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The Taxonomy, Distribution, and Affinities of *Neaphaenops*, with Notes on Associated Species of *Pseudanophthalmus* (Coleoptera, Carabidae)

THOMAS C. BARR, JR.[1]

ABSTRACT

Neaphaenops Jeannel includes one polytypic species, *N. tellkampfi*, from caves of the Pennyroyal plateau and adjacent upland in west-central Kentucky. Four subspecies are described and illustrated: *tellkampfi tellkampfi* (Erichson), *t. viator*, new subspecies, *t. henroti* Jeannel, and *t. meridionalis* Barr. A key to subspecies and a distribution map are given. It is suggested that *Neaphaenops* shares a close common ancestry with *Pseudanophthalmus* of the *pubescens* species group, and *P. princeps*, new species (Kentucky and Tennessee) may possibly represent an intermediate evolutionary stage. Taxonomic changes are proposed for *Pseudanophthalmus ciliaris orlindae* Barr, new combination, and *P. loganensis* Barr, new status.

INTRODUCTION

The monobasic cave beetle genus *Neaphaenops* was established by Jeannel (1920) for *Anophthalmus tellkampfii* Erichson (1844), a large, eyeless trechine carabid first collected by Dr. Theodor Tellkampf on a visit to Mammoth Cave, Kentucky. Erichson compared it with *Anophthalmus schmidti* Sturm, described earlier in the same year from caves in Yugoslavia, and placed it in the same genus. The Mammoth Cave species thus became the first blind trechine to be discovered in North America and the world's second described species of this group of cave beetles. Unlike most other American cave trechines, *Neaphaenops tellkampfi* is unusually elongate and slender (fig. 1); with elongation of the head, the frontal grooves end blindly on the vertex instead of continuing around the sides of the head to delimit the cervicum, a facies which Jeannel (1926-1930) called "aphaenopsian." The species is also notable for its unusually extensive distribution and relative abundance. This study is based on examination of approximately 1000 specimens of *Neaphaenops* from 95 Kentucky caves, the great majority of specimens collected by me between 1955 and 1979.

Jeannel (1926-1930, 1949) placed both *Neaphaenops* and *Pseudanophthalmus* Jeannel (1920; approximately 185 cave species and one edaphobitic species in eastern United States) in the "*Trechoblemus* series" (see also Barr, 1972) but did not comment on the precise relationship between the two genera. *Neaphaenops tellkampfi* has been the subject of recent eco-

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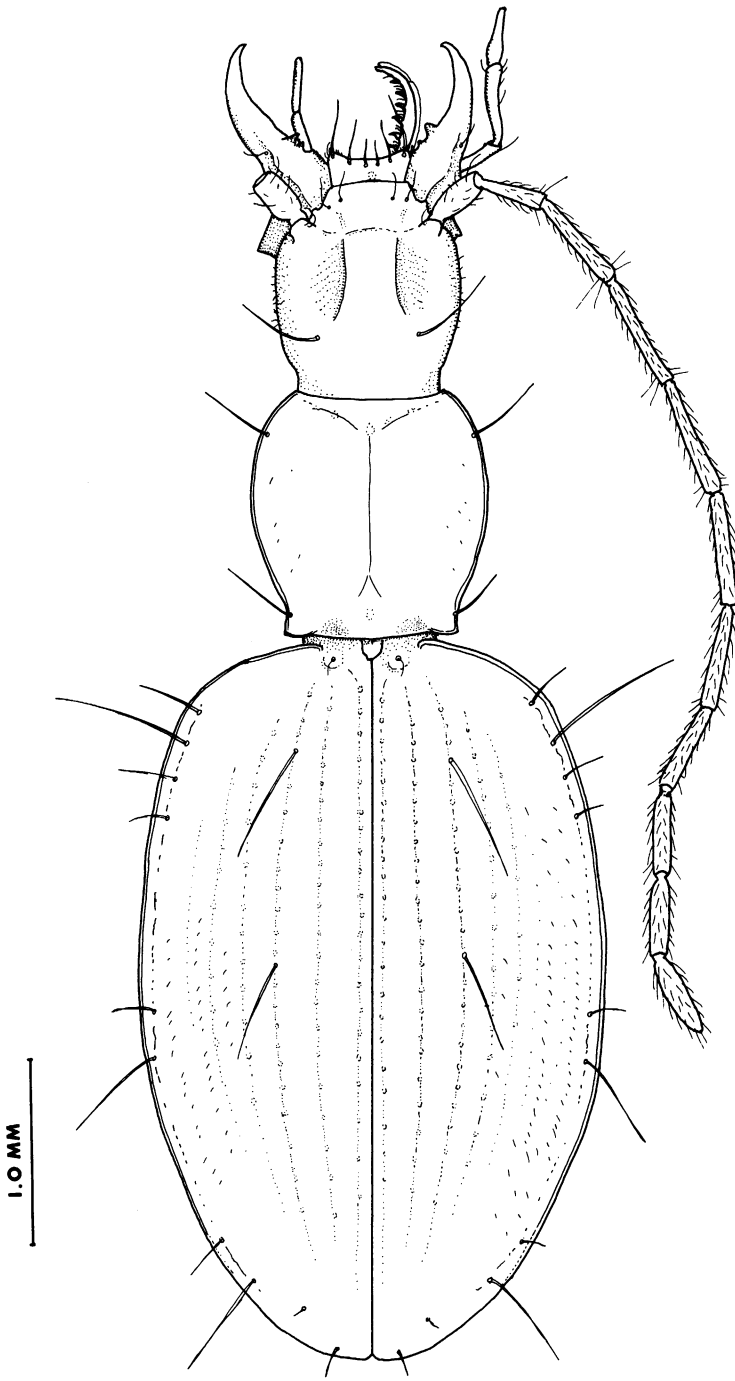

FIG. 1. *Neaphaenops t. tellkampfi* (Erichson), Diamond Caverns, Barren County, Kentucky.

logical, behavioral, and genetic studies, particularly in Mammoth Cave National Park and its immediate environs (Barr and Kuehne, 1971; Kane, Norton and Poulson, 1975; Norton, Kane and Poulson, 1975; Giuseffi, Kane and Duggleby, 1978). In contrast to most species of *Pseudanophthalmus* (including all 12 species with which it is sympatric), *Neaphaenops* feeds heavily on eggs of the rhaphidophorine "cave-cricket" *Hadenoecus subterraneus* (Scudder), which it digs from the moist silt of cave floors and ledges where they are deposited (Barr and Kuehne, 1971). This behavior presumably represents an adaptive shift away from the usual generalist feeder niches occupied by *Pseudanophthalmus* species, taking advantage of a new food and shortening the food chain from the surface to the food-poor cave environment. Crickets feed outside the caves at night, and their guano and eggs constitute an important fraction of the limited food available to the cave community (Park and Barr, 1961; Barr and Kuehne, 1971; Barr and Stoneburner, MS). *Neaphaenops* has not become so specialized that it has relinquished its feeding on other prey, but it has greatly broadened its niche by expanding it to include cricket eggs as an abundant and additional energy source. A close correspondence exists between the ranges of *Neaphaenops tellkampfi* and *Hadenoecus subterraneus* (Barr, 1968; Hubbell and Norton, 1978).

With its exclusive predation strategy *Neaphaenops tellkampfi* has far surpassed most species of *Pseudanophthalmus* in abundance. In Mammoth Cave it is so common on damp silt and sand fills that cave guides and explorers know it by the common name, "sand beetle." From modified Lincoln-Peterson estimates of local population densities in Mammoth Cave, Barr and Kuehne (1971) speculated that the total population of the species in the Mammoth Cave system alone might exceed 750,000 individuals. The range of *N. tellkampfi* (fig. 5), which is more extensive than that of any other North American cave trechine, is attributable to two factors: (a) the high vagility of this large, mobile, foraging species, and (b) the openness of solutional networks in the highly cavernous Mississippian limestones of the Pennyroyal plateau where it occurs (Barr, 1968; see also Giuseffi, Kane and Duggleby, 1978).

In Mammoth Cave National Park *N. tellkampfi* is the most abundant and most nearly ubiquitous of terrestrial troglobites. Protection of habitat and encouragement of ecological research by the National Park Service will probably result in further investigations of the biology of this species. The present paper attempts to relate nominate *tellkampfi* to other geographic races of the species and to formulate a theory of the evolutionary origin of *Neaphaenops* based on morphological and biogeographic considerations. There is no guarantee that the ecological and behavioral characteristics of *N. t. tellkampfi* in the Mammoth Cave region will be duplicated in all of its geographic races. Comparative studies of the other subspecies and of presumably related species of *Pseudanophthalmus* may shed light on the evolution of the shift in feeding strategy that appears to have proven so successful in *Neaphaenops*.

Taxonomic treatment of cave trechines in the interconnected solutional networks of the Mississippian plateaus (see Barr, 1967a) is complicated by cases of recent divergence. Pairs of closely similar taxa which cause interpretive problems fall into four categories: (1) no overlap of ranges, usually with strong geological evidence for extrinsic isolation; (2) ranges overlapping (a) broadly (several caves) or (b) narrowly (one or two caves only), with the overlap zone occupied by apparent hybrids; and (3) ranges contiguous but not overlapping, no evidence of extrinsic isolation (see Barr, 1962a, for an interpretation of (3) based on parapatric exclusion, also Wilson, 1975, for a theoretical basis for such exclusion). In *Neaphaenops* the relationships between the four taxa include (1); (2a); and (2b), respectively implying (1) no gene flow; (2a) moderate gene flow, and (2b) very limited gene flow. In the absence of genetic data I have taken a conservative approach and treated all four taxa as subspecies, but it is quite possible that *henroti* is an allopatric sibling species and *meridionalis* is a semispecies. The wide distribution and abundance of *Neaphaenops* populations offer an

unusual opportunity to assess the extent of gene flow between local populations of a terrestrial troglobite, employing both conspicuous morphological characters and electrophoretic allozyme techniques. Such studies require a sound taxonomic framework and a detailed knowledge of the distribution of putatively infraspecific taxa. Giuseffi, Kane and Duggleby (1978) have made an interesting preliminary study of six loci in populations of nominate *tellkampfi*; their results suggest that all their samples (several caves in the Mammoth Cave region) are from the same large gene pool.

ACKNOWLEDGMENTS

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TAXONOMY

NEAPHAENOPS JEANNEL

Neaphaenops Jeannel, 1920, p. 154. Type species, *Anophthalmus Tellkampfii* Erichson, by original designation. Jeannel, 1931, p. 469; 1949, p. 88.

Size large (6.3-7.5 mm.); form elongate, slender; subglabrous, rufotestaceous, shining, elytral microsculpture coarsely and somewhat irregularly transverse. Head one-fourth longer than wide, sides scarcely rounded and sparsely pubescent to glabrous; eyes absent; frontal grooves incomplete; one pair (posterior) of supraorbital setae. Pronotum slightly longer than wide, widest in apical one-third to one-half, base one-sixth wider than apex and three-fourths maximum width; basolateral impressions moderate, hind angles small, usually sharp, more or less right, and strongly reflexed. Elytra two-thirds to three-fourths longer than wide, strongly convex, deplanate around scutellum, apically attenuate; anterior discal puncture opposite second or third umbilicate; anterior apical puncture absent; humeri minutely setulose, not serrate; prehumeral borders strongly oblique; apical recurrent groove vestigial. Mandibles long and slender; last segment of maxillary palp four-fifths as long as penultimate segment; mentum tooth long and bifid; mentum and submentum fused; prebasilar setae 2 + 6. Antenna three-fourths body length. Legs very long and slender; protibia pubescent on anterior face. Aedeagus 1.28-1.45 mm. long, basal bulb large and sharply bent at right angle or more to straight, thick, apically truncate median lobe; basal opening and keel both quite small; transfer apparatus anisotopic: left (ventral) piece laterally compressed, with subparallel margins, heavily sclerotized, rounded or slightly knobbed at apex; right (dorsal) piece elongate, tentlike in cross-section, apex hyaline and slightly twisted at apex, a little longer than and partially enfolding left piece at base; parameres elongate and slender, with four or five long, apical setae.

Neaphaenops (and its single species, *N. tellkampfi*) is defined by a series of patently apomorphic characters, three of which are generically diagnostic: (1) last segment of maxillary palp shorter than penultimate segment (these segments are usually subequal in *Pseudanophthalmus* and other American trechines); (2) anterior pair of supraorbital setae and punctures absent; and (3) frontal grooves not extended onto sides of head. Other features are paralleled to a greater or lesser degree in various species of *Pseudanophthalmus*: (a) pronotum convex and hind angles strongly reflexed; (b) overall dorsal pubescence reduced; (c) humeral serrations absent, humeral setae sparse and minute; (d) elytra very convex with corresponding deplanate area near scutellum; (e) loss of the anterior apical puncture; and (f) rudimentation of the apical recurrent groove.

Neaphaenops tellkampfi is distributed along the Pennyroyal plateau and adjacent upland in west-central Kentucky from Meade and Breckinridge counties in the north, near the Ohio River, to Simpson and Allen counties in the south, near the Tennessee border. Four subspecies are recognized in the present study. Published descriptions of *N. t. henroti* (Jeannel,

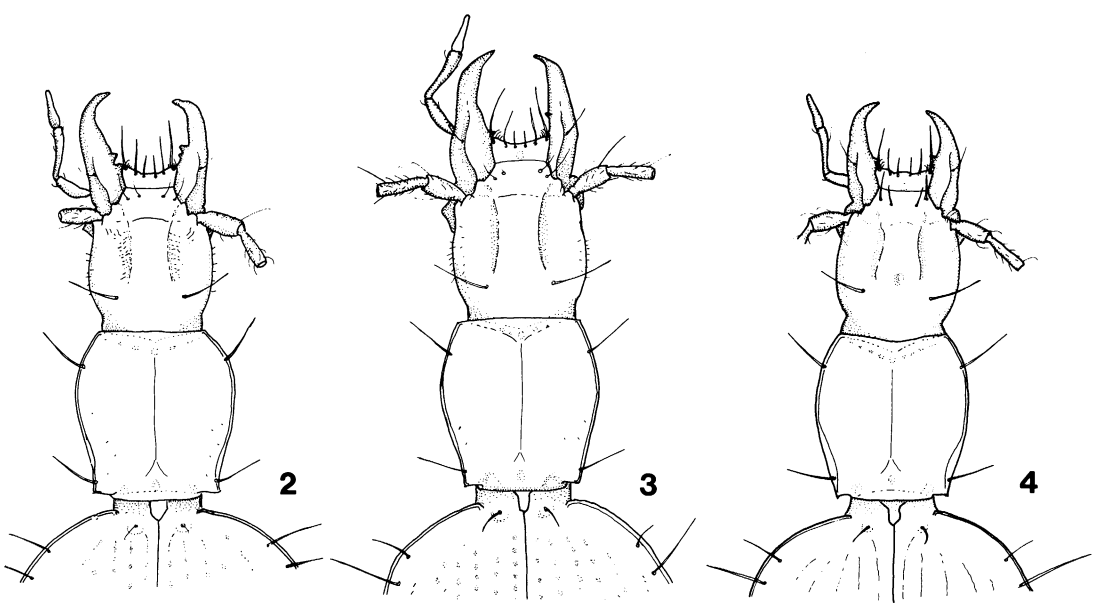
1949) and *N. t. meridionalis* (Barr, 1959) are not diagnostic in the light of the material recently examined. These subspecies are redescribed, and a new subspecies is described from the eastern part of the species' range. The four subspecies may be differentiated by the following key (which does not include *tellkampfi* × *viator* or *tellkampfi* × *meridionalis* hybrids).

KEY TO SUBSPECIES OF *NEAPHAENOPS TELLKAMPFI* (ERICHSON)

1. Elytra with single row of fine, very short pubescence on each interval, intervals flat or feebly subconvex, striae punctate; labrum singly emarginate, vertex without median pit 2
   Elytra virtually glabrous, intervals convex, striae impunctate; labrum doubly emarginate, vertex with median pit between frontal grooves; southern Warren, eastern Logan, northern Simpson, northwestern Allen counties ..... *tellkampfi meridionalis* Barr
2(1). Elytral striae shallow but distinct, intervals subconvex; pronotum sides distinctly though shallowly sinuate in basal fourth (figs. 1, 2) 3
   Elytral striae obsolescent, intervals flat; pronotum sides not sinuate (fig. 3); punctures deep, discrete; southeast Meade, eastern Breckinridge, western Hardin, and northwest Hart counties ..... *tellkampfi henroti* Jeannel
3(2). Punctures of elytral striae relatively fewer, shallower and less discrete, striae usually impunctate in apical half; easternmost Hart, northwest Metcalfe, and western Green counties. *tellkampfi viator*, new subspecies
   Punctures of elytral striae more numerous, deeper, and fairly discrete, usually extending well into apical half; southwest Hart, southeast Edmonson, northwest Barren, eastern Warren, and northern Allen counties ..... *tellkampfi tellkampfi* (Erichson)

Neaphaenops tellkampfi tellkampfi (Erichson)
Figures 1, 6, 10

Anophthalmus Tellkampfii Erichson, 1844, p. 384. Type locality, Mammoth Cave, Kentucky; type not seen. Packard, 1888, p. 73, pl. 18(1).



FIGS. 2-4. Head and pronotum of *Neaphaenops tellkampfi* subspecies. (2) *N. t. viator*, new subspecies, Brush Creek Cave, Green County, Kentucky. (3) *N. t. henroti* Jeannel, Sig Shacklett's Cave, Meade County, Kentucky. (4) *N. t. meridionalis* Barr, Hoy Cave, Simpson County, Kentucky.

Neaphaenops Tellkampfi: Jeannel, 1931, p. 471, figs. 92-103.

Neaphaenops Tellkampfi Tellkampfi: Jeannel, 1949, p. 89, figs. 90-98. Barr, 1959, p. 23 (in part); 1962b, p. 281.

DESCRIPTION: Length 6.7-7.3, mean 7.0 mm. Head without median pit on vertex; labrum singly emarginate. Pronotum sides shallowly sinuate before hind angles. Elytra with fine pubescence, at least at sides; striae shallow but distinct, intervals feebly subconvex, punctures usually fairly deep and discrete and extending well beyond middle of elytra. Aedeagus 1.29-1.45, mean 1.37 mm. long, left copulatory piece knobbed.

DISTRIBUTION: KENTUCKY: *Allen County*: Buchanan Cave, 0.8 mile W. Gainesville. *Barren County*: Brown Cave, 2.2 miles SE Coral Hill; Brushy Knob Cave, 1.9 miles ENE Park City; Buck Creek Cave, 1.3 miles SE Railton; Burnet Cave, 0.5 mile W Park City; Cave City (=Railroad) Cave, in Cave City; Crawhorn Cave, 2.3 miles NW Rocky Hill; Crystal Onyx Cave, 1.5 miles SW Cave City on Prewitts Knob; Diamond Caverns, 1.7 miles NNW Park City; Hanson Cave, 2.7 miles SW Hiseville; Neals Chapel Cave, 1.3 miles SE Lecta; Parker Cave, 1.7 miles SSW Park City; Slick Rock Cave, 0.3 mile W Slick Rock on S bank Beaver Creek; Twyman Cave, 1.4 miles N Hiseville; Vance Cave, 0.4 mile NE Park City; Walnut Hill Cave, 1.7 miles S and slightly W Park City; Wonderland Cave, 1.5 miles SW Turleys Corners. *Edmonson County*: Mammoth Cave (type locality, also extending under parts of Barren and Hart counties); other caves in Mammoth Cave National Park as follows: Blowing Spring, Bluff, Cathedral (=Buzzard), Dixon, Gothic, Great Onyx, Hickory Flat, Jim, Little Beauty, Little White, Long, Martin, Pagoda, Proctor, Running Branch, Smith Valley, White, Y Camp, also spring cave above River Styx outlet, also freshly opened sinkhole in Woolsey Valley; Coach (=Hundred Domes) Cave, 1.8 miles WNW Park City; James Cave, 1.3 miles WNW Park City; Short Cave, 2.1 miles NNW Park City. *Hart County*: Bald Knob Pit, 1.8 miles W and slightly N Hardyville on W side Bald Knob; Barnes Smith Cave, 3.4 miles N Hinesdale; Bert Burd Sink, 0.85 mile E Seymour; Buckner Hollow Cave, 1.7 miles SE Hinesdale; Hidden River (=Horse) Cave, in town of Horse Cave; Hogan Caves, 0.4 mile NE Ronalds Cave; Logsdon Valley Cave, 4 miles W Munfordville; Mammoth Onyx Cave, 2 miles N Horse Cave; Ronalds Cave, 2.5 miles N Cave City on N side Interstate 65 in Hatcher Valley; Three Springs Cave, in Three Springs; Webb Cave, 0.2 mile NW Bear Wallow; unnamed cave at Horse Cave interchange on Interstate 65. *Warren County*: Crump (=Lisenby) Cave, 0.6 mile NE Smiths Grove; Oakland Pit, 1000 feet S Oakland School; Pruett Saltpeter Cave, 0.8 mile SE Anna.

MATERIAL SEEN: Over 600 specimens from 58 caves. The distributional list was compiled from specimens in my private collection.

DISCUSSION: Nominate *tellkampfi* is widely represented in most large museums and many private collections, and the majority of specimens in those collections are from Mammoth Cave or caves in the immediate vicinity of Mammoth Cave, Cave City, or Park City (=Glasgow Junction of older literature). Some of the locations cited in the literature (for example, by Packard, 1888) are difficult or impossible to identify by the cave names given, which have changed with time; however, the distributional data presented above are far more complete and almost certainly include all the older locations within the boundaries delimited.

In Mammoth Cave the beetles are commonly observed abroad on silty floors and ledges in damp spots throughout the system, absent only in the driest and dustiest sections. They are occasionally found eating eggs or first instar nymphs of cave crickets or dead or disabled individuals of their own species. The nymphs are invariably very pale and have probably been captured as they emerged from the egg. As noted by Jeannel (1949), the beetles occur in much drier microhabitats than those frequented by sympatric *Pseudanophthalmus* species; however, "drier" in this context means an atmosphere not saturated with water vapor but with relative humidities still well above 90 percent. Beetles also occur, usually at much lower population densities, in the lowest levels of the system on mud and silt deposits along the banks of the cave rivers, where they feed on small, limicolous oligochaetes and possibly

other small invertebrates. High population densities were observed in stream passages in Brown Cave, Barren County, and Buckner Hollow Cave, Hart County.

Larvae and pupae are found, usually under silt-embedded rocks, in the drier microhabitats, where the frequency of juvenile stages peaks in late winter and early spring. Norton et al. (1975) have correlated seasonal peaks in abundance of juveniles and teneral adults with the fall peak in *Hadenoecus* oviposition; the autumn abundance of food provides a rich energy source for egg production in female *Neaphaenops*, leading to a spring peak in juveniles and a summer peak in tenerals. The life span is probably one to two years. Winter and early spring samples contain slightly more females than males; Norton et al. (1975) suggested that this is the result of greater longevity in females.

Although I believe that most local *N. t. tellkampfi* populations follow the life history pattern described by Norton, Kane and Poulson (1975) there appear to be other ecologies and other patterns, in all probability based on other prey. Ludwig (1950) predicted on theoretical grounds that selection would favor invasion of less-than-optimal subniches, and the ecological versatility of *N. tellkampfi* can be viewed as a possible example of the Ludwig effect. The low density populations of base level stream conduits are likely to be quite different, but annual flooding makes continued observation throughout the year difficult, if not impossible. Domepit populations are easier to follow. A series of 45 beetles collected February 10, 1979, in Cathedral Domes, Mammoth Cave (a wet microhabitat), included 19 tenerals (42%), indicating an oviposition peak about June 1978. On the same date a visual sample of *Neaphaenops* in Sophie's Avenue and the Radio Room (areas typical of the microhabitat category studied by Norton, Kane and Poulson) included only eight tenerals out of a total of 171 specimens (4.7%). The principal energy sources at Cathedral Domes are rotting wood of old stairs and moderately high organic content in the stream of water falling into the Dome. From total organic carbon (TOC) analyses of domepit water elsewhere in Mammoth Cave, I determined that peak TOC values (7-13 p.p.m.) occur from May to October (Barr, unpublished data). Details of energy flow between aquatic and terrestrial components of the cave community are far from clear, but *Neaphaenops* (and *Pseudanophthalmus menetriesi*) abound in areas of high TOC input. At the very least one can conclude that the propensity of *N. tellkampfi* for feeding on cave cricket eggs has not entirely replaced its ability to utilize other food sources and thus to carve out subniches that are less optimal than the principal niche occupied by the majority of populations of the species.

Where suitable microclimatic conditions prevail, *N. tellkampfi* may occur very close to entrances of caves, even in the twilight zone. In Cave City Cave, Barren County, specimens were observed walking about in daylight at the bottom of the entrance sink, where a stream crosses the floor. Roger Sperka dug open a small sinkhole in Woolsey Valley, Mammoth Cave National Park, on a warm day in November 1974, and found both *Neaphaenops tellkampfi* and *Pseudanophthalmus menetriesi* (Motschulsky) within 50 cm. of the surface, where they had probably been attracted by abundance of food.

Neaphaenops t. tellkampfi is sympatric with five species of *Pseudanophthalmus*, all of which occur in the Mammoth Cave system. Three species—*P. menetriesi, P. striatus* (Motschulsky), and *P. pubescens* (Horn)—are relatively abundant throughout most of its range. Two smaller species—*P. audax* (Horn) and *P. inexpectatus* Barr—are rather rare and quite limited in distribution (Barr, 1962b). All six trechine species coexist in White Cave (0.5 mile southwest of the Historic Entrance to Mammoth Cave), although they have never been taken in the same season. To the east, *N. t. tellkampfi* intergrades with *N. t. viator*, and to the south it intergrades with *N. t. meridionalis*.

Neaphaenops tellkampfi viator, new subspecies

Figure 2

ETYMOLOGY: Latin *viator*, "traveler."

DESCRIPTION: Length 6.7-7.3, mean 7.0 mm. Head without median pit on vertex; labrum singly emarginate. Pronotum sides shal-

lowly sinuate in basal fourth before hind angles, as in nominate *tellkampfi*. Elytra with fine pubescence; striae shallow but distinct, intervals feebly subconvex, punctures quite shallow, fewer and less discrete than in nominate *tellkampfi*, punctuation seldom extending beyond middle of elytra. Aedeagus 1.28-1.43, mean 1.38 mm. long, similar to that of *tellkampfi tellkampfi*, left copulatory piece slightly knobbed at apex.

TYPE SERIES: Holotype male (American Museum of Natural History) and 18 paratypes, Brush Creek Cave, 0.8 mile east and slightly north of Lobb on the west side of Brush Creek, in western Green County, Kentucky, September 28, 1963, T.C. Barr, J.R. Holsinger, and R.M. Norton.

MEASUREMENTS: Holotype, total length 7.2 mm., head 1.24 mm. long ×0.99 mm. wide, pronotum 1.33 mm. long ×1.30 mm. wide, elytra 4.12 mm. long ×2.48 mm. wide, antenna 4.99 mm. long.

DISTRIBUTION: KENTUCKY: *Green County*: Brush Creek Cave (type locality); Aetna Cave, 1.3 miles E Eve; Camp Branch (=Gentry) Cave, 1.0 miles NE Grab just SE forks Camp Branch; Milby Cave, 1.8 miles NW Gabe; Saltpeter Cave, 1.2 miles NE Whickerville on W side Little Barren River; Scott Cave, 1.9 miles ESE Eve on E side Brush Creek. *Hart County*: Crump Cave, 1.6 miles W Eve in E wall valley of Green River; Turner Cave, 3.7 miles SE Magnolia. *Metcalfe County*: Devils Den, 3 miles S Center in deep sink W North Metcalfe School.

MATERIAL SEEN: Eighty-seven specimens, including the type series of 19 beetles, from a total of nine caves.

DISCUSSION: This subspecies is close to nominate *tellkampfi* but differs consistently in the feebler punctuation of the elytral striae. Specimens from Bald Knob Pit and Bert Burd Sink, adjacent to the range of *tellkampfi viator* as given above and listed as nominate *tellkampfi*, are transitional in punctuation, but two late tenerals from Three Springs Cave, which is 3 miles east of Bert Burd Sink, are strongly punctured. Intergradation between *t. tellkampfi* and *t. viator* occurs gradually in eastern Hart County along a zone about 5 miles wide; there is no sharp break between the ranges of the two subspecies. Some of the specimens from Crump Cave, Hart County, have a minute depression in the middle of the vertex, but it is much smaller than that which occurs in *tellkampfi meridionalis*.

Neaphaenops tellkampfi henroti Jeannel
Figure 3

Neaphaenops Tellkampfi subsp. *Henroti* Jeannel, 1949, p. 90. Type locality, Sig Shacklett's Cave, Meade County, Kentucky; type in Museum National d'Histoire Naturelle, Paris (not seen).

Neaphaenops tellkampfi tellkampfi: Barr, 1959, p. 23 (in part).

DESCRIPTION: Length 6.6-7.5, mean 7.0 mm. Head without median pit on vertex; labrum slightly emarginate. Pronotum sides not sinuate before hind angles (except for minute emargination at site of posterior marginal seta, also present in other subspecies). Elytra with fine pubescence; striae obsolescent, intervals flat, punctures fairly deep and discrete, usually extending well beyond middle of elytra. Aedeagus 1.28-1.40, mean 1.36 mm. long, about as in nominate *tellkampfi*, left copulatory piece slightly knobbed at apex.

DISTRIBUTION: KENTUCKY: *Breckinridge County*: Glass Cave, 1.2 miles E Custer; Penitentiary Cave, 1.4 miles E Clifton Mills; Thornhill Cave, 2.1 miles WSW Big Spring. *Hardin County*: Belt Cave, 3.5 miles NW Howe Valley; Bland Cave, 1.1 miles NE Spurrier in Akers Valley; Patterson Cave, 2.5 miles NW Stephensburg; Saltpeter Cave, 2.0 miles S and slightly W Flaherty; Turkey Hollow Cave, 1.8 miles S and slightly E Old Stephensburg; Pickhandle Wilmoth Cave, 2.1 miles SW Franklin Crossroads; Wonderland Cave, 1.5 miles SE Old Stephensburg. *Hart County*: Cooch Webb Cave, 2.3 miles W Priceville on Ky. 728; Copelin Cave, 2 miles E Millerstown; Puckett Cave, 0.65 mile WSW Priceville; Rough Cave, 2.6 miles WSW Priceville on Ky. 728; Saltpeter (=Mushroom) Cave, 1.5 miles NE Lone Star; Riders Mill Cave, 2.5 miles N Priceville on Roundstone Creek. *Meade County*: Sig Shacklett's Cave (type locality), 3.0 miles N Big Spring in Stith Valley, E corner intersec-

tion Ky. 1238 and Ky. 1735; Scott Cave, near Guston (Jeannel, 1949).

MATERIAL SEEN: Eighty-nine specimens from 17 caves, including 13 topotypes from Sig Shacklett's Cave.

DISCUSSION: Jeannel (1949) described this subspecies as having more pronounced humeral angles, the prehumeral borders supposedly being less oblique than in *t. tellkampfi*. This is not the case. Previously I confused Hart and Hardin county series of *henroti* and *t. tellkampfi* (Barr, 1959). Although the subspecies is here diagnosed on a quite different basis from that originally proposed, there are no constant differences between the Meade-Breckinridge and Hart-Hardin series, and the available name *henroti* applies to all of them.

As with *viator* and *meridionalis*, the series of *henroti* are smaller than those available for nominate *tellkampfi*. At least part of this is the result of greater homogeneity of habitat in the smaller caves inhabited by the peripheral subspecies. Most of the northern caves in which *henroti* was collected are wet or damp. Dry microhabitats similar to those in the upper levels of the Mammoth Cave system were present only in Belt, Thornhill, and Wonderland caves, Hardin County. In Bland Cave, Riders Mill Cave, and Sig Shacklett's Cave the *Neaphaenops* were collected on silt banks in stream passages.

A prominent sandstone ridge and complex fault system run transversely across Hart County at the southern limit of the range of *henroti*. Close morphological similarity between *henroti*, *viator*, and nominate *tellkampfi* argue for treatment of *henroti* as a subspecies, but there are no known cases of intergradation with *t. tellkampfi* or *t. viator*, consequently *henroti* could well be an allopatric sibling species.

Neaphaenops tellkampfi meridionalis Barr
Figures 4, 7, 11

Neaphaenops tellkampfi meridionalis Barr, 1959, p. 23. Type locality, Hoy Cave, Simpson County, Kentucky; type in the American Museum of Natural History.

DESCRIPTION: Length 6.3-7.1, mean 6.8 mm. Head with distinct median pit on vertex; labrum doubly emarginate. Pronotum sides not sinuate before hind angles. Elytra virtually glabrous, 0.06-0.10 wider than in other subspecies; intervals convex, impunctate. Aedeagus 1.28-1.36, mean 1.32 mm. long, left copulatory piece not knobbed, simply rounded at apex.

DISTRIBUTION: KENTUCKY: *Allen County*: Jack Johnson (=Howell) Cave, 0.75 mile SSE Claypool in hollow S Bays Fork. *Simpson County*: Bennett Cave, 2.0 mile WNW Gold City on W side Lick Creek, 800 feet E I-65 (J.A. Hinton, legit). Hoy Cave (type locality), 1.9 miles N county courthouse in Franklin, under US 31W; Old Smoky Cave, 1.4 miles ENE Salmons; Slates Cave, at Spout Spring 1.8 miles E slightly N Gold City. *Warren County*: Blue Level Cave, 2 miles SSE Blue Level (C.J. Gray, legit); Bypass Cave, in south Bowling Green between Smith Drive and US 31W bypass (cave now closed); Horseshoe (=Vales) Cave, in C.W. Lampkin Park in west Bowling Green; McGinnis Cave, 2.5 miles SW Bowling Green (J.M. Valentine, legit); Moats Cave, 0.8 mile W Claypool; Plano Saltpeter Cave 0.5 mile SSW Plano (C.J. Gray, legit). *Logan County*: Wheeler Cave, 2.0 miles NE South Union (R.M. Norton, legit).

MATERIAL SEEN: One hundred forty-seven specimens, including the type series of 24 from Hoy Cave, from a total of 11 caves.

DISCUSSION: This subspecies is readily recognized by the vertex pit and the broad, glabrous elytra with convex intervals and impunctate striae; the labrum is distinctly trilobed; mean total length and aedeagal length are slightly smaller; pronotum sides are convergent rather than sinuate; and the left copulatory piece is not knobbed at the apex. Traces of a vertex pit (more feeble than in *meridionalis*) were seen in a few specimens from series of nominate *tellkampfi* in Pruetts Saltpeter Cave and *tellkampfi viator* in Crump Cave. There are inaccuracies and omissions in the original description of *meridionalis* (Barr, 1959): the total length range given in 1959 does not include outstretched mandibles and is thus too low, the hind angles are not smaller as stated, and the striae are not "less profound" but actually deeper.

Despite its very distinct appearance, *N. t. meridionalis* does apparently hybridize with *t. tellkampfi* in a narrow zone at the southeast margin of its range, along Trammel Fork and Bays Fork in Warren and Allen counties. Elsewhere the approximate geographic boundary between the two taxa is the Barren River. A series of 18 specimens from Friendship Cave, 1.3 miles southeast of Alvaton, Warren County, is compared with "typical" *t. tellkampfi* (Diamond, Pruett) and *meridionalis* (Hoy, Plano) in table 1. The hybrid population has the greater length of *t. tellkampfi* and resembles *meridionalis* in the broader elytra and left copulatory piece, but is intermediate between these two taxa in six other characters. A single male from Bear Cave, 3 miles southeast of Friendship Cave but in Allen County, is similar (transfer apparatus, fig. 11). Gene flow between the two taxa is probably very limited, and *meridionalis* may well be a semispecies, although a conservative treatment is adopted here.

Microhabitats selected by *N. t. meridionalis* do not seem to include the drier areas frequented by nominate *tellkampfi*; this may be a real behavioral difference, or it may be only the result of greater homogeneity of habitat afforded by the shallow, extensive cave systems which it occupies. Invariably it has been taken in wet areas near water (pools or streams); in riparian microhabitats it occurs on walls or ledges or silt banks well above the stream and not at its edge. The only feeding observation on this subspecies in its natural habitat was made in Bear Cave (August 1963), when a *Neaphaenops* was found eating a small chrysomelid beetle that had washed into the cave through an upper sinkhole entrance. *Hadenoecus subterraneus* coexists with *N. t. meridionalis* in all the caves where it has been found. In the laboratory *meridionalis* specimens dug deeply into artificial "egg holes" made by poking an *H. subterraneus* ovipositor into damp sand, a behavior also observed by Norton, Kane and Poulson (1975) in nominate *tellkampfi*.

DISTRIBUTION

The distribution of *Neaphaenops tellkampfi* (fig. 5) is essentially coextensive with distribution of outcrops of the Girkin (or Paoli to the north), Ste. Genevieve, and St. Louis limestones, all highly cavernous strata. The species range is effectively bounded by the Big Clifty sandstone member of the Golconda formation to the west and the Salem and Warsaw (or Harrodsburg in the north) limestones to the east. As a troglobite, *Neaphaenops* is limited to subterranean dispersal routes through reasonably continuous limestone; however, small streams (for example, the Green River) seldom constitute barriers to trechine dispersal if there are numerous caves on both sides of the streams (Barr, 1959; Barr and Peck, 1965). *Neaphaenops* distribution is apparently further controlled by the distribution of *Hadenoecus subterraneus*, which in turn appears dependent on moderately high cave density, so crickets

TABLE 1
Comparison of Diagnostic Characters in *Neaphaenops tellkampfi tellkampfi*, *Neaphaenops tellkampfi meridionalis* and Presumed Hybrids

	N. t. tellkampfi	*tellkampfi* × *meridionalis* (Friendship Cave)	*N. t. meridionalis*
Total length	6.7-7.3, mean 7.0 mm	6.9-7.4, mean 7.1 mm	6.3-7.1, mean 6.8 mm
Vertex pit	Absent	Present but feeble	Deep
Labrum	Singly emarginate	Feebly trilobed margin	Doubly emarginate
Pronotum sides	Sinuate	Weakly sinuate	Not sinuate
Elytral pubescence	Fine but distinct	Fine at sides	Absent
Elytral intervals	Nearly flat	Subconvex	Strongly convex
Elytral striae	Finely punctured	Punctulate	Impunctate
Elytral L/W index	1.48-1.71, mean 1.63 mm.	1.41-1.69, mean 1.58 mm.	1.54-1.65, mean 1.59 mm.
Left copulatory piece	Knobbed at apex	Apex bluntly rounded	Apex bluntly rounded

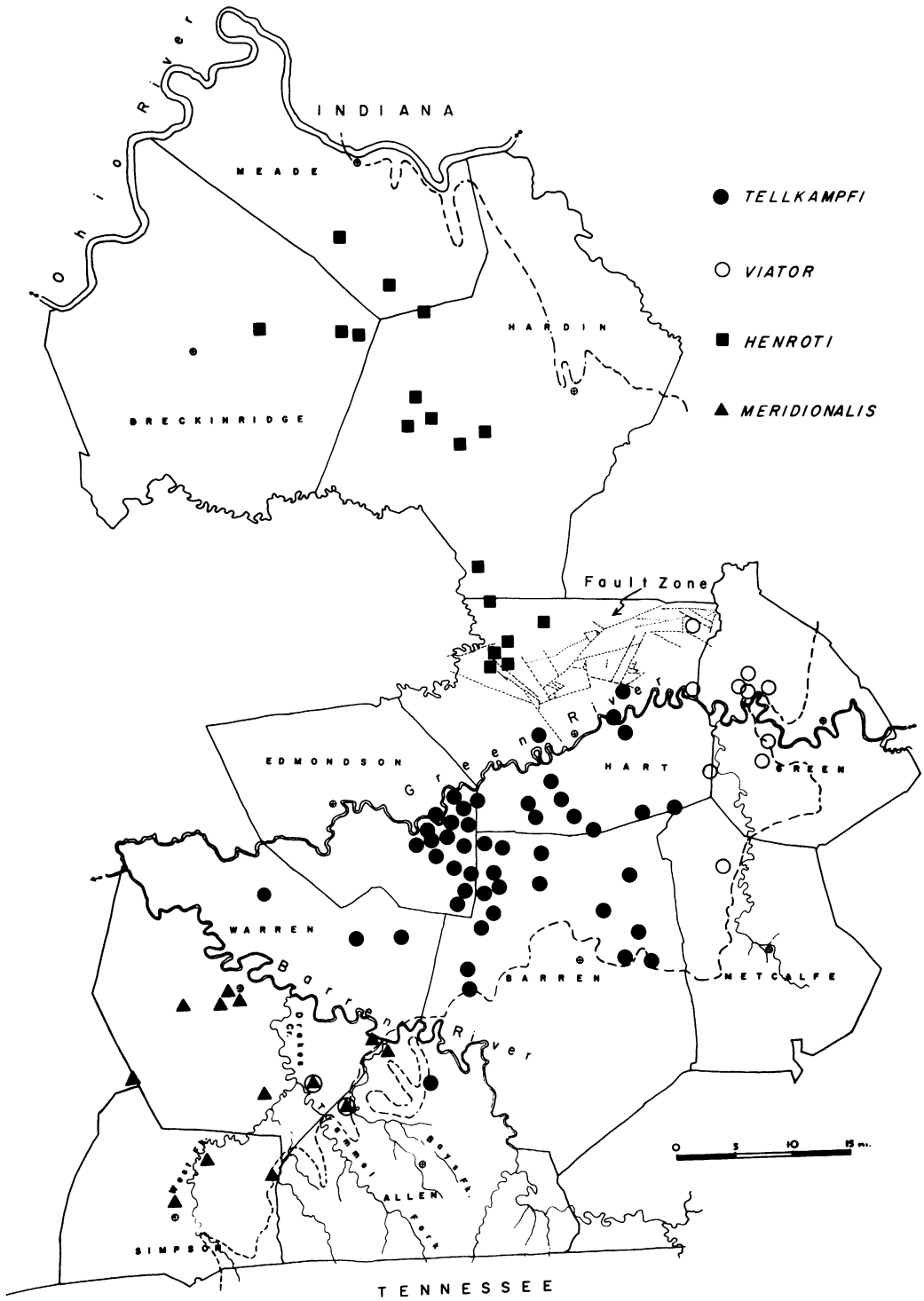


FIG. 5. Distribution of *Neaphaenops tellkampfi* in west-central Kentucky. *N. t. tellkampfi* × *N. t. meridionalis* hybrids shown by circled triangles. Small crossed circles represent county seats. Approximate location of St. Louis/Salem and Warsaw contact shown by heavy dashed line; data from United States Geological Survey 7½′ geologic maps.

can disperse from cave to cave. Locally the Salem-Warsaw unit contains a non-cavernous, arenaceous to argillaceous siltstone member which may pose a stratigraphic barrier. The few Salem-Warsaw caves occupied by *Neaphaenops* and *Hadenoecus* are close to the margin of the St. Louis outcrops. Salem-Warsaw caves are generally smaller and less frequent, and the dispersal potential of *Hadenoecus* and *Neaphaenops* is correspondingly reduced (Barr, 1968). Distributional control is probably exerted directly on *Hadenoecus subterraneus* and indirectly on *Neaphaenops*, which is dependent on cricket eggs for a large part of its diet. Several species of *Pseudanophthalmus* (of the *menetriesi* and *pubescens* groups) range widely through many of the Salem-Warsaw caves southeast of the species boundary of *N. tellkampfi*, but the caves are devoid of *H. subterraneus* populations.

Intergradation occurs in geographically intermediate populations between (a) *t. tellkampfi* and *t. meridionalis* and (b) *t. tellkampfi* and *t. viator*. Hybridization is certainly secondary in the first case and possibly also in the second, where intergradation is broader and more gradual. In contrast, gene flow between *t. henroti* and either of the subspecies to the south is probably severely restricted by a stratigraphic and structural barrier, a heavily faulted ridge with considerable thicknesses of sandstone which transversely crosses Hart County (Barr, 1968). Only a few small, isolated caves occur in this area, and if intergrading *Neaphaenops* populations exist, they have not yet been discovered. The little caves, some of which are sandstone crevices, are not barriers to *Hadenoecus subterraneus*, which, unlike *Neaphaenops*, does not require direct connection between caves, only a reasonably high density of them. Dawson Hollow Cave, 1.5 miles south-southwest of Bonnieville, Hart County, is in the ridge barrier and can serve as an example. It contains a population of thousands of *H. subterraneus*, but no trechines; other terrestrial invertebrates include linyphiid spiders and collembolans (*Sinella*, *Tomocerus*) belonging to widely distributed, opportunistic species which can probably disperse through non-cave areas by way of "microcaverns"—small spaces around tree roots, under rocks, in talus piles, and so forth—in the soil. The Hart County ridge also marks the range boundary between two species of troglobitic crayfishes, *Orconectes pellucidus* (Tellkampf) and *O. inermis* Cope (Hobbs and Barr, 1972). A distinct geographic race of *Pseudanophthalmus menetriesi* occurs north of the ridge, but two other widely distributed species in the Mammoth Cave region, *P. striatus* and *P. pubescens*, have not penetrated north of the ridge, and *P. barberi* Jeannel occurs only in caves to the north of it. Despite its allopatric distribution, *t. henroti* is morphologically closer to *t. tellkampfi* and *t. viator* than is *t. meridionalis*, yet nominate *tellkampfi* and *t. meridionalis* hybridize in at least one point where their ranges meet. The distributional and geologic evidence indicating that the ridge is an effective barrier to cave beetle dispersal leaves open the distinct possibility that both *N. t. henroti* and the northern race of *P. menetriesi* are allopatric sibling species.

Neaphaenops t. henroti is probably derived from a peripheral population of *t. tellkampfi* that worked its way northward through the small, scattered cave systems of the Hart County ridge. The two races may be descended from non-cave populations of ancestral *tellkampfi* that independently colonized caves north and south of the ridge, although close morphological similarity argues against this. Most cave trechines are believed to have descended from soil- and humus-dwellers that were widespread near the surface during the cooler, wetter climatic regimes of glacial maxima (Jeannel, 1949; Barr, 1967b). In any case, distribution of *t. henroti* at the northern part of its range, where it seems not to have occupied all the cave areas accessible to it, suggests a southern origin and gradual subterranean dispersal northward. It has not penetrated as far as caves along the Ohio River in western Meade County, nor as far west into caves of Breckinridge County as it theoretically could have gone. These caves are occupied by *Pseudanophthalmus barberi* and by *Hadenoecus subterraneus*, but not by *Neaphaenops*.

The easternmost subspecies, *N. t. viator*,

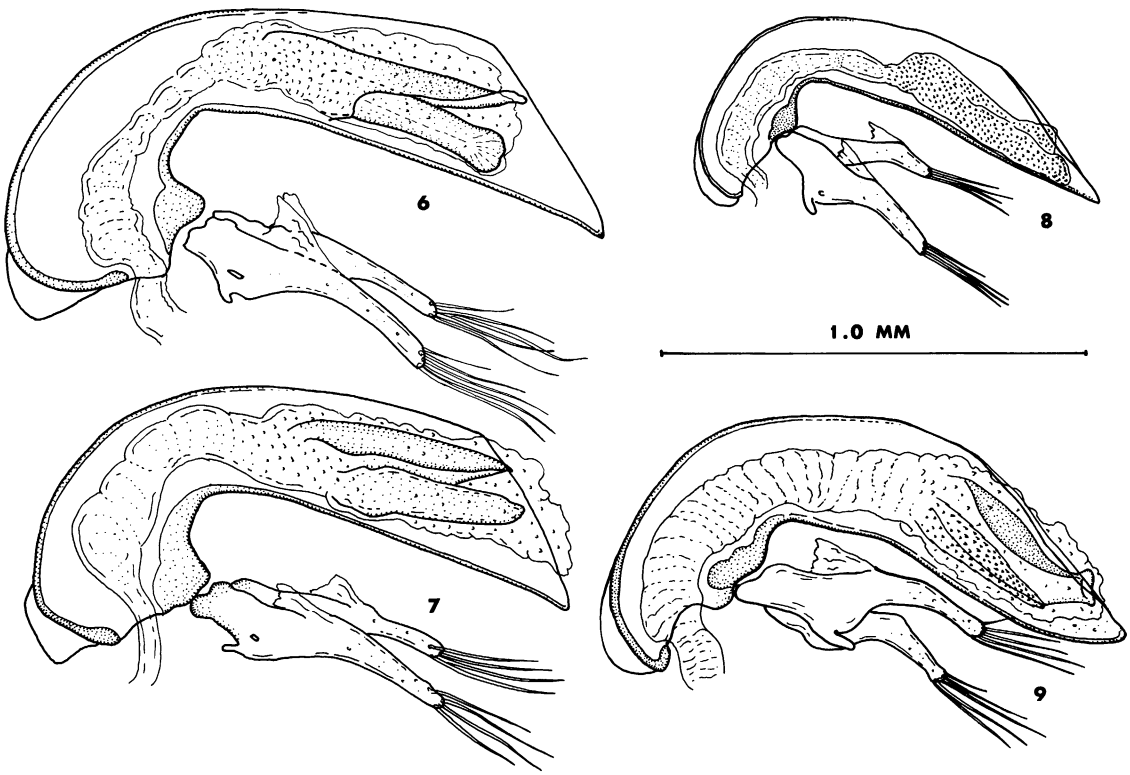
has penetrated about as far as it can go without moving into cave systems which are (a) beyond the St. Louis limestone outcrops and (b) devoid of *Hadenoecus subterraneus*. An undescribed *Pseudanophthalmus* species (*menetriesi* group), whose western species boundary closely coincides with that of *N. t. viator*, is moderately abundant in all the *viator* caves and also occurs farther east in Green County. This suggests that supposed physical barriers to dispersal in this area may be less important than the absence of *Hadenoecus subterraneus*.

Neaphaenops t. meridionalis, the southernmost and morphologically the most aberrant subspecies, occupies a range about the same size as that of *t. viator*. It coexists with two species of *Pseudanophthalmus* of the *pubescens* group and overlaps the range of *P. menetriesi* at Bowling Green. Its eastern boundary is limited by that of nominate *tellkampfi*, its northern boundary by non-caverniferous sandstones, and its southeastern boundary approximately by the St. Louis-Salem and Warsaw contact. It is not clear why this subspecies has not been taken a little farther west and south in the Pennyroyal. Throughout its range it is sympatric with *P. loganensis* Barr, which also occurs in great abundance throughout the numerous caves of Logan County, Kentucky, and northern Robertson and Sumner counties, Tennessee. *Hadenoecus subterraneus* also inhabits many of these same caves. There are no *Neaphaenops*-like trechine species there to preempt the niche of *N. tellkampfi* and thus bar it through competitive exclusion. The hypothesis that *meridionalis* is of comparatively recent origin and has had insufficient time to expand its range westward is not wholly satisfactory. The degree of the subspecies' morphological departure from nominate *tellkampfi* and its secondary hybridization with the latter indicate that it is an older isolate than either *henroti* or *viator*. Perhaps the final explanation—or at least a more palatable one—could be learned through a comparative study of the ecology and behavior of *t. tellkampfi* and *t. meridionalis*. The narrowness of the zone of hybridization implies very limited gene flow between these two taxa. I suspect that genetic (allozyme) data would support elevation of *meridionalis* to semispecies status, but I have retained a conservative treatment pending availability and analysis of such data.

AFFINITIES

If one is to look for the affinities and perhaps the origin of *Neaphaenops*, it would seem reasonable to begin with *Pseudanophthalmus*. Three other genera of troglobitic trechines inhabit caves of the Cumberland plateau margin in southeastern Kentucky (Valentine, 1952), but *Darlingtonea* and *Ameroduvalius* belong to a different phyletic series (Barr, 1972), and *Nelsonites* is a fairly clear derivative, non-aphaenopsian, from the *robustus-intermedius* section of *Pseudanophthalmus*. Within the very large genus *Pseudanophthalmus* the most promising line of attack is comparison of male genitalia. Primitively in *Pseudanophthalmus* there were two copulatory pieces placed asymmetrically on edge within the internal sac [a condition which Jeannel (1926-1930) has called "anisotopic"]. In most species groups this transfer apparatus is much the same throughout the group, although there are considerable permutations of the basic form in the *tenuis* and *audax* groups. The basic form of the aedeagus and its transfer apparatus are normally rather conservative and of diagnostic utility in distinguishing related groups of species.

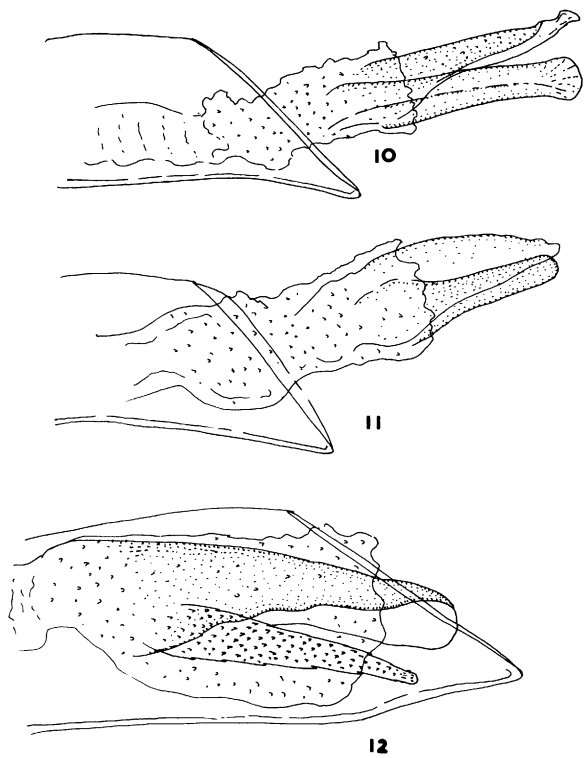
The aedeagus of *Neaphaenops tellkampfi* consists of a large basal bulb bearing a small keel and small opening, bent sharply at a right angle or more to the thick, scarcely tapered, and apically truncate median lobe (figs. 6, 7). The transfer apparatus consists of a heavily sclerotized, flattened, somewhat spatulate left piece, rounded or slightly knobbed at the apex, and an elongate, folded right piece which has the shape of an inverted V in cross-section and is slightly knobbed and twisted at its thinly sclerotized, hyaline apex. The left piece is partly enfolded by the right piece near its base (figs. 10, 11). Among the 20 species groups of *Pseudanophthalmus* the closest parallel in aedeagal shape is found in the *pubescens* group, especially in *P. pubescens* itself (fig. 8),



FIGS. 6-9. Aedeagi of *Neaphaenops* and *Pseudanophthalmus* species, left lateral view. (6) *N. t. tellkampfi* (Erichson), Crump Cave, Warren County, Kentucky. (7) *N. t. meridionalis* Barr, Hoy Cave, Simpson County, Kentucky. (8) *P. pubescens* (Horn), Crump Cave, Warren County, Kentucky. (9) *P. princeps*, new species, Plano Saltpeter Cave, Warren County, Kentucky.

where there is the same sharply deflexed basal bulb and truncate apex. The transfer apparatus in all species of the *pubescens* group consists of a broader, folded right piece, the apex of which is often twisted and slightly knobbed (least so in *pubescens*), and a heavily spinulose, rodlike left piece partly enfolded by the right piece (fig. 12). The *pubescens* and *Neaphaenops* left pieces could both be derived from the simple left piece of the *menetriesi* group, in *pubescens* becoming spinulose and in *Neaphaenops* becoming flatter, blunter, and more heavily sclerotized. The right piece in *Neaphaenops* is less folded than in the *pubescens* group, but it does have what may be a vestige of an apical knob. In *P. pubescens* the right piece has basically the same structure as that of *Neaphaenops*, and the apical knob is less developed than in other species of the group (compare fig. 10).

The male genitalia, then, offer evidence for derivation of *Neaphaenops* from the *pubescens* group. There are three additional features, no one of which alone suffices to establish affinity, but taken together with the genitalic evidence establish a strong case for joint derivation of the *pubescens* group and *Neaphaenops* from a common ancestor. (1) The anterior discal seta on the third elytral interval is normally placed at or behind the level of the fourth umbilicate (humeral) puncture in *Pseudanophthalmus*, but in *Neaphaenops* and the *pubescens* and *menetriesi* groups the anterior discal is placed opposite the second or third umbilicate. (2) The elytral microsculpture in both *Neaphaenops* and the *pubescens* group is the same: neither iso-



FIGS. 10-12. Transfer apparatus of *Neaphaenops* and *Pseudanophthalmus* species, left lateral view. (10) *N. t. tellkampfi* (Erichson), Crump Cave, Warren County, Kentucky. (11) *N. t. meridionalis* × *t. tellkampfi*, Bear Cave, Allen County, Kentucky. (12) *P. pubescens* (Horn), Smith Valley Cave, Edmonson County, Kentucky.

diametric nor finely transverse, but consisting of an irregular meshwork of transversely elongated polygons (finely transverse in the *menetriesi* group). (3) The geographic distributions of *Neaphaenops* and the *pubescens* group overlap widely in the south Pennyroyal plateau. The ancestral population from which *Neaphaenops* evolved is likely to have existed at one time in or quite near some part of the present distribution of *N. tellkampfi*. If *Neaphaenops* evolved from an epigean ancestor, then its present distribution might include several species in different cave areas, because dispersal of the ancestor would not have been limited by the distribution of continuous cavernous limestone. If *Neaphaenops* evolved from a cave ancestor, which I believe more probable, then its dispersal potential would be limited by local stratigraphy and structure (Barr, 1968). As shown in figure 5, the distribution of *Neaphaenops* is coextensive with part of the highly cavernous Pennyroyal plateau, the continuity broken only by the Hart County ridge.

Species of five groups of *Pseudanophthalmus* satisfy the requirement of proximity to the range of *Neaphaenops* in order to qualify as possible joint descendants from a common ancestor: the *tenuis, audax, inexpectatus, menetriesi*, and *pubescens* groups. There is little to suggest that the first three groups could be closely related to *Neaphaenops*, but the *menetriesi* group has the anterior discal puncture far advanced, opposite the second or third umbilicate puncture, and the apical recurrent groove is vestigial. Furthermore, *P. menetriesi* resembles *Neaphaenops* in the nonpruinose microsculpture, shallow striae with small, discrete punctures, and (in the Mammoth Cave area only) reduction of dorsal pubescence; all of these are features in which *Neaphaenops*

differs from members of the *pubescens* group. These observations indicate that *Neaphaenops* is probably also related to the *menetriesi* group, but because of the microsculpture and the shape of the aedeagus and transfer apparatus, less closely than it is to the *pubescens* group. The suggested relationship is origin of the *pubescens* and *menetriesi* groups from a common stock, with the *Neaphaenops* line branching off near the base of the *pubescens* line.

The *pubescens* group includes a dozen or more species (several undescribed) which range along the Pennyroyal from the Mammoth Cave region south, then westward to Crittenden and Livingston counties, Kentucky. Most of the species are rather robust, pubescent, and pruinose (when viewed under an oblique light, the elytral disc takes on a frosted appearance as light is reflected from many microtrichia projecting up from the posterior edge of each cuticular polygon). The pronotum is typically transverse-subquadrate, humeri are serrate and setose, and the elytral striae are (usually) impunctate or feebly punctulate. The aedeagus is remarkably similar in all species, varying principally in size, the degree of flexure of the basal bulb, and in minor details of the two copulatory pieces. The majority of the species select riparian habitats, appearing in higher levels of caves chiefly during unusually wet weather (McKinney, 1975). Alongside streams, however, they may be exceptionally abundant.

Neaphaenops tellkampfi differs from most species of the *pubescens* group in the larger, more slender body with elongate appendages; incomplete frontal grooves and loss of anterior supraorbitals; smooth humeral margin; reduction of elytral pubescence and striae; loss of pruinose microsculpture; loss of anterior apical puncture and apical recurrent groove; simpler transfer apparatus; and retention of strial punctures. All of these characters are probably apomorphic except the last two. Pruinose microsculpture is present in some (undescribed) species of the *menetriesi* group but absent in *menetriesi* and *striatus*; its adaptive significance is unknown, but may possibly be related to resistance to infection by the ectoparasitic ascomycetes of the order Laboulbeniales. Cave trechines that live along the edges of streams among leaves and sticks washed underground are most likely to have heavy infestations of *Laboulbenia subterranea* Thaxter. Selection of drier microhabitats by ancestral *Neaphaenops* would make pruinose microsculpture unnecessary and subject to rudimentation if this hypothesis is correct.

The theory just presented, that *Neaphaenops* evolved as a cave species and shares a common ancestry with the *pubescens* group and a slightly more remote relationship to the *menetriesi* group, implies a southern origin in the Mammoth Cave or Bowling Green area. Jeannel (1949) argued that *Neaphaenops* is convergent in many characters with *Trechopsis lapiei* (Peyerimhoff), a European nivicolous trechine, and that consequently its ancestor must have been a periglacial species that colonized caves following retreat of Illinoisian ice. This view ignores the absence of *Neaphaenops* from southern Indiana caves and the observation that it seems to be in the process of expanding its range northward. Furthermore, the northern origin required by the Jeannel hypothesis becomes awkward when it is seen that *N. t. meridionalis*, the southernmost subspecies, is morphologically the most aberrant and thus probably the oldest isolate.

NOTES ON THE PUBESCENS GROUP OF *PSEUDANOPHTHALMUS*

Among species of the *pubescens* group which have been described, there is little to suggest any evolutionary tendency in the direction of *Neaphaenops* with the possible exception of *P. ciliaris orlindae* Barr (1959), from caves of the upper Red River valley along the Kentucky-Tennessee border. This species is in the same size range as *P. pubescens* (5—6 mm.) but is a bit more slender and elongate, with transverse-cordiform pronotum. However, recent study of trechines collected from caves near Franklin, Kentucky, has revealed two species of the *pubescens* group coexisting with *Neaphaenops* at the southern limit of its range. One species, *P. loganensis* Barr (1959), is small (4.3-5.0, mean 4.4 mm.) and depressed.

The other species is large, elongate, and slender, with markedly convex elytra and cordiform pronotum. I was initially unable to distinguish it from *Neaphaenops* while collecting in the caves, so close is the superficial resemblance. This species, described below, is morphologically intermediate between the robust, often depressed species of the *pubescens* group and the large, convex, slender habitus of *Neaphaenops*. It may represent a stage through which ancestral *Neaphaenops* passed in its evolution from a *pubescens*-like stock.

Pseudanophthalmus princeps, new species
Figures 9, 13

ETYMOLOGY: Latin *princeps*, "first, chief, ruler."

DIAGNOSIS: Distinguished from all other species of the *pubescens* group by large size, narrow head and pronotum, and strongly convex elytra.

DESCRIPTION: Length 5.7-6.8, mean 6.2 ± 0.3 mm. Form rather slender and elongate, pubescent, shining rufous to castaneous-testaceous. Head elongate, one-fifth longer than wide; mandibles large, long, and slender; labrum distinctly and doubly emarginate; frontal grooves complete; dorsum of head subglabrous. Pronotum transverse-cordiform, nine-tenths as long as wide, width at apex and base subequal and about seven-tenths greatest width, which occurs in apical fourth; sides arcuate apical half then convergent, shallowly but distinctly sinuate in basal eighth, hind angles small and sharp; basolateral impressions moderate, minute secondary angles present on base; disc pubescence sparse but rather long. Elytra elongate-oval, two-thirds longer than wide, strongly convex on disc and deplanate near scutellum; prehumeral borders clearly oblique to midline, humeri finely serrate and setose; striae finely impressed, outer striae obsolescent, intervals subconvex, each with two or three rows of pubescence; microsculpture weakly transverse and heavily pruinose; elytral chaetotaxy normal, except anterior apical puncture placed opposite second umbilicate; apical recurrent groove subparallel, joining or directed toward apex of fifth stria slightly in advance of anterior apical puncture. Antenna rather long, seven-tenths body length. Aedeagus 1.06-1.23, mean 1.14 mm. long, thick and arcuate throughout, basal bulb not strongly deflexed as in *pubescens*; left copulatory piece apically attenuate in lateral view and densely spinulose, right piece with broad, apically truncate knob; parameres with four long apical setae, sometimes shorter fifth seta.

TYPE SERIES: Holotype male (American Museum of Natural History) and six paratypes, Hoy Cave, 1.9 miles north of county courthouse in Franklin under US 31W, Simpson County, Kentucky, July 21, 1963, T.C. Barr.

MEASUREMENTS: Holotype, total length 6.2 mm., head 1.02 mm. long ×0.87 mm. wide, pronotum 0.96 mm. long ×1.05 mm. wide, elytra 3.19 mm. long ×1.92 mm. wide, antenna 4.25 mm. long, aedeagus 1.08 mm. long.

DISTRIBUTION: KENTUCKY: *Simpson County*: Hoy Cave (type locality); Old Smoky Cave, 1.4 miles ENE Salmons; Slates Cave, at Spout Spring 1.8 miles E and slightly N Gold City; Steele Caves, 3 miles SE Franklin on E bank West Fork of Drakes Creek. *Warren County*: Plano Saltpeter Cave, 0.5 mile SSW Plano (C.J. Gray, legit). TENNESSEE: *Sumner County*: Whiteoak Cave, 2.1 miles ENE Mitchellville near mouth of Grace Creek.

MATERIAL SEEN: Thirty-eight specimens, including the type series, from a total of six caves.

DISCUSSION: *Pseudanophthalmus princeps* is clearly a member of the genus *Pseudanophthalmus* and of the *pubescens* group, but its large size, elongate form, and convex elytra demonstrate that at least one population of *pubescens* group stock was capable of evolving toward a *Neaphaenops*-like habitus. Living beetles in the caves or pinned specimens in a tray, seen with the unaided eye, resemble small *Neaphaenops*. With experience it becomes possible to distinguish the two species in the field. *Neaphaenops t. meridionalis* is redder, shinier, and a bit larger, occurring in somewhat drier and higher microhabitats than *P. princeps*. On the other hand, *princeps* is more yellowish

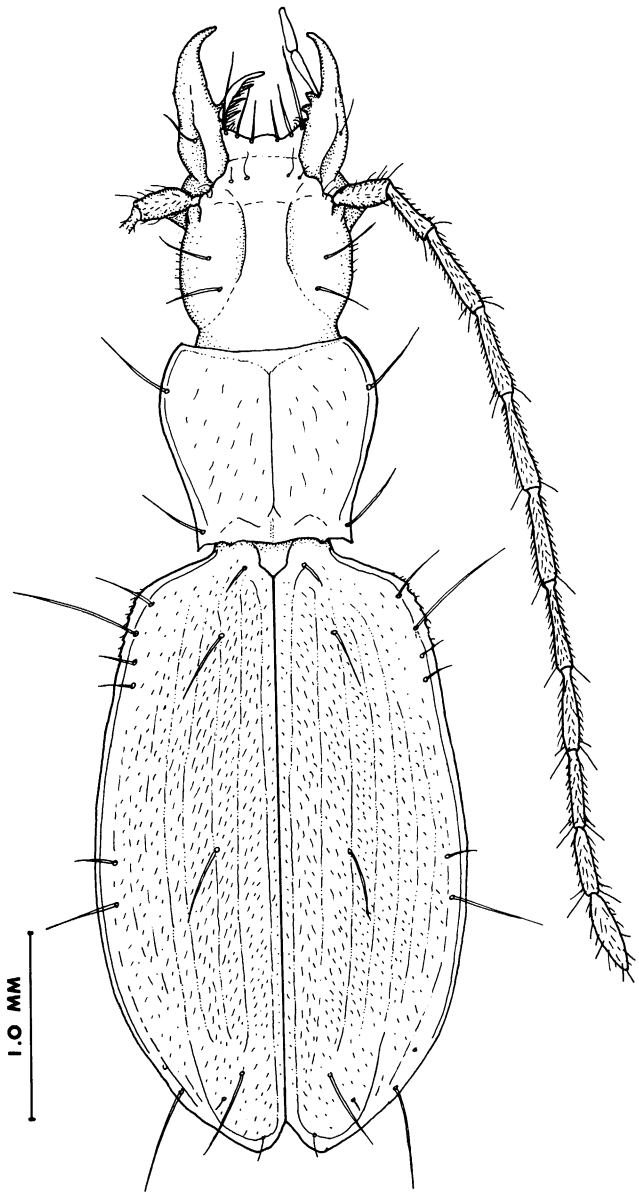


FIG. 13. *Pseudanophthalmus princeps*, new species, Hoy Cave, Simpson County, Kentucky.

brown, more opaque, slightly smaller, and occurs on wet fill near the edge of water; depressions in silt and mud of *princeps* microhabitats become filled with water seeping in from the sides.

Captive specimens of *princeps* maintained in the laboratory show little digging activity, wandering about the surface of the substrate in their container. They are aggressive feeders, quickly locating and eating bits of raw beef or dead *Hadenoecus subterraneus* much sooner than *P. loganensis* or *N. t. meridionalis*.

All the caves from which *P. princeps* has been collected are in the drainage basins of West Fork and Middle Fork of Drakes Creek, a south tributary of Barren River. *Pseudanophthalmus loganensis* occurs in all the caves listed above. *Neaphaenops t. meridionalis* was collected in Hoy, Old Smoky, Slates, and Plano Saltpeter caves, but was not taken in Whiteoak Cave or the Steele caves. It would be interesting to compare ecology and behavior of the three species of trechines coexisting in these caves. If *P. princeps* and/or *N. t. meridionalis* are ecologically and behaviorally intermediate between *P. loganensis* and *N. t. tellkampfi*, such an investigation might reveal some of the selection pressures mediating the adaptive zone shift which led to the evolution of *Neaphaenops*.

Two *Pseudanophthalmus* taxa to which reference is made in the present paper exist in caves near the southern end of the range of *Neaphaenops tellkampfi*. A change in taxonomic status is required for each of these taxa, which belong to the *pubescens* group.

Pseudanophthalmus ciliaris orlindae Barr, new combination

Pseudanophthalmus orlindae Barr, 1959, p. 7, figs. 1, 2(3). Type locality, Jesse James Cave, Robertson Co., Tennessee; type deposited in the American Museum of Natural History.

This large (5.4-5.8 mm.) form coexists in many caves of Robertson County, Tennessee, and southern Logan County, Kentucky, with the smaller *P. loganensis*. Restudy of older collections and fresh material demonstrates a clear morphological and geographic intergradation between nominate *ciliaris* and *orlindae* in Bell Witch Cave, Robertson County, Tennessee. In both subspecies of *ciliaris* the aedeagus is elongate and rather straight, with slightly produced and deflexed apex (thus differing from all other species of the group); *orlindae* differs from nominate *ciliaris* in larger size and larger aedeagus (1.3-1.4 mm. long vs. 0.9-1.0 mm. long). The range of polytypic *ciliaris* includes caves along Red River from the vicinity of Clarksville, Tennessee, eastward approximately to the point where Interstate 65 bridges South Fork of Red River. Its closest approach to the species boundary of *P. princeps* is in West Cave, 1.0 mile NNE Providence and about 7 miles SW Hoy Cave, in Simpson County, Kentucky. Overlap with the ranges of *N. t. meridionalis* or *P. princeps* has not been demonstrated; both *orlindae* and *princeps* are large riparian species with a cruising predation strategy, and mutual exclusion may determine their species boundaries with respect to each other.

Pseudanophthalmus loganensis Barr, new status

Pseudanophthalmus ciliaris loganensis Barr, 1959, p. 7, fig. 2(1). Type locality, Cook (=Savage) Cave, Logan Co., Kentucky; type deposited in the American Museum of Natural History.

Pseudanophthalmus loganensis is a medium-sized (4.6-5.2 mm.) species widely distributed in Warren (south of Barren River), Simpson, and Logan counties, Kentucky, also northeast Robertson and northwest Sumner counties, Tennessee. It is sympatric with four larger trechine species: *Neaphaenops t. meridionalis, P. menetriesi, P. ciliaris orlindae*, and *P. princeps*. Recognition of the correct status of *orlindae* as a subspecies of *ciliaris* demonstrates that *loganensis* is a full species. Principal diagnostic characters for *loganensis* are its total length range, moderately robust and feebly convex habitus, and aedeagal form: median lobe 0.83-0.92 mm. long and evenly arcuate, right copulatory piece slender with terminal button, left piece slender and pointed at apex, parameres with lateral shelves peculiarly expanded into hyaline, curved flanges. Unlike *pubescens, princeps*, or *ciliaris orlindae*, which are cruising predators, *loganensis* is an interstitial feeder, almost always encountered at the edge of cave streams in mud cracks, on rotting wood fragments, or in the interstices of cherty cobble- and gravel-bars.

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