: *delaporti* (Aubè, 1833, p. 46)

Palearctic species

## 6 (5) Mesotarsi of males abnormal (Fig. 6)

BABNORMODES new subgenus

Type: *riparius* (Say, 1824, p. 98)

Nearctic species (Group IX, Park, 1947)

Mesotarsi of males normal..... 7

## 7 (6) Front deeply impressed longitudinally between antennal tubercles in both sexes

BATRISODINUS Jeannel, 1950, pp. 351-352.

Type: *oculatus* (Aubè, 1833, p. 48)

Palearctic species

Front not as described; either declivous to clypeal margin in both sexes, or transversely excavated between the antennal cavities in the male sex..... 8

## 8 (7) Vertexal foveae densely pubescent

PUBIMODES new subgenus

Type: *nigricans* (LeConte, 1850, p. 99)

Nearctic species (Group VIII, Park, 1947)

Vertexal foveae nude..... 9

## 9 (8) Male sex with face transversely excavated between the antennal cavities; female sex with face simply declivous

EXCAVODES new subgenus

Type: *frontalis* (LeConte, 1850, p. 96)

Nearctic species (Groups IV, V, VI, Park, 1947)

Both sexes with face unexcavated between antennal cavities..... 10<sup>1a</sup>

<sup>1a</sup>At this point in the key, Group II of Park, 1947, Nearctic species, will also key out. This is a group of twelve species known only from North America west of the Rocky Mountains, whereas the subgenera *Elytroides* and *Declivodes* are unknown west of the Great Plains so that little confusion can result. This Group II was not keyed out as it represents a special problem (Park, 1947, p. 46) with the female sex of more than usual taxonomic importance. The aedeagus of this group is uninvestigated and its true relationship to the rest of the genus must await further research.

10 (9) Each elytron bifoveate

ELYTRODES new subgenus  
 Type: *ionae* (LeConte, 1850, p. 94)  
 Nearctic species (Group III, Park, 1947)

Each elytron trifoveate

DECLIVODES new subgenus  
 Type: *bistriatus* (LeConte, 1850, p. 101)  
 Nearctic species (Group VII, Park, 1947)

The preceding organization has the immediate advantage of harmonizing the Nearctic *Batrisodes* with the recent work of Jeannel (1949, 1950). Academically, the advocated organization may be unsound. For example, many Oriental and Australian species have not been examined with respect to the aedeagus, as noted by Jeannel, and similarly quite a few Nearctic species have the aedeagus undescribed. When all of this is done, certain of the subgenera may have to be elevated to generic rank, new subgenera or genera proposed, and in general subject this large genus of about 225 species to further scrutiny. For the present a conservative approach is desirable.

Material assistance to this general problem would be exact data on the aedeagi of fossil *Batrisodoes*. None has been published to the best of the author's information. Palaeontological data on pselaphids is very scanty. Schaufuss (1890, p. 134-137) described two species of "Batrisus" from the Baltic amber, presumably of the Oligocene, *Batrisus pristinus* and *Batrisus antiquus*. These may belong to *Batrisus*, *Batrisodes*, or a new genus.

Turning to the present problem, in the cave fauna under examination *Batrisodes* is the dominant element. Of the 315 cave pselaphids studied, 286 or 91% were of this genus; of the 15 cavernicolous species to be reported, nine or 60% are members of *Batrisodes*.

These nine species populations are discriminated in the following key to the known species of cavernicolous *Batrisodes* in Alabama and Tennessee.

- |        |  |    |
|--------|--|----|
| 1.     | Metatibia with a long, distinct apical spur of setae.....  | 7  |
|        | Metatibia without a distinct apical spur.....  | 2  |
| 2. (1) | Vertexal foveae pubescent.....   | 3  |
|        | Vertexal foveae nude.....  | 4  |
| 3 (2)  | Metatrochanter with an irregular tooth   | -  |
|        | male <i>troglogytes</i>  |    |
|        | Metatrochanter not toothed   |    |
|        | female <i>troglogytes</i>  |    |
| 4 (2)  | Metatrochanter with an irregular tooth.....  | 6  |
|        | Metatrochanter not toothed.....  | 5  |
| 5 (4)  | Last tergite with a pair of distinctive cusps  |    |
|        | female <i>spelaeus</i>   |    |
|        | Last tergite evenly convex   |    |
|        | female <i>quisnamus</i>  |    |
| 6 (4)  | Pronotal disc bearing a row of 2 to 3 recurved teeth on each side of the deep median sulcus                    |    |
|        | male <i>spelaeus</i>   |    |
|        | Pronotal disc not bisected by a sulcus, and with a single tooth on each side of disc                           |    |
|        | male <i>jeanneli</i>   |    |
| 7. (1) | Mesotarsi abnormal, the second tarsomere laminoid, glabrous, translucent and deeply incised ventrally.....     | 8  |
|        | Mesotarsi normal, the second tarsomere subcylindrical, normally pubescent and the ventral face unmodified..... | 11 |
| 8. (7) | Tenth antennal segment foveate on ventral face.....  | 9  |
|        | Tenth antennal segment not foveate on ventral face   |    |
|        | male <i>valentinei</i>   |    |
| 9. (8) | Face with an erect, transversely laminoid, median tubercle near the clypeal margin                             |    |
|        | male <i>jonesi</i>   |    |
|        | Face simple, unevenly declivous, not utberculated.....   | 10 |



- 7  
2  
3  
4
- 10 (9) Fovea of tenth antennal segment small (one-third the length of ventral face), circular and nude  
*male subterraneus*  
 Fovea of tenth antennal segment large (three-fourths the length of ventral face), transversely ovate, pubescent.  
*male specus*
- 6  
5
- 11 (7) Front separated from clypeus by a deep, transverse, densely pubescent excavation  
*male cavernosus*  
 Face simply declivous, not transversely excavated (females, not safely discriminated on external anatomy) .....12
- 12 (11) Known only from Hinson Cave, Butler Co., Alabama  
*female cavernosus*  
 Unknown from caves south of St. Clair Co., Alabama. 13
- on
13. (12) Known only from the western half of Colbert Co., Alabama (Dickey, Gallymore, Gist, Little Bear, McClusky and McKinney Caves)  
*female jonesi*  
 Unknown from western half of Colbert Co., Alabama. 14
- 1 a
- 14 (13) Known only from Griffith Cave, Marshall Co., Alabama  
*female subterraneus*  
 Unknown from Griffith Cave.....15
- 8  
al,  
11  
9
15. (14) Known only from caves in north-central Alabama (Cave Springs, Georgetown, Huntsville, Hutton, Lott, Pitts, Terrell and Twin Caves) and Jefferson Co., Tennessee  
*female specus*  
 Known only from Crystal Cave, Grundy Co., Tennessee and in Madison, Morgan and Jackson Counties, Alabama (Clements, Moon, Goat, Talucah and Toll Gate Caves)  
*female valentinei*
- 10

**Batrisodes spelaeus** new species

*Type Male.* Shining reddish-brown with yellowish-brown tarsi; integuments shining, subimpunctate; pubescence long, flavous, semierect except on abdomen where pubescence is semiappressed. Measurements: head 0.5 mm. long (from clypeal margin to occiput) x 0.53 mm. wide (through eyes); pronotum 0.53 x 0.53; elytra 0.77 x 0.94; abdomen 0.87 x 0.77; total length 2.67 mm.

Head with prominent eyes of about 40 facets; tempora long, evenly rounded into occiput, about twice as long as eyes; vertex with three apically converging carinae, of which the median is incomplete apically and the laterals are oblique and very strong; a strong lateral carina on each side of vertex from tempora to antennal tubercle; a shorter supraocular carina subparallel to the lateral, and between the latter and the eye; a pair of large, nude, free vertexal foveae on a line through posterior eye margins; front medianly concave between antennal tubercles, this depression limited apically by an arcuate carinoid frontal margin; clypeus evenly declivous from the frontal line, with a conspicuous, laminoid apical margin; enclosed area of clypeus between apical and frontal margins bisected by a longitudinal carina and limited laterally each side by a longitudinal carina that partially bounds the antennal acetabulum; the clypeal carinae and frontal carinoid line taken together form a capital M; labrum transverse, with a gently concave apical margin and acute lateral angles; ventral surface of head with a beard of bristling setae, medianly bisected by a longitudinal gular carina, and with a large gular fossa at base; mandibles strong, left crossed dorsal to right; maxillary palpi four-segmented, first segment minute, second elongate arcuate and pedunculate as usual, third short and subtriangular and about as wide as swollen end of second, fourth or last segment largest being one-third longer than second segment and much wider with a minute apical cone. Antennae long, slender, eleven-segmented; all segments longer than wide; segments I to VIII subcylindrical; VIII abnormal, with the ventral face produced apically into an acute, divergent spine; club weakly formed of last three segments, of which the last is as long as VIII, IX and X united, with a truncate base and long, tapering apex.

Pronotum with six poorly defined basal foveae, i. e., three on each side of a short, median, longitudinal carina that extends

from basal bead to the median antebasal fovea; an even larger lateral antebasal fovea on each side of the median fovea; medial and lateral antebasal foveae separated by a pair of acute tumuloid antebasal spines; each side of pronotum, just above the lateral antebasal fovea, bearing a short and inconspicuous tooth; disc of pronotum bisected by a long and distinct median sulcus that extends from median antebasal fovea almost to apical margin; on each side of this sulcus two recurved discal teeth; a broad sulcoid impression extends from each lateral antebasal fovea nearly to apex.

Elytra with humeral angles sloping and bearing an unarmed tumuloid swelling. Each elytron with three nude basal foveae, the sutural at base of a weak, entire sutural stria and the lateral at base of a weakly defined discal stria that extends almost to the center of disc; elytral flank with a nude subhumeral fovea at origin of a longitudinal carina that parallels the elytral margin to apex.

Metathoracic wings present.

Abdomen with five visible tergites; first tergite with a pair of slightly convergent, strong, short basal abdominal carinae about one-fourth the segmental length and dividing the segmental base into a pair of wide lateral depressions and a narrow median depression, about one-half the width of the laterals; lateral margins of first tergite formed by a pair of slightly convergent carinae, of which the external is slightly oblique and two-thirds the segmental length and the internal carina is entire from base to apex; second and third tergites with external lateral carina absent, but internal carina present and entire; last tergite simply rounded. Five sternites visible medianly, simple; last sternite as long as preceding three united, medianly with a broad and weak depression, and apical margin medianly lobed to fit into a median arcuation of the fifth tergite.

Legs relatively simple, except for metatrochanters; each metatrochanter bearing a contorted spine at center of ventral face, this spine in profile resembling an anvil and with several specialized setae curling from trochanter over the point of the anvil. Metatibia without a long spur of apical setae, but the nor-

mal setae of the tibial apex forming a pseudospur to the casual glance. Tarsi as for genus.

Aedeagus 0.5 mm. long x 0.25 mm. wide x 0.3 mm. deep (Fig. 1) with a symmetrical basal bulb (basal capsule), internal musculature, and two complicated styles. Right style transversely laminoid, sclerotized, sickle-shaped, with a thin, acute point; mesial margin with two specialized setae; internally this style has what appears to be a bifurcated system of fine canaliculi, the mesial group of which appear to end at or near the origin of the two setae noted; the right style gives origin on its ventro-basal fourth to an accessory stylet (accessory falx) that extends apically as a thin rod which is apically greatly expanded ventrally as a hemiovate process. Left style<sup>2</sup> (accessory piece) attached on the left anterior face of basal bulb, and apparently moved by internal muscles of the latter, arcuate-conical to a laminoid, diagonally expanded apex, and covered dorsally by tuberculoid tissue.

*Female.* As described for male with the following exceptions: (1) eyes vestigial, of 18 facets; (2) tempora nearly three times as long as eyes, as consequence of the smaller size of the latter; (3) antennal segment VIII simple, not bearing a spine; (4) antennal segment XI relatively shorter; (5) last tergite not simple, as in male, but medianly sulcoid, with a pair of conspicuous spinoidal lamina that bound the median impression; (6) last sternite medianly slightly longer than fourth sternite, with a simple, straight apical margin; (7) metatrochanters simple, not bearing spines.

Described on 106 specimens (43 males and 63 females),<sup>3</sup> distributed as follows: TENNESSEE: CLAY CO., Daly Cave, Butler's Landing (1); JEFFERSON CO., Indian Cave, New Market (1). ALABAMA: BLOUNT CO., Bangor Cave, Bangor (8); Horseshoe Cave, Inland (2); Ingram Cave, Greystone (10);

<sup>2</sup>In this and succeeding descriptions of the aedeagus, the terms right and left refer to the true morphological orientation. The aedeagus, on exertion, lies with its morphologically posterior end directed apically and its morphological ventral face parallel to the ventral surface of the abdomen, therefore, the true right side of the aedeagus appears to the observer as the left side, and *vice versa*.

<sup>3</sup>These 106 specimens include the type and 105 paratypes; type male collected by Flanigan and Jones, June 9, 1940 from Bangor Cave noted above.

DEKALB CO., Mantitou Cave, Fort Payne (1); LAUDERDALE CO., Bat Cave, Shoal Creek (2); LAWRENCE CO., Thomas Cave, Trinity (7); Tingling Hole (1); MARSHALL CO., Lime Point Cave (2); Warrenton Cave (3); MORGAN CO., Barrel Cave, Trinity (7); Cave Spring Cave, Hillsboro (4); Echols Cave, Trinity (18); Ladder Cave, Trinity (6); Lost Mule Cave, Trinity (1); Royer Cave, Trinity (7); Winchester Cave, Trinity (5); St. CLAIR CO., McGlendon Cave, Gallant (20).

This is an important species in Alabama and Tennessee caves. It is represented by an ample series of specimens, of both sexes, and the population sample made up 30% of all cave pselaphids taken. It is exceptional in another particular in that it has the greatest distribution of all species studied. In general the cave pselaphids have a relatively limited distribution being taken in a single cave, or a series of caves that are geographically close together. *Batrisodes spelaeus* ranges through the caves of the area studied from Clay County, Tennessee to St. Clair County, Alabama, a distance of some 250 miles. We will return to this problem later, in a general discussion of the cave species.

*Batrisodes spelaeus* is a member of the new subgenus, *Batrisymmodes* (Group I of Park, 1947). In this group it is most closely allied to *cavicrus* (Casey, 1893) of the epigeal species, but differs from the latter in many particulars. A ready method of separation of these two is afforded by the male antennae. In *cavicrus* the antennae are simple, whereas in *spelaeus* the eighth antennal segment is abnormal, the segment bearing a divergent spine from the apex of ventral face. *Batrisodes cavicrus* is known with certainty from the Black Mountains of North Carolina and the Sassafras Mountains of South Carolina, so that both *cavicrus* and *spelaeus* appear to belong to the Southern Appalachian fauna.

Several structural features are subject to considerable variation with the population sample at hand. First, the median clypeal carina varies from strong and entire to weak and apically incomplete; it tends to be less developed in females. Second, the median pronotal sulcus varies from strong to evanescent. Third, the two discal teeth on the pronotum, on each side of the median sulcus, are difficult to discern at best as a consequence of the

pubescence. The apical teeth are always much smaller than the basal pair, but both pairs vary and in some specimens the apical teeth are so small as to be vestigial.

Of especial interest was the presence of two callows, e. g., specimens killed so soon after pupation that the integument is straw yellow, thin and translucent. Such callows suggest that pupation took place from one to three days previous to the collecting date, and hence throw some light on life cycle. The two specimens noted were taken in McGlendon Cave, near Gallant, St. Clair County, Alabama on September 27, 1939. Presence of pselaphid callows in the collection will be discussed later.

Finally, an abnormal specimen was present. Abnormal pselaphids have been described so rarely that such an event is noteworthy. This was a female from Echols Cave, near Trinity, Morgan County, Alabama on September 13, 1947. The specimen was normal in all particulars except for the right metaleg. The latter had both femur and tibia very strongly bent medianly in the same plane, so that when the tibia was retracted against the femur, both segments curved around the side of the abdomen. Such a condition must have reflected an injury during the pupal or callow period, and is substantiated by the callow data above from McGlendon Cave.

***Batrisodes quisnamus*** new species

*Type Female.* Shining reddish-brown with yellowish-brown tarsi; integuments shining, subimpunctate; pubescence long, flavous, semierect except on abdomen where pubescence is semiappressed. Measurements: head 0.45 mm. long (from clypeal margin to occiput) x 0.47 mm. wide (through eyes); pronotum 0.47 x 0.47; elytra 0.63 x 0.74; abdomen 0.87 x 0.67; total length 2.42 mm.

Structure as for the female of *spelaeus* except for the following differences: (1) eyes smaller, of 10 facets; (2) vertexal foveae on a line behind the posterior eye margin; (3) median frontal depression relatively deeper and smaller, not extending to the frontal margin; (5) pronotum with only four basal foveae, e. g., two on each side of median basal carina; (6) the three ante-

basal pronotal foveae relatively deeper and smaller, and in consequence the small tooth of the pronotal margin is more remote from the associated lateral antebasal fovea; (7) the last tergite is notably different, its surface being evenly convex and perfectly simple; (8) last sternite as long as the preceding two sternites united, with straight apical margin.

Male sex unknown.

Described on a single specimen, collected in Bunum Cave, Byrdstown, PICKETT County, TENNESSEE.

This new species is most closely allied to *spelaeus*, and the females of these two can be quickly separated on the structure of the last tergite, which in *spelaeus* bears a pair of prominent cusps, and in *quisnamus* is simple and evenly convex. When the male sex can be discovered, the aedeagus will make an interesting study in contrasting it with the aedeagus of *spelaeus*.

In all probability, *quisnamus* belongs in *Batriasymmodes*, as it has all of the external features of the *monstrosus* group. A glance at the aedeagus, when the male is found, will settle the matter.

**Batrisodes jeanneli** new species

*Type Male.* Color, integumental structure, and pubescence as in *spelaeus*. Measurements: head 0.48 mm. long (clypeal margin to occiput) x 0.47 mm. wide (through eyes); pronotum 0.5 x 0.47; elytra 0.77 x 0.87; abdomen 0.70 x 0.74; total length 2.45 mm.

Head as in *spelaeus* except that the short supraocular carina is absent, the three vertical labial carinae are absent, and the gular carina is very weakly developed. Maxillary palpi as in *spelaeus*. Prominent eyes of about 48 facets.

Antennae with segment IX shorter than VIII, with the ventral face produced into a conspicuous laminoid spine at right angles to the long axis of the segment; segment X also very abnormal, the ventral face bearing an oblique and flattened area with carinoid margins, and the apical half depressed and overhung by the expanded and fimbriated apical margin.

Fronotum with only two basal foveae on each side of the median longitudinal carina, as in *quisnamus*; three deep small antebasal foveae and two large antebasal tumuloid spines as usual; the median and lateral longitudinal sulci are absent; there is only a single recurved tooth on each side of disc; lateral tooth, above each lateral antebasal fovea, small.

Elytra as in *spelaeus*. Abdomen as in *spelaeus* except that the basal abdominal carinae are more distant, separated by one-fifth of total segmental width, so that the median basal depression is broader. Last sternite of same form as in *spelaeus* males, but longer, nearly as long medianly as the preceding four sternites united.

Metathoracic wings present.

Prothoracic legs abnormal, each tibia with a subglabrous arcuation at median fifth of length on dorso-anterior face. Metathoracic legs with the typical contorted spine on the ventral face of each metatrochanter, so characteristic of the males of *Batriasymmodes*; no metatibial spur.

Aedeagus 0.6 mm. long x 0.3 mm. wide x 0.3 mm. deep (Fig. 2) with a symmetrical basal bulb in which the sclerotized dorsal ring is asymmetrically triangular, powerful internal musculature arising over the posterior internal face of the bulb and converging to insert at the base of the right style. Right style with a heavy base that bears a small tooth at its mesial angle, and extending apically as a very long, arcuate falx. Left style very complex, base formed by an oblique subquadrate plate that is gradually depressed from about center to lateral margin; this basal part bearing an acute, slender falx at its apico-mesial angle; basal part with remainder of apical margin heavier, forming flattened bead that extends apico-laterally to form a bifurcated process; this bifurcated process with a recurved hook basally and a secondarily bifurcated and broadened apical extension.

Female sex unknown.

Described on two males (type and paratype). Type from Lindsay Williams Cave, Doweltown, DEKALB CO., TENNESSEE. Paratype from Burial Cave, Flynn's Lick, JACKSON CO., TENNESSEE.



This species is a member of the subgenus *Batriasymmodes*. In this group it is not closely allied to any species, but both in the slightly abnormal protibia and especially in the structure of the aedeagus *jeanneli* is most similar to *monstrosus* (LeConte, 1850). Named in honor of the distinguished speleologist, Dr. R. Jeannel, of the National Museum of Natural History, Paris, France.

This similarity in basic aedeageal structure is notable. Whereas *spelaeus* has the left style moved by intrinsic bulbar muscles and the right style fixed (Fig. 1), both *jeanneli* (Fig. 2) and the epigean *monstrosus* (Fig. 3) have the right style moved by bulbar muscles and the left style fixed. This cleavage within the subgenus *Batriasymmodes* is reminiscent of a similar cleavage in aedeageal symmetry within the genus *Cedius* (Park, 1949). The bearing of these data in the evolution of cavernicolous species will be discussed later. For the present it is necessary to separate the subgenus into two species groups: the species in which the moving style is on the morphological right (*Batridextrodes*, new group) with *monstrosus* as its type, and including *jeanneli*; the species in which the moving style is on the morphological left (*Batrisinistrodes*, new group) with *spelaeus* as its type.

***Batrisodes troglodytes* new species**

*Type Male.* Reddish-brown with yellowish brown antennal clubs and legs; head, pronotum and elytra with microscarified integuments, abdomen punctulate; pubescence abundant and appressed except for bristling genal beard.

Measurements: head 0.42 mm. long (clypeal margin to occiput) x 0.42 mm. wide (through eyes); pronotum 0.45 x 0.42; elytra 0.56 x 0.74; abdomen 0.47 x 0.67; total length 1.90 mm.

Head with relatively small eyes of 28 facets; tempora three times as long as eyes and rounded into cervicum; occiput with a single median, longitudinal carina bisecting cervicum, occiput and extending over vertex to a point opposite posterior eye margins; vertex with a pair of free, deep, densely pubescent vertexal foveae on a line through tempora, well back of eyes; front deeply and abruptly excavated from a line through anterior

margins of eyes to frontal margin; frontal margin medianly acute and extended partially over clypeus as an incomplete carina; lateral carinae and supraocular carinae well developed; face relatively strongly narrowed between antennal cavities. Maxillary palpi, mandibles, labrum and ventral surface of head as described for *spelaeus*. Antennae relatively short and simple, not abnormally modified.

Pronotum with three basal foveae on each side of the median basal carina, the latter extending to median antebasal fovea as usual; three deep antebasal foveae; a relatively low, inconspicuous spinoid tumulus between lateral and median antebasal foveae each side; three broad, weak longitudinal impressions, the median of which is marked off by three strong, low, recurved teeth on each side of disc; pronotal lateral margins not toothed.

Elytra exceptional, each elytron with only two basal foveae; sutural stria entire from sutural fovea; discal fovea at origin of a relatively very deep and broad discal impression to discal center, the walls of the impression so sharply defined mesially as to form a costa; flank as in *spelaeus*.

Abdomen with five visible tergites, with lateral carinae on the first three as in *spelaeus*; base of first tergite with the usual three transverse, pubescent depressions, and a pair of basal abdominal carinae, these latter one-eighth the segmental length and separated by one-sixth the total segmental width. Five visible sternites, simple, fifth sternite as long as first four united, with a strongly lobed apical margin as in *spelaeus*.

Legs with protibiae abnormal, each dilated in apical half and arcuate-slender in basal half; metatrochanters with the usual contorted, anvil-shaped spine of the subgenus.

*Female* as for male with the following exceptions: (1) small, flat, vestigial eyes of nine facets; (2) discal teeth of pronotum two on each side; (3) fifth sternite as long as preceding two united, with a gently arcuate apical margin; (4) legs unmodified.

Described on a pair of specimens, male type and a female paratype collected by W. B. Jones, November 10, 1946 from Rock Cave, Greenville, BUTLER CO., ALABAMA.

This is a radically divergent species. It is a member of the subgenus *Batriasymmodes* on external anatomy, e. g., contorted metatrochantal spines and absence of metatibial spurs, but it has no close allies in the subgenus. Within the latter it is most closely allied to *carolinae* (Casey, 1893) known only from the mountainous areas about Asheville, Buncombe County, North Carolina. It is readily separated from this species, since both sexes of *troglydytes* have pubescent vertexal foveae and each elytron with but two basal foveae, and the male protibiae are abnormal whereas *carolinae* has nude vertexal foveae, each elytron with three basal foveae, and normal protibiae in the male.

The female paratype is a callow, so that it emerged from the pupal condition from one to four days prior to November 10.

It is a great pity that the aedeagus could not be examined, but the author was unwilling to sacrifice the abdomen of the type for this purpose. When additional males are found and their aedeagi reported, it may well be that *troglydytes* will form a new group within the subgenus. The reasons for this suggestion are the pubescent vertexal foveae and the two basal foveae on each elytron. The former condition is unknown in any of the species in *Batriasymmodes*; the latter condition is found only in one other North American species (Park, 1947), namely, *Batrisides (Elytrodus) ionae* (LeConte, 1859) with which the present species has nothing else in common, the two being in different subgenera.

The remaining five undescribed species are all distantly related to *Batriasymmodes*: the males have aedeagus reduced to a relatively thin and simple sclerotized frame, without bulbar muscles and lacking styles; the metatibiae are provided with long apical spurs; the metatrochanters of the males are not provided with the peculiar anvil-shaped spines.

**Batrisodes cavernosus** new species

*Type Male.* Yellowish-brown; integument strongly shining and sparsely punctulate; pubescence golden, sparse, semiappressed except for bristling genal beard.

Measurements: Head 0.42 mm. (clypeal margin to occiput) x 0.47 mm. wide (through eyes); pronotum 0.42 x 0.42; elytra 0.60 x 0.74; abdomen 0.47 x 0.67; total length 1.91 mm.

Head with prominent eyes of about 40 facets; sloping tempora slightly longer than eyes; lateral vertexal carinae strong; cervicum bisected by a strong median carina that becomes evanescent on the occiput and is just discernible on vertexal base as a just discernible carinoid line; vertex with a pair of deep, nude foveae of exceptional size, each with the diameter of nearly three ocular facets; each fovea at base of a deep, glabrous, arcuate sulcus that ends apically without joining its fellow; front gently and obliquely declivous between the slight antennal tubercles to terminate in a sharply defined frontal margin; face deeply and transversely excavated beneath this overhanging margin between antennal cavities; this excavation very densely setose; clypeus medianly elevated into a densely setose subconical swelling below this frontal margin; labrum, mandibles, maxillary palpi and ventral surface of head as described for *spelaeus*.

Antennae with segment IX asymmetrical, the ventral face oblique, with a transversely acute base; X abnormal, very large, slightly wider than eleventh segment, subspherical, with the ventral face bearing a minute fovea, with a diameter of an ocular facet, at the extreme base; XI normal, unmodified.

Pronotum with four basal foveae but without a basal bisecting carina; three nude antebasal foveae, weakly connected by the usual biarcuate, evanescent transverse sulcoid impression; a weak, acute tumulus between each lateral antebasal fovea and median fovea; disc lacking recurved teeth but with a weak, median impression to apical fourth; lateral sulcoid impressions also weak; sides of pronotum not toothed.

Elytra each with an unarmed, tumuloid humeral angle; three nude, deep, basal foveae; sutural fovea at base of entire sutural stria; lateral fovea at base of a weak discal impression through basal third; flank as for *spelaeus*.

Metathoracic wings present.

Abdomen with five visible tergites, with lateral margins on first three as for *spelaeus*; first tergite with a pair of basal abdominal carinae one-sixth the segmental length and separated by one-fifth total segmental width. Five visible sternites; fifth sternite as long as preceding two united, with apical margin not medianly lobed but broadly concave instead.

Legs simple with two exceptions: mesotibiae each with an apical spine; metatibiae each with the subgeneric apical spur.

Aedeagus (Fig. 4) 0.27 mm. long x 0.13 mm. wide x 0.07 mm. deep; bilaterally symmetrical, and of the form illustrated.

*Female* as for description of male with the following exceptions: (1) Eyes of 14 facets; (2) interfoveal sulcus complete on the vertex; (3) face not transversely excavated between the antennal cavities, the front steeply declivous to the untuberculated and oblique clypeus; (4) antennal segment IX symmetrical; (5) antennal segment X simple, subspherical, obviously narrower than eleventh segment, and not foveate on ventral face; (6) mesotibiae with apical ends normally rounded, not spined.

Described on 9 specimens (five males and four females). All specimens (type and eight paratypes) collected by W. B. Jones on November 13, 1946 in Hinson Cave, Greenville, BUTLER CO., ALABAMA.

This very distinctive species is a member of the subgenus *Excavodes*, and of Group V (Park, 1947). Within this small group it is most closely allied to *beyeri* Schaeffer (1906, p. 261), but differs markedly from the latter in the relatively simple nature of the transverse facial excavation of the male. So far, *beyeri* is known only from the Black Mountains of North Carolina.

***Batrisodes jonesi*** new species (Figs. 5, 6)

*Type Male.* Dark reddish-brown; integument shining, lightly punctulate except for clypeus, front, genae and area of vertex external to interfoveal sulcus which are coarsely punctate; pubescence moderately abundant and flavous, semiappressed except for bristling genal beard.

Measurements: head 0.42 mm. long (clypeal margin to occiput) x 0.42 mm. wide; pronotum 0.42 x 0.37; elytra 0.64 x 0.67; abdomen 0.64 x 0.60; total length 2.12 mm.

Head with prominent eyes of about 40 facets; tempora about twice as long as eyes, arcuate to cervicum; cervicum, occiput and vertex to a line through anterior third of eyes bisected by a median carina; lateral carinae strong; a pair of nude, deep vertexal foveae, on a line through posterior margins of eyes, united by a deep U-shaped interfoveal sulcus; front lengthily declivous to terminate in an apically setose fronto-clypeal horn; labrum, mandibles, maxillary palpi and ventral surface of head as described for *spelaeus*.

Antennae with segment IX transversely trapezoidal, with ventral face medianly produced apically; X large, wider than XI, transversely subovate, with ventral face bearing a conspicuous and pubescent excavation which in turn bears a deep fovea at its ventro-mesial area.

Pronotum with two basal foveae, on each side of a short median carina; three antebasal foveae connected by a biarcuate transverse sulcus; an acute tumulus on each side of median antebasal fovea; sides of pronotum not toothed; lateral longitudinal sulci extend nearly to margin; discal longitudinal sulcus crosses disc to about apical fourth.

Elytra each with three nude basal foveae; entire sutural stria; evanescent discal stria to about discal third; flank as for *spelaeus*.

Metathoracic wings present.

Five visible tergites, the last simple and, as usual, not visible from above; lateral margins of first three tergites as described for *spelaeus*; first tergite with a pair of basal abdominal carinae separating the three, subequal basal impressions, these carinae not quite one-fourth the segmental length and separated by about two-ninths of total segmental width. Five visible sternites; last sternite as long as preceding two united, with median third of apical margin slightly convex.

Legs with protibiae each with apical third of ventral face bearing a fringe of setae that becomes progressively prostrate from proximal to distal areas; mesotarsi abnormal, as diagnostic for subgenus *Babnormodes* (Fig. 6: 6, 7), the second tarsomere greatly compressed and glabrous, with the ventral face strongly incised; metatibiae each bearing a long apical spur of setae.

Aedeagus 0.28 mm. long x 0.13 mm. wide x 0.10 mm. deep (Fig. 6: 9, 10, 11), of the simple type, without styles, and with a median, membranous, apically bicornuate process.

*Female* as for description of male except that: (1) eyes reduced to about 20 facets; (2) face evenly declivous, with no fronto-clypeal horn; antennae simple, segments IX and X progressively larger and obviously not as wide as eleventh, symmetrical, trapezoidal, with X not excavated or foveate on ventral face; (3) fifth sternite with apical margin broadly concave; (4) legs with normally pubescent protibiae and normal mesotarsi.

Described on 62 specimens (29 males, 33 females). This is one of the most satisfactory cavernicoles from a zoogeographic viewpoint since all of this ample material (type male and 61 paratypes) was collected from caves in the western half of COLBERT CO., ALABAMA as follows: Dickey Cave, Gallymore Hollow (5); Gallymore Cave, Allsboro (14); Gist Cave, Allsboro (10); Little Bear Cave, Tuscombua (11); McClusky Cave, Maud (1); McKinney Cave, Pride Station (9); Wolf Den Cave, Wolf Den Hollow (12).

Three callows were taken on September 26, 1940 which suggests that pupation was during the previous three or four days.

*Batrisodes jonesi* is a member of *Babnormodes* and of Group IX (Park, 1947). In this group it is distinctive on the combination of the fronto-clypeal horn and the tenth antennal segment. It is most closely allied structurally to *cavicornis* (Casey 1897, p. 579) which has a wide range from Westmoreland County, Pennsylvania south to Edmonson County, Kentucky and west through Hamilton County, Ohio and Pope County, Illinois; and is also closely allied to *foveicornis* (Casey, 1887, p. 462)

which has a known range that includes Tennessee and Robertson County, Kentucky.

This species is named in honor of Dr. Walter B. Jones, State Geologist of Alabama, under whose continuous enthusiasm the cavernicoles of this report were collected and made available for study.

The type male, six male paratypes, and four female paratypes were collected by W. B. Jones in Little Bear Cave, Tusculumbia, Colbert County, Alabama on March 27, 1942.

**Batrisodes subterraneus** new species

*Type Male.* Dark yellowish-brown, shining; pubescence sparse and semiappressed, with genal beard reduced. Integuments diverse in appearance: clypeus subgranular; pronotum subglabrous; abdomen lightly punctulate; elytra with large, very shallow, foveoid impressions that give a scarified, peculiar appearance. Measurements: head 0.37 (clypeal margin to occiput) x 0.40 mm. wide (through eyes); pronotum 0.37 x 0.40; elytra 0.57 x 0.74; abdomen 0.60 x 0.57; total length 1.91 mm.

Head with vertex subquadrate, with small eyes of about 40 small facets; tempora arcuate, twice as long as the eyes; median vertexal carina absent, the vertex slightly tumid between vertexal foveae; a pair of nude vertexal foveae, on a line passing through posterior margins of eyes, with an interfoveal sulcus that is obvious near the foveae but becomes evanescent apically; lateral vertexal carinae present; frontoclypeus simply declivous, not modified by a transverse excavation or teeth or tubercles, and ending in an expanded clypeus with a subtruncate apical margin; labrum, mandibles, maxillary palpi, and ventral surface of head as noted for *spelaeus*.

Antennae with segment X very slightly narrower than the eleventh segment, subspherical, with a distinct fovea on the ventral face, this fovea near base and with a diameter about one-third of the ventral face length; segment XI simple.

Pronotum with very reduced structure; four broad, shallow basal punctures or foveae; median, longitudinal basal carina



not present; three antebasal foveae connected by a shallow, biarcuate sulcoid impression; two basal tumuli present but low, blunted and vestigial; discal sulcus vestigial, only discernible in basal fourth of disc; lateral sulci vestigial; lateral margins not toothed; an unusual feature is a very inconspicuous tumulus just apical of each antebasal tumulus, in about the position of a recurved discal tooth in some species of the subgenus *Batriasymodes*.

The peculiar integumental modification of the elytra has been noted; each elytron with sloping, inconspicuous humeral angle, three basal foveae, weak sutural stria, weak discal impression weakly formed through basal third of disc; elytral flank with a vestigial longitudinal impression and the usually strong subhumeral fovea reduced to a vague impression. Metawings present.

Abdomen with five visible tergites; first three tergites with typical carinal patterns as noted for *spelaeus*; first tergite with basal abdominal carinae as for *spelaeus*. Five visible sternites; fifth sternite as long as preceding two united, with the median portion of apical margin slightly lobed.

Legs with protibiae each slightly contorted in apical half; mesotarsi abnormal, as diagnostic for subgenus *Babnormodes*; each metatibia with a long apical spur.

*Aedeagus* (Fig. 7) simple, without styles, bilaterally symmetrical, with a membranous toadstool-shaped median process; aedeagus is 0.23 mm. long x 0.15 mm. wide x 0.10 mm. deep.

*Female* as for male with the following exceptions: (1) vestigial eyes of 16 small facets; (2) antennal segment X distinctly smaller than eleventh, rounded trapezoidal, and not foveate on ventral face; (3) fifth sternite not as long as preceding two united, with the apical margin very slightly lobed; (4) protibia normal, not contorted; (5) mesotarsi normal.

Described on three specimens (type male and two paratype females) collected by W. B. Jones on December 29, 1938 from Griffith Cave, Guntersville, MARSHALL CO., ALABAMA.

This new species is a member of the subgenus *Babnormodes*, as a consequence of the very abnormal mesotarsi of the male, but within this subgenus is not closely related to any epigean species; its nearest ally structurally is *schaefferi* Park (1947, p. 104), known only from North Carolina. The new species is distinguished in both sexes by very reduced pronotal and elytral structure, and by the peculiar integumental modification of the elytra; on the other hand, the male sex is strongly marked by the foveate tenth antennal segment and abnormal mesotarsi. The slightly contorted protibiae of the male, and the vestigial accessory tumulus on each side of the pronotal disc are an approach to the condition in some species of *Batriasymmodes*. It can be readily told from *schaefferi*; the latter has a strongly excavated face, whereas *subterraneus* has a simply declivous face in the male sex.

***Batrisodes valentinei*** new species

*Type Male.* Dark reddish-brown with yellowish-brown legs, palpi and antennae; pubescence sparse and semiappressed except for bristling genal beard; integument shining and sparsely punctulate except for the clypeus and the vertex external to interfoveal sulcus which are coarsely granulate-punctate. Measurements: head 0.42 mm. long (clypeal margin to occiput) x 0.42 mm. wide (through eyes); pronotum 0.42 x 0.42; elytra 0.60 x 0.67; abdomen 0.62 x 0.60; total length 2.06 mm.

Head with subquadrate vertex and moderately prominent eyes of about 40 facets; arcuate tempora about one and one-half times as long as eyes; lateral vertexal carinae present; occiput and vertexal base with vestiges of a median, longitudinal carina (this carina varies among the paratypes from complete, to a line through anterior margins of eyes, to wholly absent); vertex moderately vaulted between foveae; vertexal foveae, on a line through posterior margins of eyes, connected by a wide U-shaped interfoveal sulcus (this sulcus varies among the paratypes from deep to shallow, but is entire); antennal tubercles obsolete.

The face is difficult to describe. The front becomes sharply declivous on a line through antennal bases; this declivity is longitudinally concave, subglabrous and narrows rapidly so that it presents a triangular field that is surrounded by the granulate-

punctate clypeus; there is a transversely ovate depression at the start of the declivity that bears a few setae; the face is not transversely excavated between antennal cavities, and this triangular declivous field is bounded by a "frontal margin" that is formed by a subcarinoid, V-shaped outline of the triangular field; clypeus not modified with tubercles or other excesses, and with a semi-circular apical margin; labrum, mandibles, maxillary palpi, and ventral surface of head as in *spelaeus*.

Antennae simple, with a trapezoidal tenth segment that is distinctly narrower than eleventh, and with an unmodified ventral face; distal (eleventh) segment simple, not modified by basal teeth or concavities.

Pronotum essentially as for *subterraneus*, even to the accessory tumuli apical of each antebasal tumulus, except that in the present species the median longitudinal basal carina is distinct (this basal carina varies in the paratypes from strong to wholly absent).

Elytra as in *subterraneus*, except that the subhumeral fovea is more obvious.

Metathoracic wings present.

Abdomen with five visible tergites; first three tergites with entire marginal carinae as described for *spelaeus*; first tergite with the usual three depressions separated by a pair of basal abdominal carinae; these carinae are one-fifth the segmental length and separated by slightly more than one-fifth of total segmented width. Five visible sternites, simple, the fifth slightly longer than preceding two united and with an almost straight apical margin.

Legs with protibiae abnormal, contorted in apical half, this sinuosity much more marked than in *subterraneus*; mesotarsi abnormal as in *jonesi*; metatibiae each with a long apical spur of setae.

Aedeagus 0.28 mm. long x 0.15 mm. wide x 0.10 mm. deep, without lateral styles (Fig. 8). When the median process is evagi-

nated, it is seen to be of the same type as in *subterraneus*. The aedeagi of these two species are readily separated: in *subterraneus* (Fig. 7) the aedeagus is bilaterally symmetrical; in *valentinei* it is bilaterally asymmetrical (over a dozen aedeagei of *valentinei* have been studied), with the declivous, acute apex well to the morphological left of the median line, and the morphological right-apical margin of the median lobe slightly to strongly elevated.

*Female*. As for male with the following exceptions: (1) eyes of 20 facets; (2) tempora slightly more than twice the eye length; (3) face evenly declivous and not longitudinally concave, and with no precise delimitation of front and clypeus; front basally subglabrous but apically gradually coarsely punctate, these punctures becoming smaller and subgranular apically to merge into clypeal granulate-punctate condition; (4) protibiae normal, not contorted; (5) mesotarsi normal.

Described on 55 specimens (male type, 17 male and 38 female paratype), and named in honor of Dr. J. Manson Valentine of Highlands, North Carolina. The collected population sample is as follows: TENNESSEE: Crystal Cave, Mont-eagle, GRUNDY CO. (1); ALABAMA: JACKSON CO., Clements Cave (5); MORGAN CO., Talucah Cave (2); MADISON CO., Goat Cave (Great Cave), Keel Mountain (43), Moon Cave, Newmarket (1), Toll Gate Natural Well, Monte Sano (3).

This is another species which, like *spelaeus*, has a relatively large area of distribution. It is a member of the subgenus *Babnormodes* as a consequence of its abnormal mesotarsi in males. Within this subgenus, *valentinei* is obviously most closely allied to *subterraneus*, and in the opinion of the author the latter is either derived from *valentinei* or both from a relatively recent ancestor. The internal sac (median process) of the aedeagi of both is strikingly similar, as are also the general habitus and detailed structure of pronotum and elytra, the weakly contorted protibiae of male *subterraneus* and markedly contorted male protibiae of male *valentinei*, and so on through a long series of structural similarities. In both species the males have about 40 ocular facets, whereas the females differ in that *valentinei* has 20 facets but *subterraneus* has a still more vestigial eye of 16 facets, which may

indicate a more derived and specialized condition. This idea is supported by the distribution in Alabama. For example, the known distribution of *subterraneus*, a single cave (Griffith Cave, Marshall County, Alabama) does not overlap the wide distribution of *valentinei*, but is more or less surrounded by the latter.

These two species can be readily told apart, as between the males. In *subterraneus* the male tenth antennal segment is swollen and bears a conspicuous fovea on the ventral face, the face is simply declivous, and the aedeagus bilaterally symmetrical. In *valentinei* the tenth antennal segment is small and unfoveate, the face is peculiar in that the "frontal margin" is a carinoid edge separating a granular clypeal field from a subglabrous, triangular frontal field, and the aedeagus is bilaterally asymmetrical.

Both species can be separated in both sexes by elytral sculpture, which is simply punctulate in *valentinei* and peculiarly scarified-punctate in *subterraneus*.

The epigeal allies within *Babnormodes* would appear to include *appalachianus* Casey, 1903 known from Westmoreland County, Pennsylvania, and *schaefferi* Park, 1947 known from North Carolina, both in the Appalachian system.

There were three callows in the *valentinei* collected. These were a male and two females from Toll Gate Natural Well taken on October 8, 1939 which presumes pupation in the first week of October.

The male type, eleven male paratypes, and 31 female paratypes were collected by W. B. Jones in Goat Cave (Great Cave), Keel Mountain, Madison County, Alabama on July 24, 1946.

#### ***Batrisodes specus* new species**

*Type Male.* Dark reddish-brown with yellowish-brown palpi and antennal clubs; pubescence moderately abundant, flavous and semiappressed except for bristling genal beard; integuments shining, lightly punctulate except for clypeus which is granulate-punctate, and the vertex external to interfoveal sulcus which is sparsely, coarsely punctate.

Measurements: head 0.37 mm long (clypeal margin to occiput) x 0.42 mm. wide (through eyes); pronotum 0.42 x 0.42; elytra 0.60 x 0.67; abdomen 0.56 x 0.60; total length 1.95 mm.

Head with prominent eyes of about 40 facets; tempora one and a half the eye length; vertex subquadrate, with lateral vertexal carinae; median vertexal carina absent (weakly formed in some paratypes); a pair of nude vertexal foveae, on a line through eye centers, connected by an entire, U-shaped, interfoveal sulcus; face simply declivous, neither transversely excavated nor provided with horn or tubercle, the subglabrous front narrowing to merge into the granular clypeus; labrum, mandibles, maxillary palpi, and ventral surface of head as in *spelaeus*.

Antennae with a heavy club, segment IX right-triangular from a mesial view; segment X distinctly narrower than eleventh, but swollen, irregularly spherical, with the ventral face bearing a very large fovea, this fovea is fossoid, occupies the basal two-thirds of the ventral face and is very deep with a setose margin; segment XI broad, with the ventral face longitudinally concave in basal two-thirds (reminiscent of *cavicornis* Casey, 1897, p. 579).

Pronotum as for *jonesi*, except that the antebasal tumuli and discal and longitudinal sulci are vestigial.

Elytra as in *jonesi*.

Metathoracic wings present.

Abdomen as for *jonesi*.

Legs with protibiae each with the apical half contorted (as in *valentinei*), and bearing the lateral setose fringe (as in *jonesi*); mesotarsi abnormal, as diagnostic for the subgenus *Barnormodes*; each metatibia with a long apical spur of setae.

Aedeagus (Fig. 9) 0.23 mm. long x 0.14 mm. wide x 0.07 mm. deep; slightly asymmetrical in that the right apical sclerotized margin of median lobe is longer than the left apical margin; evaginated internal sac of the general form of *valentinei* and sub-

*terraneous*, but longer, and more acute. Eight aedeagi examined.

*Female* as for male with the following exceptions: (1) eyes of 18 facets; (2) tempora nearly three times the eye length; (3) antennal club normal; segment X larger than ninth, trapezoidal, much smaller than eleventh, and with a nonfoveate ventral face; (4) protibiae normal, not contorted; (5) mesotarsi normal.

Described on 46 specimens (17 males and 29 females) as follows: TENNESSEE: Indian Cave, New Market, JEFFERSON CO., (4); ALABAMA: COLBERT CO., Georgetown Cave, Georgetown (1); MADISON CO., Cave Spring Cave, Certain Gap (2), Huntsville Cave, Huntsville (2), Hutton Cave, Sharp's Cove (17), Lott Cave, Big Cove (1), Pitts Cave, Big Cove (2), Twin Cave, Brownsboro (4); MARSHALL CO., Terrell Cave, Guntersville (13).

Type male, four paratype males and twelve paratype females collected by W. B. Jones in Hutton Cave, Sharp's Cove, Madison County, Alabama on January 3, 1942.

This new species is a member of the subgenus *Babnormodes*, by virtue of the abnormal mesotarsi in the male sex. Within the subgenus it is allied distantly to *foveicornis* (Casey, 1887, p. 462) and *cavicornis* Casey (1897, p. 579) more than to any other epigean species. The resemblance of *specus* to these species is strong enough to suggest a direct ancestral connection, with the face similar to *foveicornis* and the antennal club similar to *cavicornis*. Among the Alabama-Tennessee cavernicoles, *specus* is closely allied to *jonesi*, so much that, in the opinion of the author, on the basis of anatomical and geographic grounds, *jonesi* was derived from *specus*, or an immediate ancestor.

These latter two can be separated readily: male *specus* have a simple, declivous fronto-clypeus; male *jonesi* have the front terminating near the clypeal margin in a horn (Fig. 6).

Among other things, the collection of *specus* was rich in callows: one male on October 9, 1939 in Cave Spring Cave, Madison County, Alabama; one male on January 3, 1942 from Twin Cave, Madison County, Alabama; two males on January 3, 1942 from Hutton Cave, Madison County, Alabama; one female on





Evaginated internal sac with apical margin not truncate, but in the outline of a toad-stool..... 5

- 5. (4) Median lobe with strongly declivous apex acute and median in position..... 6

Median lobe with strongly declivous apex acute but asymmetrical, placed on the morphological left side of the midline (Fig. 8)

*valentinei*, new species

- 6. (5) Median lobe strictly bilaterally symmetrical in dorsal view, and with the evaginated internal sac with an ogival apical outline (Fig. 7)

*subterraneus*, new species

Median lobe with morphological right side longer than left side from a dorsal view, and with the evaginated internal sac acute-triangular in outline with a finely drawn-out apex (Fig. 9).

*specus*, new species

**Arianops** (Brendel, 1893)

This genus has no Western Hemisphere allies, but is closely allied to the relatively large Amauropsoid fauna of southern Europe, holding many blind cavernicoles and recently reorganized by Jeannel (1950).

*Arianops* up to the present held two species. The genotype is *Arianops amplyoponica* (Brendel, 1890, p. 80)<sup>4</sup> taken with ants in Westmoreland County, Pennsylvania. I have a series from St. Vincent, Westmoreland County that is conspecific with the type, and this species has been reported from Retreat, North Carolina (Brimley, 1938).

The second species is *Arianops plectrops* Casey, 1897, p. 582 from Round Knob, North Carolina. My series of this species is from the Black Mountains, collected in deep leaf mold in rich forest near Montreat, Buncombe County and Hamrick, Yancey County, North Carolina.

The genus, then, appears to be restricted to central and southern Appalachians. Deep forest leaf mold and the dark, moist galleries of ants are habitat niches that are consistent with many features of the cave environment. The points of resemblance include partial to complete darkness, high relative humidity, relatively cool air temperature and a marked degree of constancy in the general microclimate. All *Arianops* lack eyes, and the absence of eyes would not appear to handicap dwellers of deep leaf mold, ant nests or caves. Both from a consideration of these ecological matters, as well as the phylogenetic similarity of cavernicolous Amauropsoids of southern Europe, it is not surprising that *Arianops* should have cavernicolous species in the Appalachian system and its adjacent plateaus.

The discovery of a new species of *Arianops* in a northern Alabama cave has necessitated a reorganization of the genus as follows:

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<sup>4</sup>*Anops amplyoponica* Brendel, 1890, p. 80; *Arianops amplyoponica* Brendel 1893, p. 279; *Arianops amblyoponica* Leng, 1920 and Bowman, 1934.

- 1. Pronotum with a distinct median fovea near base  
     Subgenus *Arianops* Brendel, 1893 s. str. .... 2

Pronotum lacking any foveae, tubercles or sulci, being a perfectly simple oboval

Subgenus *Arispeleops* new subgenus

Type: *cavernensis* new species

- 2. (1) Vertexal foveae minute; pubescence abundant; pronotum wider than long

Type: *amplyoponica* (Brendel, 1890)

Vertexal foveae large: pubescence sparse; pronotum longer than wide

*plectrops* Casey, 1897

***Arianops cavernensis* new species**

*Type Female.* Shining brown; pubescence very short (0.054 mm.) and very sparse except for genae and labrum; integuments lightly punctulate.

Measurements: 0.45 mm. long (clypeal margin to occiput) x 0.37 mm. wide (through widest part of head); pronotum 0.47 x 0.42; elytra 0.53 x 0.80; abdomen 0.80 x 0.74; total length 2.25 mm.

Head subovate, including clypeus; tempora very long and arcuate; eyes absent, replaced each side by a short and acute spine; vertexal foveae vestigial, reduced to a pair of small pits; face declivous and simple, from a point between the antennal tubercles to the arcuate clypeal margin; labrum broad, nearly straight, with apical angles produced and acute; mandibles long, left crossed dorsal to right; ventral surface of head with neither gular suture nor median gular carinoid line, but with the usual gular fossa at base.

Maxillary palpi four segmented, simple; first segment minute; second segment pedunculate; third as wide as second, elongate-subtriangular; fourth (distal) segment wider than second

and distinctly longer, acute-subfusiform, broadest behind middle, with a very minute palpal cone at apex.

Antennae eleven-segmented, simple; I to VII elongate, with IV and VI slightly shorter than adjacent segments; VIII smallest; club of last three segments, of which XI is conspicuously larger, as long as preceding three united, with a pedunculate base and a narrowly rounded apex.

Pronotum elongate, oboval with a subtruncate base; notable for its lack of any foveae, tubercles or sulci; the only structural feature is a peculiar area at extreme base that is microstriate.

Elytra also very simple, with very long, sloped humeri, and lacking any trace of basal foveae or impressions, and without any discal impression; flank not modified; each elytron does have a fine but distinct and entire sutural stria.

Abdomen with five visible tergites, in a length ratio of: 6/1/0.5/3/1.5 and without marginal carinae except for the first tergite; first tergite with an entire external carina on the extreme margin of segment, and with a vestigial, divergent internal carina that appears only in basal fourth; first tergite with a pair of basal abdominal carinae that are flat, parallel, one third of segmental length, and separated by two elevenths of total segmental width; first tergite without lateral depressions and with the base between basal carinae only lightly impressed; fifth tergite transversely trapezoidal, divided by a transverse carina into a basal subglabrous and an apical punctulate half, the apical margin slightly concave medianly.

Six visible sternites, the first more or less obscured by the dense pubescence at this point; these sternites in a length ratio of: 1/3.5/1/0.8/0.8/3.6 with the fifth sternite with a deeply arcuate apical margin to partially enclose the large sixth sternite; sixth sternite with a large median lobe on apical margin.

Metasternum simple.

Legs long and simple; tarsi slender, second tarsomere longer than third; tarsi bearing a single short tarsal claw, and a just discernible accessory seta or setoid claw.

Described on a single specimen, the female type, collected by W. B. Jones on June 18, 1938 in Salpetre Cave, MARSHALL CO., ALABAMA.

Unfortunately the male sex is unknown and no comparison of aedeagi within the genus was possible.

**Bythinopsis** (*sensu* Jeannel, 1950)

Raffray (1890) proposed the tribe Bythinini for certain Bythinoid species, and later (1903-1904) placed these with other genera in the tribe Tychini. The latter course has been adopted generally since that time (Raffray, 1908, 1911; Leng, 1920; Bowman, 1934; Park, 1942).

Recently, Jeannel (1950) has studied the European Bythinoid and Tychoid genera and has reestablished the Bythinini and Tychini as distinct tribes. The author is in accord with Jeannel's point of view.

*Bythinopsis* was erected by Raffray (1908, p. 282) and has been reorganized by Jeannel, 1950. Our North American species up to the present numbered two: *tychoides* (Brendel, 1865, p. 259) is known from New Jersey (Essex County), New York (Long Island,) Pennsylvania and eastern Ohio; *carolinae* (Casey, 1897, p. 614) is known only from the Black Mountains of North Carolina. From data presented previously in this paper, it is not surprising that these essentially Appalachian populations should be allied with an undescribed cavernicole from northern Alabama.

**Bythinopsis jonesi** new species

*Type Female.* Pubescence sparse, semiappressed; integuments shining, punctulate except for the coarsely punctate elytra. Measurements: head 0.17 mm. long (clypeal margin to occiput) x 0.20 mm. wide (through eyes); pronotum 0.23 x 0.27; elytra 0.45 x 0.47; abdomen 0.20 x 0.42; total length 1.05 mm.

Head with small, posteriorly-placed eyes of about 16 coarse facets; vertex simply convex, not medianly carinated, and bearing

a pair of deep, nude vertexal foveae<sup>5</sup> on a line through anterior margins of eyes; a sulcus from each fovea, these sulci extending apically to merge with the deep depression between the antennal tubercles, this depression consequently being deeper on each side; antennal tubercles at apical corners of a subquadrate rostrum that bears median depression; rostrum truncate apically, where it becomes subvertically declivous to form the simple face; face transversely divided in basal third by the fronto-geno-clypeal line. Ventral surface of head not bisected by a carina.

Maxillary palpi as illustrated (Fig. 10), and typical of the genus. A novelty to the author were several dentoid tubercles near apex of second segment.

Antennae eleven-segmented, simple and typical of genus; segments united 0.48 mm. long e. g., distinctly longer than the head and pronotum united, and almost one-half as long as body; segment I elongate-cylindrical, four times as long as wide, and one-third as long as entire antenna; II symmetrically oval, slightly wider than first; III to VII as long as first segment, III obconical, IV to VII subequal and moniliform; distinct club of last three segments, IX transversely suboval and distinctly wider than eighth, X much wider than ninth and about twice as wide as long, XI almost as long as preceding four segments united, of conical form with a rounded base.

Pronotum as in *tychoides* and *carolinae*, except for the transverse antebasal sulcus that connects the lateral foveae; in *jonesi* this sulcus is rudimentary, just discernible.

Elytra with similarly rudimentary development; each elytron with humeral angle obtuse, two basal foveae, an entire but feeble sutural stria, and a vague discal impression; the elytral flank bears a large subhumeral fovea.

Abdomen very short as seen from above, with narrow but distinct lateral margins on the first three tergites. Five tergites in

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<sup>5</sup>In cleared whole-mounts under high magnification these vertexal foveae are seen to be relatively long and conical, with the floor of each attached to an arm of the supratentorium, as usual for Pselaphidae (cf. Stickney, 1923 and Park, 1942).

a length ratio of 1.5/1/1/1/1. Six sternites in a length ratio of 0.8/1/0.25/0.25/0.3/1.

Metasternum with a fine, longitudinal stria that extends from just before the posterior margin through the posterior half of disc.

Legs simple; each tarsus bears a short, broad tarsal claw and an exceptionally thick and distinctive paraungial seta.

Described on one female specimen, the type, collected by W. B. Jones on September 25, 1940 in Wolf Den Cave, near Maud, COLBERT CO., ALABAMA. Named in honor of the late Nelson B. Jones.

This specimen is a callow, so that mature coloration is not known. The sex precluded analysis of the aedeagus of the species.

This species can be readily separated from other American species of the genus by many criteria, including the rudimentary condition of pronotal and elytral impressions.

**Machaerites** (Miller, 1855)

As limited by Jeannel (1950, p. 170) this is a genus of two European species known, up to the present, only from caves in Carniola (northeastern Italy—northwestern Yugoslavia).

The collection under examination contained two new species of this remarkable genus, and necessitated a reorganization of *Machaerites*.

This is the first time that this genus has been reported from the Western Hemisphere and the several subgenera and species may be delimited as follows:

- 1. Each elytron with two large basal foveae..... 5
- Basal elytral foveae either absent, or each elytron with two vague, foveoid impressions:
- Speleochus* new subgenus..... 2

2. (1) Head ovoidal in dorsal outline (Fig. 11)  
*stygius* new species (type of subgenus)..... 3  
 Head subtriangular in dorsal outline  
*ferus* new species..... 4
3. (2) Each metatibia armed with a blunt spine (Fig. 11): males  
 Metatibiae simple, not spined: females
4. (2) Ventral surface of head deeply excavated from side to side, the floor of excavation in the form of a thin, complicated shelf (Fig. 13): males  
 Ventral surface of head simple: females
5. (1) Pronotum with a distinct transverse, antebasal sulcus:  
*Bythoxenus* (Motschulsky, 1859)  
 Type: *subterraneus* Motschulsky, 1859  
 Pronotum with sulcus absent:  
*Machaerites s. str.* (*sensu* Jeannel, 1950)  
 Type: *spelaeus* Miller, 1855

*Speleochus* new subgenus of *Machaerites*

Subgenus Type: *stygius* new species (Fig. 11)

*Diagnosis:* Bythinini (*sensu* Jeannel, 1950) with the following morphological features: (1) Head elongate, narrowed anteriorly with antennae articulated subcontiguously; (2) eyes wholly absent in both sexes; (3) Maxillary palpi four-segmented, with first segment minute, second segment very long and gradually thicker from base to apex and studded with small tubercles, third segment short and elongate-triangular and also studded with a few small tubercles, fourth segment very long and slender with a falciform outline and bearing apically a long and translucent palpal cone<sup>a</sup>; (4) Antennae simple, eleven-segmented, not

<sup>a</sup>The palpal cone is regarded by Jeannel (1950, p. 7-8) as a vestigial fifth segment of the maxillary palpus; it is regarded as a sensory structure homologous to antennal cones by Park (1935, p. 133; 1942, p. 18, 22) and Park, Auerbach and Wilson (1950).



geniculate; (5) Pronotum simple, with a pair of small lateral antebasal foveae united by a just discernible, vestigial impression; (6) Elytra simple, with evanescent humeri, flank unmodified, with a weak sutural stria on each elytron but no discal impression, and with basal foveae either wholly absent or weakly represented by a pair of vague basal impressions on each elytron; (7) Abdomen with five visible tergites and six visible sternites in both sexes, with the first visible sternite obvious from side to side; (8) First three visible tergites with narrow but distinct lateral margins; (9) Both sexes with procoxae and protibiae studded with small tubercles on the ventro-anterior faces; (10) femora articulated very obliquely on trochanter, so that femora and coxa are subcontiguous; (11) three-segmented tarsi, in which the first tarsomere is very short and the last two very long, the second tarsomere being distinctly longer than the third, the third tarsomere bearing a single tarsal claw and an unusually distinct unguiform seta; (12) metathoracic wings absent; (13) aedeagus with suboval median lobe and supplied with numerous diagonal bulbar muscles that extend from the dorsolateral to the ventral surface of the basal bulb, internal sac (median process) supplied with apically symmetrical and paired basal armature and a pair of exsertile basal teeth.

*Machaerites (Speleochus) stygicus* new species (Fig. 11)

*Type Male.* Reddish-brown when mature varying to light straw-yellow in immaturity; pubescence moderately abundant and semi-appressed, except on ventral surface of head where the setae are more sparse and longer; integuments polished, shining and punctulate except for elytra which are much more punctate. Measurements: head 0.35 mm. long (clypeal margin to occiput) x 0.27 mm. wide (through widest part of head); pronotum 0.37 x 0.42; elytra 0.63 x 0.68; abdomen 0.37 x 0.67; total length 1.7 mm.

Morphology as described for subgenus and as illustrated.

Head with a long lateral carina each side originating where eye usually is placed, and continuing anteriorly to form clypeal margin; eyes wholly absent; vertexal foveae small but distinct; ventral surface of head with a weakly developed median carinoid ridge and a weak basal gular fovea.

Second segment of maxillary palpus with about 40 small but distinct tubercles arranged in three irregular rows.

Prosternum long, not medianly bisected by a carina, but with a slight carinoid ridge between coxae in basal fourth.

Elytra without trace of basal foveae (in some of the paratypes there is a vague impression at base of sutural stria where sutural fovea would ordinarily be placed).

No metathoracic wings.

Sternites in a median length ratio of 1/1.2/0.4/0.4/0.5/2 and the last tergite is ogival in outline and normally vertical in position and not visible from above except when aedeagus is exerted. Abdomen slightly concave in lateral outline.

Legs long, with swollen femora, especially the metafemora; metatibiae each arcuate near apex and bearing a short, stout spinoid process.

*Female.* As for the male with the following exceptions: (1) Abdomen with ventral surface straight to slightly convex in lateral outline; (2) legs more slender, especially notable when metafemora are compared with those of the male; (3) the metatibiae are much less arcuate and lack the apical spine.

This eyeless, wingless species is described on 16 specimens (type male, eight male paratypes, seven female paratypes) collected as follows, all from MADISON CO., ALABAMA: Barclay Cave, King Mountain (1); Cave Spring Cave, Certain Gap (2); Toll Gate Natural well, Monte Sano (4 on 6. VIII. 39 and 3 on 28. XI. 40); Huntsville Spring Cave, Huntsville (2); Kelly Natural Well, King Mountain (2); Lott Cave, Big Cove (1); Twin Cave, Brownsboro (1).

Type Locality: Toll Gate Natural Well, Monte Sano.

One female callow was present, collected on October 8, 1939 in Cave Spring Cave, Certain Gap, nr. Huntsville.

Aedeagus typical of the subtribe Machaeritina in general, and of *Machaerites* in particular, e. g., the internal sac is supplied with a pair of large, apically symmetrical processes, and a basal armature of two large teeth. In *stygicus* the aedeagus is 0.53 mm. long x 0.23 mm. wide x 0.17 mm. deep. Its complicated structure is illustrated (Fig. 12). The internal sac is provided with a pair of basal teeth, these teeth are hyaline, laminoid, apically bifurcated and on exertion of the internal sac these teeth become divergent.

*Machaerites (Speleochus) ferus* new species (Figs. 13, 14)

*Type Male.* Reddish-brown when mature, varying to light straw-yellow in immaturity; pubescence semiappressed on abdomen, semierect on elytra and pronotum; integuments shining and rather coarsely punctate throughout.

*Measurements:* head 0.30 mm. long (clypeal margin to occiput) x 0.27 mm. wide; pronotum 0.33 x 0.36; elytra 0.56 x 0.64; abdomen 0.30 x 0.60; total length 1.5 mm.

Head subpyriform, with strongly rounded tempora that merge with the oblique genae to the subquadrate antennal rostrum; lateral carinae, vertexal foveae, frontal depression on rostrum, face, labrum and mandibles as in *stygicus*; eyes entirely absent; antennae essentially as in *stygicus*, but a little more robust, e. g., intermediate segments (III-VIII) are more elongate-oval than elongate-subcylindrical.

Maxillary palpi differing in two details. The second segment has fewer tuberosities, e. g., about 30 in two irregular rows. The fourth segment is more sinuate-falciform, with a concave lateral and a convex mesial outline (Fig. 13).

Pronotum as for *stygicus*.

Elytra with a pair of elongate, weakly formed, foveoid impressions at base of each elytron. Metathoracic wings absent.

Abdomen as described for subgenus. Five visible tergites in a median length ratio of 2/1.8/1.4/1.3/1.4 with fifth ogival in

outline. Six sternites in a median length ratio of 1.4/1.6/0.5/0.3/-0.2/1.5 and without abnormal modifications.

Legs as described for subgenus, the femora relatively less swollen than in *stygicus*, and metatibiae lacking the apical spinoid process found in male *stygicus*.

Two morphological features require special attention. These are the ventral surface of the head, and the aedeagus.

The ventral surface of the head (Fig. 13) is remarkably modified. In sharp contrast to the simple condition in *stygicus*, the entire gular-genal floor is very deeply hollowed out, and the bottom of this excavation is formed by an arcuate shelf that arises near the cervical constriction. This shelf is thin and trilobed: the lateral lobes are sickle-shaped and attached to the median lobe by a thinner integument; the median lobe is longer, truncate and bears a pair of parallel canals. At the base of this shelf, and curling upward over its lower face is a transverse row of six, excessively long setae: the outer two are slender, but the inner four are very wide and laminoid and tend to coil.

The aedeagus (Fig. 14) has the apical ends of the median lobe drawn out into a pair of very long, ventrally directed, thin apical processes; these latter lie beneath the exerted internal sac, and each bears four setae in a linear series, the third of which is very much thicker than the others. The internal sac bears a pair of large basal teeth. When the sac is withdrawn these teeth lie vertically appressed; when the sac is exerted these teeth gradually diverge so that at full exertion the teeth are nearly at right angles to one another. This aedeagus is smaller than in *stygicus*, measuring 0.37 mm. long x 0.17 mm. wide x 0.09 mm. deep. In perfectly relaxed examples a gentle pressure on the bulb of the median lobe would force out the internal sac easily and rapidly. In life, the method of operation may include the contraction of two sets of muscles alternately. The first set are composed of the bulbar contractors. These are numerous, about twelve to a side and extend diagonally from the dorso-lateral walls of the basal bulb of the median lobe to its ventro-lateral and ventral walls. Their contraction must suddenly reduce the volume of the basal bulb and exert hydraulic pressure on the

internal sac, bathed in haemolymph. This should exert the internal sac. When the latter is fully extended, it will be seen that there are about four very long, thin, muscles on each side of the median line, easily visible beneath the membranous epithelium of the sac. These are the internal sac retractors. On their contraction the internal sac would be rapidly withdrawn and the divergent basal teeth gradually appressed. These basal teeth appear to be articulated to a sclerotized basal collar to which some of the retractor muscles are attached. When these sac retractors are contracting, the bulbar muscles in all probability are in antagonistic relaxation and, the hydraulic pressure on the bulb being released, this would also serve to pull back the sac.

*Female.* General morphology as described for the male, with the following exceptions: (1) ventral surface of head perfectly simple and gently convex; (2) femora slightly less swollen.

Described on six specimens (male type, 4 male paratypes and 1 female paratype) collected in ALABAMA as follows: MADISON CO., Aladdin Cave, Sharp's Cove (3), Hutton Cave, Sharp's Cove (1); JACKSON CO., Devil Stair Steps Cave, Keel Sinks (1) and Hambrick Cave, Hambrick Sinks (1). Type Locality: Aladdin Cave, Madison Co.

One callow was present in the collection. This was a male collected by W. B. Jones on January 3, 1942 in Hutton Cave.

#### SPELEOBAMINI new tribe (Fig. 15)

Pselaphidae with the following diagnostic combination of morphological features: (1) Eyes absent; (2) vertexal foveae absent; (3) eleven-segmented, subcontiguously articulated antennae; (4) four-segmented maxillary palpi, the first segment short, second segment very elongate and apically enlarged, third segment very elongate and apically enlarged, fourth segment very elongate, subfalciform and bearing a long apical palpal cone; (5) pronotum elongate suboval, without foveae, sulci or tuberosities; (6) prosternum long, simple, not medianly bisected by a carina; mesosternum long, bisected by a strong median carina; metasternum long, not bearing sulci; (7) elytra without basal foveae, without discal impression, flank simple, entire sutural stria present; metathoracic wings absent; (8) five tergites visible, the

first very long, and first three tergites bearing a distinct margin on each side; (9) seven sternites in the male sex visible, first nearly hidden by dense pubescence, second very long, sixth with apical margin medianly and semi-circularly incised to contain the minute seventh segment or penial plate; (10) all legs brachysceline, with femora very obliquely articulated on trochanters so that femur and coxa are subcontiguous; (11) tarsi three segmented, first segment small, next two long, with second distinctly longer than third, third bearing a single claw, no paraungual seta; (12) aedeagus with a style on each side, free and inserted on the ventral face of the basal capsule.

Type of Tribe: *Speleobama vana* new genus and new species.

SPELEOBAMA new genus (Fig. 15)

Genotype: *Speleobama vana* new species.

So far, but one genus is known in this tribe, *Speleobama*, with the characters of the tribe as set forth previously.

It is known only from a cave in northern Alabama, and represents the peak of specialization through loss or reduction of parts. The eyes, wings, vertexal foveae, pronotal foveae and elytral foveae are all absent. Only the male sex is known, but in this there is a unique structural feature: the very long head has a deep cervical constriction which is hidden by a large ruff of long, golden setae. The ruff is conspicuous and formed in part by setae arising from the cervicum and arching apically and in part by setae arising from vertex and genae and arching posteriorly.

The proper discrimination of this genus has been a long and difficult task as it holds a combination of critical features that has necessitated a reorganization of our knowledge of pselaphid tribes. Thus, the Pselaphinae have been separated into two groups of tribes, Brachyscelina and Macroscelina, based on two diagnostic features. These are the type of articulation of the femora (Raffray, 1890), and the insertion of aedeageal styles (Jeannel, 1949, 1950).

*Speleobama* has brachysceline femoral articulations and the aedeageal styles are macrosceline. Consequently this new tribe and genus of cavernicolous pselaphids spans the gap between the two great divisions, and has important evolutionary implications discussed later. The position of this tribe and genus are given in a general key to pselaphid tribes of the Western Hemisphere (p. 56).

***Speleobama vana*** new species (Fig. 15)

*Type Male.* Very elongate, with slender and elongate appendages; uniform deep yellowish-brown; pubescence short and sparse except for the elaborate cervical ruff, apical margin of elytra, and at base of venter; integuments lightly punctulate, polished. Measurements: head 0.51 mm. long (apical margin of clypeus to posterior limit of cervicum) x 0.22 mm. wide; pronotum 0.33 x 0.29 mm.; elytra 0.53 x 0.56 mm.; abdomen 0.53 x 0.56.; total length 1.9 mm.

Head much longer than wide, with a deep and complicated cervical constriction that is hidden by the remarkable cervical ruff previously described, and this ruff in turn hides the occiput and gular areas; eyes wholly absent; vertexal foveae wholly absent; no median vertexal carina and no lateral carinae; a short longitudinal carina below each antennal tubercle; the antennae articulated subcontiguously on a short rostrum, this rostrum medianly impressed; anterior margin of rostrum forms a frontal carina which roofs over the shallow antennal acetabulae; these acetabulae separated medianly by a short vertical carina that arises at center of frontal margin; face otherwise not modified; labrum short; mandibles long, slender, left crossed dorsal to right.

Antennae long, slender and simple; eleven-segmented; first nine segments 0.60 mm., last three segments 0.45 mm. long, that is, the antennae measure about 1.0 mm., or slightly more than half of body length; shape and relative size of segments as illustrated.

Maxillary palpi four-segmented; first segment short; second segment elongate, gradually clavate to apex; third segment also elongate and widest in apical three-fourths of length; fourth seg-

ment elongate, falciform, with its surface thickly studded with large, elongate-oval tuberosities, and bearing a long, oblique, apical palpal cone.

Pronotum simple and unmodified.

Elytra simple, each elytron with an entire scutellar stria that expands in basal third into a deeper and broader, ovoidal impression, but this is not a fovea; no fovea; flank simple; apical margin bearing about twelve to fifteen long, golden setae that project posteriorly over impressions of first tergite.

Abdomen with five visible tergites, with proportions as illustrated; first three with a distinct margin on each side; first tergite with a longitudinally hemiovate depression on each side.

Seven visible sternites, in a median length ratio of 1/4.3/0.3/0.4/0.6/1/0.3 and all simple; first greatly obscured by pubescence; second very long, longer than other sternites united; sixth sternite medianly incised on apical margin to contain the minute, ovoidal seventh or penial plate. This penial plate is exerted to the morphological right on exertion of the aedeagus, e. g. a dextral asymmetry as in *Cedius* (*Cedius*) described previously (Park, 1949).

Prosternum, mesosternum and metasternum as described in the tribe Speleobamini.

Legs all very long, slender, wholly unmodified, with slender femora; typically brachysceline articulation, the femur being very obliquely articulated on the trochanter, so that the femur is very close to its coxa, as illustrated; tarsi long and three-segmented, first segment very short, last two very long, with third distinctly shorter than second, and third bearing a long tarsal claw but no paraungual seta.

Aedeagus long and slender, 0.54 mm. long x 0.15 mm. wide; exerted through the aperture formed by the exertion of the penial plate to the right, elevation of fifth tergite and depression of sixth sternite; bilaterally symmetrical, with a long internal sac on evagination; a free style, bearing a pair of apical setae, lengthily



inserted on the ventral face of the median lobe (basal bulb or basal capsule) on each side (Fig. 15, E).

Female sex unknown.

Described on one specimen, the male type, collected by W. B. Jones in September, 1937 in the McClunney Alabama Caverns, near Clay, JEFFERSON CO., ALABAMA.

To summarize this very important addition to the known pselaphid fauna of the world, it will be seen that the femoral articulations are brachysceline, and the aedeagus is that of the macrosceline tribes; the very long third segment of the maxillary palpi is of the Tychini, but the whole habitus is that of the Pselaphini. In fact, except for the maxillary palpi and brachysceline articulation, *Speleobama* would fit perfectly in Pselaphini both on general structural grounds as well as the aedeagus. The aedeageal structure is thought by the author to be of especial weight in considering evolutionary lines in the family. The macroscelines are thought of as being more specialized than the brachyscelines in general, e. g. less staphylinoid, and *Speleobamini* is thought of as an ancient tribe that bridges the gap in part between the contemporary Pselaphini and brachysceline aggregates.

On the other hand, the loss of eyes, wings and foveae are regarded collectively as the byproduct of the long millenia of evolution in the dark, moist, cool environment of the cave habitat.

#### *Tmesiphorus* (LeConte, 1850)

In the entire collection under report, only one epigeal species was represented. This was the widely dispersed and well known *Tmesiphorus costalis* LeConte.

Of this species two females were collected by W. B. Jones on June 11, 1938 in Terrell Cave, near Guntersville, MARSHALL CO. and one female was taken by Jones and Royer on September 13, 1947 in Lost Mule Cave, near Trinity, MORGAN CO., ALABAMA.

This was the only previously undescribed species in the collection. Its presence in two caves, collected some ten years apart suggests a relatively very recent and facultative penetration into the Alabama cave system.

This species is known to feed upon the larvae of its occasional host ant, *Aphaenogaster fulva* (Park, 1933). It inhabits the society of ants much less often than the dark, moist leaf and log mold of rich deciduous forests. The cavernicolous records further add to its known vagility.

The species is widely dispersed throughout eastern North America, and is known from a wide variety of counties in Alabama, Florida, Illinois, Indiana, Kansas, Kentucky, Mississippi, Pennsylvania and Tennessee, but always associated with rich, deciduous woodlands, either directly or in the nests of forest-inhabiting ants.

It is worth mentioning once more that the ecological conditions that are common to caves, ant nests and forest log mold are numerous.

#### KEY TO THE TRIBES OF THE WESTERN HEMISPHERE

The following key to the tribes, and in some instances, subtribes of Pselaphidae of the Western Hemisphere has become desirable in order to bring into alignment our knowledge of this area with current research on this family in other parts of the world. It is based in part on new data, and in part on Raffray (1908), Park (1942, 1947, 1949), and Jeannel (1949, 1950). It is not a global key.

#### *Subfamilies*

1. Tarsi apparently of two segments under ordinary dissecting binocular magnification (in reality of three segments, the first two minute and connate and the third very long when examined under oil immersion at 1000 diameters); body 0.75 mm.; eyes absent; metathoracic wings vestigial; habitat in deep soil

Tribe MAYETINI of Pselaphinae.

- Tarsi of three segments..... 2
- 2. (1) First two segments of tarsi very short, third segment very long relatively..... 3
- First segment of tarsi very short, last two segments very long relatively

PSELAPHINAE.

- 3. (2) Abdomen with at least five free tergites, the first four of which are margined on each side.

FARONINAE.

Abdomen with dorsal surface composed largely of a single disc formed by fusion of three tergites; myrmecophilous

CLAVIGERINAE.

SUBFAMILY FARONINAE (Jeannel, 1949)

- 1. Antennae eleven-segmented; maxillary palpi normal, of four segments which are distinct and unmodified

Tribe FARONINI (Raffray, 1890, reorganized by Jeannel, 1949).<sup>7</sup>

Antennae nine-segmented; maxillary palpi four-segmented, very complex, in repose contracted to form an arcuate mass within a palpal fossa of each gena

Tribe PYXIDICERINI (Raffray, 1903).<sup>8</sup>

SUBFAMILY CLAVIGERINAE (Redtenbacher, 1849 and reorganized by Jeannel, 1949)

- 1. Eyes absent; antennae of three segments (first not visible from above); body pubescence largely bifurcated; head longer than wide, subobconical

<sup>7</sup>*Megarafonus* (Oregon, Mexico), *Sonoma* (United States), *Caccoplectus* (Mexico and Guatemala), and *Golasa*, *Prosagola*, and *Salagosa* (Chile). See foot-note No. 6 in regard to a difference of opinion on segmentation of maxillary palpi.

<sup>8</sup>*Bythinoplectus* (Arizona, Mexico, South America, Antilles)

Tribe ADRANIINI new tribe.<sup>9</sup>

Eyes present; antennae of three segments; body pubescence simple

Tribe FUSTIGERINI (Jeannel, 1949).<sup>10</sup>

SUBFAMILY PSELAPHINAE (Redtenbacher, 1849)

Reorganized by Raffray, 1903-1904, 1908, Park, 1942, and Jeannel, 1949, 1950.

1. All trochanters short, with the femora inserted very obliquely on the trochanters, so that each femur is near its associated coxa

Division BRACHYSCELIA (Raffray, 1890).

Meso and metatrochanters long, more or less clubbed, femur articulated on the distal end of trochanter, so that each femur is distant from its associated coxa

Division MACROSCELIA (Raffray, 1890)

Division BRACHYSCELIA

1. Tarsi apparently of two segments (in reality of two minute and connate segments, and a long third segment when examined under oil immersion at 1000 diameters), body 0.75 mm. or less; eyes absent; metathoracic wings vestigial, habitat in deep soil

Tribe MAYETINI (Park, 1947).<sup>11</sup>

Tarsi of three segments, first small and last two relatively very long..... 2

<sup>9</sup>*Adranes* (United States).

<sup>10</sup>*Fustiger* (United States, Mexico, Antilles, Central America and South America); *Pseudofustiger* (Virgin Islands); *Neofustiger* (Argentina). The subfamily has been placed in a separate family by some authors, but as a subfamily of pselaphids by many others. This question has been discussed at length by Park (1942, p. 350-353); Jeannel (1949, p. 28) expresses the same view, and for much the same reasons, e. g., the clavigerids are true Pselaphidae in respect to basic morphology, and their divergence is a consequence of evolution that has been associated with their social parasitism.

<sup>11</sup>*Mayetia* (United States).

2. (1) Aedeagus with a long, free style on each side, the two styles inserted on ventral face of basal capsule; a conspicuous ruff of long setae enclosing a deep cervical constriction; eyes, metathoracic wings, vertexal foveae, pronotal foveae and elytral foveae wholly absent; cavernicolous

Tribe SPELEOBAMINI new tribe.<sup>12</sup>

Aedeagus with styles absent or if present usually inserted on or near the distal border of the basal capsule; other characters noted not in the same combination..... 3

3. (2) Mentum very wide, largely covering mouth and mouth-parts; cardo of each maxilla extended obliquely as a long projection

Tribe JUBININI (Raffray, 1903-1904).<sup>13</sup>

Mentum normally small; cardo not so extended..... 4

- 4 (3) Abdomen with a distinct margin on each side of the first three visible tergites, this margin varying from wide to narrow but present..... 12

Abdomen either with no margins at all, or with a weak margin at base of first tergite, or with sides of first three visible tergites bearing one or two entire or incomplete carinae ..... 5

5. (4) Antennae strongly geniculate

*Barrometopia* of METOPIINI.

Antennae not geniculate..... 6

- 6 (5) Tarsi bearing a pair of distinct, but unequally developed claws

<sup>12</sup>*Speleobama* (Alabama).

<sup>13</sup>Strictly American tribe: *Pselaphomorphus* (Argentina to Panama), *Macta* (Brazil), *Arctophysis* (Colombia), *Jubomorphus* (Venezuela), *Sebaga* (Brazil to Mexico), *Jubus* (Mexico, Central America, South America, Antilles), *Barrojuba* (Panama), *Balega* (Mexico, Antilles), *Phamismus* (Bolivia, Colombia, Mexico), *Stratus* (Panama, Mexico), *Endytocera* (Panama). Following the system advocated by Jeannel (1949), the Jubinini are sufficiently distinct to form a new section, the Jubomorphi.

- Tribe BATRISINI (Raffray, 1890)..... 7
- Tarsi bearing either one claw, or a claw and a fine unguis seta ..... 8
- 7 (6) Last two tarsal segments subequal in length; the tarsal claws strongly formed
- Subtribe BATRISINI *s. str.* (Raffray, 1890).<sup>14</sup>
- Second tarsal segment much longer than third; the tarsal claws much more unequally developed, with the second claw very small
- Subtribe AMAUROPSINI (Jeannel, 1948).<sup>15</sup>
8. (6) Maxillary palpi with third segment lenticular, the long axis vertical and bearing spongy pubescence on external face
- Bythinogaster* of BRACHYGLUTINI.
- Maxillary palpi not as described above..... 9
9. (8) Venter with only five fully visible sternites
- Globa* of BRACHYGLUTINI.
- Venter with six sternites fully visible
- Tribe TANYPLEURINI (Jeannel, 1949).....10
- 10 (9) Head with a narrow, longitudinal sulcus extending each side from antennal tubercle posteriorly above the eye
- Subtribe INIOCYPHINI new subtribe.<sup>16</sup>
- Head not as described.....11
11. (10) Each elytron with two to three antebasal foveae
- 

<sup>14</sup>*Arthmius* (North, Central and South America), *Syrbatus* (Brazil, Paraguay, Argentina), *Syrmocerus* (Brazil), *Oxarthrius* (Central and South America), *Iteticus* (Brazil, Bolivia), *Batoctenus* (Panama, Brazil, Bolivia), *Batrisodes* (numerous subgenera in United States and Canada), *Euphalepsus* (Mexico, Central and South America), *Phalepsoides* (Brazil).

<sup>15</sup>*Arianops* (two subgenera in United States).

<sup>16</sup>*Iniocyphus* (Brazil).

- Subtribe DALMODIINI new subtribe.<sup>17</sup>  
 Elytra without antebasal foveae  
 Subtribe TANYPLEURINI *s. str.* (Jeannel, 1949).<sup>18</sup>
12. (4) Venter with only five sternites completely visible.....13  
     Venter with six to seven sternites fully visible sternites..18
13. (12) Antennae strongly geniculate  
     Females of Tribe METOPIINI.  
     Antennae never geniculate.....14
14. (13) Maxillary palpi with third segment very long, almost as  
     long as fourth  
     Tribe TYCHINI (*sensu* Jeannel, 1940).<sup>19</sup>  
     Maxillary palpi with third segment not as described  
     Tribe BRACHYGLUTINI<sup>20</sup>.....15
- 15 (14) Ventral surface of head with either a median longitudinal  
     carina or a median fossa.....16  
     Ventral surface of head simple, lacking either of these  
     structures.  
     Subtribe EUPSENIINI new subtribe.<sup>21</sup>
16. (15) Ventral surface of head with a large, median, ovate fossa  
     Subtribe DECARTHONINI new subtribe.<sup>22</sup>

<sup>17</sup>*Dalmodes* (Brazil, Mexico), *Dalmonexus* (Panama), *Harmomima* (Bolivia), *Harmophola* (Brazil), *Harmophorus* (Brazil).

<sup>18</sup>*Bythinophysis* (Mexico, Guatemala, Venezuela, French Guiana, Guadeloupe), *Dalmomima* (Brazil), *Buris* (Mexico), *Dalmoburis* (Panama), *Batriphysis* (Panama), *Phybytharsis* (Panama), *Dalmophysis* (Mexico), *Anoplobraxis* (British Guiana), *Batrybraxis* (Mexico, Panama, Venezuela, Brazil).

<sup>19</sup>*Tychus* (America, north of Mexico), *Cylindrarctus* (America, north of Mexico).

<sup>20</sup>Brachyglutini *sensu* Raffray, 1908, Park, 1942; Bryaxini of Jeannel, 1949, 1950.

<sup>21</sup>*Eupsenius* (United States, Mexico, Colombia, Antilles), *Eupsenina* (Brazil, Paraguay, Panama.)

<sup>22</sup>*Decarthron* (North, Central and South America, Antilles), *Euteleia* (Mexico, Brazil), *Itamus* (Brazil).

- Ventral surface of head with a median, longitudinal carina .....17
- 17 (16) Posterior coxae absolutely contiguous  
 Subtribe BARADIINI new subtribe.<sup>23</sup>  
 Posterior coxae distant  
 Subtribe BRACHYGLUTINI s. str.<sup>24</sup>
18. (12) Tarsi with a pair of distinct claws.....19  
 Tarsi with either a single tarsal claw, or with a tarsal claw and an accessory unguial spine or seta set behind and obliquely to the claw.....20
- 19 (18) Tarsal claws long, of the same length but not of equal thickness; antennae not geniculate

*Valda* of Tribe BYTHININI.

Tarsal claws strong, unequally developed; antennae always geniculate

Males of Tribe METOPIINI (Raffray, 1904).<sup>25</sup>

<sup>23</sup>*Barada* (Venezuela).

<sup>24</sup>*Achillia* (Chile, Cuba), *Anchylarthron* (United States, Mexico), *Berdura* (Antilles, Panama), *Brachygluta* (United States), *Braxyda* (Bolivia), *Briaraxis* (Florida), *Bryaxina* (Brazil), *Bunoderus* (Mexico, Brazil), *Bythinogaster* (Hispaniola), *Caligocara* (Mexico), *Cryphorhinula* (Brazil, Venezuela, Guatemala, Mexico), *Dranisaxa* (Mexico), *Drasinus* (Mexico, British Honduras, Panama, Brazil), *Ectopocerus* (Chile), *Eremomus* (Brazil, Bolivia), *Eutrichites* (United States), *Globa* (Bolivia, Colombia, Venezuela), *Mitona* (Bolivia, Colombia, Venezuela, Mexico), *Nisaxis* (United States), *Nodulina* (Brazil, Dutch Guiana), *Panabachia* (Panama, Guatemala, Mexico), *Phoberus* (Bolivia), *Itamus* (Brazil), *Pselaptus* (United States, Mexico, Central America, South America, Antilles), *Raxybis* (Argentina), *Reichenbachia* (North, Central and South America, Antilles—the division of genus into genera on basis of number of elytral foveae by Jeannel, 1949 is not feasible for American fauna, as number found to vary within a species population by Park, 1945), *Rybaxis* (United States), *Scalenarthrus* (SW United States, Mexico, Central and South America, Antilles), *Strombopsis* (Brazil), *Xybarida* (Brazil, Panama, Mexico), *Xybaris* (Brazil, Panama).

<sup>25</sup>*Metopias* (South America, Panama), *Metopiellus* (Brazil, Argentina), *Metopiosoma* (Brazil, Argentina), *Metopioxys* (Argentina, Brazil, Colombia), *Barrometopia* (Panama).



20 (18) Maxillary palpi large and conspicuous, second segment elongate and distally swollen, third small, fourth very large, second and third segments often covered with tubercles; abdomen short, conical and contracted; in part cavernicolous

Tribe BYTHININI (*sensu* Jeannel, 1949).<sup>26</sup>

Maxillary palpi always small; not cavernicolous.....21

21. (20) Mesial portions of posterior coxae, *viz.* the area of articulation with trochanter, conically produced; abdomen elongate and subparallel; antennae geniculate or not

Tribe EUPLECTINI *s. lat.* (Park, 1942).....22

Mesial portions of posterior coxae noted broadly triangular or globular; abdomen short and conical; antennae always geniculate

Tribe GONIACERINI (Raffray, 1890).<sup>27</sup>

22. (21) Very broad head abruptly narrowed to a small, subcylindrical cervicum and this cervical peduncle closely invested by an exceptionally small apical lobe of prothorax; antennae always strongly geniculate.

Subtribe RHEXINI new subtribe.<sup>28</sup>

Head never articulated to a special prothoracic lobe in the manner described; antennae rarely slightly geniculate .....23

23. (22) Tarsi bearing a single strong claw and a distinct accessory claw or claw-like spine.....24

Tarsi bearing either a single claw, or a claw and a thin, short, accessory setiform bristle.....26

<sup>26</sup>*Bythinopsis* (United States), *Machaerites* (*Speleocheus*) (Alabama), *Machaerodes* (United States), *Pselaptrichus* (California), *Valda* (California).

<sup>27</sup>*Adrocerus* (Brazil), *Bibrax* (Panama), *Goniaceroides* (Paraguay), *Goniacerus* (Brazil, Venezuela, Panama), *Goniastes* (Brazil), *Listriophorus* (Mexico).

<sup>28</sup>*Rhexius* (United States, Mexico, Panama, Brazil).

24. (23) Head with semicircular front and straight occiput, this expanded surface so great that the large eyes are invisible from a dorsal view

Subtribe MITRACEPHALINI new subtribe.<sup>29</sup>

Head may or may not be laterally expanded but eyes visible from above if present.....25

25. (24) Head with front greatly modified, expanded as an elongate tubercle, or prolonged with parallel sides, or in the form of a long median spur; exclusively termitophilous

Subtribe PHTEGNOMINI new subtribe.<sup>30</sup>

Head not so modified

Subtribe TROGASTRINI (Jeannel, 1949).<sup>31</sup>

26. (23) Mesothoracic coxal cavities not confluent, distant to subcontiguous mesocoxae separated by processes of the mesosternum and metasternum

Subtribe PANAPHANTINI (Jeannel, 1950).<sup>32</sup>

Mesothoracic coxal cavities confluent, the mesocoxae contiguous or nearly so.....27

27. (26) Prosternum entirely bisected by a median, longitudinal carina

Subtribe BIBLOPORINI new subtribe.<sup>33</sup>

Prosternum not medianly carinate.....28

<sup>29</sup>*Mitracephala* (Brazil).

<sup>30</sup>*Phtegnomus* (Brazil, Venezuela).

<sup>31</sup>*Anarmodius* (Brazil, Venezuela), *Aporhexius* (Bolivia), *Eurhexius* (South and Central America), *Faronoma* (Chile), *Fletcherexius* (Mexico), *Oropus* (Pacific Coast of United States), *Rhexidius* (United States, Mexico), *Rhexinia* (Colombia, Guadeloupe), *Xherius* (Venezuela).

<sup>32</sup>*Acotebra* (Chile), *Thesium* (United States, Mexico, Guatemala, Panama, Brazil—this genus described in 1884 by Casey, and *Apothinus* described by Sharp in 1887 is a synonym), *Verabarolus* (Panama).

<sup>33</sup>*Biblomimus* (Antilles), *Bibloporus* (United States), *Eutyphlus* (United States), *Mexipectus* (Mexico), *Pteracmes* (Chili), *Pteroplectus* (Chili),

28. (27) Front prolonged into a conspicuous rostrum, with the antennae articulated at distal end of this structure, and the latter contiguous or nearly so

Subtribe RHINOSCEPSINI (Bowman, 1934).<sup>34</sup>

Front not so formed ..... 29

29. (28) Antennae with the last segment relatively very large, and forming the antennal club, this segment as long as the four preceding segments united or longer

Subtribe TRIMIINI (Bowman, 1934).<sup>35</sup>

Antennae with the club formed of the last three or four segments.

Subtribe EUPLECTINI *s. str.* (Raffray, 1890).<sup>36</sup>

#### Division MACROSCELIA

1. Tarsi with second segment bilobed, the third segment cylindrical and inserted between the lobes of the second

Tribe ARHYTODINI (Raffray, 1890).<sup>37</sup>

Tarsi with the second segment never bilobed..... 2

<sup>34</sup>*Rhinoscepsis* (Florida, Mexico, Dutch Guiana, Brazil, Argentina), *Morius* (California).

<sup>35</sup>*Actinoma* (Mexico), *Actium* (United States, Mexico, Chile), *Allotrimium* (Mexico), *Basolum* (United States), *Cupila* (Oregon, Mexico), *Dalmoplectus* (Brazil), *Dalmosella* (United States), *Melba* (North, Central, and South America—numerous subgenera, cf. Park, 1942, 1943), *Melbamima* (Brazil), *Neodalmus* (Venezuela), *Pseudotrimium* (Mexico), *Ramelbida* (Virgin Islands), *Simplona* (Arizona), *Trimiodina* (Guatemala), *Trimiomelba* (United States), *Trimiopsis* (Mexico, Guatemala, Panama, Colombia), *Trimiosella* (Virgin Islands).

<sup>36</sup>*Acolonia* (Florida), *Adrogaster* (Brazil), *Allobrox* (Mexico), *Barroeuplectoides* (Panama), *Biblopectus* (United States), *Euplectus* (United States, Mexico, Guatemala, Colombia, Venezuela, Antilles), *Lioplectus* (Argentina), *Oropodes* (United States), *Panaramecia* (Panama), *Ramecia* (United States), *Thesiastes* (United States, Dutch Guiana, Chile, Windward Islands), *Tomoplectus* (Mexico), *Trigonoplectus* (United States), *Trimiopectus* (United States).

<sup>37</sup>*Arhytodes* (Argentina, Bolivia, Brazil, Venezuela).

2. (1) Tarsi with a single large claw, no accessory claw or unguiform seta present  
 Tribe PSELAPHINI (Raffray, 1890, Jeannel, 1951).<sup>38</sup>  
 Tarsi with a pair of claws, large or small, equal or very unequal..... 3
3. (2) Tarsi with a pair of large, obviously equal to subequal tarsal claws..... 4  
 Tribe PHALEPSINI (Jeannel, 1949).<sup>39</sup>  
 Tarsi with the claws short and very unequal, one claw and a claw-like accessory seta
4. (3) Maxillary palpi penicillate, *viz.*, external face of one or more segments bearing a bundle of projecting setae, or a distinct lateral lobe..... 5  
 Maxillary palpi variously modified but never penicillate as noted..... 6
5. (4) Clypeus laterally dilated; general body pubescence of scales or squamiform setae  
 Tribe CTENISTINI (Raffray, 1890).<sup>40</sup>  
 Clypeus not laterally dilated; general body pubescence of setae  
 Tribe TMESIPHORINI (Jeannel, 1949).<sup>41</sup>
6. (4) Pronotum always with one to three antebasal foveae; elytra usually with basal foveae; maxillary palpi usually large and conspicuous..... 7  
 Pronotum and elytra without foveae; maxillary palpi minute; known so far only from nests of leaf-cutting ants  
 Tribe ATTAPSENINI (Bruch, 1933).<sup>42</sup>

<sup>38</sup>*Pselaphus* (United States, Canada), *Neopselaphus* (Brazil, Dutch Guiana), *Pselaphellus* (Mexico, Guatemala, Brazil, Argentina).

<sup>39</sup>*Phalepsus* (Brazil, Paraguay, Mexico).

<sup>40</sup>*Anitra* (Arizona), *Atinus* (United States), *Biotus* (California), *Ctenisis* (Arizona, Mexico, Guatemala, Colombia, Brazil, Argentina), *Ctenisodes* (Mexico), *Pilopius* (United States, Mexico).

<sup>41</sup>*Tmesiphorus* (Eastern half of United States).

7. (6) Pubescence complex; tempora, genae and ocular areas with squamous setae; antennae densely pubescent, articulations obscured; general body pubescence dense, formed of appressed thick-shafted setae

Tribe ODONTALGINI (Jeannel, 1949).<sup>43</sup>

General body pubescence of simple setae..... 8

8. (7) Antennae lacking any semblance of a club, moniliform; always myrmecophilous

Tribe CEOPHYLLINI new tribe.<sup>44</sup>

Antennae always with a distinct club..... 9

9. (8) Maxillary palpi of various forms, but the internal face of fourth segment never sulcate

Tribe TYRINI (Raffray, 1890, reorganized by

Jeannel, 1949, 1950).<sup>45</sup>

Maxillary palpi with the internal face of the fourth segment longitudinally sulcate, this sulcus broad to narrow and entire or short

Tribe HAMOTINI new tribe.<sup>46</sup>

<sup>42</sup>*Attapsenius* (Argentina, Brazil).

<sup>43</sup>*Ephimia* (Pearl Islands, Virgin Islands, Windward Islands), *Juxtahamotopsis* (Panama).

<sup>44</sup>*Ceophyllus* (Eastern half of United States).

<sup>45</sup>*Cedius* (Eastern half of United States), *Lethenomus* (Chile), *Tyrus* (United States), *Neotyrus* (Brazil, Argentina, Panama), *Tyroгатunus* (Panama), *Tyropsis* (Brazil, Chile).

<sup>46</sup>*Hamotus* (Florida, Mexico, Central and South America, Windward Islands), *Cercocerus* (Eastern half of United States), *Pseudohamotus* (Brazil, Panama, Guatemala), *Aploderina* (Bolivia), *Hamotocellus* (Brazil), *Phamisulus* (Brazil), *Apharus* (Brazil, Colombia, Venezuela), *Cercocerulus* (Brazil), *Pselaphocompsus* (Brazil), *Cercoceropsis* (Brazil, Paraguay), *Cercoceroides* (Brazil, Paraguay, Venezuela).

### GENERAL DISCUSSION OF AMERICAN CAVERNICOLOUS PSELAPHIDAE

It is the purpose of this last section to bring together the available data on this recently discovered fauna and its habitat and attempt a partial synthesis.

Although the several points of view and bodies of information are in reality inextricably related and mutually supportive, it is convenient to discuss the problem under three general topics, namely, general ecology, zoogeography and evolution.

In the first place, the cave community is one of the more remarkable ecological entities. It is a natural community, clearly defined, and with a distinctive fauna (cf. Allee, Emerson, Park, Park and Schmidt, 1949 for literature). In certain ways this community is unique. Chlorophyll-bearing plants do not grow in caves and consequently natural cave herbivores are absent. The absence of green plants and herbivores is novel among other major communities. Therefore, there is no normal base to the food supply of the community and the animals tend to be either (1) predators, (2) saprophagous, or a combination of these two feeding types. This means that caves must obtain their energy input from epigeal sources, e. g., chiefly periodic floods (Hawes, 1939; Park, Roberts, and Harris, 1941), and in special instances from bat dung.

It is remarkable that pselaphid beetles have not been reported previously from American cave systems. For example, Mammoth Cave, Kentucky has a large and relatively well-known fauna (Park, Allee, and Shelford, 1939, pp. 117-126) but no pselaphids are known from this large limestone cavern. As opposed to this there is the remarkable pselaphid fauna reported here from limestone caves in Alabama and Tennessee.

The general ecology of epigeal pselaphids is such that the family should not have undue difficulty in penetrating the cave environment, adjusting to it and maintaining their ecological position in the cave community. In general (Park, 1947a) these beetles are nocturnal and predaceous. Their normal food includes oribatoid and parasitoid mites, small worms, and small insects and their larvae. All of these food items are often present in the

cave habitat; even if they were not, it is not impossible to imagine that the evolution of cave pselaphids might be accompanied by a change of food habits, at least to a combination of predatism and saprophagous habits.

Natural selection could operate upon food habits as easily as upon other biological demands. These latter include adjustment to the physical environment. Again, pselaphids are naturally fitted, at least in part, for cave existence. Their natural nocturnalism is supported by laboratory observations, e. g., under controlled conditions the few species so far tested, including several species of *Batrisodes*, select the dark end of a light intensity gradient and the moist end of a moisture gradient. This suggests that the cave habitat would be ecologically possible both from the standpoint of physical and biological requirements.

Exact data on the natural enemies of pselaphids are scanty. Red-backed salamanders (*Plethodon cinereus*) are known to feed on three genera of pselaphids (Park, 1947; Park and Edgren, 1950) and ectoparasitic mites of the families Parasitidae and Uropodidae have been found on *Euplectus confluens*. No ectoparasitic mites were found on the cave pselaphids. In caves pselaphids might be attacked by cave-cricket and pseudanophthalmids. Two species of *Pseudanophthalmus* have been taken from the gut of the Mammoth cave-cricket (*Hadenoeus subterraneus*), and the cave food-chain may include the small cave arthropods.<sup>47</sup>

Practically nothing is known regarding the life cycle of pselaphid beetles. This is strange in a family of some 5000 species, and it may be that some species are parasitic in the larval stage (Park, 1947a), or that some species are ovoviviparous. Copulation has been observed, but eggs, larval life, pupation are unknown. Some three larvae have been described and a cast pupal skin observed, but no more data have accumulated. These matters have been summarized previously (Park, 1942, 1947a; Jeanne, 1949).

<sup>47</sup>Park, Orlando, Nelson Hairston and Eliot Williams. Studies in Community Structure: Mammoth Cave, Kentucky. *In preparation*.

At present the collecting dates for callows, *viz.*, very recently pupated specimens of pale yellow tint and with an imperfectly sclerotized cuticle, afford a suggestion as to when pupation took place. The data on callows is given in the accompanying Table I.

TABLE I  
CALLOWS IN CAVERNICOLOUS PSELAPHIDAE

Genus	Species	No.	Date Collected	Locality
<i>Batrisodes</i>	<i>spelaeus</i>	2	September 27, 1939	McGlendon Cave St. Clair, Alabama
	<i>troglydytes</i>	1	November 10, 1946	Rock Cave, Butler Co., Alabama
	<i>jonesi</i>	3	September 26, 1940	
	<i>valentinei</i>	3	October 8, 1939	Toll Gate Natural Well, Madison Co., Alabama
	<i>specus</i>	1	October 9, 1939	Cave Spring Cave, Madison Co., Alabama
		1	January 3, 1942	Twin Cave, Madison Co., Alabama
		2	January 3, 1942	Hutton Cave, Madison Co., Alabama
		1	March 15, 1931	Huntsville Spring Cave, Madison Co., Alabama
		1	May 25, 1934	Indian Cave Jefferson Co., Tennessee
<i>Bythinopsis</i>	<i>jonesi</i>	1	September 25, 1940	Wolf Den Cave Colbert Co., Alabama
<i>Machaerites</i>	<i>stygicus</i>	1	October 8, 1939	Cave Spring Cave, Madison Co., Alabama
	<i>ferus</i>	1	January 3, 1942	Hutton Cave, Madison Co., Alabama



If we assume that the elapsed time for sclerotization of the cuticula, that is, the callow period, is not appreciably different for epigeal and hypogean species, then the data in Table I are suggestive of several alternative views.

It is possible that each species has its own callow period, and that within a genus the species tend to have a more or less similar callow period. Admittedly, there are far too few callow records for positive statements, but with latitude in mind it is of interest to note that the great bulk of the records fall in two periods: out of eighteen specimens, eleven or 61% are in the period September 25 to October 9, and four or 22% are in the period January 3. In addition, one is in middle November, one in middle March, and one in the end of May.

Lumping these records in this way suggests that the majority of the species are pupating in the autumn. But with a constant cave environment, with light absent and temperatures and moisture relatively constant in the larger and deeper caverns, this seasonal event must be a carry-over from the ancestral breeding periodicity—unless periodic vernal floods, with their influx of food supplies and water, tend to act as seasonal activators in the cave community.

It may be that several species can not be lumped in this way, and that each species must be examined separately. If this is so, then the only species with more than one callow date is *Batrisodes specus* and this has a broad period of callow production, from January 3 to May 25 over a period of years.

Assuming that the years between 1931 and 1942 were more or less the same in so far as the cave habitat is concerned, and there is no justification for this, then there is too much seasonal spread for a one-generation-per-annum hypothesis for this species.

This interesting problem may not be solved with the information at hand. First, it is possible that the cavernicolous pselaphids have one generation per annum, but through long periods of time below ground each cave occupied by the species as a whole tends to develop its own cave breeding population, and

hence the several cave populations would gradually become "seasonally" isolated. This might tend to foster subspeciation at first, and speciation eventually.

Second, it is possible that some of the species at least have two generations per annum, and the relatively constant cave environment might eventually account for a broader period of callow production in each generation so that some overlap may develop. Of course, the point made above, that isolation in caves of intraspecies breeding populations would tend to foster subspeciation could apply in a two generation per annum species as well.

Third, it is possible that through time all breeding periodicity has been lost and that copulation may occur much more frequently.

Natural darkness of the caves would tend to place emphasis on sensory functions other than compound eyes. This general point would apply to finding a mate, as well as obtaining food and escaping from enemies. Here again pselaphids are suited for cave penetration. The pselaphid eye has relatively few facets as compared with many other groups of insects, and in the cave species under examination there was a general reduction of these organs. For example, *Batrisodes* showed a general reduction both in eye size and facet number in the females of the nine species examined; *Arianops* lacks eyes in both epigean and hypogean species; *Speleochus* and *Spelobama* lack eyes. On the other hand, the facultative cave dweller, *Tmesiphosus costalis* showed no reduction in facet number from the abundant epigean fauna of this species.

Probably sensory functions most important to cave pselaphids are tactility and order perception. In unpublished experiments on the role of antennae in order perception,<sup>48</sup> it was found that in species of the genus *Cedius* the distal antennal segment was of chief importance. In this connection, it is worth noting that it is this distal segment that bears the remarkable antennal cones

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<sup>48</sup>Park, Orlando and Glenna Corley. Behavior of Myrmecophilous Beetles of the Genus *Cedius*. In preparation. Abstract in Bull. Ecol. Soc. America, 1949, vol. 30, No. 2, p. 52.

(Park, 1935, 1942). These diverse structures were present in the cave species, where examination on slides at high magnification was feasible, and these cones may subservise the tactile function in the family.

Turning to broader, zoogeographic speculations, it is fitting that a complete list of the fauna be presented. This is set forth in Table II.

TABLE II

CONSPECTUS OF AMERICAN CAVERNICOLOUS PSELAPHIDAE

Tribe Batrisini (*sensu* Raffray, 1904, 1908, 1911)

Subtribe Batrisini (Tribe Batrisini, *sensu* Jeannel, 1950)

Genus *Batrisodes* (*sensu* Raffray, 1904, 1908, 1911; Park, 1947, 1948)

Subgenus *Batriasymmodes* new subgenus

*spelaeus* new species

*quisnamus* new species

*jeanneli* new species

*troglydites* new species

Subgenus *Excavodes* new subgenus

*cavernosus* new species

Subgenus *Babnormodes* new subgenus

*jonesi* new species

*subterraneus* new species

*valentinei* new species

*specus* new species

Subtribe Amauropsini (Tribe Amauropsini, *sensu* Jeannel, 1950)

Genus *Arianops* (Brendel, 1893)

Subgenus *Arispeleops* new subgenus

*cavernensis* new species

Tribe Bythinini (*sensu* Jeannel, 1950)

Subtribe Machaeritina (Jeannel, 1950)

Genus *Bythinopsis* (*sensu* Jeannel, 1950)

*jonesi* new species

Genus *Machaerites* (*sensu* Jeannel, 1950)

Subgenus *Speleochus* new subgenus

*stygicus* new species

*ferus* new species

Tribe Speleobamini new tribe

Genus *Speleobama* new genus

*vana* new species

Tribe Tmesiphorini (Jeannel, 1949)

Genus *Tmesiphorus* (LeConte, 1850)

*costalis* LeConte (1850)

The general area of known dispersal is given in Fig. 16. Although the north-south distance is about 512 miles, in reality the cavernicolous species are separable into two relatively isolated areas. *Batrisodes troglodytes* and *Batrisodes cavernosus* are known from separate caves in Butler County; all of the others are known from caves in north-central Alabama and scattered localities in eastern Tennessee.

The Butler County caves are in the Clayton Formation. This is white limestone and white to red micaceous sand. The formation is relatively recent, of Eocene age.

The northern area, with the great bulk of the cavernicolous species, contains numerous caves in very much older strata. In Alabama these are primarily limestone of Carboniferous age: Fort Payne chert on the north-east in a narrow belt, followed southward by Tuscumbia limestone through the northern half of Colbert County eastward into Madison and parts of Jackson Counties; then an irregular fringe of the Gasper Formation formed of Bethel Sandstone and Ste. Genevieve Limestone; southward in a broad north-east to southwest lobe lies the Pottsville Formation which is shot on the east by diagonals of still older strata, e. g., Cambrian dolomites, limestones and sandstones.

This brief summary of the geological features is made because, although there is no correlation between the age of a cave-bearing stratum and the length of time an animal may have existed in such caves, it seems clear that the cavernicolous pselaphids are now living in caves of greatly differing ages. If we assume that the rate of cave formation has been about the same between the Eocene limestone and Carboniferous limestones, then there would have been a much more extensive series of caves in the northern area ready for penetration by epigeal stocks. On the basis of present data, the southern area (Butler County) appears to be very isolated from the northern area. Undoubtedly there is no subterranean connection between these two areas, whereas there may be many subterranean connections between the numerous caves in northern Alabama and Tennessee.

Such connections, when they can be demonstrated, are of great zoogeographic importance since they would form avenues of dispersal through time.

Of the 58 caves reported upon here, 52 were in Alabama and six in Tennessee. These caves were in large majority in limestone; a very few were in sandstone and limestone (Royer Cave, Barrel Cave, Ladder Cave, all in Morgan County), or sandstone (Lott Cave, Madison County).

Of the total caves discovered (157 in Alabama and 10 in Tennessee), 58 caves or 34% harbored pselaphids and the percentage is probably higher. This is a high proportion of caves to be penetrated and it is to be hoped that the systematic investigation of this cave system is just starting. Of particular interest would be (a) exploration to locate and study other caves in the Clayton Formation that stretches across southern Alabama in a narrow belt passing through Butler County and (b) location and study of caves in eastern Tennessee.

The first of these two desiderata should result in the discovery of new species allied either to *Batrosodes troglodytes* or *Batrisodes cavernosus*, as well as other genera perchance. The second is greatly to be desired from the point of subspeciation.

Of the fourteen new species of cavernicoles described here, eleven occupy relatively compact areas of one to eight caves in one to two contiguous counties. Where more than one cave is involved in the known range, it is probable that small to large connections exist, or existed in the past, between these caves.

The other three species belong to the genus *Batrisodes*, and *spelaeus*, *specus*, and *valentinei* have ranges from the extreme northern or central Tennessee to northern Alabama, with a relatively great gap of limestone strata from which cavernicolous pselaphids have not been reported. One would think that in these three populations subspeciation might be a possibility, and there are some indications that this has taken place in the material available. Such an analysis was not made for the present, as they are too few specimens from critical areas to attempt a study of morphological intergradation.

Some interesting features are discoverable from an examination of the Alabama caves where size is reported. Forty-one caves of the 58 that harbored pselaphids had an average length of 490 feet, with a maximum of 5000 feet and a minimum of seven

feet; the average height was 21 feet, with a maximum of 150 feet and a minimum of three feet. These caves were usually in limestone, were neither excessively wet nor excessively dry, and ranged from Manitou Cave, DeKalb County (5000 x 20) to Cave Spring Cave, Madison County (65 x 4). Manitou Cave yielded one *Batrissodes spelaeus*, whereas Cave Spring Cave yielded two specimens of *Batrissodes specus* and two specimens of *Speleochus stygicus*.

The average number of pselaphids collected was five individuals per cave so that the largest cave was much below and the smallest cave near the average yield. This may be coincidence or unequal collecting time. On the other hand it may suggest that the ecological conditions of the microhabitat are the important determining influences in regulating the interspecies and intraspecies population densities.

Five caves gave relatively heavy yields. These are McGlen-don Cave, St. Clair County (20 specimens); Gallymore Cave, Colbert County (14); Hutton Cave, Madison County (18); Goat Cave, Madison County (43); Echols Cave, Morgan County (18).

The 52 Alabama caves that harbored pselaphids had an unequal county distribution: Blount (3 caves), Butler (2), Colbert (8), DeKalb (1), Jackson (3), Jefferson (1), Lauderdale (1), Lawrence (3), Madison (16), Marshall (5), and Morgan (8). The last three counties contained more than half of these caverns.

The cave temperature is usually more medial than extra-cave temperature, being warmer in winter and cooler in summer, and is relatively constant, this degree of constancy depending upon the size of the cave and its amount of communication with the surface and its subterranean depth. This is a more or less general rule. Some data are available on Alabama caves. Where air temperatures were reported, there was a variation of fourteen degrees Fahrenheit between six caves, e. g., Rock Cave, Butler County (46.4°); Moon Cave, Madison County (47°); Twin Cave, Madison County (48°); Sublett Cave, Madison County (50°); Wolf Den Cave, Colbert County (56°); Dickey Cave, Colbert County (61°). If these represent relatively constant cave tem-

peratures, at least in respect to cave relative to cave, then such a differential in temperature may act as a selective factor through time, or the difference from one extreme to another may not be of sufficient magnitude to be of operational importance.

With this general background in mind, the question of faunal affinities of these cavernicoles may be studied. The pertinent information is summarized in Table III.

TABLE III  
 ZOOGEOGRAPHIC AFFINITIES OF AMERICAN CAVERNICOLOUS  
 PSELAPHIDAE

Cavernicolous species	Range	Nearest living ally (?)	Range of ally
<i>Batrisodes</i>			
<i>spelaeus</i> n. sp.	NE Tenn. to N. Ala.	<i>cavicus</i> (Casey)	Black Mts., N. C.
<i>quisnamus</i> n. sp.	Pickett Co., Tenn.	<i>spelaeus</i> n. sp.	
<i>jcanneli</i> n. sp.	N. Tenn.	<i>monstrous</i> (LeConte) (myrmecophile)	N. Y. to Ga., west to Ill.
<i>trogodytes</i> n. sp.	Butler Co., Ala.	<i>carolinae</i> (Casey)	Black Mts., N. C.
<i>cavernosus</i> n. sp.	Butler Co., Ala.	<i>beyeri</i> Schaeffer	Black Mts., N. C.
<i>specus</i> n. sp.	NE. Tenn. to N. Ala.	<i>cavicornis</i> Casey & <i>foveicornis</i> (Casey)	SW. Penna. to Ky. and S. Ill. Tenn. and Ky.
<i>jonesi</i> n. sp.	Colbert Co., Ala.	<i>specus</i> n. sp.	
<i>valentinei</i> n. sp.	S. Tenn. to N. Ala.	<i>appalachianus</i> Casey & <i>schaefferi</i> Park	SW. Penna. Black Mts., N. C.
<i>subterraneus</i> n. sp.	Marshall Co., Ala.	<i>valentinei</i> n. sp.	
<i>Arianops</i>			
<i>cavernensis</i> n. sp.	Marshall Co., Ala.	<i>plectrops</i> Casey	Black Mts., N. C.



<i>Bythinopsis</i> <i>jonesi</i> n. sp.	Colbert Co., Ala.	<i>carolinae</i> (Casey)	Black Mts., N. C.
<i>Machaerites</i> <i>stygicus</i> n. sp.	Madison Co., Ala.	<i>subterraneus</i> (Mots.)	Carniola, Europe
<i>ferus</i> n. sp.	Madison and Jackson Co., Ala.	<i>stygicus</i> n. sp.	
<i>Speleobama</i> <i>vana</i> n. sp.	Jefferson Co., Ala.	contemporary Pselaphini?	Holarctic ?
<i>Tmesiphorus</i> <i>costalis</i> LeConte	Caves of N. Ala.	Epigeal population of the species throughout eastern United States	

Examination of Table III brings out a singularly consistent thesis—one, it should be noted, that was arrived at long after the species descriptions were completed. The cavernicolous pselaphids of Alabama and Tennessee have their closest contemporary allies either (a) within the hypogean fauna, or (b) in the epigeal fauna of the southern Appalachians.

This suggests that the ancient Appalachian system, extending from the St. Lawrence River valley near Quebec some 1,500 miles south-westward to the Gulf Coast plain in Alabama has fostered the pselaphid fauna of eastern North America and, more especially has in the remote past been an evolutionary center for the cavernicoles of the genera *Batrisodes*, *Arianops*, and *Bythinopsis*. These three genera contain eleven out of fourteen cavernicoles.

Three of these eleven species, on the basis of structure, appear to have been secondarily derived from cave species: *Batrisodes quisnamus* from *B. spelaeus*; *B. subterraneus* from *B. valentinei*; *B. jonesi* from *B. specus*. The remaining eight species have structurally closest allies in the extreme southern part of this mountain system, e. g., Black Mountains westward to the Cumberland Plateau.

The remaining two genera, containing three species, do not follow this thesis. They belong to much older stocks, assuming that the evolutionary rate has been more or less the same for pselaphids. There is no justification for this assumption. At least, we can say that these two genera have no allies in North America known so far. *Machaerites* is a palaeartic genus, with numerous species in southern Europe, primarily in caves from the Balkans to Spain. The two American species belong to a strictly American subgenus, *Speleochus*, and appear to be most closely allied to *Machaerites subterraneus* of Carniola.

The other genus, *Speleobama*, is without any close allies in the known world fauna. It will be remembered that this genus represents a new tribe, with morphological features that bridge the gap between the two great divisions of the subfamily Pselaphinae. It is unique, and its presence in a cave suggests great age of the stock. It is distantly allied to the holarctic Pselaphini.

Another notable feature of this southern cave fauna is the general tendency for species within a given genus to occupy separate caves, or separate cave systems. *Arianops*, *Bythinopsis*, and *Speleobama*, with one species each, occupy three widely separated caves from which no other pselaphids are reported. *Machaerites*, with two species, has no overlap between the two populations, although eleven of the thirteen caves occupied by the genus are in Madison County, and many of them presumably may be connected by subterranean passages.

Within the large genus *Batrisodes*, with nine cavernicolous species divided between three subgenera, this principle is especially evident. For example, *quisnamus* occupies one cave in Tennessee; *spelaeus* two caves in Tennessee and seventeen caves in Alabama; *trogloodytes* one cave in Alabama; *jeanneli* two Tennessee caves; *cavernosus* one Alabama cave; *subterraneus* one Alabama cave; *jonesi* seven Alabama caves; *specus* one Tennessee cave and eight Alabama caves; *valentinei* one Tennessee cave and five Alabama caves. These nine species, with a collected sample of 286 specimens, have been collected from 46 caves. In only one instance were two species taken in the same cave! This latter case was in Indian Cave, near New Market, Jefferson County, Tennessee in which *Batrisodes spelaeus* and *Batrisodes specus* occurred. It should be pointed out that these are not closely related species; the reverse is true, they belong to widely separated subgenera as the previous taxonomic section demonstrates.

On the other hand, pselaphid genera may occupy the same cave. For example, *Machaerites stygicus* is confined to Madison County, Alabama where it occupies seven caves; of these seven, four are also occupied by *Batrisodes specus* and two other caves are occupied by *Batrisodes valentinei*. In other words *stygicus* was found alone in only one out of seven caves that are known to harbor this species.

The same pattern is found for the other species of this genus. *Machaerites ferus* is known from two caves in Jackson County and three caves in Madison County; of these five caves, one also contained *Batrisodes specus*.

Finally, the epigeal *Tmesiphorus costalis* with an apparent cavernicolous tendency was found in two caves; one of these also held *Batrisodes specus* and the other cave contained *Batrisodes spelaeus*.

The genus *Batrisodes* is the dominant genus in the cave system under discussion and has been discussed in detail in previous pages. The largest subgenus, *Babnormodes*, has been studied sufficiently to discuss its hypothetical evolution. Some of the data to be used are assembled in Table IV.

TABLE IV  
ASSAY OF BATRISODES (BABNORMODES) BASED ON MALE  
SECONDARY SEX CHARACTERS

Species	Face transversely excavated	Clypeus tuberculated	Antennal segment IX abnormal	Antennal segment X excavated or foveate	Antennal segment XI excavated	Antennal segment XI spined	Score
Epigeal Populations							
<i>antennatus</i> .....	+	0	+	+	+	0	4.0
<i>appalachianus</i> .....	+	+	0	0	0	0	2.0
<i>cavicornis</i> .....	$\frac{1}{2}$	0	0	+	+	0	2.5
<i>foveicornis</i> .....	$\frac{1}{2}$	0	0	+	$\frac{1}{2}$	0	2.0
<i>hairstoni</i> .....	+	$\frac{1}{2}$	0	+	$\frac{1}{2}$	$\frac{1}{2}$	3.5
<i>punctifrons</i> .....	+	+	0	0	0	0	2.0
<i>riparius</i> .....	+	0	+	+	0	+	4.0
<i>rossi</i> .....	+	0	0	+	0	0	2.0
<i>schaefferi</i> .....	+	+	0	+	0	0	3.0
<i>spretus</i> .....	+	0	0	+	0	0	2.0
<i>uncicornis</i> .....	+	0	0	+	0	+	3.0
Hypogean Populations							
<i>jonesi</i> .....	0	+	0	+	0	0	2.0
<i>specus</i> .....	0	0	+	+	0	0	2.0
<i>subterraneus</i> .....	0	0	+	0	0	0	1.0
<i>valentinei</i> .....	0	0	0	0	0	0	0.0
Subgenus average .....							2.3
Hypogean average .....							0.3

In Table IV six different secondary sex characters of the males of the fifteen species populations of the subgenus *Babnormodes* are tabulated and scored. It will be seen that the subgenus average score is 2.3 whereas the subterranean populations have a greatly reduced average of these features at 0.33. The subgenus is American, occupying the deciduous forest biome of eastern United States. It is the largest subgenus of *Batrisodes* in America and the ancestral home of these several stocks is thought of as the south and central Appalachian system, e. g., Sassafras Mts., Black Mts., Smoky Mts., Blue Ridge Mts., Allegheny Mts.

The tabular data has been combined with comparative detail of the aedeagus to give a hypothetical pattern of evolution (Fig. 17). The distribution of the cavernicolous species of the entire genus *Batrisodes* (representing three subgenera) is given in Fig. 18, so far as reported.

The entire cavernicolous pselaphid fauna of Alabama and Tennessee is old. The limestone strata, in which most of the caves are located, is ancient: Eocene in the Butler County caves and Carboniferous or older in the northern Alabama cave system. We do not know how long a time was required for the caves to form. Probably a great many years with change in the water table, and the erosion and dissolution of the limestone by seepage and subterranean water currents. Probably the caves formed at rates varying through time and became open to colonization from above at varying periods. Undoubtedly the several pselaphid aggregates penetrated caves very slowly and, if the external anatomy is any guide to the length of evolution, some groups have been cavernicolous for a much greater time than others.

Based on the amount of structural modification of the cavernicoles as contrasted with allied epigeal genera and species, a speculative order of cave colonization may be given; *Speleobama* very early, followed much later by *Machaerites* at a time in the earth's history when this genus was represented by epigeal stock in what is now the United States; *Arianops* and *Batrisodes* (*Batrisymmodes*) may have come in still later; the subgenera *Babnormodes* and *Excavodes* of *Batrisodes* still more recently; *Bythinopsis* appears to be less modified from contemporary

species living an epigean existence; *Tmesiphorus* is not a cavernicolous genus, as yet, and *costalis* is probably at the threshold of facultative cave occupation.

In concluding this study, it is suitable that the pselaphid fauna of eastern North America as a whole should be examined briefly with respect to its several major components.

1. The overwhelming majority of species inhabit the rich deciduous forests, presumably the ancestral habitat type of the family (Park, 1947, 1947a). This component was thought to be populated from the wooded slopes of the ancient Appalachian system.

2. The cavernicolous component of fourteen known species. This may be subdivided roughly into (a) the majority derived from epigean stocks, representatives of which now exist in the southern Appalachians; (b) an ancient component (*Machaerites* and *Speleobama*) without allies in the contemporary American fauna.

3. A northern component, of species that now exist through the northern United States and southern Canada but remain as far south as northern Illinois and southwestern Michigan as glacial relicts in the floating mat of bogs. It is thought that these species, such as *Reichenbachia borealis* and *Reichenbachia corporalis*, moved southward in front of the advancing Wisconsin Glacier, and now maintain a scattered distribution along the limits of penetration of the last ice sheet.

4. A western component, of species that moved eastward with the Prairie Peninsula following the retreat of the Wisconsin Glacier. This grassland contingent (Park, Auerbach and Wilson, 1949), including *Reichenbachia subsimilis*, exists now in meadows and modified prairie often surrounded by the encroaching forest and vacant lots.

5. A southern component from the Neotropical Region (Park, 1942). This includes such genera as *Hamotus*, *Eupsenius*, *Arthmius*, and *Decarthron*.

### ABSTRACT

There are three sections in the paper. The first is a taxonomic examination of 315 pselaphid beetles collected from 58 caves in 19 counties of Alabama and Tennessee. These specimens represented a new North American cave fauna, comprising 4 tribes, 6 genera, and 15 species, as follows: Batrisini, genus *Batrisodes spelaeus* n. sp., *B. quisnamus* n. sp., *jeanneli* n. sp., *trogloodytes* n. sp. in new subgenus *Batriasymmodes*; *B. cavernosus* n. sp. in new subgenus *Excavodes*; *B. jonesi* n. sp., *B. subterraneus* n. sp., *B. vaentinei* n. sp., *B. specus* n. sp. in new subgenus *Babnormodes*; genus *Arianops*, new subgenus *Arispeleops*, *cavernensis* n. sp. Bythinini, genus *Machaerites*, new subgenus *Speleochus*, *M. stygicus* n. sp., and *M. ferus* n. sp.; *Bythinopsis jonesi* n. sp.; Speleobamini new tribe, *Speleobama* new genus, *S.vana* n. sp.; Tmesiphorini, genus *Tmesiphorus costalis* LeConte.

Of especial interest is *Speleochus* with no American allies but allied to other *Machaerites* of Carniola, and Speleobamini with no contemporary allies and combining features of the two great divisions of modern Pselaphinae.

Second section is a key to the tribes and subtribes of the Western Hemisphere in which the following are new: Adraniini, Speleobamini, Iniocyphini, Dalmodini, Eupseniini, Decarthronini, Baradiini, Rhexini, Mitracephalini, Phtegnomini, Bibloporini, Ceophyllini and Hamotini. The generic composition of each tribe and subtribe in the Western Hemisphere is given.

Third section is a general discussion of the American cavernicolous pselaphid fauna, organized under three chief topics of general ecology, zoogeography, and evolution.

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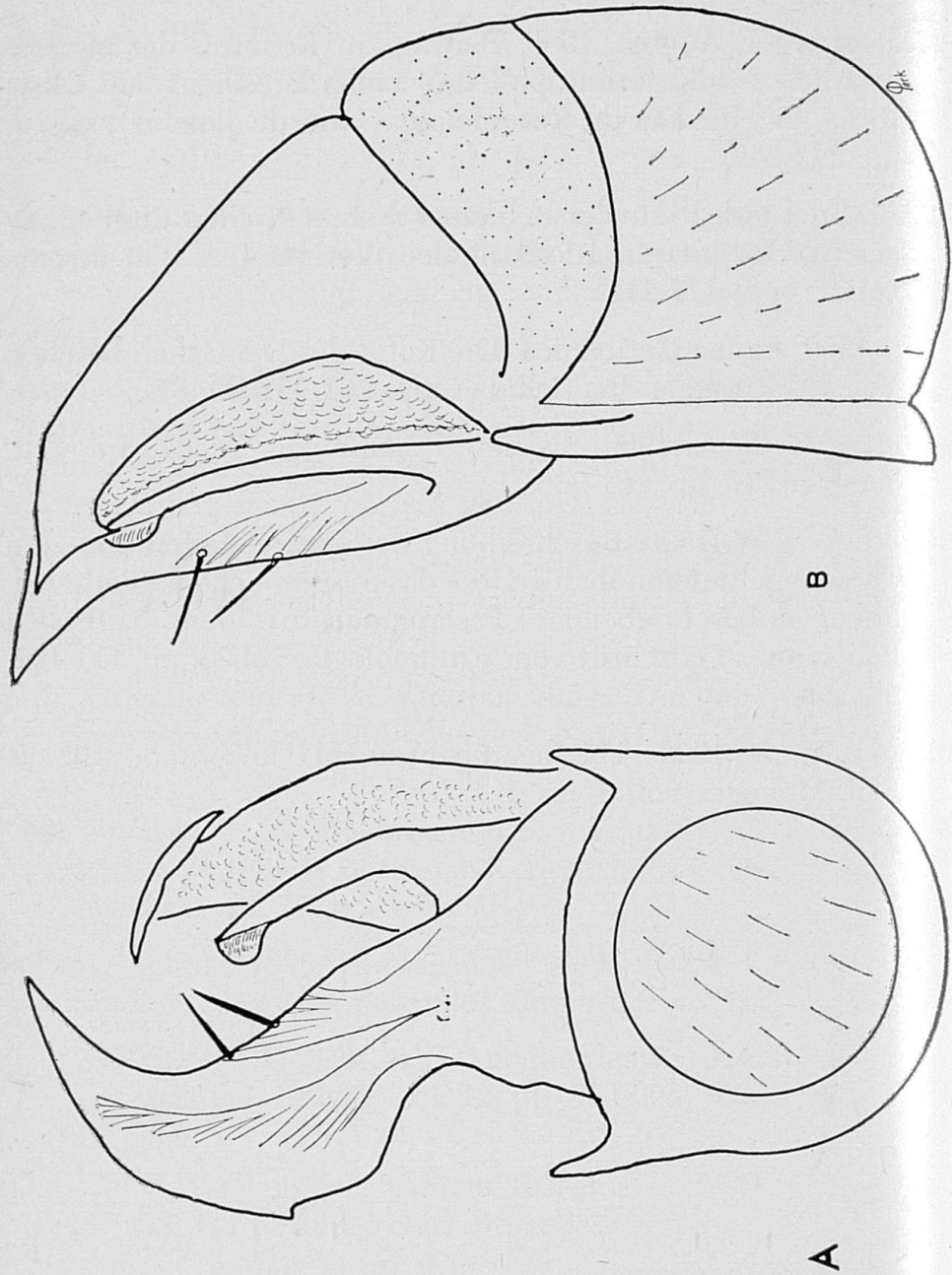


Fig. 1. Aedeagus of *Batrisodes (Batriasymmodes) spelaeus*.  
A. Dorsal view. B. Left lateral view.

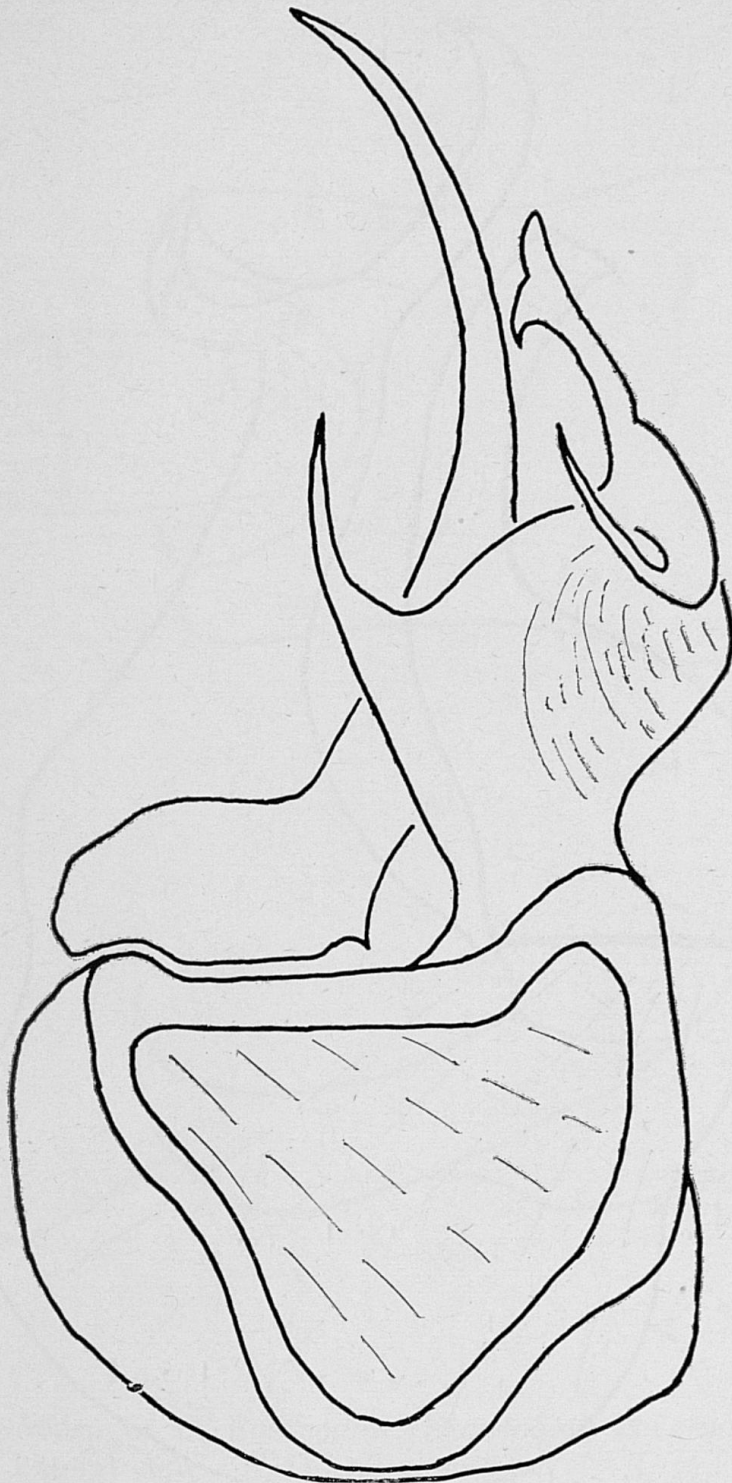


Fig. 2. Aedeagus of *Batrisodes (Batriasymmodes) jeanneli*, dorsal view.



Fig. 3. Aedeagus of *Batrisodes (Batriasymmodes) monstrosus*, dorsal view, after Park, 1942.

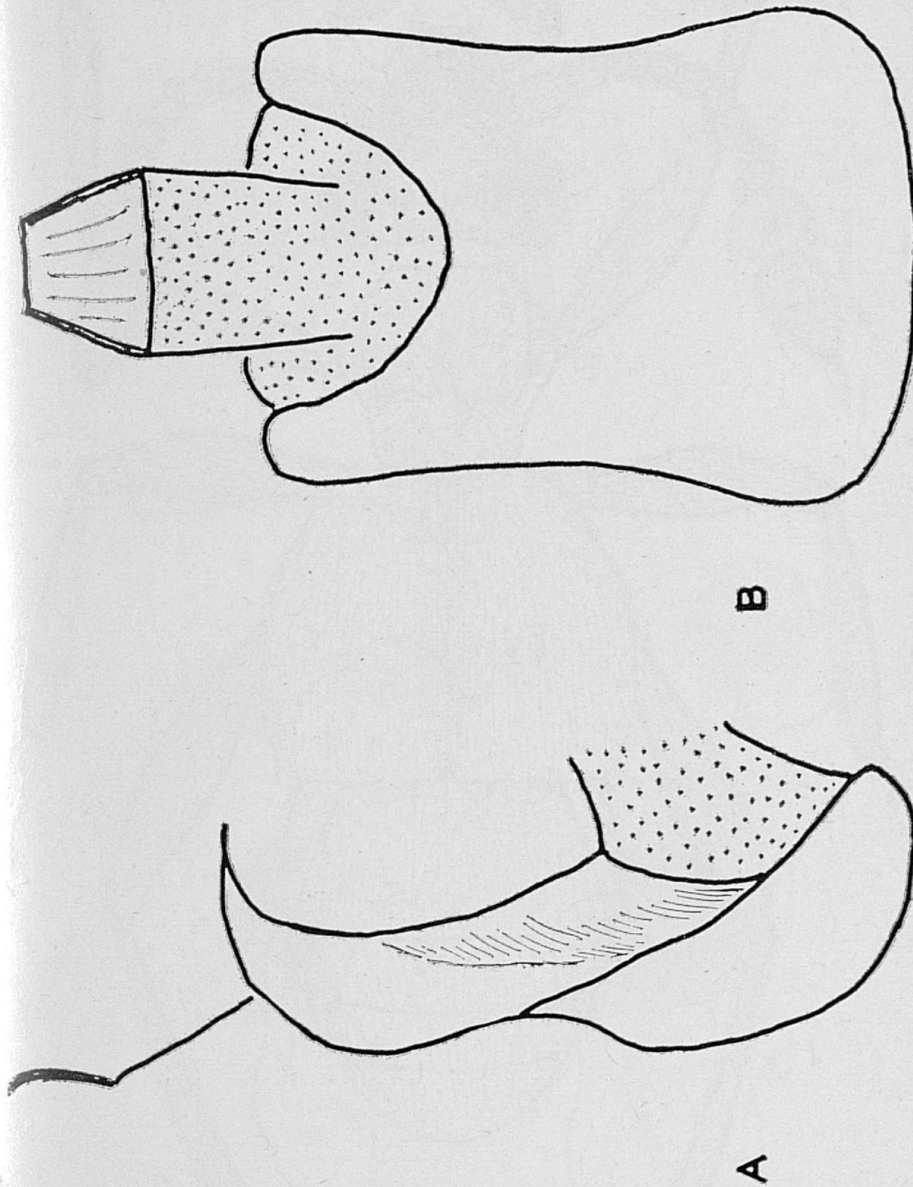


Fig. 4. Aedeagus of *Batrisodes (Excavodes) cavernosus*. A. Lateral view. B. Dorsal view.

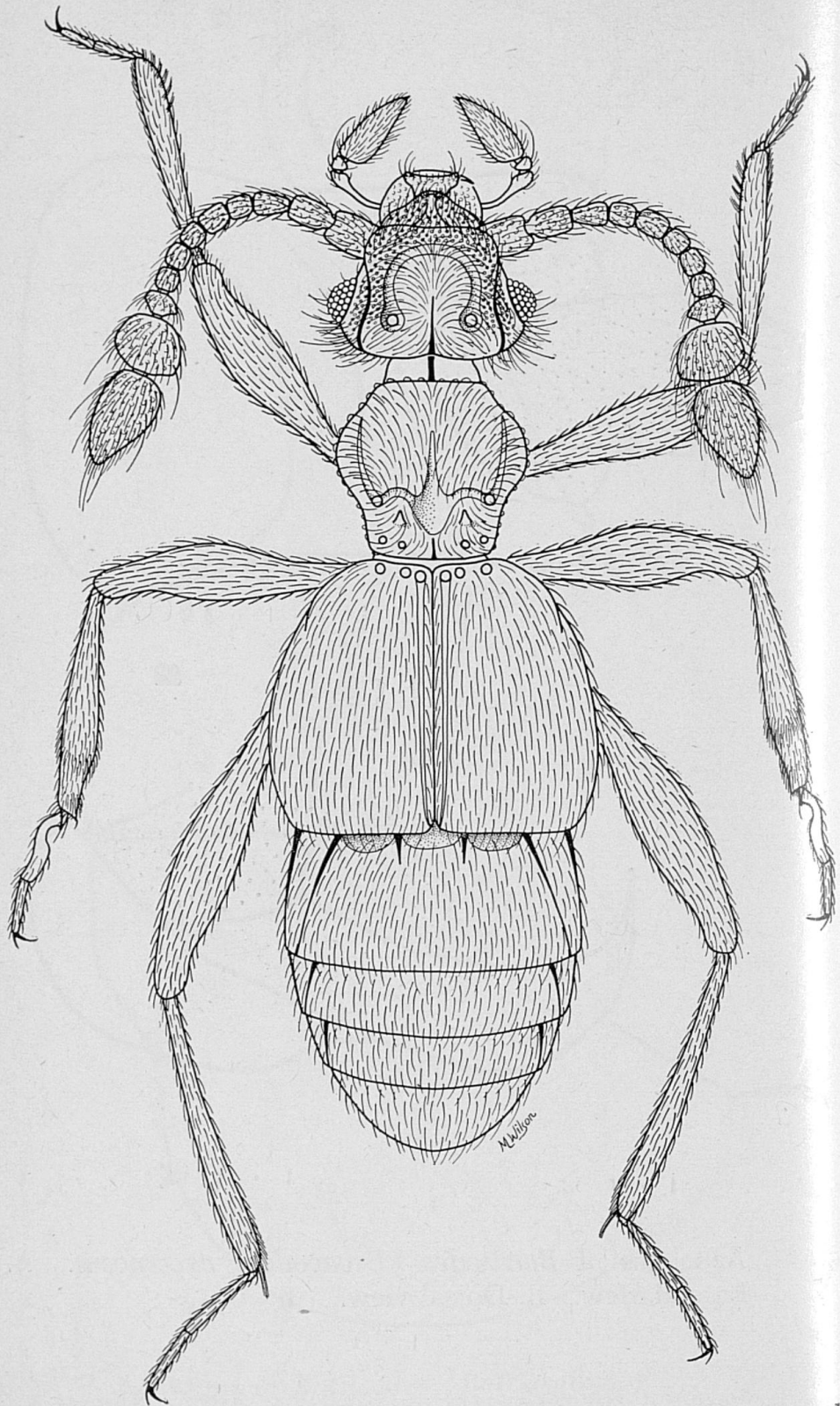


Fig. 5. Dorsal view of *Batrisodes* (*Babnormodes*) *jonesi* male, 70 x.



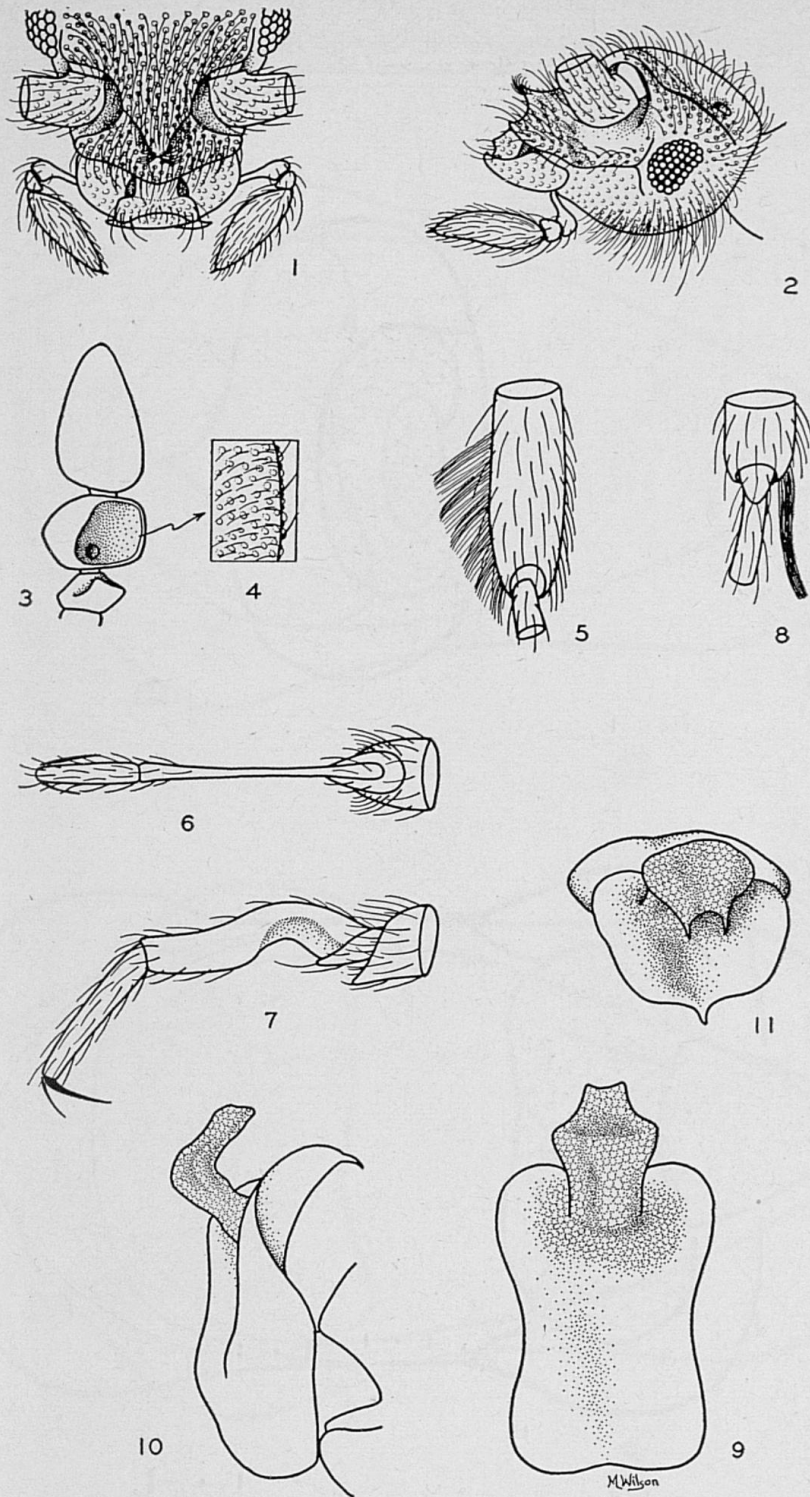


Fig. 6. *Batrisodes (Babnormodes) jonesi* male, 70 x. 1. Face; 2. Head, lateral aspect; 3. Antennal segments IX, X, XI from ventral aspect; 4. Detail of excavation of tenth antennal segment. 5. Protibia apex, to show comb of setae; 6. Mesotarsus, dorsal aspect; 7. Mesotarsus, lateral aspect; 8. Metatibia, apex to show spur; 9. Aedeagus, dorsal aspect; 10. Aedeagus, lateral aspect; 11. Aedeagus, apical aspect.

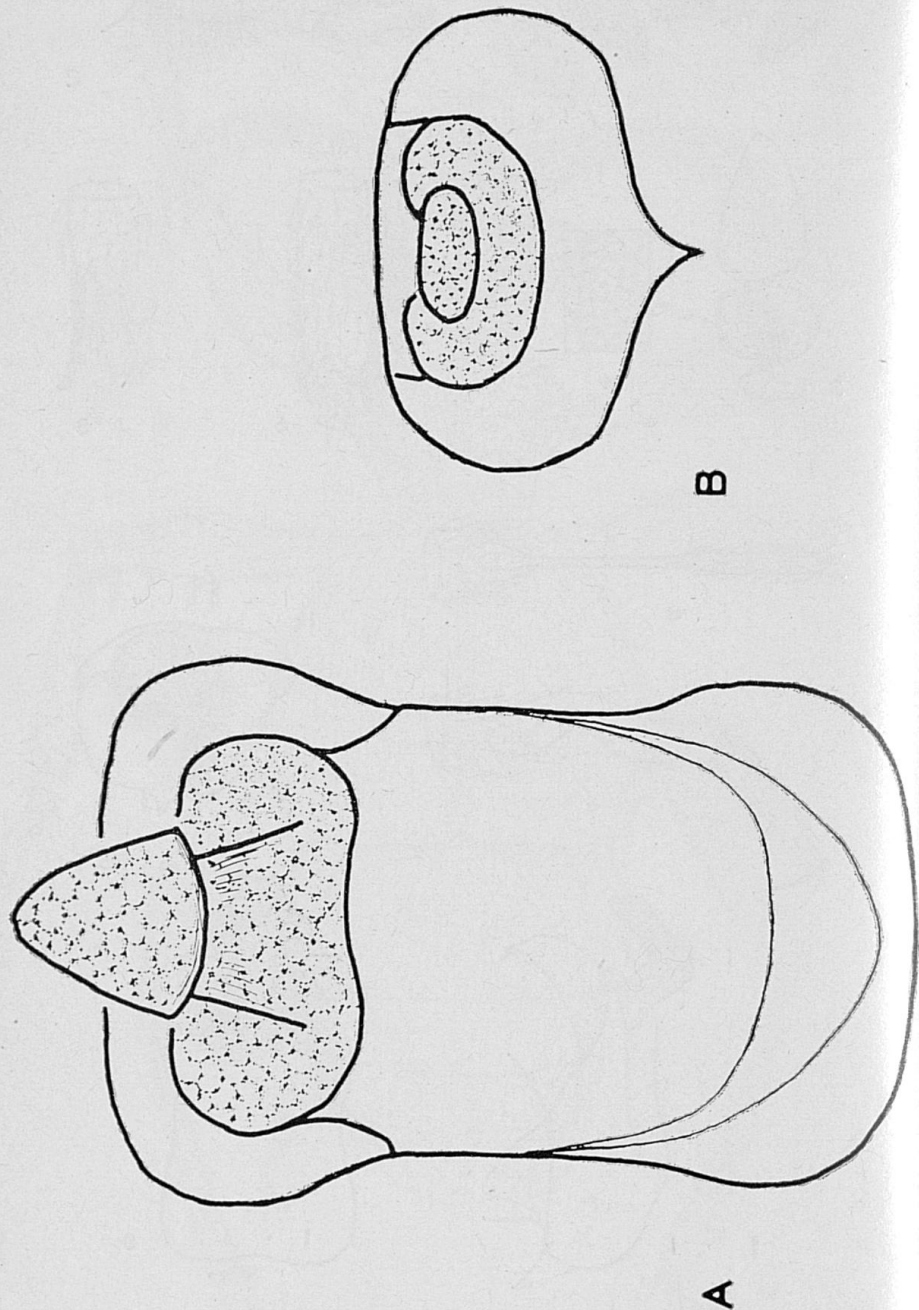


Fig. 7. Aedeagus of *Batrisodes (Babnormodes) subterraneus*,  
A. Dorsal view. B. Apical view.

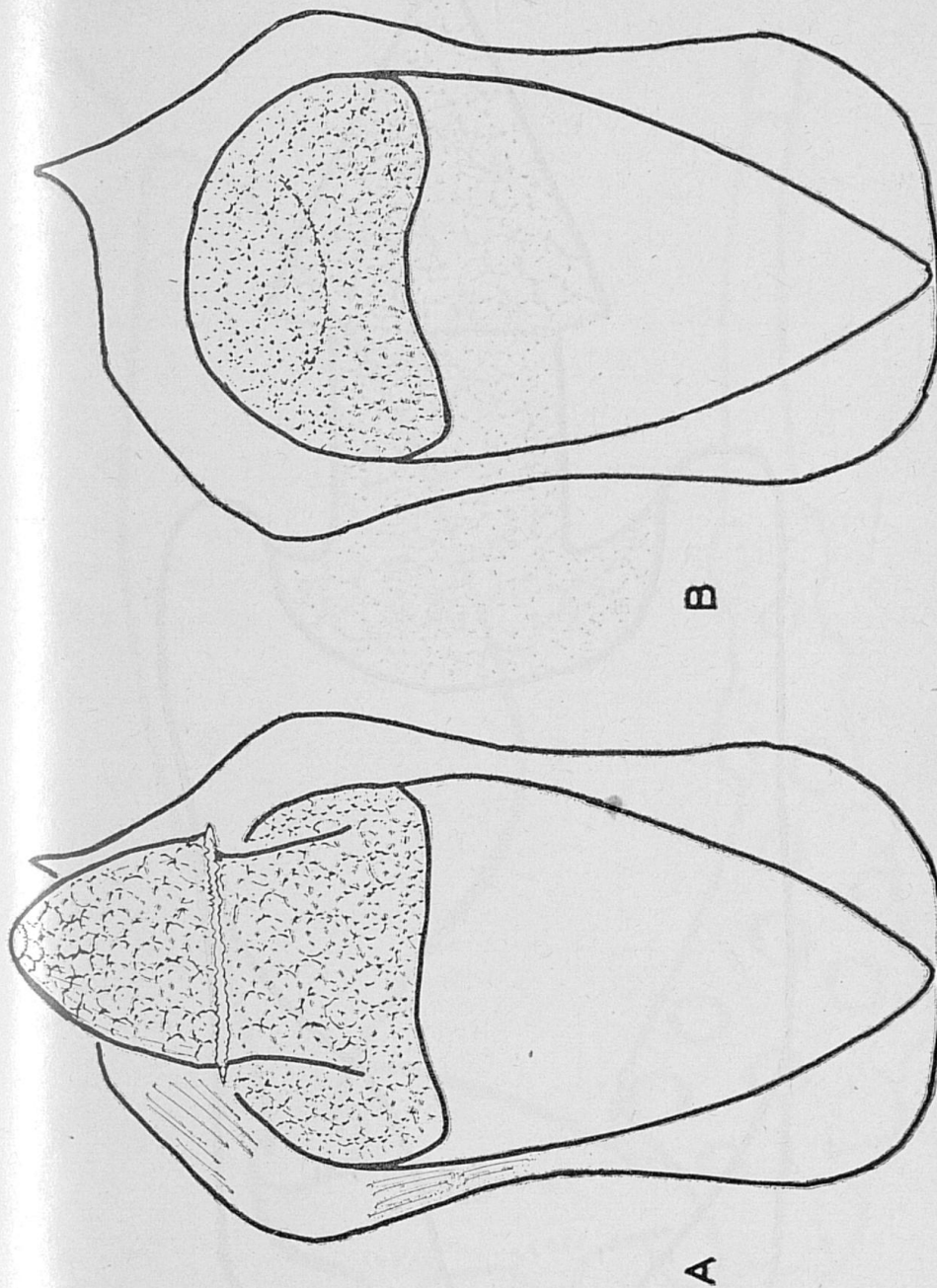


Fig. 8. Aedeagus of *Batrisodes (Babnormodes) valentinei*, dorsal view. A. Median process (internal sac) evaginated; B. Median process (internal sac) invaginated.

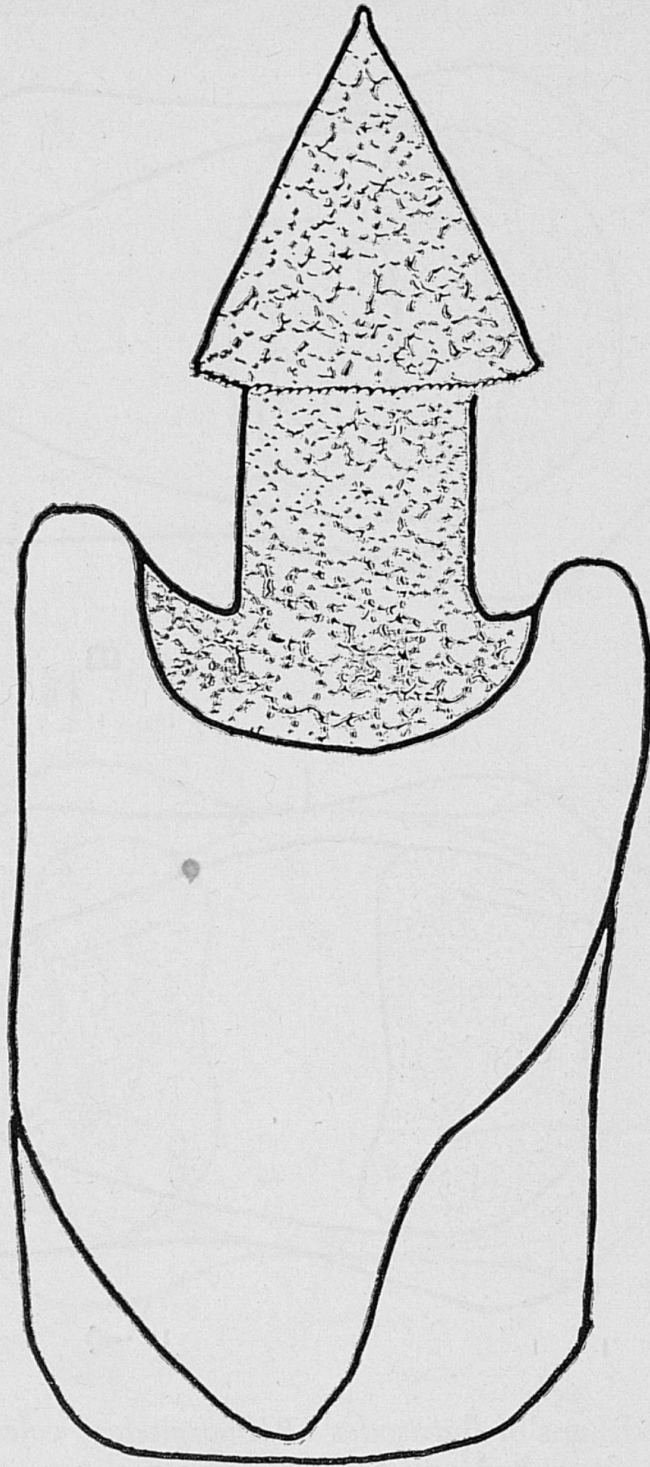


Fig. 9. Aedeagus of *Batrisodes* (*Babnormodes*) *specus*, dorsal view, with median process (internal sac) evaginated.



Fig. 10. Right maxillary palpus of *Bythinopsis jonesi*, ventral view.

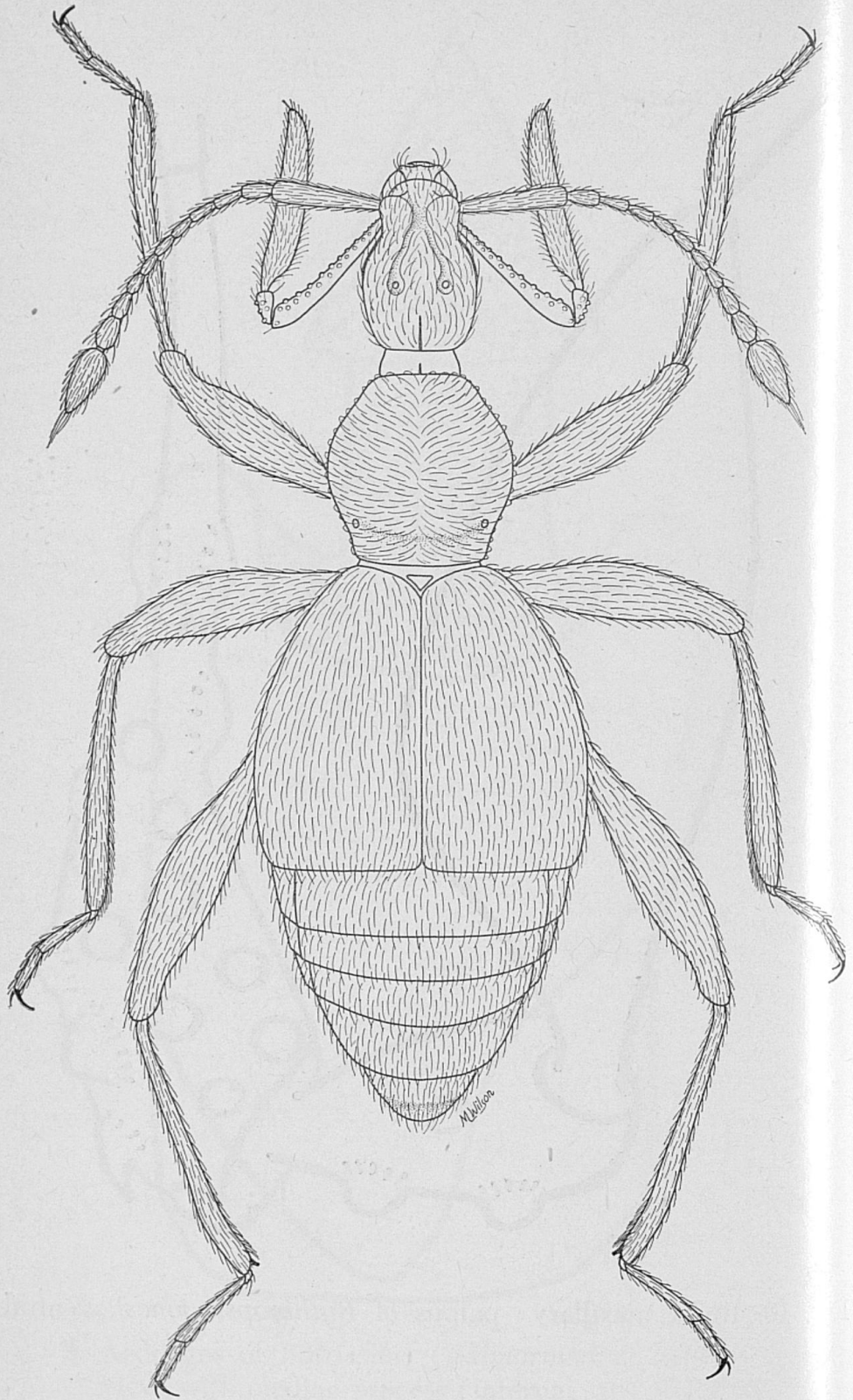
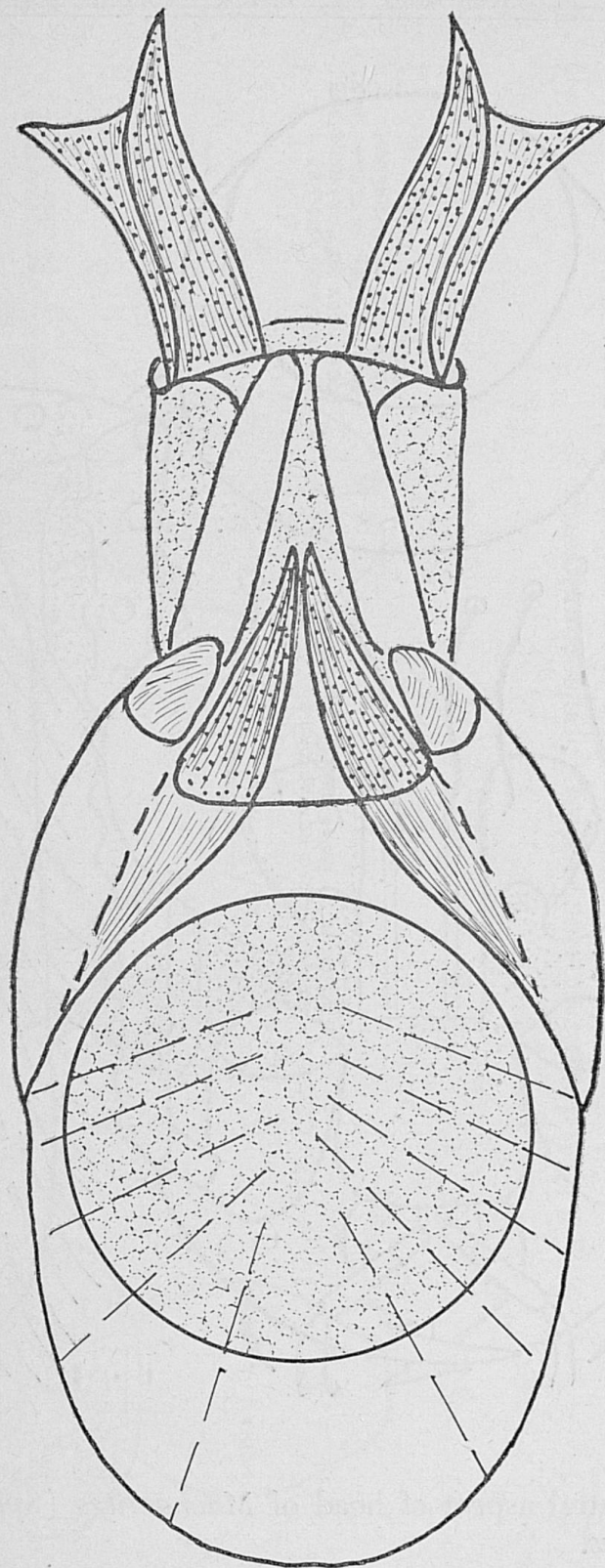


Fig. 11. *Machaerites (Speleochus) stygicus*, dorsal view, 70 x.



x. Fig. 12. Aedeagus of *Machaerites* (*Speleochus*) *stygicus*, dorsal view.

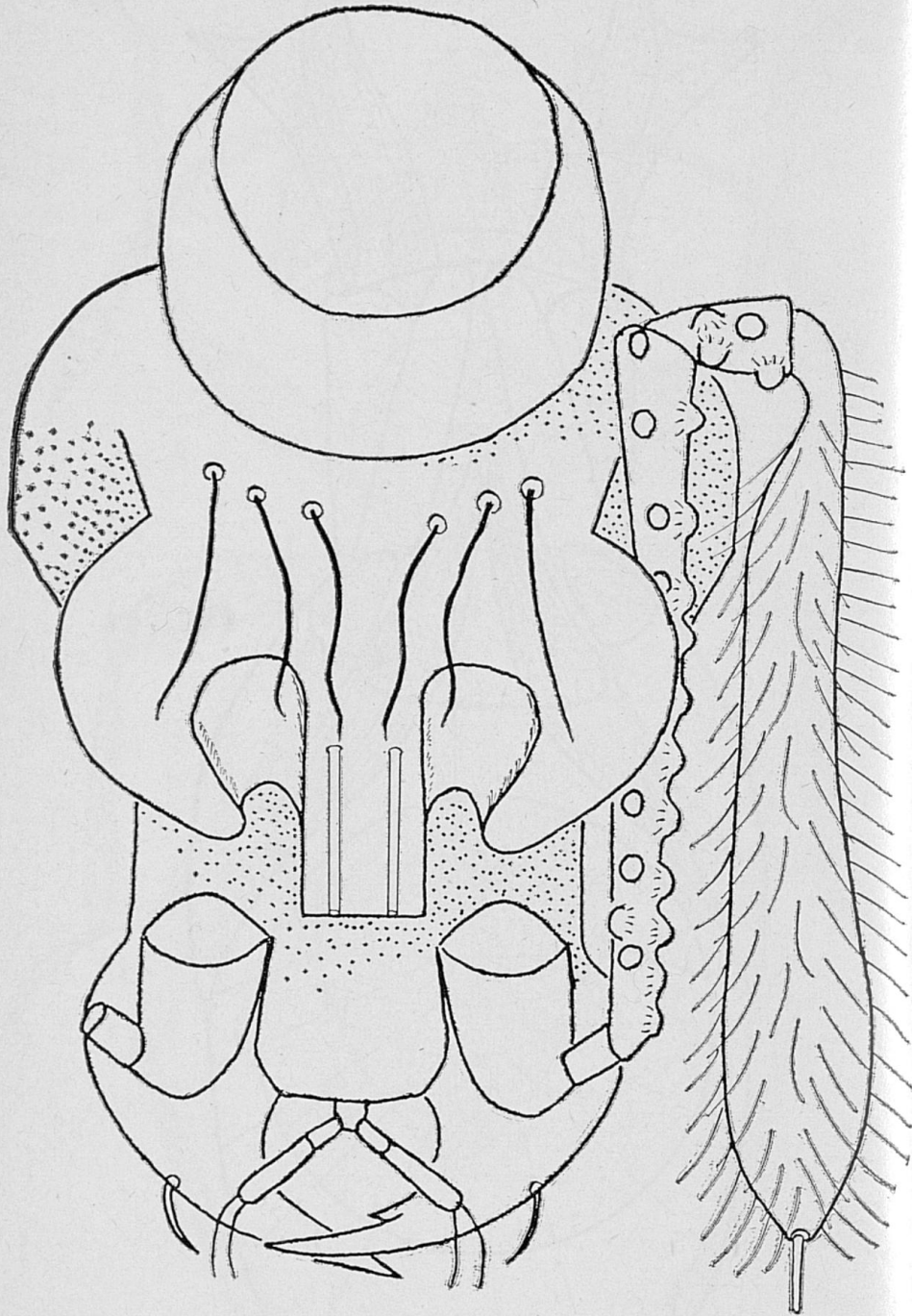


Fig. 13. Ventral aspect of head of *Machaerites (Speleochus) ferus*.



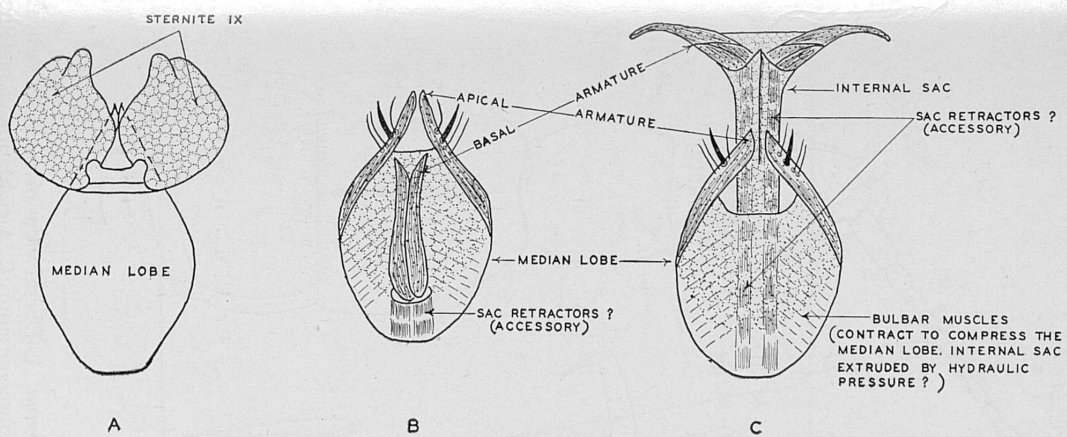


Fig. 14. Aedeagus of *Machaerites (Speleochus) ferus*.  
 A. Outline of aedeagus beneath the morphological ninth sternite. B. Aedeagus with internal sac withdrawn, and basal teeth appressed. C. Aedeagus with internal sac exerted, and basal teeth divergent.

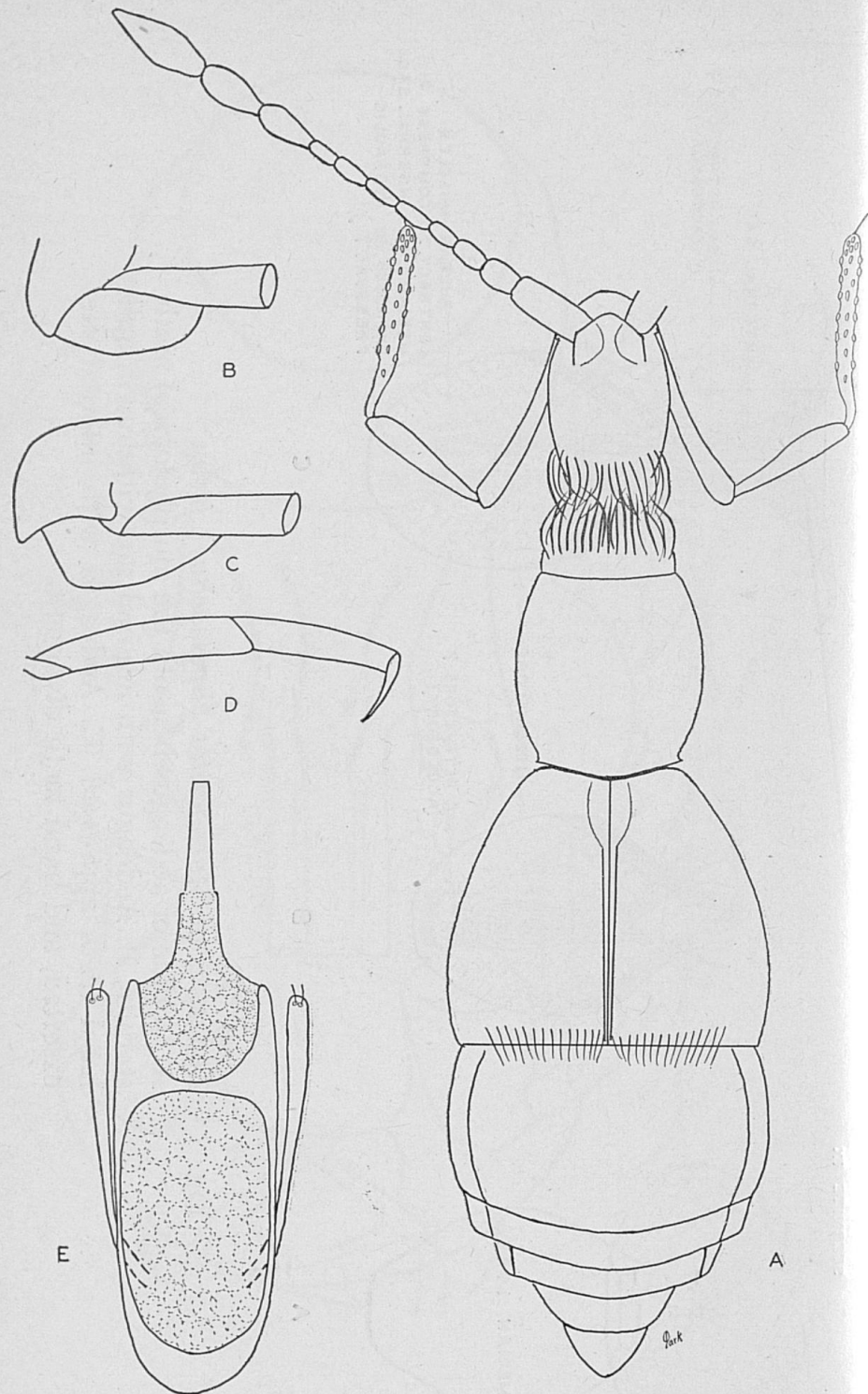


Fig. 15. *Speleobama vana*. A. Dorsal view of male; B. Articulation of mesothoracic femur; C. Articulation of metathoracic femur; D. Metatarsus; E. Aedeagus. All at 70 diameters, but B to E at twice the enlargement of A.

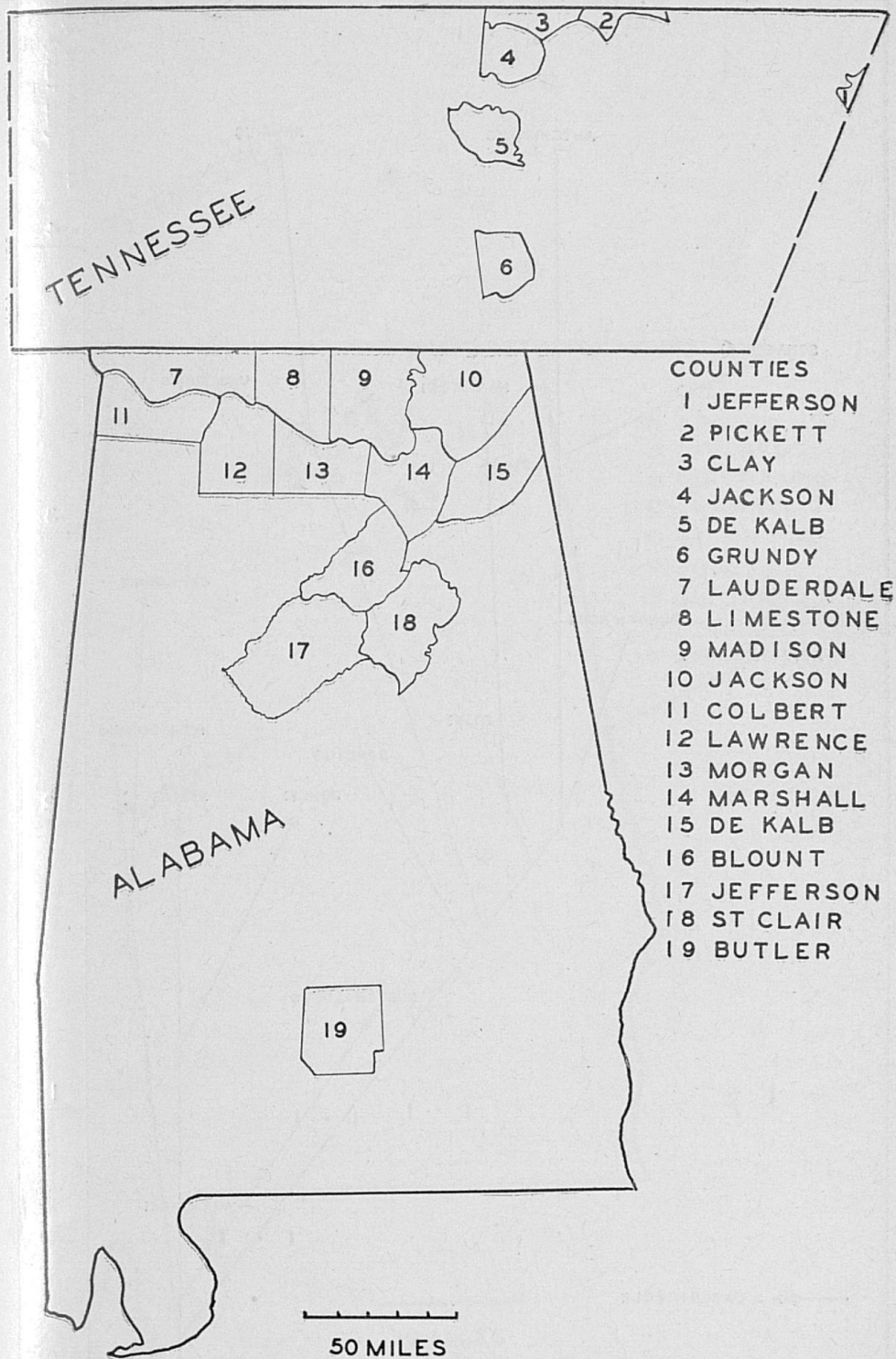


Fig. 16. Counties in Alabama and Tennessee from which cavernicolous Pselaphidae have been reported.

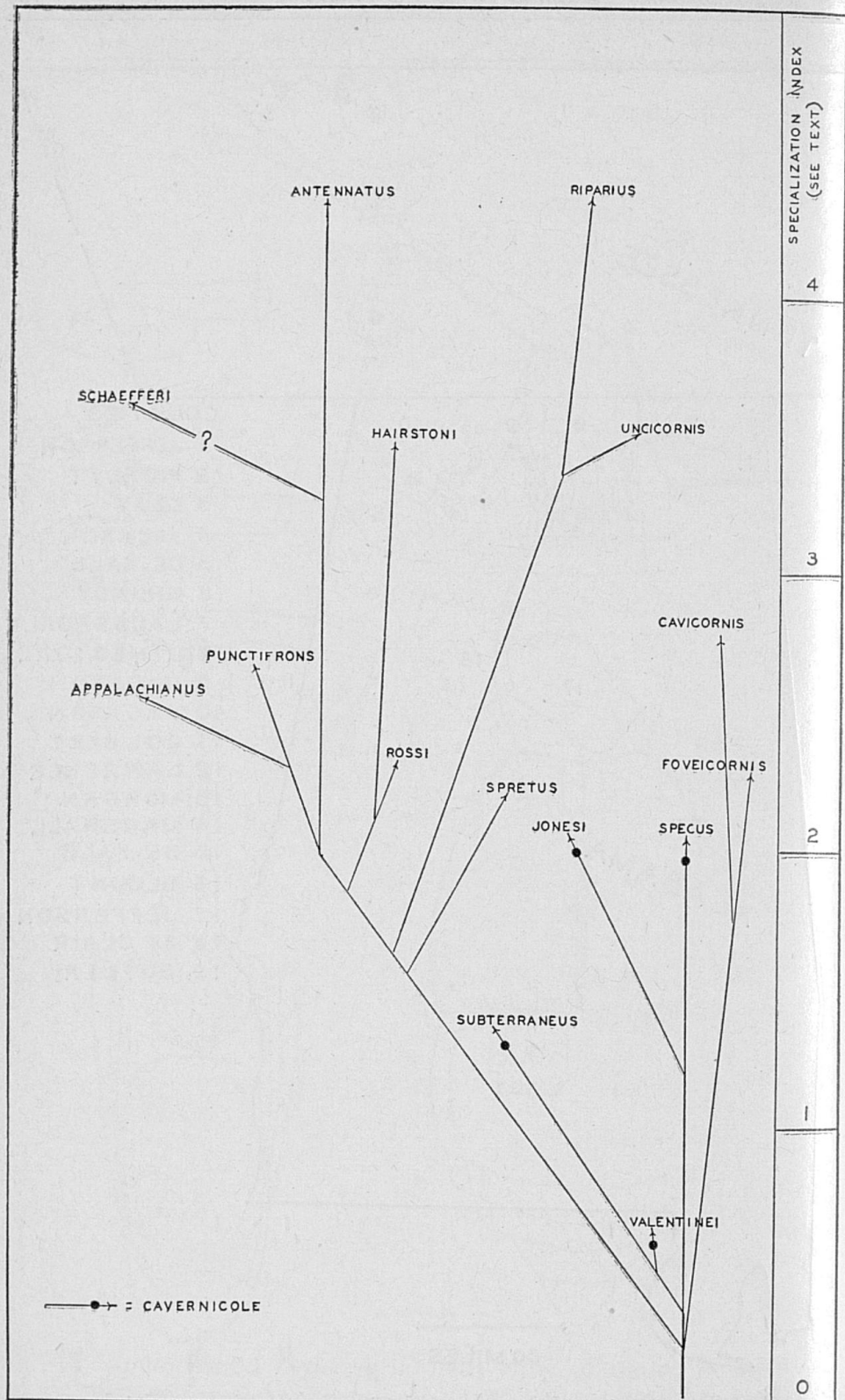


Fig. 17. Hypothetical pattern of evolution in the subgenus *Babnormodes* of the genus *Batrisodes*. See text for explanation.

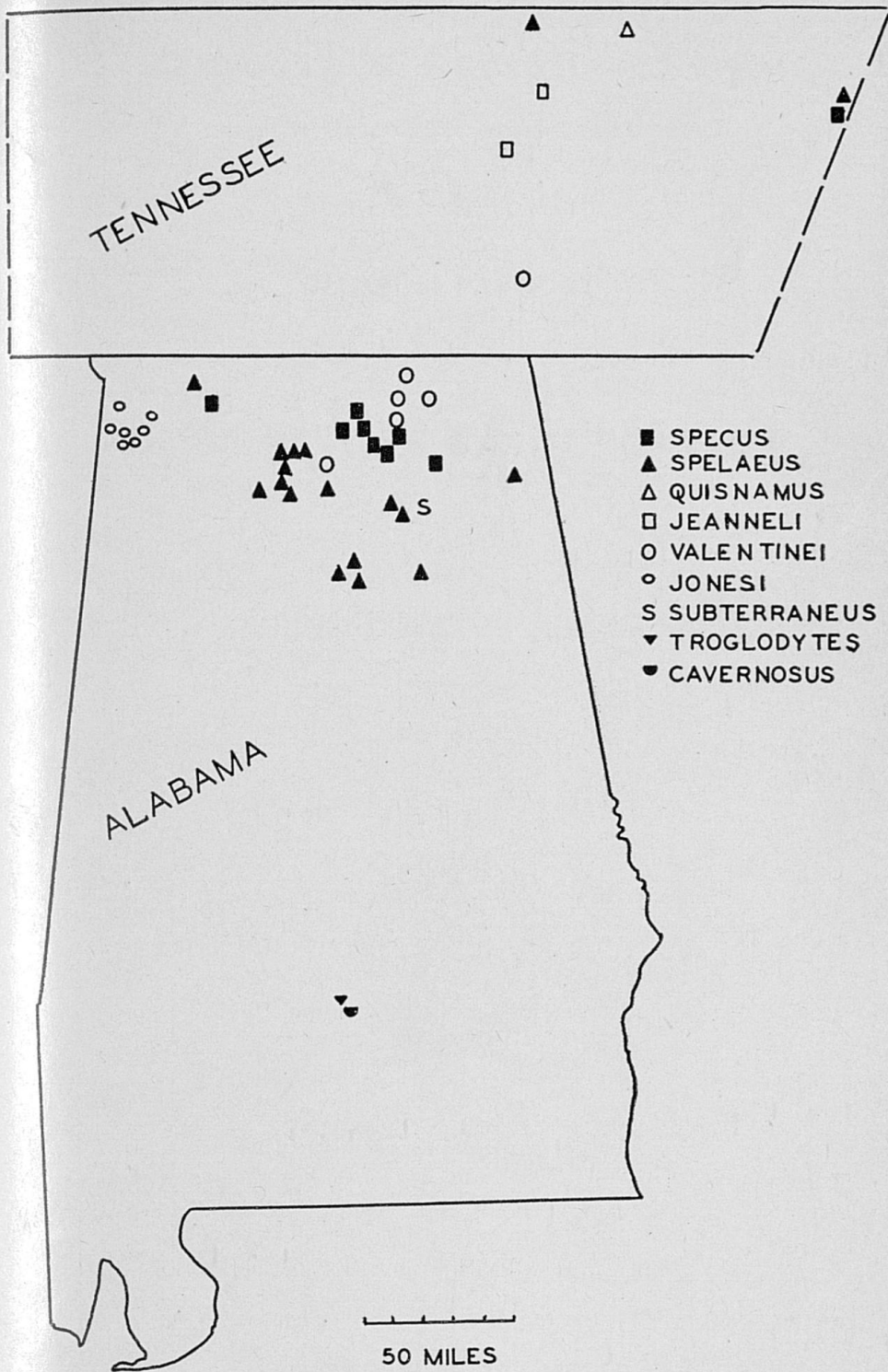


Fig. 18. Distribution of the cavernicolous species of *Batrisodes* in Alabama and Tennessee.

