JOURNAL OF THE TENNESSEE ACADEMY OF SCIENCE
Volume 34, Number 1, January, 1959

NEW CAVE BEETLES (CARABIDAE, TRECHINI) FROM TENNESSEE AND KENTUCKY[1]

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Five genera of eyeless cave beetles of the carabid tribe Trechini have been described from eastern North America. Three of these genera (*Neaphaenops* Jeannel, *Darlingtonea* Valentine, and *Ameroduvalius* Valentine) are monotypic, and are apparently endemic to Kentucky. *Nelsonites* Valentine contains but two known species, from caves in the Cumberland Plateau of Kentucky and Tennessee. Species of *Pseudanophthalmus* Jeannel, the largest and most widely distributed genus of these beetles, have been described from Kentucky, Tennessee, Indiana, Alabama, West Virginia, and Virginia.

The cave trechines, sometimes known as the "anophthalmid" beetles, are small (3mm-8mm), depigmented cavernicoles with rather slender appendages. Eyes and wings have been lost. These insects are predaceous, feeding on other cavernicoles. Within the caves they are found crawling about on the walls and floors or beneath stones and piles of sticks and leaves washed into the caves from the exterior. With very few exceptions they occur in those parts of the caves where a high relative humidity (about 98% to saturation) prevails.

The cave trechines collected by the writer were preserved in 70% ethyl alcohol or Barber's fluid (the latter was found to leave them more flexible for subsequent study). Aedeagi of the males were dissected out with insect pins and cleaned of excess connective tissue, then were mounted directly on slides in Down's medium. Thirty-six to forty-eight hours after mounting, the aedeagi had cleared sufficiently to permit examination of the internal sac and copulatory pieces. Measurements were made in millimeters, using a calibrated ocular micrometer disc. The following abbreviations are used throughout the present paper:

Tl	total length
Hl	head length
Hw	head width
Pl	pronotum length
Pw	pronotum width
El	elytra length
Ew	elytra width
Ant	antenna length

[1]This paper is based on part of a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, Department of Biology, Vanderbilt University.

Lengths were measured along the mid-line. Widths are maximum widths. All measurements are for normally articulated specimens. Rounded surfaces were measured as chords of arcs.

Type specimens have been deposited in the American Museum of Natural History, New York City.

The writer wishes to express his appreciation to Dr. Charles E. Farrell, Vanderbilt University, for advice and assistance. Mr. Leslie Hubricht, Louisville, Kentucky, collected some of the beetles discussed in the present paper. Personnel of the Natural Park Service, especially Naturalist Richard Burns, were most cooperative during collecting endeavors in Mammoth Cave National Park. Catherine Barr, the writer's wife, assisted in collecting many of the beetles and patiently endured a large number of the cave explorations.

Genus *Pseudanophthalmus* Jeannel

pubescens group

Pseudanophthalmus ciliaris ciliaris Valentine

P. ciliaris Valentine, 1937. J. Elisha Mitchell *Sci. Soc.* vol. 53, p. 95

This beetle was described from Dunbar Cave, 3 miles east of Clarksville, Montgomery Co, Tennessee. Both Valentine (1937) and Henrot (Jeannel, 1949) found it very abundant at the type locality. The writer took four specimens on August 14, 1956, in wet silt along the banks of the river in Dunbar Cave. Eight specimens were collected June 24, 1957, under rocks and wood in a small grotto in the same cave.

New records for this race are as follows:

Bell Witch Cave, 1 mile NE Adams, Robertson Co., Tenn., June 24, 1957 (TCB); 27 specimens collected under rocks along the stream 100 yards from the entrance.

Buzzard Cave, 1 mile S Keysburg, Ky., but in Robertson Co., Tenn., on the north side of Red River, July 16, 1957 (TCB); 6 specimens in crawlway to left of entrance chamber.

Durham Cave, on the south branch of Passenger Creek, in the Sango Community of eastern Montgomery Co., Tenn., June 24, 1957 (TCB); 4 specimens under rocks along stream, 75 yards from the entrance.

Glover Cave, 4 miles SW Trenton, in the eastern edge of Christian Co., Ky., June 9, 1957 (Catherine Barr and TCB); 48 specimens, crawling on wet silt a half mile from the entrance.

P. ciliaris ciliaris is a highly variable form, ranging in total length from 4.85 to 5.60. The pronotal index (pl/pw) varies between 0.88 and 1.20. The aedeagus measures 0.98-1.08 in length, and the right copulatory piece is about 2½ times as wide as the left piece. A median sagittal keel, not shown in Jeannel's (1949) figure, is present on the basal bulb of all aedeagi of this race examined by the writer.

Pseudanophthalmus ciliaris colemanensis n. subsp.

Type series: Holotype male, allotype female, eight male and four female paratypes, Coleman Cave, 8 miles west of Clarksville, Montgomery Co., Tennessee, on a tributary of Blooming Grove Creek. June 22, 1957 (Leslie Hubricht and TCB).

Holotype: Tl 5.10; hl 1.24; hw 0.86; pl 0.96; pw 1.19; el 2.88; ew 1.88; ant 3.86.

Allotype: Tl 5.25; hl 1.14; hw 0.93; pl 1.02; pw 1.23; el 3.02; ew 1.94; ant 3.70.

Description: Longer and more robust than *P. ciliaris ciliaris*. Head wider. Pronotal index 1.21-1.24; anterior and posterior pronotal angles more prominent; sides less arcuate; base much wider. Elytra very full; longitudinal striae deeper and punctations more distinct than in the nominate race. Aereagus of paratype 1.00; almost identical with that of a topotype *P. ciliaris ciliaris*.

Remarks: Coleman Cave is located on a north tributary of the Cumberland River (Blooming Grove Creek) which empties into the Cumberland downstream from the mouth of Red River. The beetles were collected in the south fork of the cave, from among small rocks at the bottom of a rapid drip of water from the ceiling.

Pseudanophthalmus ciliaris loganensis n. subsp.

Type series: Holotype male, allotype female, and 0 paratypes, Cook Cave, 1 mile east of Adairville, Logan Co., Kentucky, June 25, 1957 (TCB). Additional paratypes 197, as follows:
45 from Collier Saltpeter Cave, 2.4 miles N Dot, Logan Co., Ky., June 25, 1957 (TCB); 40 from Buzzard Cave, 2 miles S Schochoh, Logan Co., Ky., July 25, 1957 (E. S. Davis and TCB); 92 from Double Cave, 1 mile E Milldale, Robertson Co., Tenn., July 25, 1957 (E. S. Davis and TCB); 12 from Christian Cave, 3 miles SE Milldale, Robertson Co., Tenn., Jan. 2, 1958 (TCB); 7 from Jesse James Cave, 1.5 mile SE Orlinda, Robertson Co., Tenn., April 1, 1957 (TCB).

Holotype: Tl 4.35; hl 1.10; hw 0.75; pl 0.79; pw 1.00; el 2.46; ew 1.54; ant 3.9; length of aedeagus 0.86.

Allotypes Tl 4.35; hl 1.07; hw 0.77; pl 0.82; pw 0.93; el 2.45; ew 1.56; ant 3.09.

Description: Length 3.9-4.9, av. 4.4. Smaller, slenderer, and paler than *P. ciliaris ciliaris*. Sides of pronotum more nearly subparallel, the pronotal index ranging from 0.75 to 0.87, av. 0.83. Slope of prehumeral border less oblique with respect to the mid-line. Aedeagus smaller (0.86-0.87), the median lobe a little thicker; right copulatory piece much broader, the apex blunt and deflected slightly upward.

Remarks: *P. ciliaris loganensis* occurs in large numbers in damp places in the caves of the upper Red River valley, where it is apparently more abundant in the summer than in the winter. Like the nominate race, it is predominantly cursorial. A few abnormally small individuals occur in the populations, but there are all graduations from the smaller to the larger specimens, and the aedeagi of various sizes are indistinguishable. *P. ciliaris loganensis* overlaps the known range of a larger and closely related species of *Pseudanophthalmus*, to be described below.

Pseudanophthalmus orlindae n. sp.

Type series: Holotype male, allotype female, and fourteen paratypes, Jesse James Cave, 1.5 miles southeast of Orlinda, Robertson Co., Tennessee, April 1, 1957 (TCB). Additional paratypes as follows: 45 from Cook Cave, 1 mile east of Adairville, Logan Co., Kentucky, June 25, 1957 (TCB); 1 from Cheeks Tavern Cave, 4 miles north of White House, Robertson Co., Tennessee, April 1, 1957.

Holotype: Tl 5.70; hl 1.31; hw 0.89; pl 0.96; pw 1.19; el 3.39; ew 2.00; ant 4.02.

Allotype: Tl 5.71; hl 1.35; hw 0.98; pl 1.00; pw 1.23; el 3.36; ew 2.05; ant 3.82.

Description: Length 5.4-5.8, av. 5.7. Pale, reddish brown. Form very similar to *P. ciliaris*, but larger. Head elongate; labrum trilobed. Pronotum convex, pubescent; wider than long, pronotal index 1.15-1.20; anterior angles

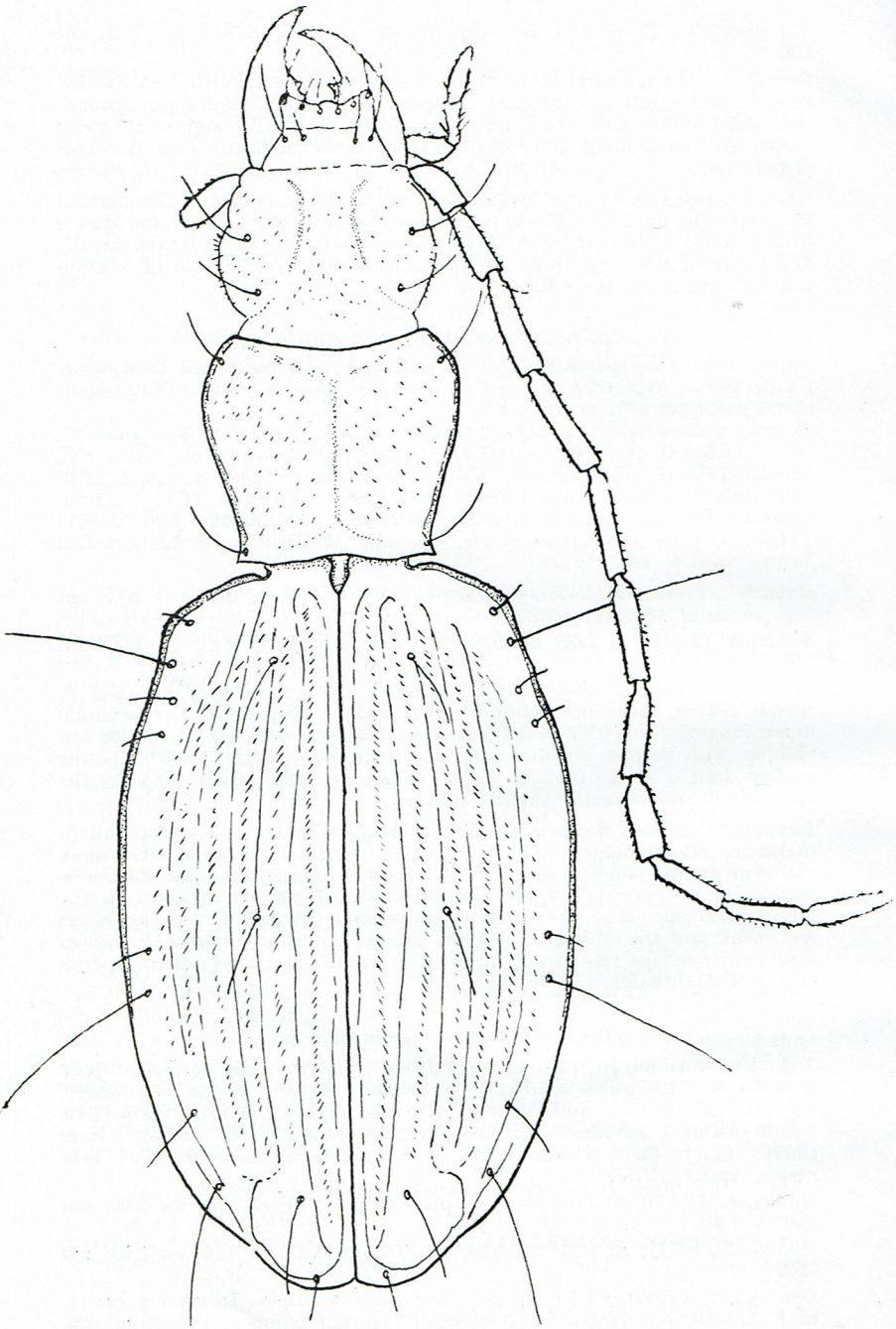

FIGURE 1. *Pseudanophthalmus orlindae* n. sp. Holotype male, X23.

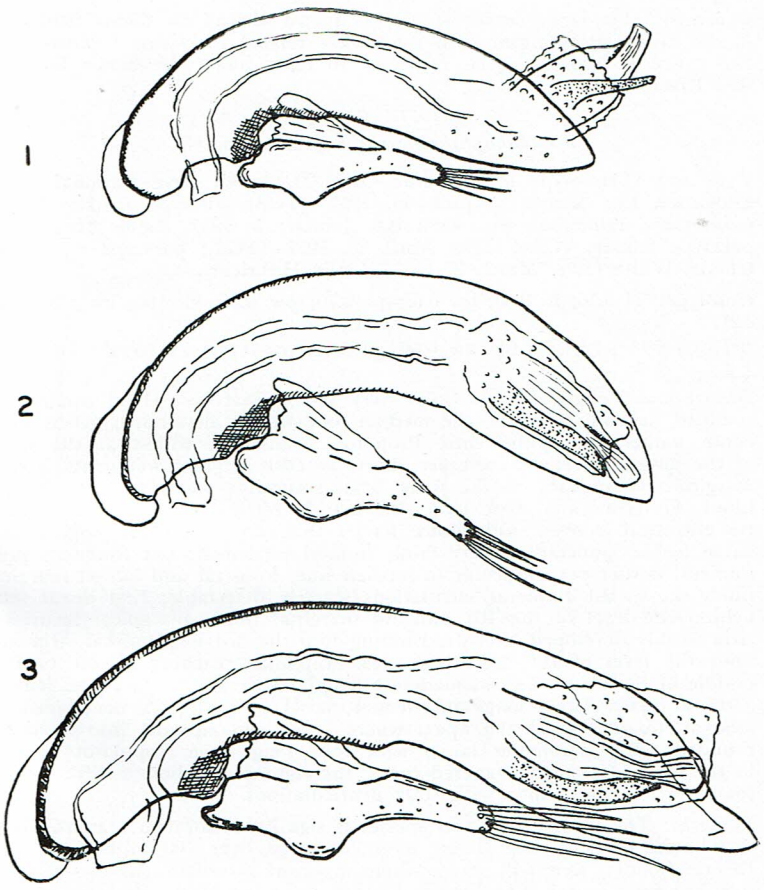

FIGURE 2. Aedeagi of *Pseudanophthalmus*, X62. (1) *P. ciliaris loganensis* n. subsp., holotype. (2) *P. ciliaris colemanensis* n. subsp., paratype. (3) *P. orlindae* n. sp., paratype, Jesse James Cave.

reduced; sides little rounded, basal sinuosity poorly developed; posterior angles small, more-or-less acute. Elytra as in *P. ciliaris*, with the following differences: proportionately shorter, pubescence less dense, longitudinal striations slightly more profound, humeri more angular; apical recurrent stria basally arcuate, flexed outward, and running parallel to the elytral suture anterior to the flexure; an impressed groove passing laterally from the anterior end of the apical stria to the 3rd longitudinal stria, and a faint groove toward the 5th stria. Antennae very long, reaching back three-fourths the length of the elytra. Mandibles large and powerful. Aedeagal length

1.33-1.37; basal bulb strongly bent; apex slightly produced; copulatory pieces elongate, of the same general form as *P. ciliaris;* parameres with four long setae.

Remarks: This large, active species is found abroad in damp situations in the caves, intermingled with the closely related *P. ciliaris loganensis* in two caves. It appears to be restricted to caves along the South Fork of Red River.

horni group

Pseudanophthalmus inexpectatus n. sp.

Type series: Holotype male, White Cave, Mammoth Cave National Park, Edmonson Co., Kentucky, June 19, 1957 (TCB); allotype female, Mammoth Cave, Edmonson Co., Kentucky, January 5, 1957 (Leslie Hubricht); paratype female, White Cave, April 20, 1957 (TCB); paratype male and female, White Cave, March 2, 1957 (Leslie Hubricht).

Holotype: Tl 3.50; hl 0.80; hw 0.63; pl 0.70; pw 0.86; el 2.00; ew 1.26; ant 2.21.

Allotype: Tl 3.72; hl 0.93; hw 0.69; pl 0.64; pw 0.78; el 2.00; ew 1.27; ant 2.35.

Description: Length 3.3-3.7. Color very pale, testaceous. Head small and rounded; labrum trilobate, the median lobe weakly developed; genae with dense, rather long pubescence. Pronotum transverse, widest at the level of the anterior setae; pubescence short; anterior angles prominent; lateral margins arcuate back to the weak basal sinuosity; posterior angles large, blunt, subrectangular; base large, the margin retcilinear, not concave. Elytra ellipitical, convex; pubescence longer than on pronotum; longitudinal striae feeble; punctations very faint; humeri prominent but rounded; prehumeral border perpendicular to median line; humeral and *lateral* margins finely setose, the humeral serrulations scarcely detectable; first discal seta behind the level of the 4th humeral marginal puncture; apical recurrent stria weakly developed, arcuate, running into the 3rd longitudinal stria behind the level of the 3rd discal seta. Antennae reaching almost to the middle of the elytra; legs of moderate length. Aedeagus of paratype: length 0.94, unusually large, long and slender; basal bulb slightly bent; median lobe attenuate toward the apex, where it is bent upward into a small, rounded bulb; parameres large, with four long steae; copulatory pieces in the form of elongate, tapered cones; the right piece about a fifth longer than the left and armed with scaly denticulations.

Remarks: The discovery of this species is significant for two reasons. First, it inhabits caves in the Green River drainage over 100 miles from the Fayette County, Kentucky, caves where *P. horni* (Garman), its closest relative, has been found. The Fayette County caves are in the drainage of the Kentucky River. Second, its occurrence in Mammoth Cave, hitherto unsuspected despite a hundred and thirteen years of biological collecting in the cave, raises to six the number of species of cave trechines known from the Mammoth Cave region.

All five specimens of the type series were collected from beneath wet, decaying wood. Four were taken at a pit in the back of White Cave, and one near the top of Mammoth Dome in Mammoth Cave. These two areas are separated by a breakdown, impenetrable to man, but probably readily penetrable by the beetles.

robustus group

Pseudanoprthalmus robustus robustus Valentine

1931. J. Elisha Mitchell Sci. Soc., vol 46, p. 250

The type locality for *P. r. robustus* is Johnson Cave, near Calfkiller, Putnam Co., Tennessee, where beetles abound under rotting boards in the vast entrance chamber. In May, 1957, thirty specimens were collected in

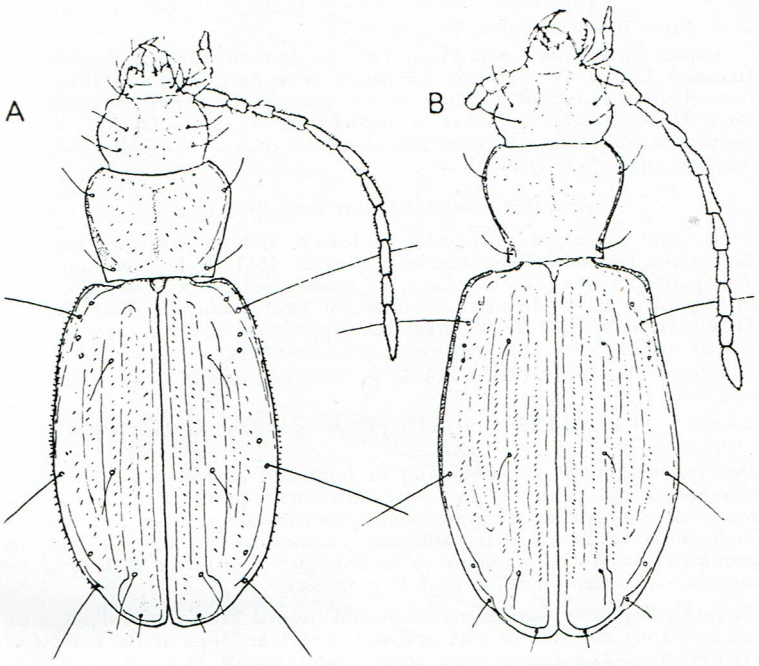

FIGURE 3. (A) *Pseudanphthalmus inexpectatus* n. sp. Holotype male, X23. (B) *Pseudanophthalmus packardi* n. sp. Holotype male, X23.

an hour's time in Johnson Cave. Most of this huge cave is dusty and quite xeric, although there are undoubtedly deeper, more humid portions, as was indicated by the presence of a troglobious crayfish. *Orconevtes pellucidus australis* (Rhoads), in an intermittent pool in the entrance chamber.

The following collections represent new records for the nominate race of *P. robustus,* previously known only from the type locality.

Mott Cove Cave, in Key Community, White Co., Tenn., Mar. 24, 1957 (TCB); one male on a damp ledge 400 feet from the mouth.

Haskell Sims Cave, 1.5 miles E Doyle, White Co., Tenn., Dec, 24, 1956 (Leslie Hubricht and TCB); four specimens under rocks embedded in silt at the edge of the cave stream near the bottom of the entrance sink. These are the darkest anophthalmids the writer has seen, almost the color of port wine. The body form and the form of the aedeagus do not seem to warrant racial separation.

Indian Cave, 2 miles S Quebeck, White Co., Tenn., Dec. 24, 1956 (Leslie Hubricht and TCB); two specimens taken near the back of the cave near a wet place on the wall.

Calfkiller Saltpeter Cave, 0.5 mile W Calfkiller School, Putnam Co., Tenn.,

May 6, 1957 (B. C. Stewart); one female. This cave is a mile north of Johnson Cave.

Pseudanophthalmus robustus neglectus Jeannel

1949, Notes Biospeologiques, Fasc. 4, p. 51

Known only from Cumberland Caverns (formerly) Higgenbotham and Henshaw Caves), Warren Co., Tennessee. This race is widely distributed throughout the damper portions of the cave, having been taken near all three known entrances, where it occurs with *P. macradei* Val. and *P. templetoni* Val. It is somewhat less abundant than *P. macradei,* but more common than *P. templetoni.*

Pseudanophthalmus robustus megosteus n. subsp.

Type series: Holotype male, allotype female, and 39 paratypes from Big Bone Cave, Van Buren Co., Tennessee, July 21, 1957 (C. L. Bush and TCB). Two paratypes from McElroy Cave, 1.5 miles northeast of Bone Cave P. O., in Big Bone Cave Mountain, Van Buren Co., Tennessee, June 23, 1957 (Leslie Hubricht and TCB); eight paratypes from McElroy Cave, January 1, 1958 (TCB).

Holotype: Tl 4.80; hl 0.98; hw 0.78; pl 0.93; pw 1.08; el 2.74; ew 1.81; ant 2.98.

Allotype: Tl 4.75; hl 1.03; hw 0.78; pl 0.88; pw 1.08; el 2.64; ew 1.72; ant 2.89.

Description: Length 4.2-5.0. Similar in color and general appearance to *P. r. robustus* Val., with the following differences: pronotum distinctly narrower; anterior angles less prominent; posterior angles small and subdued. Prehumeral border of elytra obliquely inclined to the mid-line, not perpendicular as in the nominate race. Aedeagus of paratype 0.94 long; not differing appreciably from that of *P. r. robustus.*

Remarks: Big Bone Cave is a famous and historic cavern, mined for nitrocalcite during the War of 1812 and the Civil War. Most of the cave is excessively dry. The beetles were taken under boards in moderately damp places near the entrance to the cave, and far in the interior in a large avenue known as the Muster Ground. The writer has never observed anophthalmids in drier situations. In McElroy Cave the beetles occur under wet rocks or in rotting vegetation carried into the cave through sinkholes.

The range of *P. r. robustus* extends down through the Calfkiller Valley into southern White County to the Caney Fork River. Across the Caney Fork the *robustus* populations have apparently diverged. McElroy and Big Bone Caves are located south of the Caney Fork in the northwestern corner of Van Buren County. They are separated from the type locality of *P. r. neglectus* by the Rocky River, a tributary of the Caney Fork.

Pseudanophthalmus robustus farrelli n. subsp.

Type series: Holotype male, allotype female, one male and three female paratypes. Indian Grave Point Cave, in Dry Creek Valley, DeKalb Co., Tennessee, December 27, 1956 (C. E. Farrell, Catherine Barr, TCB). Additional paratypes 14, all from nearby DeKalb County caves:

1 from Avant (Lindsay Williams) Cave, Dec. 23, 1956 (Leslie Hubricht and TCB); 2 from Avant Cave, June 26, 1957 (Leslie Hubricht); 1 from Cripp's Mill Cave, Dec. 27, 1956 (C. E. Farrell, Catherine Barr, TCB); 1 from Fox Cave, Dec. 27, 1956 (C. E. Farrell and TCB); 6 from Snow Hill Cave, Dec. 23, 1956 (Leslie Hubricht and TCB); 4 from Jim Cave, Dec. 23, 1956 (Leslie Hubricht and TCB).

Holotype: Tl 5.60; hl 1.35; hw 0.98; pl 1.05; pw 1.24; el 3.17; ew 2.19; ant 3.75; aedeagus 1.12.

Allotype: Tl 5.50; hl 1.28; hw 0.98; pl 1.02; pw 1.23; el 3.10; ew 2.03; ant 3.80.

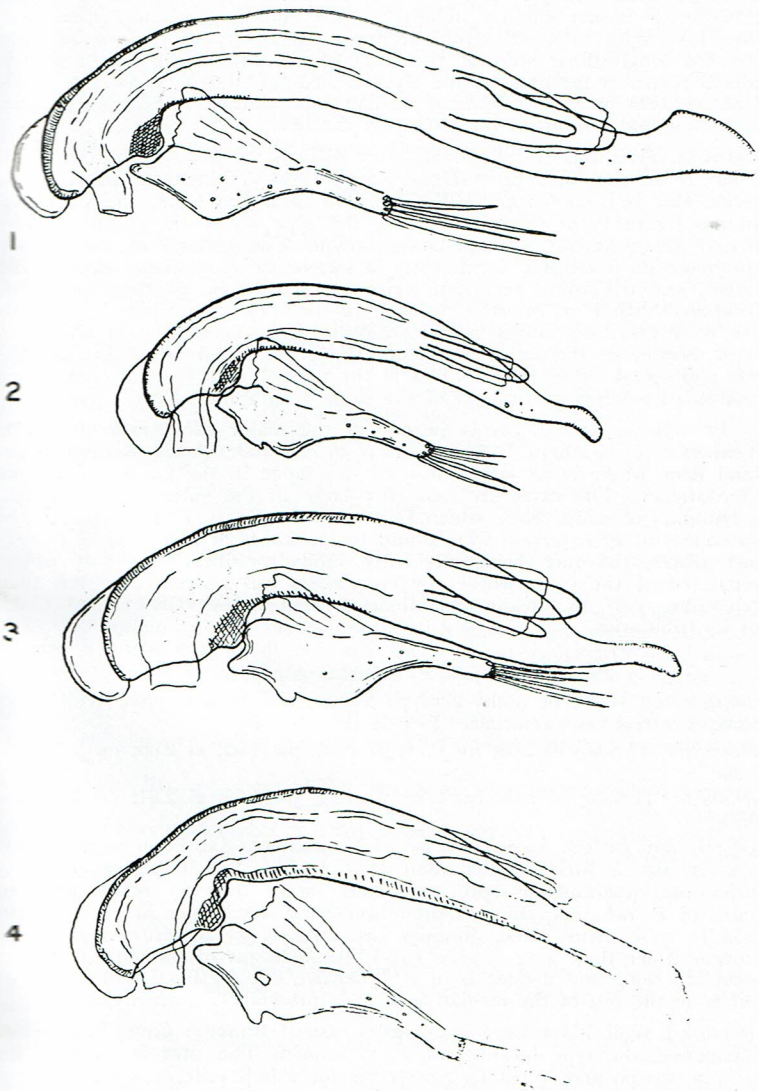

FIGURE 4. Aedeagi of *Pseudanophthalmus*. (1) *P. templetoni vanburenensis* n. subsp., paratype, X62. (2) *P. robustus megosteus* n. subsp., paratype, Big Bone Cave, X62. (3) *P. robustus farrelli* n. subsp., holotype X62. (4) *P. robustus lupus* n. subsp., paratype, X82.

Description: Length 4.3-5.6, av. 5.4, larger than any other described race of *P. robustus*. Pronotum less transverse (index 0.83-0.85). Elytra proportionately wider; longitudinal striae more profound; punctations clearer; prehumeral border slightly oblique to the mid-line in most specimens; humeral angles rounded; apical recurrent stria very short, running into the 3rd longitudinal stria at the level of the 3rd discal seta, which is placed relatively far back on the elytron. Aedeagus 1.01-1.12, av. 1.05 (0.88-1.02, av. 0.96 in *P. r. robustus*); median lobe thicker; apex spout-shaped, as in nominate *robustus,* but relatively shorter.

Remarks: Five smaller individuals, very difficult to distinguish from *P. r. robustus* on the basis of external morphology, are included in the type series. One is from Cripp's Mill Cave, two from Jim Cave, and two from Indian Grave Point Cave. Sixteen of the type series (80%) are proportioned about as the holotype and allotype. The aedeagi of the smaller specimens do not differ significantly in size or structure from those of the larger, and the apical recurrent striae are shorter in all the type series, compared with *P. r. robustus*. In view of the very great similarity of both the small and large forms to *P. r. robustus,* the cohabitation of small and large beetles in the same caves, and the general correlation in aedeagal size and apical striae, it seems best at the present time to treat both larger and smaller forms as variants of the same geographic race.

P. robustus farrelli occurs in one of the major cave areas of Middle Tennessee, in southern DeKalb County at the base of the Eastern Highland Rim, where many large caves are developed in the Cannon limestone (Ordovician). The caves are especially large in the valley of Dry Creek, a tributary of Smith Fork, which flows into the Caney Fork River. All the specimens of *P. r. farrelli* were found under stones or rotten wood in very wet places, the race being decidedly subhydrophilic. The most widely separated of the caves where the type series was collected are less than ten miles apart, by stream, and all are located in the valley of Dry Creek or its tributaries.

Pseudanophthalmus robustus lupus n. subsp.

Type series: Holotype male, allotype female, and 18 paratypes, Wolf River Cave, Fentress Co., Tennessee, July 7, 1957 (TCB).

Holotype: Tl 4.60; hl 1.08; hw 0.74; pl 0.83; pw 1.03; el 2.60; ew 1.76; ant 3.36.

Allotype: Tl 5.10; hl 1.18; hw 0.88; pl 0.98; pw 1.08; el 2.84; ew 1.86; ant 3.70.

Description: Length 3.8-5.1, average of 20 specimens 4.6. Form more slender, average size a little smaller than *P. r beaklei* Val. Posterior angles of pronotum quadrangular, proportionately larger than in other described races of *P. robustus;* sides of pronotum less curved than in *P. r. beaklei* and *P. r. robustus;* basal sinuosity just anterior to posterior angles; pronotum wider than long (index 1.10-1.24). Aedeagus of paratype 0.86; median lobe long and slender as in *P. r. beaklei,* but the basal bulb is not set off from the rest of the median lobe by a pronounced constriction.

Remarks: Wolf River Cave is 30 miles east of Bunkum Cave, Pickett Co., Tennessee, the type locality for *P. r. beaklei*. The cave is traversed by a large stream and is readily penetrable for a half mile or more. It opens at the base of the Cumberland Plateau near the head of Wolf River, and is locally called "Blowing Cave". The beetles were collected 100 yards inside the cave in a pile of leaf debris on a shelf above the stream.

Pseudanophthalmus macradei Valentine

1948, Geol. Surv. Alabama, Mus. Pap. No. 27, p. 9

P. macradei is the most abundant anophthalmid in Cumberland Caverns, Warren Co., Tennessee, which is the type locality. It was collected by

Valentine (1948) and Henrot (Jeannel, 1949) near the Historic Entrance. The writer has found it near all three entrances, in the Oasis Room, in the Long Crawlway, and at Dudleys Waterfall. The last two of these localities are far in the interior of the caverns, remote from any known entrance. The coexistence of *P. macradei* with the closely related *P. robustus neglectus*, similar in size and many other features, may be explained on the basis of the considerable genital differentiation. Both forms are found under rocks in wet places, or crawling about over wet flowstone walls or on damp silt in the crawlways.

A single male of this species, not distinguishable from specimens from Cumberland Caverns, was collected in Turkeyscratch Cave, on Rocky River in eastern Warren County, 8 miles northeast of Cumberland Caverns, January 1, 1958.

Pseudanophthalmus t. templetoni Valentine

P. templetoni Valentine, 1948. Geol. Surv. Alabama, Mus. Pap. No. 27, p. 7

Known only from the Historic Entrance section of Cumberland Caverns, Warren Co., Tennessee, *P. t. templetoni* is the largest known species of its genus. It ranges in length between 6.5 and 7.0 mm. Two specimens were taken April 27, 1957, in the drier parts of the cave, 600 feet from the Historic Entrance, and two additional specimens were found in damper places, 250 feet from the entrance, June 23, 1957.

Pseudanophthalmus templetoni vanburenensis n. subsp.

Type series: Type male and four paratype males, McElroy Cave, 1.5 miles northeast of Bone Cave P. O., Van Buren Co., Tennessee, June 23, 1957 (Leslie Hubricht and TCB).

Type: Tl 6.25; hl 1.40; hw 0.98; pl 1.12; pw 1.17; el 3.42; ew 2.06; ant 3.26; aedeagus 1.52.

Description: Length 6.0-6.5. Features similar to those of smaller individuals of *P. t. templetoni*, with the following differences. Head wider. Anterior margin of pronotum rectilinear, without a slight concavity; basal sinuosity of lateral margins of pronotum less profound; posterior angles not produced. Humeri rounded, not angular; prehumeral border less obliquely inclined. Apex of median lobe of aedeagus slightly produced obliquely forward and backward into a knob the shape of a boot; 4 or 5 setae on parameres.

Remarks: The five specimens of the type series were collected from beneath rocks at the base of a flowstone formation 400 feet from the entrance and from under rocks near a shallow pool 500 feet from the entrance. *P. t. vanburenensis* is much less common than *P. robustus megosteus*, found in the same cave.

engelhardti group

Pseudanophthalmus hesperus n. sp.

Type series: Type male and three paratype males, Bethel Cave, Perry Co., Tennessee, February 14, 1957 (TCB); one paratype male from Bethel Cave, June 16, 1957 (Catherine Barr and TCB).

Type: Tl 4.11; hl 0.94; hw 0.77; pl 0.70; pw 0.93; el 2.47; ew 1.40; ant 2.68.

Description: Length 3.7-4.1, av. 4.0. Pale, reddish brown. Head small and rounded; genae with rather long pubescence. Pronotum wider than long, medium convex; pubescence sparse, a few short discal hairs; anterior margin slightly concave; lateral margins curved anterior three-fourths, parallel posterior fourth; posterior angles rectangular; base wide. Elytra somewhat depressed, elliptical; pubescence dense; humeri angular; prehumeral border perpendicular to median line; posthumeral border setose but not serrulate; longitudinal striae poorly developed but distinct; punctations not visible; first discal seta at level of 4th humeral marginal

puncture; apical recurrent stria as in *P. engelhardti,* rather long, slightly indented, parallel to the elytral suture, and running into the 3rd longitudinal stria well in advance of the level of the 3rd discal seta. Antennae of moderate length, reaching back to the level of the 2nd discal seta. Legs of moderate length. Aedeagus of paratype: length 0.54; median lobe short and thick; basal bulb thick, only slightly flexed; apex of median lobe spatulate, as in *P. rotundatus* Val.; parameres short and stout, armed with five rather short setae.

Remarks: The discovery of this species considerably extends the recorded range of *Pseudanophthalmus* of the *engelhardti* group, previously known in the Tennessee Valley from Claiborne County, Tennessee, southward and westward along the Tennessee River Basin to Chattanooga, Tennessee, and Huntsville, Alabama. Bethel Cave is in the valley of the Buffalo River, a tributary of the Tennessee. The cave is penetrable for 1500 feet, and is developed in the Bob limestone (Silurian). In wet weather, surface wash enters the cave, carrying logs, sticks, and leaves, which are deposited along the banks of the stream. The beetles were found under logs and stones, but were not abundant.

Pseudanophthalmus tiresias tiresias n. sp. and subsp.

Type series: Holotype male allotype female, three paratype males, and one paratype female, Indian Grave Point Cave, 6 miles southwest of Smithville, DeKalb Co., Tennessee, December 27, 1956 (C. E. Farrell, Catherine Barr, and TCB).

Holotype: Tl 3.56; hl 0.79; hw 0.65; pl 0.65; pw 0.79; el 2.11; ew 1.22; ant 2.45.

Allotype: Tl 3.38; hl 0.79; hw 0.63; pl 0.63; pw 0.79; el 1.95; ew 1.21; ant 2.11.

Description: Length 3.4-3.6. Color very pale, testaceous. Slender, somewhat depressed, elongate. Head rounded, rather wide; labrum distinctly trilobate. Pronotum rather large and slightly transverse, convex; sparsely pubescent; anterior angles prominent; sides strongly curved; basal sinuosity strong and short; posterior angles small, rectangular. Elytra elongate, depressed, finely pubescent; humeri angular; prehumeral border obliquely inclined to the mid-line; post-humeral border setose, not serrulate; first discal seta slightly posterior to level of 4th marginal puncture; longitudinal striae converging to puncture of first discal seta, and usually to puncture of 2nd discal seta; punctations very fine; apical recurrent stria rounded, not indented or flexed, running into 3rd longitudinal stria just anterior to the 3rd discal seta. Antennae and legs of moderate length. Mandibles rather slender. Aedeagus of paratype: small (0.46); median lobe short, fairly thick; basal bulb little developed; apex rod-like, not spatulate; copulatory pieces short, with a wide base and blunt apex; parameres short, stout, with four short setae.

Remarks: The type locality is a huge, damp cave in the valley of Dry Creek, which flows into Smith Fork, a tributary of Caney Fork of Cumberland River. The beetles were collected under rotten wood under a slow drip from the ceiling, far in the depths of the cave. *P. robustus farrelli* was collected in the same cave, although in different places. *P. tiresias* is the first species of the *engelhardti* group to be discovered outside the Tennessee Valley.

P. tiresias differs from other species in the *engelhardti* group principally in the short, rounded (not indented) apical stria of the elytra, in the reduced basal bulb of the aedeagus, and in the simple, unmodified (never spatulate or truncate), aedeagal apex. Beetles conforming to this broad diagnosis were obtained from thirteen Middle Tennessee caves (including the type locality of the nominate race). Seven distinct but closely related forms are recognized in this paper, and are described as subspecies. In-

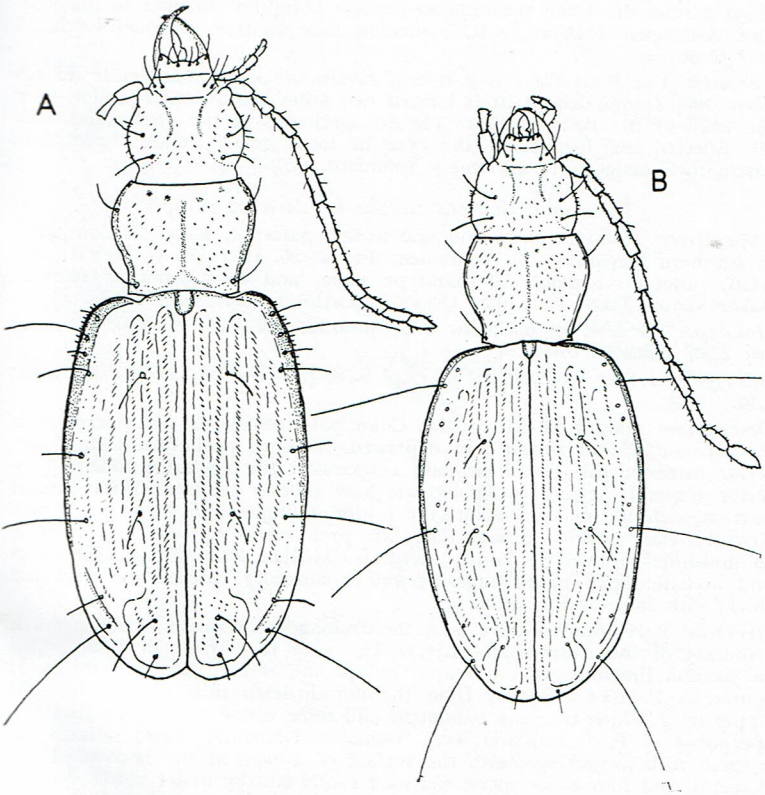

FIGURE 5. (A) *Pseudanophthalmus hesperus* n. sp., type male, X23.
(B) *Pseudanophthalmus tiresias tiresias* n. sp. and subsp., holotype male X23.

adequte material from five of the caves has not yet been diagnosed below the species level.

Pseudanophthalmus tiresias catherinae n. subsp.

Type series: Holotype male, allotype female, and 33 paratypes, Petty Cave, Marshall Co., Tennessee, August 10, 1957 (Catherine Barr and TCB).

Holotype: Tl 5.10; hl 1.03; hw 0.79; pl 0.93; pw 1.08; el 2.80; ew 1.72; ant 3.00.

Allotype: Tl 5.10; hl 1.03; hw 0.81; pl 0.93; pw 1.13; el 2.80; ew 1.72; ant 3.24.

Description: Length 4.2-5.1, av. 4.8. Color pale, reddish-brown, testaceous. Form robust, depressed. Lateral margin of pronotum strongly curved, basal sinuosity very short; posterior angles small but salient. Longitudinal striae

of elytra feebly impressed; usually 3rd and 4th striae converging to the puncture of the first discal seta; striae more or less disorganized on anterior surface of elytra; prehumeral borders obliquely inclined to the mid-line. Aedeagus of paratype 0.55; median lobe arcuate; parameres with 3 or 4 setae.

Remarks: The Petty Cave is a stream cavern of large to moderate dimensions, 1000 feet in length. It is located two miles northwest of Talley, near the head of the Petty Hollow. The 35 specimens of the type series were all collected 250 feet inside the cave in loose gravel beside the stream, where the beetles were extremely abundant.

Pseudanophthalmus tiresias insularis n. subsp.

Type series: Holotype male and one female paratype, Baker Station Cave, in northern Davidson Co., Tennessee, August 26, 1957 (B. C. Stewart and TCB); allotype female, one paratype male, and four paratype females, Baker Station Cave, December 18, 1956 (Catherine Barr and TCB).

Holotype: Tl 3.94; hl 0.88; hw 0.71; pl 0.76; pw 0.83; el 2.20; ew 1.35; ant 2.50; aedeagus 0.45.

Allotype: Tl 3.82; hl 0.88; hw 0.71; pl 0.78; pw 0.88; el 2.06; ew 1.35; ant 2.50.

Description: Length 3.8-4.1, av. 4.0. Color pale, testaceous, but darker than *P. t. tiresias*. Form robust and depressed. Sides of pronotum arcuate anterior three-fourths, rectilinear and subparallel the posterior fourth; posterior angles large and quadrangular; base slightly concave in the medial portion with the margins below the posterior angles oblique or excavated. Elytral striae shallow; humeri angular; prehumeral border perpendicular to mid-line; posthumeri faintly serrulate. Median lobe of aedeagus short and arcuate; apex blunt, tapering rather abruptly; parameres large and thick, with four flexible setae.

Remarks: Baker Station Cave is in the drainage of Mansker Creek, a north tributary of the Cumberland River. The cave is a small one, developed in Silurian limestone of the Wayne group, and is used as a private water source. A 150-foot crawlway from the mouth leads into a more spacious upper level, which contains a domepit and some rotten wood. The first two specimens of *P. t. insularis* were found in December, 1956, isolated on a small rock projecting above the surface of a pool at the bottom of the domepit, and four other specimens were found nearby under rotten boards. Both of the two specimens collected in August, 1957, were taken from loose gravel at the point where the crawlway joins the upper gallery.

Pseudanophthalmus tiresias occidentalis n. subsp.

Type series: Holotype male, De Priest Branch Cave, Lewis Co., Tennessee, February 10, 1957 (TCB); paratype male from De Priest Branch Cave, January 3, 1958 (TCB); allotype female and four female paratypes, Cave Branch Cave, Hickman Co., Tennessee, June 16, 1957 (TCB).

Holotype: Tl 3.92; hl 0.82; hw 0.69; pl 0.73; pw 0.84; el 2.33; ew 1.40; ant 2.41; aedeagus 0.62.

Allotype: Tl 3.83; hl 0.84; hw 0.72; pl 0.77; pw 0.84; el 2.16; ew 1.33; ant 2.28.

Description: Length 3.8-3.9. Pale reddish, testaceous. Form medium convex, slender. Pronotum subquadrate; anterior border not concave; sides arcuate the anterior three-fourths, subparallel posterior fourth; posterior angles large, slightly elevated, quadrangular, but smaller than in *P. t. insularis*. Prehumeral borders of elytra perpendicular to the mid-line. Aedeagus large (0.53); median lobe extended, less arcuate; basal bulb with a large keel; parameres rather slender, slightly curved, bearing three long setae.

Remarks: De Priest Branch Cave is on the right side of Cane Creek, a tributary of Buffalo River, and is located a quarter mile from the creek

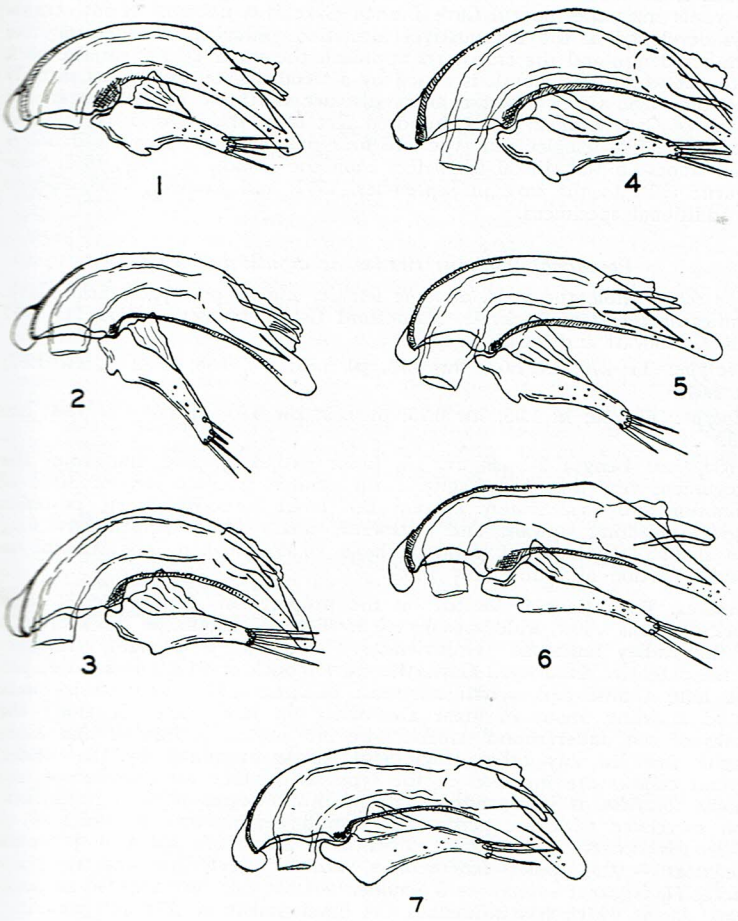

FIGURE 6. Aedeagi of *Pseudanophthalmus tiresias* subsp., X82.
(1) *P. t. tiresias* n. sp. and subsp., paratype.
(2) *P. t. insularis* n. subsp., holotype.
(3) *P. t. bendermani* n. subsp., paratype.
(4) *P. t. catherinae* n. subsp., paratype.
(5) *P. tiresias tullahoma* n. subsp., paratype.
(6) *P. t. acherontis* n. subsp., paratype.
(7) *P. t. occidentalis* n. subsp., holotype.

in a tributary hollow, in the Farmers Exchange Community. It is a small, damp cave developed in limestone of the Wayne group (Silurian). Both beetles from this cave were taken from beneath stones in a damp place 100 yards from the mouth. Cave Branch Cave is a network of low crawlways developed in the Beech River formation (Silurian). The entire cave is rather damp, and the crawlways approach the water table near the back of the network. The mouth is closed by a wooden gate, and opens directly onto the Cane Creek Road a short distance north of Rt. 100, near the mouth of Cave Branch, a few hundred feet from the right bank of Cane Creek. The five females (allotype and four paratypes) were collected under small stones on wet silt 50 to 80 feet from the mouth, in June, 1957. Subsequent visits to the cave in September, 1957, and January, 1958, yielded no additional specimens.

Pseudanophthalmus tiresias acherontis n. subsp.

Type series: Holotype male, allotype female, and 50 paratypes; Echo Cave, 2 miles northeast of Rockvale, Rutherford Co., Tennessee, August 26, 1957 (Bill C. Stewart and TCB).

Holotype: Tl 4.70; hl 1.03; hw 0.73; pl 0.83; pw 0.98; el 2.64; ew 1.57; ant 3.04.

Allotype: Tl 4.50; hl 1.03; hw 0.73; pl 0.83; pw 0.93; el 2.44; ew 1.54; ant 2.79.

Description: Length 3-7-4.8, av. 4.5. Color extremely pale, testaceous, the integument very thin and fragile. Form slender, medium convex. Sides of pronotum only moderately curved, the basal sinuosity short; posterior angles projecting upward and backward, small, acute. Appendages long and slender. Aedeagus of paratype large (0.53); median lobe straight in middle portion and unusually thick.

Remarks: Echo Cave is located on the property of Tenner Ferris, near Rockvale. It is a low, wide stream cave 1500 feet in length, and is developed in the Ridley limestone (Ordovician). The stream is probably tributary to the extensive Snail Shell Cave, the chief mouth of which is a huge, pit-like hole a mile and a half northeast of Echo Cave. The beetles were found crawling about in great abundance on loose, wet silt along the banks of the underground stream. The integument is thinner and more fragile than in any other troglobious beetle examined by the writer. Several callows are included in the type series; they are translucent and almost colorless. It is suggested that the thin integument is a rudimentation correlated with the perpetually humid environment in which *P. t. acherontis* occurs. An apparent absence of the more common potential predators — the spider *Liocranoides unicolor* Keyserling and the cave cricket *Hadenoecus subterraneus* Scudder — from this cave may be an additional factor which has influenced the development of thin integument.

Pseudanaphthalmus tiresias tullahoma n. subsp.

Type series: Holotype male, allotype female, and two male paratypes; Carroll Cave, Coffee Co., Tennessee, July 27, 1957 (Catherine Barr and TCB).

Holotype: Tl 4.60; hl 1.03; hw 0.74; pl 0.88; pw 0.93; el 2.50; ew 1.61; ant 3.23.

Allotype: Tl 4.05; hl 0.88; hw 0.69; pl 0.76; pw 0.83; el 2.20; ew 1.42; ant 2.54.

Description: Length 4.0-4.6. Color reddish-brown, testaceous. Form of moderate depth and width. Sides of pronotum moderately rounded; posterior angles small and blunted. Prehumeral border obliquely inclined to the mid-line; 3rd and 4th elytral striae not converging at first discal puncture. Aedeagus of paratype 0.49; median lobe dorsally flattened in profile view and rather thick (but thinner than in *P. t. acherontis*).

Remarks: Carroll Cave is located on the left bank of Carroll Creek, a tributary of Duck River, about 3 miles north of Tullahoma. It is a large network-pattern cave developed in the Catheys formation (Ordovician). All four beetles were collected from beneath rocks in a loop passage to the north of the vast entrance chamber, near a fresh deposit of dung of the wood rat (*Neotoma magister Baird*).

Pseudanophthalmus tiresias bendermani n. subsp.

Type series: Holotype male, allotype female, three male and two female paratypes, Benderman Cave, Maury Co., Tennessee, August 10, 1957 (TCB). *Holotype*: Length 3.8-4.1, av. 4.0. Form slender, moderate depth. Color pale, light reddish. Posterior angles of pronotum quadrangular, blunted, and slightly salient, smaller than in *P. t. insularis*. Prehumeral border oblique; 3rd and 4th longitudinal striae of elytra not convergent at 1st discal seta; apical recurrent stria rounded in some specimens, in others the anterior portion of the groove is oblique (not arcuate) to the 3rd longitudinal stria. Aedeagus 0.49 long; median lobe arcuate.

Remarks: The Benderman Cave is located 2 miles west of Southport on property of Carl Benderman. It is a narrow, long cave traversed by a small but permanent stream, and is developed in the Hermitage formation and Bigby limestone (Ordovician). The cave is inhabited in the summer by a large colony of bats (*Myotis grisescens* Howell). All of the beetles were found by sifting gravel at the stream's edge not far from a bat guano deposit. Benderman Cave is in the drainage of the Duck River.

Key to Subspecies of *Pseudanophthalmus tiresias* n. sp.

1 3rd and 4th elytral striae converging to puncture of first discal seta ... 2
3rd and 4th elytral striae not converging at first discal seta ... 3

2 Size small (3.5-4.0 mm); form slender and deep ... *P. tiresias tiresias* n. sp. and subsp.
Size larger (4.2-5.1 mm); form robust and depressed ... *P. tiresias catherinae* n. subsp.

3 Prehumeral border perpendicular to mid-line, or nearly so ... 4
Prehumeral border obliquely inclined to mid-line ... 5

4 Posterior angles of pronotum large and quadrangular; aedeagus smaller (0.45 mm), median lobe arcuate ... *P. tiresias insularis* n. subsp.
Posterior angles of pronotum smaller; aedeagus large (0.53 mm), median lobe extended, less arcuate ... *P. tiresias occidentalis* n. subsp.

5 Integument thin and fragile; color very pale, testaceous; aedeagus large (0.55 mm), median lobe straight in middle portion and unusually thick ... *P. tiresias acherontis* n. subsp.
Integument normal; color less pale, reddish-brown; aedeagus smaller (0.49 mm), median lobe less thick ... 6

6 Size larges (4.0-4.6 mm); median lobe of aedeagus almost straight in middle portion and rather thick (but thinner than in *P. t. acherontis*) ... *P. tiresias tullahoma* n. subsp.
Size smaller (3.8-4.1 mm); median lobe of aedeagus strongly arcuate ... *P. tiresias bendermani* n. subsp.

packardi group (new group)

Size small (3.7-3.8); form moderately robust and depressed; coloration pale; head rounded; labrum concave; both pronotum and elytra pubescent;

first discal seta at level of 4th humeral marginal seta; longitudinal elytral stria well developed, punctation absent; apical recurrent stria basally oblique, indented, then running parallel to the suture into the 3rd longitudinal stria at the level of the 3rd discal seta. Aedeagus short and thick, basal bulb greatly reduced; copulatory pieces a pair of subequal, leaf-like plates. Type: *P. packardi* n. sp.

Pseudanophthalmus packardi n. sp.

Type series: Holotype male, allotype female, two male and three female paratypes, Bat Cave, Carter Caves State Park, Carter Co., Kentucky, May 26, 1957 (TCB).

Holotype: Tl 3.72; hl 0.72; hw 0.61; pl 0.75; pw 0.84; el 2.24; ew 1.33; ant 2.16.

Allotype: Tl 3.79; hl 0.86; hw 0.75; pl 0.72; pw 0.86; el 2.19; ew 1.42; ant 2.10.

Description: Length 3.7-3.8. Color pale, reddish, testaceous. Form moderately robust and depressed. Head rounded; labrum concave; genae globose, with a few small setae. Pronotum medium-convex, pubescent; anterior angles large and projecting; sides curved to the basal sinuosity, then subparallel to the large, rectangular posterior angles; base rather wide, rectilinear. Elytra elongate, rather depressed, pubescence well developed in longitudinal rows on the interstriae; humeri subangular; prehumeral border setose, faintly serrulate, nearly perpendicular to the mid-line; first discal seta at level of 4th humeral marginal seta; longitudinal striae prominent; punctations not visible; apical recurrent stria oblique, indented, then running parallel to the suture into the 3rd longitudinal stria at the level of the 3rd discal seta. Antennae of moderate length, extending back to the middle of the elytra. Legs rather long. Aedeagus of paratype 0.68; median lobe short and thick, homogeneously arcuate throughout its length; basal bulb greatly reduced; mid-sagittal keel on basal bulb very small; apex bluntly rounded; copulatory pieces a pair of simple, lamellar plates, subequal in size; left piece broadly notched toward the apex; parameres fairly short, armed with four stout setae, the uppermost (dorsal) very short.

Remarks: This is undoubtedly the species collected by A. S. Packard (1888) at Carter Caves and erroneously identified as *Anophthalmus pusio* Horn by LeConte. *P. pusio* (Horn) is a species from Montgomery Co., Virginia, only remotely related to *P. packardi*. After Packard's visit to Carter Caves, other attempts to secure specimens of anophthalmids from Bat Cave (Bolivar and Peannel, 1931; Jeannel, 1949) were unsuccessful.

Bat Cave occurs in the drainage basin of the Little Sandy River, a tributary of the Ohio. It is a large tunnel cave, with upper and lower entrances, and is traversed by a stream. The cave is developed in the Ste. Genevieve limestone (Mississippian). The beetles were collected from organic debris deposited along the stream banks, 750 feet from the lower mouth.

Genus *Nelsonites* Valentine

Nelsonites walteri Valentine

1952, Geol. Surv. Alabama, Mus. Pap. No. 34, p. 18

A male of this species was collected in McElroy Cave, Van Buren Co., Tennessee, June 23, 1957. *N. walteri* is otherwise known only from the type locality, Johnson Cave, Putnam Co., Tennessee, twenty miles north of McElroy Cave. The writer's specimen, like Valentine's entire type series, was a teneral. It was found beneath a rock on wet flowstone, 400 feet from the mouth of the cave. Measurements of this specimen are as follows: tl 6.65; hl 1.67; hw 1.00; pl 1.10; pw 1.24; el 3.82; ew 2.28; ant 5.7; aedeagus 1.62.

Genus *Darlingtonea* Valentine

Darlingtonea k. kentuckensis Valentine

1952, Geol. Surv. Alabama, Mus. Pap. No. 34, p. 22

Fifty-one specimens of this beetle were taken December 16 and 17, 1956, in three caves in Pulaski Co., Kentucky: Wind Cave, 5 miles southeast of Somerset (12 specimens); Tater Cave, 0.5 mile southeast of Sloans Valley. 100 yards south of US 27 (9 specimens); and Piney Grove Cave, 0.25 mile north of Piney Grove Church and School, near Dykes (30 specimens). In all three caves *D. k. kentuckensis* was found to be a common cavernicole, crawling about in damp places.

Although Valentine (1952) states that the number of pre-basilar setae in *Darlingtonea* is eight, the writer found a certain amount of variation. Of 51 specimens, 25 (49%) have eight prebasilar setae, 19 (37%) have seven setae, and 7 (14%) have 9 setae. This variation was not correlated with any of the three populations studied. The 9th seta, where present, is a very small, median one.

Genus *Neaphaenops* Jeannel

Neaphaenops tellkampfi tellkampfi Erichson

Anophthalmus tellkampfii Erichson, 1844, Mullers Arch. Anat, u. Phys., p. 384

Neaphaenops Tellkampfi (Erichson). Jeannel, 1920, Bull. Soc. Entom. France, p. 154

Neaphaenops T. Tellkampfi Er., Jeannel, 1949, Notes Biospeologiques, Fasc. 4, p. 90

This is the first anophthalmid beetle to be discovered from North America. It ranges from Barren County, Kentucky, northward and eastward through eastern Edmonson County, most of Hart County, and into southern Hardin County. It is perhaps the most conspicuous cavernicole in Mammoth Cave, the type locality, where it is found on wet silt along the receding waters of Echo River, crawling about on wet flowstone, or abroad on sandy flats near the walls of galleries. *N. t. tellkampfi* was collected at the following places in Mammoth Cave: Audubon Avenue, Echo River, Gratz Avenue, Labyrinth, Mammoth Dome, Marion Avenue, Olive's Bower, Radio Room, Serena's Arbor. In Floyd Collins Crystal Cave, in Flint Ridge 5 miles east of Mammoth Cave, *N. t. tellkampfi* is exceptionally widespread and abundant, and occurs along the sandy floor of Floyds Lost Passage, in the long crawlways leading to Floyds Passage, and on the damper floors and walls of Pohl Avenue.

Collections referable to this race were made in the following Kentucky caves:

Edmonson County — Colossal Cave, Long Cave, Mammoth Cave, Proctor Cave, Floyd Collins Crystal Cave, White Cave, Little White Cave

Barren County — Brushy Knob, Burnet, Coach, James, Short, and Vance Caves near Park City; Railroad Cave, at Cave City (Cave City Cave)

Hart County — Ronalds Cave, Hogan Cave, and Little Hogan Cave, 3 miles NE Cave City; Copelin Cave, 2 miles W Millerstown (Leslie Hubricht); Cooch Webb Cave, 3 miles SW Priceville (Leslie Hubricht); Blind Snail Cave, 7 miles ENE Munfordville and 0.2 mile north of Rt. 357

Hardin County — Bland Cave, 1.5 miles NE Spurrier (Leslie Hubricht); Star Mills Cave, 1.5 W Star Mills (Leslie Hubricht)

Neaphaenops tellkampfi meridionalis n. subsp.

Type series: Holotype male, allotype female, and three paratypes, Hoy Cave, 2 miles north of Franklin, Simpson Co., Kentucky, March 2, 1957 (Leslie Hubricht); 19 paratypes, Hoy Cave, January 2, 1958 (TCB).

Holotype: Tl 6.15; hl 1.58; hw 0.92; pl 1.21; pw 1.14; el 3.52; ew 2.28; ant 4.16.

Allotype: Tl 6.13; hl 1.55; hw 0.92; pl 1.19; pw 1.16; el 3.52; ew 2.26; ant 4.33.

Description: Length 6.0-6.2 mm. Smaller and more slender than N. t. *tellkampfi*. The posterior angles of the pronotum are smaller, more acute, and slightly elevated. Longitudinal striations of elytra less profound. Aedeagus of paratype 1.32, differing from that of the nominate race in having a short keel on the basal bulb; apex of median lobe broadly truncate, not tapered; apex of right copulatory piece bluntly rounded, not quadrangular as in *N. t. tellkampfi*.

Remarks: The type locality is a spacious, muddy cave which extends underneath US 31-W. The main passage is devoid of fauna. The series of beetles taken on January 2, 1958, was found (a) at the end of a side passage on a wet wall, and (b) on damp walls and ceiling in a lateral fissure known locally as "The Narrows". The beetle fauna of this cave differs markedly from that of the Red River valley caves fifteen miles to the south. Hoy Cave is in the drainage basin of the Barren River, forty miles south of the Mammoth Cave region, where *N. t. tellkampfi* is abundant. No *Neaphaenops* have yet been collected in the intervening caves of Warren Co., Kentucky.

Discussion

A relatively homogeneous group of organisms such as the cave trechines would appear prima facie to be excellent material for investigation of the effects of isolation upon speciation. Discussions of cave isolation and its influence on raciation and speciation have been given by Valentine (1931, 1932, 1937, 1945, 1948, 1952) and Krekeler (1958). Both of these authors have assumed rather complete isolation of beetle populations in individual caves. Such an assumption is a critical one, because of its bearing on a genetical species concept, and consequently on the systematic interpretation of the cave animals under consideration.

In recent papers by students of American trechines, two antithetical taxonomic approaches are evident. Krekeler (1958) has treated certain of the southern Indiana *Pseudanophthalmus* as full species although they differ only in minor characters and inhabit caves a short distance apart. *P. eremita stricticollis* Jeannel is known from Marengo Cave, 10 miles from Wyandotte Cave, type locality for *P. e. eremita* (Horn), yet *stricticollis* is accorded full specific rank. A systematic approach based principally on morphology has been employed by Valentine (op. cit.) and Jeannel (1931, 1949) in describing American cave beetles. Both authors have made extensive use of trinomials.

In studying Tennessee and Kentucky cave material, one is confronted with an array of beetle populations from many caves, some of which differ conspicuously, some of which differ in only minor characters, and some of which are morphologically indistinguishable. Few caves may be connected by direct exploration. That openings penetrable to beetles extend between two given caves is in most cases not directly determinable.

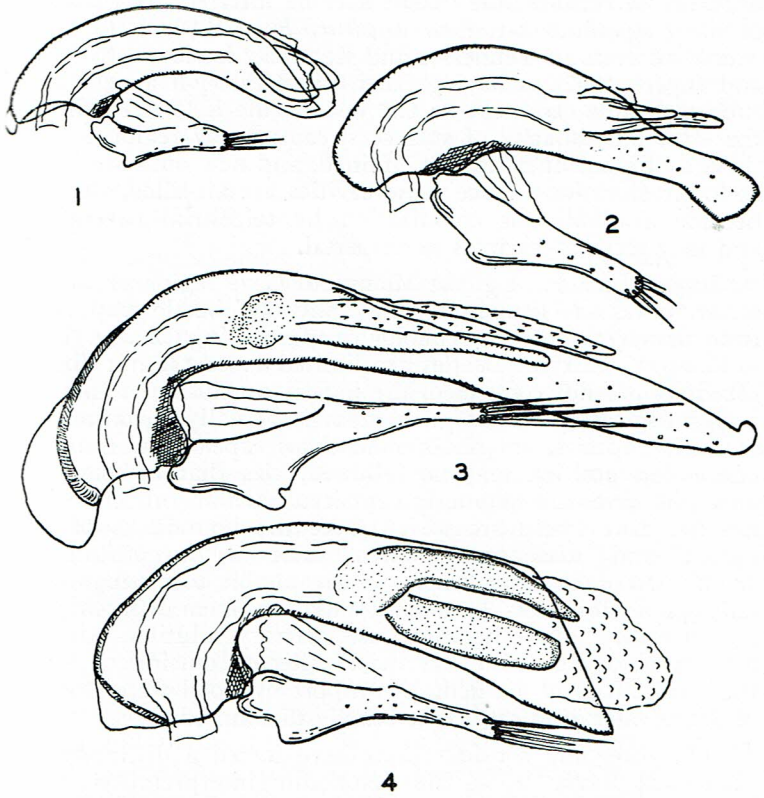

FIGURE 7. Aedeagi of *Pseudanophthalmus* and *Neaphaenops*.
(1) *P. packardi* n. sp., paratype, X62.
(2) *P. hesperus* n. sp., paratype, X100.
(3) *P. inexpectatus* n. sp., paratype, X100.
(4) *Neaphaenops tellkampfi meridionalis* n. subsp., paratype, X50.

The entrances to caves are, in general, fortuitous. Collapse of the roof or erosion by a surface wash cutting into an underground passage are the chief mechanisms which open caves to man. There are thus probably many more caves available for population by cavernicoles than are accessible to man. In limestone terrains a system of underground solution channels is developed at or slightly below the water table (cf. Civjic, 1918; Piper, 1932; Swinnerton, 1932). Flow of ground water

through such channels is locally amenable to study with the use of fluorescein dyes and other tracing techniques, and continuous openings of considerable extent may be inferred. The dispersal of the troglobious blindfish *Typhlichthys subterraneus* Girard over wide areas in Tennessee and Kentucky is viewed by Woods and Inger (1957) as having taken place through a network of sub-water-table channels. As the water table is lowered through the erosional capacity of surface streams or by regional uplift, these solutional openings are drained, and new ones are formed at lower elevations. Once these cavities are air-filled, they may become available for colonization by terrestrial cavernicoles, and may serve as avenues of dispersal.

In certain areas, e.g. the Mammoth Cave region or the Red River valley of Tennessee and Kentucky, beetle populations from many caves are morphologically indistinguishable. If one assumes (a) that the beetles are limited to caves, and (b) that the caves are not connected, the logical conclusion is that each morphological species in such areas is actually a constellation of sibling species, and taxonomic chaos supervenes. A middle-of-the-road position may be followed, viz., that in some karst areas the caves are ovbiously connected, and in others they are isolated. But where are we to stake the boundaries of "connected" and "disconnected" areas? The *circulus vitiosus* that "connected" areas exist where we are unable to distinguish, on a morphological basis, between populations from different caves, is a tempting but otherwise unsatisfactory solution. Although no troglobious trechine has been collected outside of a cave, the possibilities of accidental transport by flood waters or even of active migration cannot be wholly discounted.

The foregoing considerations have forced a distinctly morphological flavor upon the taxonomic interpretation of the beetles described in this paper. This approach is tempered with strong emphasis on the male genital apparatus, very similar aedeagi being construed as indicative of participation in the same gene pool. Decidedly dissimilar aedeagi per se indicate a mechanical barrier to gene flow between populations.

2

Valentine's (1932) observation that genital type in the genus *Pseudanophthalmus* appears to be correlated with river drainage basins deserves reevaluation in the light of recent findings. While this generalization holds rather well for the subgeneric groups which Valentine had studied at that time, it breaks down when applied to certain of the beetles described in this paper. *P. inexpectatus,* found in the Green River valley, is a hundred miles from the caves in the Kentucky River drainage where its closest known relative, *P. horni,* occurs. By stream the two localities are approximately four hundred miles distant. *P.*

tiresias has been collected in caves in the drainage areas of Buffalo River, Caney Fork River, Duck River, Elk River, Piney River, Stones River ,and two minor, north tributaries of the Cumberland. On the other hand, there is an abrupt and striking change from the beetle fauna of the Green and Barren drainages of south-central Kentucky (*Neaphaenops, menetriesi* and *pubescens* groups) to the Red River drainage to the south (*pubescens* group only). *P. robustus,* a widespread species with many races, appears to be well confined to the upper Cumberland River drainage in Tennessee, on the south side of the Cumberland.

Why there should be any correlation at all between lineage and drainage is probably explainable on geological grounds. Piper (1932) has described subterranean erosion in north-central Tennessee as a cyclic phenomenon, with stages of youth, maturity, and old age, corresponding to the three stages of W. M. Davis' classic cycle of surface erosion. The subterranean cycle need not proceed at the same pace as the surface cycle in the same terrain, so that surface divides and subterranean divides may not always coincide. As the water table is lowered and the underground spaces become air-filled, secondary streams may find their way into the cavities, further enlarging them and discharging into surface valleys. In Middle Tennessee most caves which have their mouths in valleys trend headward, subparallel to the long axes of the valleys (Barr, 1954).

In a river valley in a limestone terrain there appears thus to be a system of solution cavities, often interconnecting, trending headward, providing a route for the dispersal of cave trechines and other cavernicoles. In a comparatively long river valley one might expect partial isolation of large populations of cavernicoles, which could lead to genetic fixation, raciation, and ultimately speciation. In the Red River valley extensive collecting of *Pseudanophthalmus* has yielded two races of *P. ciliaris* and the closely related *P. orlindae,* which are not found in the caves of the Barren River drainage to the north, nor in the caves of the Cumberland River valley near Nashville, to the south.

Why does Valentine's generalization appear to hold in some instances and break down in others? If subterranean divides do not coincide with surface divides, as Piper (1932) has suggested, it is not unlikely that overlapping of subgeneric groups may occur, particularly near the headwaters of drainage systems. This phenomenon of overlapping was noted by Valentine (1932). His observation that the representative of the "allochthonous" group was often somewhat aberrant could signify a relatively long term isolation, effected by subterranean stream piracy, from the other species of its group.

The subgeneric groups mentioned by Valentine in his 1932 paper inhabit caves of the faulted and folded Appalachian valley of Virginia and West Virginia. The caves and streams are largely developed in narrow strike belts of limestone separated by non-caverniferous strata. Even the caves of the Greenbrier valley, where the strata are but slightly inclined, occur in a comparatively limited limestone area. Although underground avenues of dispersal from one cave to another are possible, such avenues between adjacent limestone valleys are stratigraphically and structurally highly improbable. In central Tennessee and Kentucky, however, the rocks are relatively flat-lying, and wide areas are floored with limestone. Caves have been discovered in nearly all of the stratigraphic formations recognized in the Central Basin of Tennessee. The Central Basin corresponds approximately to the range of the widespread *P. tiresias*.

A final consideration is that further, more intensive collecting is needed, particularly in the Appalachian valley and in east-central Kentucky, before the distributions of the various sub-generic groups are adequately understood. When these additional data are at hand, the lineage-drainage relationship may not be as close as it now appears to be.

3

The occurrence of pairs of closely related species of *Pseudanophthalmus* within the same cave has been discussed by Valentine (1945), who postulates a sympatric origin for the pairs, terming the process "associative speciation". Barriers between two segments of a population are thought to arise as macromutations. Such barriers may be physiologic or ethologic, according to Valentine. Examples of sympatric pairs of closely related species are *P. menetriesi* and *P. striatus* in the Mammoth Cave region, and *P. engelhardti* and *P. rotundatus* in English Cave, Claiborne Co., Tennessee. In the present paper the pair *P. ciliaris loganensis* and *P. orlindae* constitutes a new example of this phenomenon.

In the case of the latter pair, extensive collecting has demonstrated an apparent overlapping of ranges. Morphologically indistinguishable populations of the two species have been obtained from several caves at different points along the Red River valley. In low bluffs near the river the writer has explored extensive networks of crawlways excavated during a period when the water table was higher than it is today.

The Red River valley is believed to contain a vast network of solutional openings connecting its caves. Small crawlway caves may be inhabited by immense beetle populations. In Double Cave, near Milldale, Robertson Co., Tennessee, 92 specimens of *P. ciliaris loganensis* were collected by two per-

sons in half an hour ,yet the cave is only 3 feet high, 5 feet wide, and 60 yards in length.

One cannot completely negate the possibility of a sympatric origin for *P. ciliaris loganensis* and *P. orlindae*. A more likely mode of speciation, in the writer's opinion, is the following. Ancestral *pubescens* group stock, finding its way into the headwaters of the Red River by crossing the divide (or being transferred across by subterranean stream piracy) between the Barren and Red Rivers, became established in Red River caves.

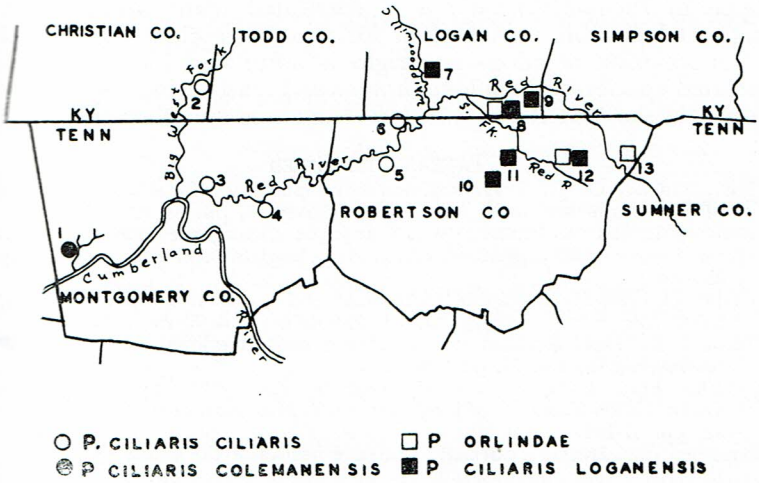

FIGURE 8. Distribution of *Pseudanophthalmus* in the Red River valley. (1) Coleman Cave, (2) Glover Cave, (3) Dunbar Cave. (4) Durham Cave, (5) Bell Witch Cave, (6) Buzzard Cave (Keysburg), (7) Collier Saltpeter Cave, (8) Cook Cave, (9) Buzzard Cave (Schochoh), (10) Christian Cave, (11), Double Cave, (12) Jesse James Cave, (13) Cheeks Tavern Cave.

The population gradually spread downstream. At some time in the past downstream and upstream segments of the population were isolated and diverged, the upstream segment giving rise to *P. orlindae*, the downstream to *P. ciliaris*. Subsequently *ciliaris* began moving upstream, perhaps because of the opening of recently excavated cavities again linking the two segments. *P. ciliaris* itself shows minor differences between upstream and downstream populations, possibly indicating that free migration (between Collier Saltpeter Cave, Logan Co., Kentucky, and Buzzard Cave, near Keysburg, Kentucky, just south of the Kentucky line in Tennessee) is again becoming restricted. *P. ciliaris*

loganensis, the upstream portion of the *ciliaris* population, has invaded the range of *P. orlindae,* the two species successfully competing in the same caves.

Summary

Seventeen new species and subspecies of *Pseudanophthalmus* and one new subspecies of *Neaphaenops* are described from the caves of central Tennessee and Kentucky. The degree to which populations of troglobious beetles are isolated from each other in different caves is discussed. It is concluded that cave isolation may not be as restricted as some authors have supposed. Exceptions are noted to Valentine's observation that genital type in *Pseudanophthalmus* is correlated with surface drainage, and possible explanations for these exceptions are offered. A mechanism of allopatric origin is postulated for two closely related species of *Pseudanophthalmus* found living together in caves of the Red River valley in Tennessee and Kentucky.

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