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Cave Beetles of the Genus Pseudanophthalmus (Coleoptera, Carabidae) from the Kentucky Bluegrass and Vicinity

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The first true cave carabids known from America, blind, depigmented forms known as anophthalmids, were found in Mammoth Cave in Kentucky (Erichson, 1844). Between their discovery and 1957 about ten additional forms of anophthalmids were described from Kentucky by Motschoulsky (1862), Horn (1868, 1883), Garman (1892), and Jeannel (1931, 1949).

In the same years, however, almost 50 species and subspecies of anophthalmids were described from Tennessee, Virginia, and West Virginia where collecting had been more intensive. All but a few of these forms were described between 1928 and 1952 by Jeannel and Valentine. Suspecting (correctly, as it turned out) that a rich Kentucky anophthalmid fauna remained to be found, we spent about five weeks of the summer of 1957 searching for anophthalmids in central Kentucky. Specimens collected at that time constitute the majority of the specimens on which this paper is based. At about the same time, Dr. Thomas C. Barr, Jr. became interested in the anophthalmid fauna of Kentucky and has subsequently described (1959, 1962a) several Kentucky forms. In order to avoid duplication of effort, Dr. Barr and I have agreed that each of us will focus his attention on certain geographic areas and/or species groups. Hence his papers in which Kentucky anophthalmids are considered have dealt with anophthalmids of the Mammoth Cave area and the

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Pennyroyal Plateau and the *menetriesi, pubescens, audax,* and *robustus* groups. Considered in this paper are other species groups and species from the Kentucky Bluegrass and vicinity.

I am indeed grateful to Dr. Thomas C. Barr, Jr., for his co-operation in the arrangement described above, for his generous exchange of specimens and ideas with me, for his patience while this work was in progress, and for his helpful criticism of this manuscript. I am also most grateful to John Rittman who assisted me so capably in the 1957 collecting and to Signe Heide who prepared the distribution map. I acknowledge with appreciation the assistance of the National Science Foundation whose grant G-3888 supported the 1957 collecting and whose grant G-5637 supported the analysis of the material.

The holotypes and allotypes of all the new species described herein are deposited in the collection of Field Museum of Natural History (FMNH). Except for *Pseudanophthalmus puteanus* and *P. conditus,* paratypes are in both my collection and that of Thomas C. Barr, Jr. The single paratype of *puteanus* is in the collection of Dr. Barr and the single paratype of *conditus* is in my collection.

The measurements (in mm.) used are those proposed and described by Valentine (1932, 1945) and used by me (1958) previously. The abbreviations used are: TL—total length; HL—head length; HW—head width; PL—pronotum length; PW—pronotum width; EL—elytron length; EW—elytra width; DE—depth; ANT—antenna length; AED—aedeagus length. I have included the extended mandibles in the head length, and in total length, as does Valentine; Barr's recent measurements do not include the mandibles. Most of the indices which Valentine proposed as being useful can be determined from the measurements given if they are desired. A useful index that cannot be determined from the measurements, the chaetotaxial index (abbreviated "c"), is given with the measurements. It should be noted that though the drawings of the aedeagi are dorsal views of the organ as it lies *in situ,* it is convenient and customary to refer to this as a lateral view and hence to the convex portion as dorsal, the concave as ventral, that surface toward the viewer as left, that away from him as right.

All but one species of the anophthalmids of the Kentucky Bluegrass and vicinity may be assigned to four species groups. In all the species two discal setae are found, with the first of them typically at the level of the 4th humeral papilla, and the recurrent stria joins either the 3rd or the 5th elytral stria. A key by means of which the

four groups and the species not assigned to a group may be distinguished is provided below. First it is appropriate that comments be made concerning some of the key characters.

The mesosternum in anophthalmids typically slopes gently, or follows a broad convex curve, to an anterior narrowing of the mesothorax. Barr (1966) has noted, however, that in some central Kentucky forms this portion of the mesosternum is distinctly angulate and that in many cases there is a tubercle at this angle.

In most anophthalmids the posterior margin of the last (6th) abdominal sternite of the male is gently arched without interruption. Barr (1967a) has pointed out that in males of the *gracilis* and *inexpectatus* groups there is a shallow but distinct indentation in this margin. A similar, though usually not as distinct an indentation, is often found in males of the *horni* group.

Another character of considerable utility in distinguishing between groups is the nature of the microsculpture, especially that of the elytra. The surface of anophthalmids is generally alutaceous (leathery) in appearance. Some forms, however, when viewed under relatively low magnification have a matte surface. Barr (*pers. comm.*) has termed this "pruinose." The difference in microsculpture is most distinctive under the higher magnifications of a dissecting microscope. The sculpturing of the alutaceous surface is transverse and irregular. The pruinose surface, in contrast, is composed of minute uniform-sized polygons, each with a minute hair (microtrichia?).

Key to the Species Groups, and Species Not Assigned to a Group, of *Pseudanophthalmus* From the Kentucky Bluegrass and Vicinity

1	Inner margin of femora of anterior legs distinctly angulate about one-third the distance from their base . . . . . *barri* group
1′	Inner margin of profemora broadly rounded 2
2 (1′)	Humeri of elytra with distinct or feeble serrations (because the reflexed margin sometimes extends vertically these serrations may be visible only when the specimen is examined from a lateral angle) 3
2′	Humeri of elytra lacking serrations 4
3 (2)	Aedeagus with single copulatory piece; last (6th) abdominal sternite of male sometimes feebly indented . . . . . *horni* group
3′	Aedeagus with two long, slender copulatory pieces; last (6th) abdominal sternite of male shallowly, but distinctly, indented . *inexpectatus* group
4 (2′)	Forms from the southeast portion of the Kentucky Bluegrass and the adjacent Cumberland Plateau with two copulatory pieces which basally are two concentric cylinders . . . . . *rittmani* group

4′ Form from the southwestern portion of the Kentucky Bluegrass with a single copulatory piece . . . . . *P. conditus* n. sp.

HORNI GROUP

Length 3.3–5.3 mm. Microsculpture alutaceous or pruinose. Labrum with low, broad, weakly to well-defined median tooth. Posterior angles of pronotum sharply rectangular to somewhat acute with straight or slightly concave lateral margins. Mesosternum distinctly angled except in *ohioensis*, *exoticus*, *krameri*, and *pholeter*. Humeri of elytra distinctly serrate; striae fairly distinct on disc, becoming indistinct laterally (except in *exoticus*); 1st discal seta just posterior to level of 4th marginal humeral papilla (except in *exoticus*); recurved portion of apical groove weakly impressed and so variable (either curving medially to the 3rd stria or curving laterally or extending subparallel to the elytral suture and interpretable as joining either the 3rd or 5th stria) that it is of no diagnostic value.

Aedeagus moderately to extremely elongate; ranging in shape from those flattened ventrally and weakly arched dorsally with a distinct basal flexure to those arched both ventrally and dorsally and lacking a distinct basal flexure; apex moderately to very extensively produced; transfer apparatus short to moderately long, consisting of a single element which in lateral view tapers from a thick base to a pointed tip. Parameres moderately long, bearing 4 or 5 setae.

The only species of anophthalmid heretofore described from the Bluegrass is *Pseudanophthalmus horni* after which this group is named. Jeannel grouped this species at one time (1931) with *pusio* and at another (1949) with *robustus*. Valentine (1932) considered this species as forming a distinct group related to the *menetriesi* group. Barr (1959), like Valentine, distinguished between the *horni* and *robustus* groups and having compared the forms recently retains this distinction (Barr, *pers. comm.*). I concur with Valentine and Barr in considering this a distinct group.

The *horni* group species are similar in external appearances to those of the *inexpectatus* group. But species of the *horni* group can be distinguished from those of the *inexpectatus* group on the basis of the following external characteristics. 1) The posterior margin of the last abdominal sternite of males of the *inexpectatus* group is typically rather clearly indented; there is often an indentation here in males of the *horni* group also, but this indentation is rather shallow and poorly defined. 2) In caves where they coexist (Reid's= Picadome, Swope, Arnold, Dix Dam, Clifton, Robinson, and Hay-

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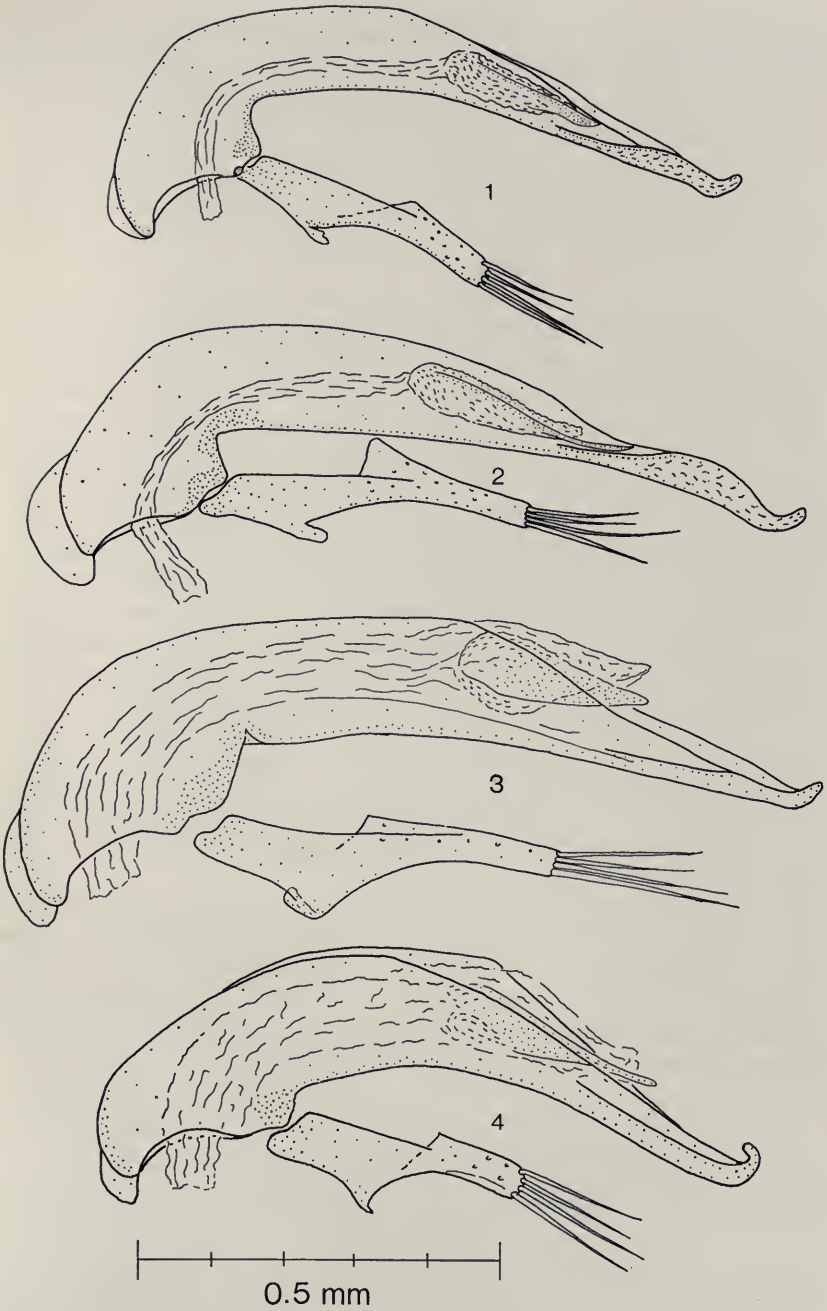
FIGS. 1–4. Aedeagi of *Pseudanophthalmus* species of *horni* group. **1.** *P. horni abditus*, n. ssp. **2.** *P. solivagus*, n. sp. **3.** *P. tenebrosus*, n. sp. **4.** *P. desertus desertus*, n. sp. and ssp.


1
2
3
4
0.5 mm

den) the *horni* group form is larger than the *inexpectatus* group form, though the range of size is not sharply discontinuous in the first two caves listed. 3) In caves where they coexist the *horni* group forms have a distinctly angulate mesosternum in contrast to the gradually sloping mesosternum of the *inexpectatus* group. It should be noted, however, that certain forms of the *horni* group, namely *ohioensis*, *exoticus*, *krameri*, and *pholeter*, do not have a distinctly angulate mesosternum.

It is, however, on the basis of the aedeagal characteristics, and specifically those of the copulatory pieces, that the *horni* and *inexpectatus* groups are most sharply distinguished. The copulatory pieces of species of the *inexpectatus* group are in the form of two long subparallel blades which regularly protrude through the aperture of the median lobe. In species of the *horni* group there is a single copulatory piece which in lateral view tapers from a thick base to a pointed tip. When viewed dorsally or ventrally (cf. fig. 5a), this single element is seen to be a blunt-tipped elongate triangular extension of a flattened cylinder; denticles are often found at its tip. The membranous internal sac sheaths the copulatory piece for much of its length. Ventrally the membranous sac extends toward the produced tip of the median lobe and forms a distinct chitinized "floor" within the U-shaped tube which extends beyond the copulatory piece. In certain preparations and/or when viewed at a particular angle this chitinized membrane may appear to be a second copulatory piece. In no case, however, is it detached from the median lobe so as to extend through the aperture in association with the copulatory piece which lies dorsal to it.

Forms of the *horni* group are found in greatest concentration in the Kentucky River basin of the Bluegrass. They are scattered also in the Licking River drainage of the Bluegrass and north of the Ohio River in southeastern Indiana and southwestern Ohio. One species tentatively assigned to this group is found in the Cumberland Plateau immediately to the east of the Bluegrass.

Key to the Species and Subspecies of the *horni* Group

1	Body, especially elytra, with alutaceous microsculpture	2
1′	Body, especially elytra, with pruinose microsculpture	12
2 (1)	Apex of aedeagus directed downward	3
2′	Apex of aedeagus directed upward	4
3 (2)	Apex of aedeagus broadly rounded (fig. 5)	*chthonius* n. sp.
3′	Apex of aedeagus blunt (fig. 7)	*exoticus* n. sp.

4 (2′) Apex of aedeagus curved gently upward (fig. 6) . . . . . *ohioensis* n. sp.

4′ Apex of aedeagus recurved or with tip extending upward at an angle . 5

5 (4′) Apex of aedeagus with tip extending upward at an angle (figs. 1, 2, 3, 9) 7

5′ Apex of aedeagus recurved (fig. 4) . . . . . *desertus* n. sp. 6

6 (5′) Smaller body (3.87–4.84 mm.) and aedeagus (0.91–1.17 mm.) *desertus* n. sp.

6′ Larger body (4.93–5.30 mm.) and aedeagus (1.29 mm.) *desertus major* n. ssp.

7 (5) Apex of aedeagus much produced beyond the aperture (figs. 2, 3, 9) . 10

7′ Apex of aedeagus only slightly produced beyond the aperture (fig. 1). *horni* (Garman) 8

8 (7′) Aedeagus less than 0.8 mm. long . . . . . *horni* s. str.

8′ Aedeagus more than 0.8 mm. long 9

9 (8′) Aedeagus 0.85–0.96 mm. long . . . . . *horni abditus* n. ssp.

9′ Aedeagus more than 1.0 mm. long . . . . . *horni caecus* n. ssp.

10 (7) Apex of aedeagus distinctly swollen beyond the aperture (figs. 2, 9) . 11

10′ Apex of aedeagus not distinctly swollen beyond the aperture (fig. 3). *tenebrosus* n. sp.

11 (10) Swollen portion of produced apex of aedeagus very long (fig. 9); aedeagus more than 1.35 mm. long; copulatory piece more than 0.3 length of aedeagus . . . . . *elongatus* n. sp.

11′ Swollen portion of produced apex of aedeagus moderately long (fig. 2); aedeagus less than 1.2 mm. long; copulatory piece less than 0.3 length of aedeagus . . . . . *solivagus* n. sp.

12 (1′) Smaller body (3.40–4.07 mm.) and aedeagus (1.11–1.17 mm.) *krameri* n. sp.

12′ Larger body (3.94–4.94 mm.) and aedeagus (1.55 mm.) . *pholeter* n. sp.

Pseudanophthalmus horni horni (Garman), new status

Anophthalmus horni Garman, 1892, p. 241. Type locality: caves and quarry fissures within the corporate limits of Lexington, Fayette Co., Ky. Barber, 1928, p. 196.

Pseudanophthalmus horni: Jeannel, 1928, p. 128, figs. 1,372–1,376; Jeannel, 1931, p. 456, figs. 69–73; Valentine, 1932, p. 276, pl. 23, fig. 4.

Pseudanophthalmus horni horni: Jeannel, 1949, p. 49, fig. 27. Type locality: as above, though designated by Jeannel as a "small cavern on the site of the University of Kentucky."

Pseudanophthalmus horni garmani: Jeannel, 1949, p. 49, fig. 37. Type locality: Reid's Cave (one mile west of Lexington), Fayette Co., Ky. (Mus. Nat. Hist. Nat., Paris). (NEW SYNONYMY.)

Pseudanophthalmus horni minor: Jeannel, 1949, p. 49, fig. 36. Type locality. Phelp's Cave (five miles southwest of Lexington), Fayette Co., Ky. (coll: Henrot; cotype Mus. Nat. Hist. Nat., Paris). (NEW SYNONOMY.)

Though specimens of *P. horni* were set aside by Garman as types they were not available to Jeannel or Valentine and have, in fact, only recently been located (Barr, *pers. comm.*, May 9, 1968). Partially as a result of this there is, unfortunately, a good deal of confusion about this species in the literature. Jeannel's 1928 figures of *horni*, labelled simply "from Lexington," must be of a Reid's Cave specimen (where he collected two specimens in 1928): they are identical to those in his 1931 paper identified more specifically as being from Reid's Cave. In 1949 Jeannel described three subspecies of *horni:* 1) *horni* s. str., on the basis of a specimen in his possession collected by Garman which he acknowledged receiving from the U. S. National Museum; 2) *horni garmani* on the basis of two specimens he had collected from Reid's Cave and one collected by Henrot in Picadome Cave; 3) *horni minor*, on the basis of 15 specimens from Phelp's Cave. In the meantime, Barr and his associates (*pers. comm.*) have concluded that "Reid's Cave" and "Picadome Cave" are two names applied to the same cave. Finally, when Garman's types were located the holotype was identified as coming from Reid's Cave. There is no question, therefore, that *garmani* must be placed into synonymy. As a matter of fact, the characters cited by Jeannel as diagnostic of subspecies *minor*—smaller size, less deeply insinuated pronotal margin, and less recurved aedeagal apex—are variations not restricted to the Phelp's Cave population. Hence *minor*, too, is placed into synonymy.

We were able to collect only two specimens from Reid's (=Picadome) Cave in 1957. Fortunately, both were males. When I removed the genitalia I discovered that there were two quite distinct forms: 1) that figured by Jeannel (1928, 1931, 1949) and Valentine (1932) for *horni*; 2) that described below for *umbratilis*. Fortunately, the specimens which Jeannel and Valentine used for their dissections and figures were of the form of the recently located holotype which Barr (*pers. comm.*) confirms as being the "robust local species with prominent mesosternal spine."

The forms of *P. horni* are most readily distinguished from other species of the group by the shape of the apex of the aedeagus: its tip extends upward at a rather distinct angle but it is produced only slightly beyond the aperture. The nominate subspecies is the smallest form of the species, being 3.72 $\pm$ 0.04 mm. in length. The

aedeagus is likewise small, the seven measured ranging from 0.77–0.78 mm. There is a great amount of variation in the chaetotaxial index (range 0.56–1.13) and a comparatively high mean chaetotaxial index (0.73). There are several long hairs anteriorly on the pronotum on either side of the midline among the short pubescence.

This form has been collected from several caves in the vicinity of Lexington, Kentucky: Reid's (=Picadome) Cave (type locality), immediately north of Picadome Elementary School, 2 miles southwest of Lexington courthouse, Fayette Co., Ky., July 1, 1957 (C. H. K. and J. Rittman); Phelp's Cave, 5 miles west-southwest of Lexington courthouse, Fayette Co., Ky., Oct. 8, 1961 (T. C. Barr); Russell Cave, 6 miles north-northeast of Lexington courthouse, Fayette Co., Ky., Nov. 16, 1963 (J. Holsinger), Aug. 5, 1964 (S. Peck and W. Andrews); Church Cave, 2.5 miles west-northwest of Georgetown, Scott Co., Ky., Sept., 1964 (R. McAdams and W. Andrews). Included in the measurements are five specimens in the U. S. National Museum labelled as being collected in Lexington by Hubbard and Schwarz on Oct. 9, 1892. These caves are located in the Inner Bluegrass in the drainage basins of North Elkhorn Creek and South Elkhorn Creek (including its Town Branch). Also found in Reid's Cave, as noted above, is *P. umbratilis*, a species of the *inexpectatus* group.

Pseudanophthalmus horni caecus, new subspecies

Type series.—Holotype, allotype, and 22 paratypes, from Clifton Cave, 0.6 mile east-southeast of Clifton, Woodford Co., Ky., June 24, 1963 (T. C. Barr).

Holotype male (FMNH). TL 4.37, HL 1.17, HW 0.80, PL 0.80, PW 1.00, EL 2.40, EW 1.57, DE 0.97, ANT 2.73, AED 1.01, c 0.58.

Allotype female (FMNH). TL 3.74, HL 1.00, HW 0.67, PL 0.70, PW 0.83, EL 2.03, EW 1.23, DE 0.80, ANT 2.23, c 0.67.

P. h. caecus, though not significantly larger in size (3.80 ± 0.08 mm.) than *horni* s. str., has a distinctly longer aedeagus (the three measured range from 1.01–1.05 mm.); as a result the genital index is slightly higher (on the order of 0.24 as compared to 0.21). In this form also there is great variation in the chaetotaxial index (range 0.53–1.04) and a relatively high mean chaetotaxial index (0.78).

Clifton Cave is very near the Kentucky River several miles upstream from Frankfort. Occupying the same cave is *P. umbratilis* of the *inexpectatus* group, a form noticeably smaller in size.

Pseudanophthalmus horni abditus, new subspecies

Type series.—Holotype, allotype, and 29 paratypes, from Swope Cave, 4.5 miles north of Versailles, Woodford, Co., Ky., holotype, allotype, and 23 paratypes, July 3, 1957 (C. H. K. and J. Rittman), 6 paratypes Sept. 17, 1961 (T. C. Barr); 4 paratypes from Weber #2 Cave, 3 miles southeast of Versailles, Woodford Co., Ky., Aug. 10, 1963 (T. C. Barr); 4 paratypes from Meece Cave, 4.5 miles north-northwest of Nicholasville, Jessamine Co., Ky., April 7, 1964 (R. McAdams and W. Andrews).

Holotype male (FMNH). Fig. 1. TL 4.10, HL 1.05, HW 0.70, PL 0.80, PW 0.95, EL 2.25, EW 1.40, DE 0.80, ANT 2.40, AED 0.88, c 0.63.

Allotype female (FMNH). TL 3.80, HL 0.95, HW 0.65, PL 0.75, PW 0.85, EL 2.10, EW 1.25, DE 0.80, ANT 2.20, c 0.74.

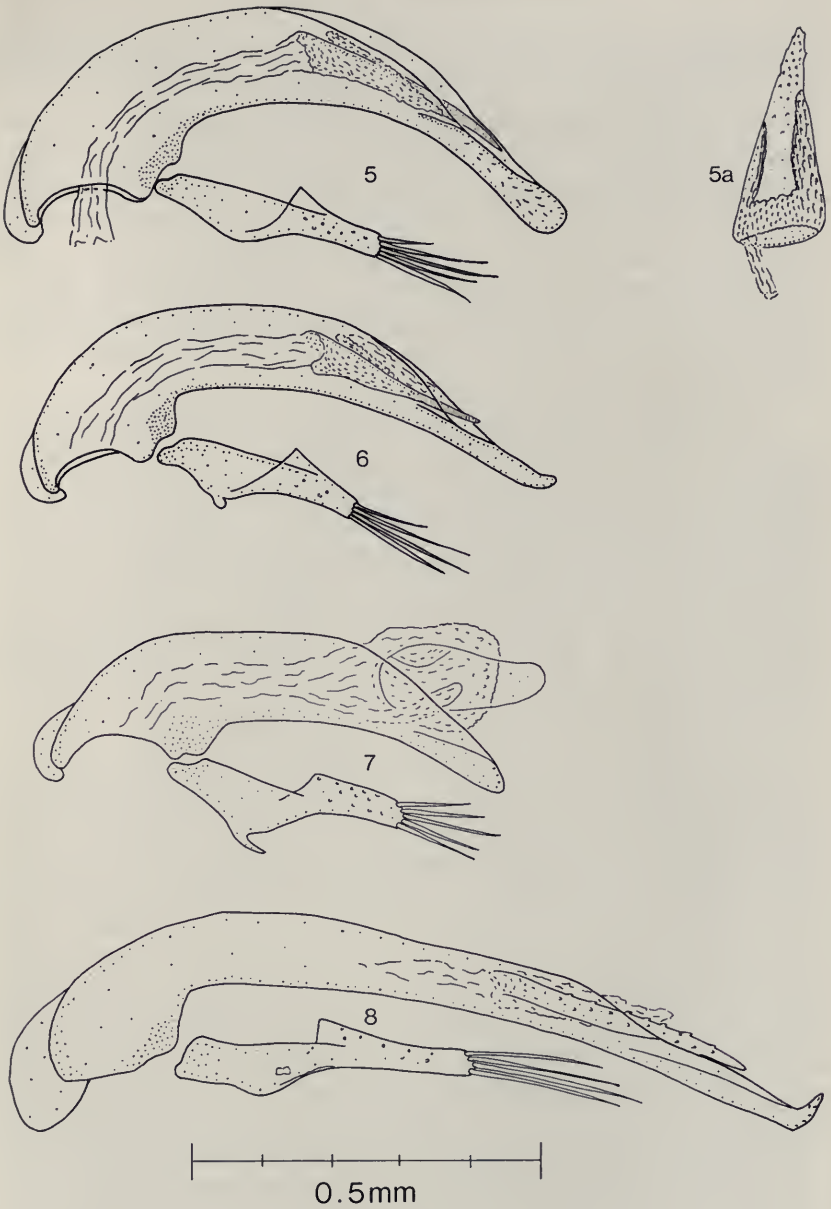
P. h. abditus is the largest of the three subspecies of *horni* here recognized (3.93 ± 0.04 mm.); but its aedeagus is smaller (the 11 measured range from 0.85–0.96 mm., average 0.91 mm.) than that of *h. caecus*. The variation in the chaetotaxial index (range 0.54–0.77) is much less, and the mean chaetotaxial index (0.66) is lower than in the other forms.

The caves from which this form has been taken are in the vicinity of Versailles. Swope Cave, north of Versailles, is near Lee Branch which drains into South Elkhorn Creek. Weber #2 Cave and Meece Cave, southeast of Versailles, are in the karst area lying between Clear Creek and South Elkhorn Creek. Living with *h. abditus* in Swope Cave is *P. umbratilis,* a species of the *inexpectatus* group; there is no appreciable size difference between these two forms.

Pseudanophthalmus solivagus, new species

Type series.—Holotype, allotype, and 62 paratypes from Weber Cave, 2 miles northwest of Nonesuch, Woodford Co., Ky., July 2, 1957 (C. H. K. and J. Rittman); 39 paratypes from Nonesuch Cave, 2.5 miles east-northeast of Nonesuch, Woodford Co., Ky., Oct. 8, 1961 (T. C. Barr); 5 paratypes from Britton Cave, 4.5 miles southwest of Troy, Woodford Co., Ky., Nov. 4, 1962 (T. C. Barr); 1 paratype from Keene Cave, 1 mile east of Keene, Woodford Co., Ky., July 16, 1965 (W. Andrews and N. Hornback).

Holotype male (FMNH). Fig. 2. TL 4.35, HL 1.20, HW 0.75, PL 0.80, PW 0.95, EL 2.35, EW 1.55, DE 0.90, ANT 2.80, AED 1.08, c 0.68.



FIGS. 5–8. Aedeagi of *Pseudanophthalmus* species of *horni* group. **5.** *P. chthonius*, n. sp.; **5a**, transfer apparatus, ventral aspect. **6.** *P. ohioensis*, n. sp. **7.** *P. exoticus*, n. sp. **8.** *P. krameri*, n. sp.

Allotype female (FMNH). TL 4.30, HL 1.20, HW 0.75, PL 0.80, PW 0.95, EL 2.30, EW 1.50, DE 0.85, ANT 2.60, c 0.74.

P. solivagus, horni, elongatus, and *tenebrosus* seem to form a natural subgroup of the *horni* group. In general form, color, and pubescence these species are so similar as to be indistinguishable. The pronotum and elytra are covered with a short and sparse pubescence, and in most specimens (but not all) there are several long hairs anteriorly on the pronotum on either side of the midline. Moreover, the aedeagi of these species are similar in that the produced apex has a tip which extends upward at a rather distinct angle and the parameres bear four setae.

P. solivagus, with a length of 4.14 ± 0.02 mm., is distinctly smaller in size than *elongatus* and *tenebrosus;* it can also be distinguished from these species by aedeagal shape as described below. On the other hand, *solivagus* is larger than any of the *horni* subspecies. Also the aedeagus of *solivagus* is longer than that of any of the *horni* subspecies: the nine aedeagi measured range from 1.03–1.19 mm., and average 1.12 mm., in length. *P. solivagus* is distinguished most readily from *horni* by the shape of the aedeagus: the produced tip of *solivagus* is distinctly swollen beyond the copulatory piece, while in *horni* there is no such swelling of the produced tip.

P. solivagus was found in the greatest abundance of all the species reported in this paper. In Weber's Cave approximately 30 specimens were taken in the flat crawlway which forms its entrance; the remainder were collected with the diminished effort which ensued when we found that a water channel opened into virgin cave. The caves in which *solivagus* is found are north and east of the deeply entrenched Kentucky River where, shortly after being joined by the Dix River, it changes its generally westward course to a generally northern one. Weber's Cave stream flows into Clear Creek, a tributary of the Kentucky River; Nonesuch Cave lies along the East Fork of Clear Creek; and Keene Cave is in the upland a short distance north of the intermittent headwaters of the East Fork of Clear Creek. Britton Cave is in the upland above a bend in the Kentucky River, more than 200 ft. higher in altitude than, and less than a mile north and less than a mile southeast of, the river.

Pseudanophthalmus elongatus, new species

Type series.—Holotype, allotype, and 54 paratypes from Old Fort Cave, 1.2 miles northeast of Harrodsburg, Mercer Co., Ky.,

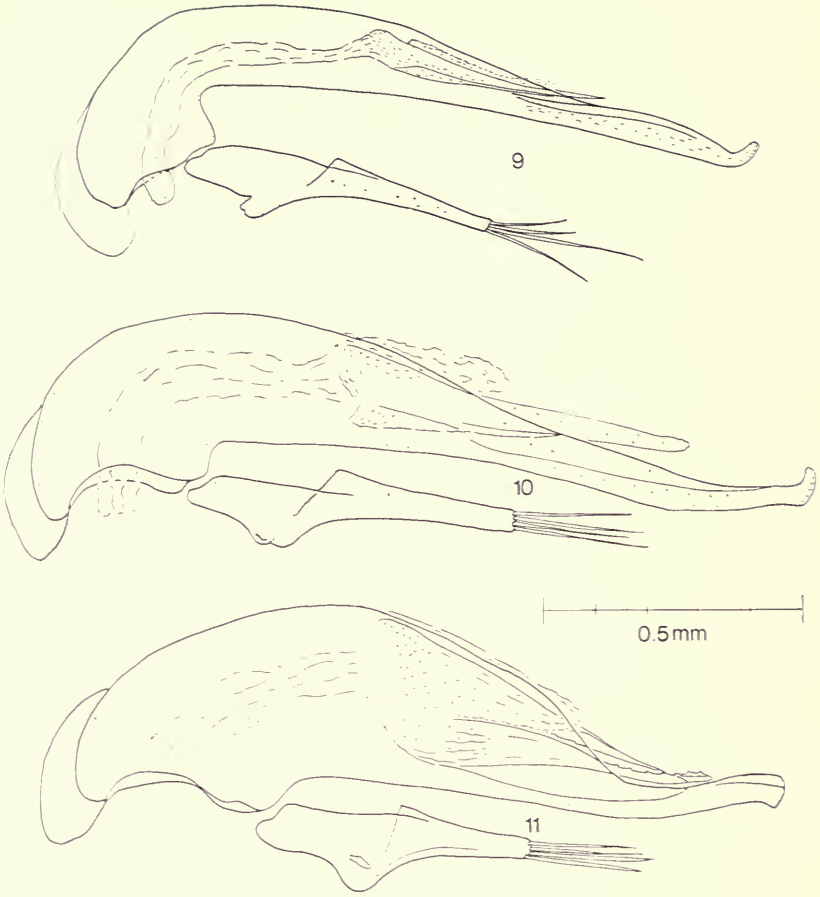
July 2, 1957 (C. H. K. and J. Rittman); 2 paratypes from Dix Dam Cave, 2 miles northwest of Buena Vista, Garrard Co., Ky., July 2, 1957 (C. H. K. and J. Rittman); 3 paratypes from Robinson Cave, 4.5 miles west-northwest of Lancaster, Garrard Co., Ky., Aug. 16, 1957 (C. H. K. and J. Rittman); 8 paratypes from Arnold Cave, 1.2 miles west-northwest of Bryantsville, Garrard Co., Ky., July 2, 1957 (C. H. K. and J. Rittman).

Holotype male (FMNH). Fig. 9. TL 4.65, HL 1.30, HW 0.75, PL 0.80, PW 1.00, EL 2.55, EW 1.50, DE 1.10, ANT 2.75, AED 1.38, c. 0.64.

Allotype female. TL 4.75, HL 1.30, HW 0.80, PL 0.90, PW 1.10, EL 2.55, EW 1.60, DE 0.95, ANT 3.05, c 0.58.

P. elongatus, with a length of 4.71 ± 0.02 mm., and *P. tenebrosus,* with a length of 4.75 ± 0.05 mm., are the largest species of the *horni* group. The aedeagus of *elongatus* is by far the longest in the group; the seven measured range from 1.35–1.43 mm., and average 1.38 mm., in length. As in *horni, solivagus,* and *tenebrosus,* the apex of the aedeagus of *elongatus* is produced and has a tip which extends upward at a distinct angle. As in *solivagus,* but unlike in *horni* and *tenebrosus,* the apex is clearly swollen beyond the position of the copulatory piece. The apex of *elongatus* is much more produced, however, than that of *solivagus;* moreover, the copulatory piece is approximately one-third the length of the aedeagus in *elongatus* (the seven measured range from 0.31–0.37, average 0.35) as compared to less than three-tenths the length of the aedeagus in *solivagus* (the eight measured range from 0.25–0.30, average 0.27).

Old Fort Cave lies in a karst plain about 6 miles southwest of the Kentucky River at the southwest margin of the Inner Bluegrass. Whether the waters of this cave drain north and east via Shaker Creek into the Kentucky River or west via Town Creek into Salt River is not known. Dix Dam Cave, Arnold Cave, and Robinson Cave lie immediately east of Dix River, a major tributary of the Kentucky River. In these last three caves is found also *P. umbratilis,* a species of the *inexpectatus* group, which is clearly smaller in size than *elongatus.* The three Robinson Cave specimens listed as paratypes of *elongatus* are all females hence cannot be assigned to this species with certainty. They are, however, clearly of the *horni* group, are in geographic proximity to the other populations of *elongatus,* and are of the size of *elongatus.*



FIGS. 9–11. Aedeagi of *Pseudanophthalmus* species of *horni* and *rittmani* groups. **9.** *P. elongatus* n. sp. **10.** *P. pholeter* n. sp. **11.** *P. rittmani* n. sp.

Pseudanophthalmus tenebrosus, new species

Type series.—Holotype, allotype, and 11 paratypes from Stevens Creek Cave, 0.85 mile east-southeast of Orville, Henry Co., Ky., July 9, 1966 (T. C. Barr and R. Norton).

Holotype male (FMNH). Fig. 3. TL 4.87, HL 1.30, HW 0.80, PL 0.87, PW 1.00, EL 2.70, EW 1.63, DE 1.10, ANT 3.00, AED 1.12, c. 0.52.

Allotype female (FMNH). TL 4.90, HL 1.23, HW 0.87, PL 0.90, PW 1.03, EL 2.77, EW 1.73, DE 1.23, ANT 3.10, c 0.51.

Although the body length of *tenebrosus* and *elongatus* is comparable, their aedeagi are quite different in length. The three aedeagi of *tenebrosus* measured average 1.16 mm. in length (ranging from 1.12–1.19 mm.) as compared to the average 1.38 mm. length of *elongatus*. As a result there is, of course, a difference in genital index: that of *tenebrosus* which averages 0.24 (range 0.23–0.24) is lower than that of *elongatus* which averages 0.29 (range 0.28–0.30). The apex of the aedeagus of *tenebrosus*, like that of *elongatus* but unlike that of *horni*, is extensively produced beyond the copulatory piece. The produced portion of the aedeagus is, however, like that of *horni* but unlike that of *elongatus*, not clearly swollen.

Stevens Creek Cave is about 20 miles north of Clifton Cave and even farther from the other caves in which are found the other forms of its subgroup (*horni, solivagus,* and *elongatus*). It lies near Stevens Creek less than a mile from where it enters the Kentucky River.

Pseudanophthalmus desertus desertus, new species and subspecies

Type series.—Holotype, allotype, and 8 paratypes from Jones Cave, 0.8 mile northeast of Locust Grove, Clark Co., Ky., June 17, 1963 (T. C. Barr); 5 paratypes from Price Cave, 1.8 miles east-northeast of Eminence, Henry Co., Ky., July 9, 1966 (T. C. Barr and R. Norton); 2 paratypes from Slack's Cave, 3 miles west-southwest of Georgetown, Scott Co., Ky., Jan. 18, 1963 (T. C. Barr); 1 paratype from Hayden Cave, 0.5 mile south-southeast of Gratz, Owen Co., Ky., July 9, 1966 (R. Norton).

Holotype male (FMNH). Fig. 4. TL 4.03, HL 1.03, HW 0.73, PL 0.70, PW 0.90, EL 2.30, EW 1.40, DE 0.83, ANT 2.47, AED 0.93, c 0.64.

Allotype female (FMNH). TL 4.53, HL 1.30, HW 0.73, PL 0.83, PW 0.90, EL 2.40, EW 1.53, DE 1.07, ANT 3.00, c 0.70.

The size of *P. desertus desertus* (4.39 $\pm$ 0.08 mm.) is intermediate in the size range of the *horni* group. There is a considerable range of variation both in body length (from 3.87–4.84 mm.) and in aedeagus length (from 0.91–1.17 mm., average 1.01 mm., in the nine specimens measured), and more than one form may be represented in this sample. I am, however, unable to distinguish any such forms on the basis of the small number of specimens available. This species is distinguished from *horni, solivagus, elongatus,* and *tenebrosus* by the fact that its pronotum and elytra are covered with abundant and

medium length hairs rather than short and sparse pubescence; also the longer hairs often found anteriorly on the pronotum of these species are not found in *desertus*. The apical groove of *d. desertus* is rather distinctly impressed and clearly joins the 3rd stria. The chaetotaxial index of this form ranges from 0.52–0.77, averages 0.64. Most distinctive of this species is the apex of the aedeagus: it forms a distinct hook with the tip pointing back toward the base of the aedeagus. The transfer apparatus is clearly of the *horni* type.

P. d. desertus is found, apparently in small populations, in several widely scattered caves. Price, Hayden, and Slack's caves are north and west of Lexington, the former two about 40 miles distant, the latter about 10 miles. Jones Cave, on the other hand, is about 10 miles southeast of Lexington. All four caves are in the Kentucky River drainage basin. Found also in Hayden Cave is *P. umbratilis* of the *inexpectatus* group, a form which is clearly smaller in size than *d. desertus*.

Pseudanophthalmus desertus major, new subspecies

Type series.—Holotype, allotype, and one male paratype, from Beaver Cave, 3 miles northeast of Oddville, Harrison Co., Ky.,July 17, 1966 (T. C. Barr).

Holotype male (FMNH). TL 4.97, HL 1.30, HW 0.83, PL 0.90, PW 1.13, EL 2.77, EW 1.70, DE 1.10, ANT 3.24, AED 1.29, c 0.56.

Allotype female (FMNH). TL 5.30, HL 1.40, HW 0.90, PL 0.97, PW 1.17, EL 2.93, EW 1.80, DE 1.17, ANT 3.30, c 0.48.

P. d. major is noticeably larger (range 4.93–5.30 mm., mean 5.04 ± 0.10 mm.) than *desertus* s. str. In addition the single aedeagus measured, at 1.29 mm., is considerably larger than any of *desertus* s. str. *P. d. major* also has somewhat more distinct lateral striae on the elytra and has a smaller chaetotaxial index (range 0.48–0.56, mean 0.52). The apical groove joins either the 3rd or the 5th stria.

Beaver Cave, about 35 miles northeast of Lexington, is 30 miles distant from the nearest cave (Slack's Cave) from which the nominate subspecies has been taken. It lies near Beaver Creek, a tributary of Licking River.

Pseudanophthalmus chthonius, new species

Type series.—Holotype, allotype, and 28 paratypes from Wilson Cave 1.5 miles northwest of Kent, Jefferson Co., Ind., holotype, allotype, and 22 paratypes, June 9, 1957 (C. H. K. and J. Rittman),

6 paratypes, Aug. 9, 1964 (T. C. Barr); 22 paratypes from Morris Cave, 4.5 miles south-southwest of Kent, Jefferson Co., Ind., Aug. 3, 1959 (C. H. K. and W. Bloom); 2 paratypes from Lowry Cave, 0.5 mile east of Commiskey, Jennings Co., Ind., June 9, 1957 (C. H. K. and J. Rittman); 1 paratype from Indian Cave, 0.5 mile southwest of Charlestown, Clark Co., Ind., Aug. 2, 1959 (C. H. K. and W. Bloom); 1 paratype from Peyton Beechwood Cave, 3 miles southwest of Charlestown, Clark Co., Ind., Aug. 2, 1959 (C. H. K. and W. Bloom).

Holotype male (FMNH). Figs. 5, 5a. TL 4.65, HL 1.20, HW 0.80, PL 0.85, PW 1.00, EL 2.60, EW 1.55, DE 0.90, ANT 2.55, AED 0.85, c 0.63.

Allotype female (FMNH). TL 4.45, HL 1.10, HW 0.80, PL 0.85, PW 1.05, EL 2.50, EW 1.55, DE 0.95, ANT 2.70, c 0.56.

P. chthonius, with a length of 4.31 $\pm$ 0.02 mm., is intermediate in the size range of the *horni* group. The aedeagus, however, is short (the six measured range from 0.77–0.86 mm., average 0.82 mm.), hence the genital index is low (range 0.18–0.20, mean 0.18). The mesosternum is distinctly angled. The pronotum and elytra are covered with a short and sparse pubescence. Most, but not all, specimens have several longer hairs anteriorly on the pronotum on either side of the midline. The pronotal angles are somewhat acute by virtue of the fact that the posterior margin is rather deeply concave as it joins the rather prominent basal angle.

The tip of the aedeagus is most distinctive: it is club shaped and broadly rounded. The parameres bear 4 or 5 setae. The general form of the copulatory piece is like that of the other species of the *horni* group. The copulatory piece is approximately four-tenths the length of the aedeagus (from 0.39–0.44, mean 0.42, in the six measured), distinctly longer proportionately than in any other species of the group. The portion of the membranous sac which forms the floor of the produced apical tube of the aedeagus is well chitinized and may appear to be a second copulatory piece. It remains attached to the tube, however, rather than extending freely through the aperture as the copulatory piece does, hence is not interpreted as a copulatory piece. Small spurs are also visible at the base of the copulatory piece of this species. On careful examination these spurs are seen to be rather heavily chitinized portions of the base of the flattened cylinder from which the copulatory piece in this group typically arises.

The caves from which this species is known are in southeastern Indiana, across the Ohio River from where the forms described above are found. Indian Cave and Peyton Beechwood Cave lie near Pleasant Run, a tributary of Silver Creek which after a short distance flows into the Ohio River. In these caves *P. chthonius* is the rare associate of *P. barri* described below. The other caves are in the drainage basin of the Muscatatuck River which drains by a long route (via the White and Wabash rivers) into the Ohio River. All five caves in which *P. chthonius* is found are in rocks covered with glacial drift of Kansan and Illinoian ages. All previously described anophthalmids have come from non-glaciated areas, and the significance of this and other exceptions reported below in this paper will be discussed later. The rocks in which these caves are found correspond to those of the Bluegrass section of the Interior Low Plateaus province of Kentucky. However, southeastern Indiana, where glacial rather than bedrock controlled topography predominates, is classified by physiographers (Thornbury, 1965) as the Till Plains section of the Central Lowland province. For convenience the boundary between these sections northeast of Louisville is placed at the Ohio River.

Pseudanophthalmus ohioensis, new species

Type series.—Holotype, allotype, and 5 paratypes from Freeland Cave, 6 miles southeast of Peebles, Adams Co., Ohio, holotype, allotype, and 2 paratypes, June 7, 1957 (C. H. K. and J. Rittman), 3 paratypes, March 13, 1960 (F. Kramer and W. Menrath).

Holotype male (FMNH). Fig. 6. TL 4.10, HL 1.00, HW 0.70, PL 0.75, PW 0.90, EL 2.35, EW 1.45, DE 1.00, ANT 2.35, AED 0.78, c 0.55.

Allotype female (FMNH). TL 4.30, HL 1.20, HW 0.80, PL 0.80, PW 0.95, EL 2.30, EW 1.45, DE 0.90, ANT 2.45, c 0.62.

P. ohioensis, like *chthonius*, is of intermediate length (4.24 ± 0.06 mm.) among the species of the *horni* group and has an aedeagus which is short (the two measured are 0.78 and 0.85 mm.) so that its genital index is low (0.19 and 0.20). The pronotum and elytra are covered with a short and sparse pubescence. Most, but not all, specimens have several long hairs anteriorly on the pronotum on either side of the midline. As in *chthonius* the pronotal angles are somewhat acute by virtue of the posterior margin being rather deeply concave as it joins the rather prominent basal angle. The lateral

striae are somewhat more distinct in *ohioensis* than in *chthonius*, and the apical groove of *ohioensis* regularly joins the 3rd stria rather than either the 3rd or 5th as in *chthonius* and many other species in this group. In contrast to all species of the *horni* group considered to this point, the mesosternum of *ohioensis* is not distinctly angulate nor does it have a tubercle. The general habitus otherwise is that of the *horni* group. The characteristics of the aedeagus, and particularly of the transfer apparatus, are clearly those of the *horni* group. Thus there is no question of its placement here. The apex of the aedeagus is slightly produced; the tip curves gently upward and comes to a slightly rounded point.

P. ohioensis is the first anophthalmid to be taken from Ohio. Freeland Cave is in a valley of a deeply dissected, relatively narrow plateau which lies between the extension of the Bluegrass into Ohio and the Illinoian glacial boundary on the west and the Cumberland Plateau to the east. This plateau, the Highland Rim, corresponds to the plateau west and southwest of the Bluegrass in Kentucky which I refer to below, following Barr (1967b), as the Pennyroyal Plateau, though many geomorphologists restrict the term Pennyroyal Plateau to that portion of the plateau south of the Mammoth Cave Plateau and refer to the remainder as the Highland Rim. Freeland Cave lies on Turkey Creek whose waters drain eastward via the South Fork of Scioto Brush Creek and then southward via the Scioto River to the Ohio River.

Pseudanophthalmus exoticus, new species

Holotype male from Townsend Cave, 4 miles west-northwest of Zachariah, Estill Co., Ky., Aug. 15, 1957 (C. H. K. and J. Rittman).

Holotype male (FMNH). Fig. 7. TL 4.34, HL 1.13, HW 0.73, PL 0.80, PW 1.00, EL 2.40, EW 1.53, DE 1.00, ANT 2.63, AED 0.70, c 0.59.

Four anophthalmid specimens were taken from Townsend Cave. Two of them are assigned to *P. exiguus* and another to *P. rittmani*, both described below. The fourth constitutes another species herewith named *exoticus*. *P. exoticus* is tentatively included in the *horni* group because of the form of the copulatory piece, though it differs rather markedly from other species of this group in several respects. The species is of moderate size (4.34 mm.) but its aedeagus is short (0.70 mm.), hence the genital index is very low (0.16). The general body form and humeral serrations are those of the *horni* group. The

pronotum and elytra are covered with moderately long and dense pubescence. The apical groove joins the 3rd stria. As in *ohioensis* the mesosternum is not distinctly angulate. The following characteristics of *exoticus* are in contrast to all other forms assigned to the *horni* group: 1) the 1st discal seta is approximately at the level of the 3rd humeral papilla; 2) the discal striae are distinctly impressed and punctate.

The apex of the aedeagus of *exoticus* is not produced as it is in other species assigned to the *horni* group. Rather the tip of the aedeagus is broad and blunt. The parameres are relatively short and bear five short setae. The copulatory piece is very similar in its ventral aspect (that shown in the drawing because the aedeagus was flattened in preparation) to that of other species of the *horni* group examined from this aspect.

Townsend Cave is in the uplands of the Cumberland Plateau immediately to the east of the Bluegrass. It lies about 300 ft. above the floodplain of the nearby Kentucky River to which its waters drain by way of Billy Fork and Millers Creek.

Pseudanophthalmus krameri, new species

Type series.—Holotype, allotype, and 9 paratypes, from Cave Hill Cave, 5 miles northwest of West Union, Adams Co., Ohio, holotype, allotype, and 8 paratypes, Aug. 28, 1962 (C. H. K. and N. Krekeler), 1 paratype, March 13, 1960 (F. Kramer and W. Menrath.

Holotype male (FMNH). Fig. 8. TL 3.47, HL 0.87, HW 0.67, PL 0.70, PW 0.83, EL 1.90, EW 1.13, DE 0.67, ANT 1.93, AED 1.17, c 0.76.

Allotype female (FMNH). TL 3.63, HL 1.07, HW 0.70, PL 0.70, PW 0.83, EL 1.87, EW 1.13, DE 0.67, ANT 2.00, c 0.79.

P. krameri and the remaining species of this group, *P. pholeter,* may be considered an aberrant subgroup of the *horni* group. In contrast to all the other species of the *horni* group, they have pruinose microsculpture. Moreover, as in *ohioensis* and *exoticus,* the mesosternum is not angulate. The disc of the pronotum is pubescent. The recurved portion of the apical groove is relatively short and well impressed, curving inward proximally to join the 3rd stria. The fact that the transfer apparatus of these two species is, as described below, so similar to that of the species of the *horni* group described above, seems to warrant including them in this group.

P. krameri is relatively small in size, averaging 3.67 ± 0.06 mm. in length. The posterior angles of the pronotum are somewhat acute by virtue of the lateral and posterior margins being slightly concave; the basal margin is straight or very shallowly concave. The humeri of the elytra slope more distinctly and the elytral margins are more gently arcuate in *krameri* than *pholeter*. The striae on the disc of the elytra of *krameri* are somewhat less distinct than in *pholeter;* this is particularly noticeable apically: the 3rd stria, where it is joined by the recurrent stria, is feebly impressed in *krameri*. The chaetotaxial index of *krameri* is high (range 0.67–0.88, mean 0.82).

The two aedeagi of *krameri* measured are 1.11 and 1.17 mm. in length; the genital index is 0.32. The median lobe of the aedeagus is quite thin; and the basal bulb, though only of moderate size, is rather well demarcated from the median lobe. The apex of the aedeagus is produced and terminates in an extension which angles sharply dorsally so that the tip has a boot-like appearance. The copulatory piece is approximately one-third the length of the aedeagus (the two measured were 0.33 and 0.34 the aedeagal length) and is covered apically with rather large denticles.

Cave Hill Cave is high on a hill from which water drains eventually into the Ohio River. The hill forms a divide so that drainage is either 1) northeastward via Cherry Fork and thence east and south by way of the West Fork of Brush Creek and Ohio Brush Creek to the Ohio, or 2) south and west via the East Fork of Eagle Creek and Eagle Creek to the Ohio. The cave lies just within the boundaries of Illinoian glaciation. It is formed in the limestones which comprise the bedrock of the Outer Bluegrass. Because of the fact that the area has been glaciated, however, geomorphologists include it within the Central Lowlands province.

I am pleased to name this species after Frank Kramer of Cincinnati who first collected this form.

Pseudanophthalmus pholeter, new species

Type series.—Holotype, allotype, and 4 paratypes, from Adams Cave, 5 miles south-southwest of Richmond, Madison Co., Ky., Aug. 15, 1964 (T. C. Barr and S. Peck).

Holotype male (FMNH). Fig. 10. TL 4.64, HL 1.23, HW 0.83, PL 0.87, PW 1.03, EL 2.53, EW 1.60, DE 1.00, ANT 2.80, AED 1.55, c 0.55.

Allotype female. TL 4.13, HL 1.13, HW 0.73, PL 0.77, PW 0.93, EL 2.23, EW 1.33, DE 0.83, ANT 2.47, c 0.53.

P. pholeter is significantly larger (averaging 4.42 ± 0.15 mm. in length) than *krameri;* there is, however, an overlapping of size ranges (*krameri*, 3.40–4.07 mm.; *pholeter*, 3.94–4.94 mm.). The posterior angles of the pronotum are distinctly rectangular, rather than acute as in *krameri;* the basal margin is concave, though shallowly so. The humeri of the elytra are rounded and the elytral margins are gently arcuate. The striae on the disc of the elytra are quite distinct and regular; the lateral striae are less distinct. The chaetotaxial index (range 0.50–0.72, mean 0.56) is much lower than that of *krameri*. The ciliated reflexed margin of the elytra in the humeral region extends about 45° above horizontal so that its distinct, but shallow, serrations are not readily visible when the specimen is viewed dorsally.

The length of the aedeagus of *pholeter* is much greater (that measured being 1.55 mm.) than that of *krameri*. But inasmuch as the body length of *krameri* is smaller than that of *pholeter* the genital index of the two forms is essentially the same (*krameri*, 0.32; *pholeter*, 0.33). The median lobe of the aedeagus of *pholeter* is much thicker than that of *krameri;* the basal bulb is large but poorly demarcated from the median lobe. As in *krameri*, the produced apex has a bootlike appearance. The copulatory piece of the single aedeagus examined is 0.45 the length of the aedeagus. As in *krameri*, the copulatory piece is covered apically with denticles, but those of *pholeter* are much smaller and less conspicuous than those of *krameri*.

Adams Cave is in rocks of the Outer Bluegrass and lies near Silver Creek, a tributary of the Kentucky River. Adams Cave is almost 90 miles distant from Cave Hill Cave where *krameri* is found. In addition, the two caves are separated by the Ohio River. On the basis of numerous common features of *krameri* and *pholeter* as described above, particularly of the aedeagi, the two species are considered to be closely related.

INEXPECTATUS GROUP

Length 3.2–4.2 mm. Labrum with low, broad, weakly defined median tooth. Posterior angles of pronotum sharply rectangular with straight or concave lateral margins; disc of pronotum pubescent. Margin of elytra with ciliated obsolete serrations throughout length, the serrations very feeble and widely spaced along margins, less feeble and more closely spaced at humeri, the cilia along margins larger than in *horni* group; striae evident though quite broad, shallow, and irregu-

lar, becoming indistinct laterally; 1st discal seta approximately at level of 4th marginal humeral papilla; chaetotaxial index variable but generally high (averages range from 0.72 to 0.99); recurved portion of apical groove weakly impressed and so variable (either curving medially to the 3rd stria or curving laterally or extending subparallel to the elytral suture and interpretable as joining either the 3rd or 5th stria) that it is of no diagnostic value.

Aedeagus moderately elongate; relatively flat ventrally and moderately arched dorsally, with a moderate basal flexure; apex produced. Transfer apparatus proportionately quite long, ranging from one-half to two-thirds the length of the aedeagus; composed of two elements each of which is semicylindrical at its base but becomes blade-like (flattened, slender, and pointed) toward its apex. Parameres moderately long, bearing 2 or 3 setae.

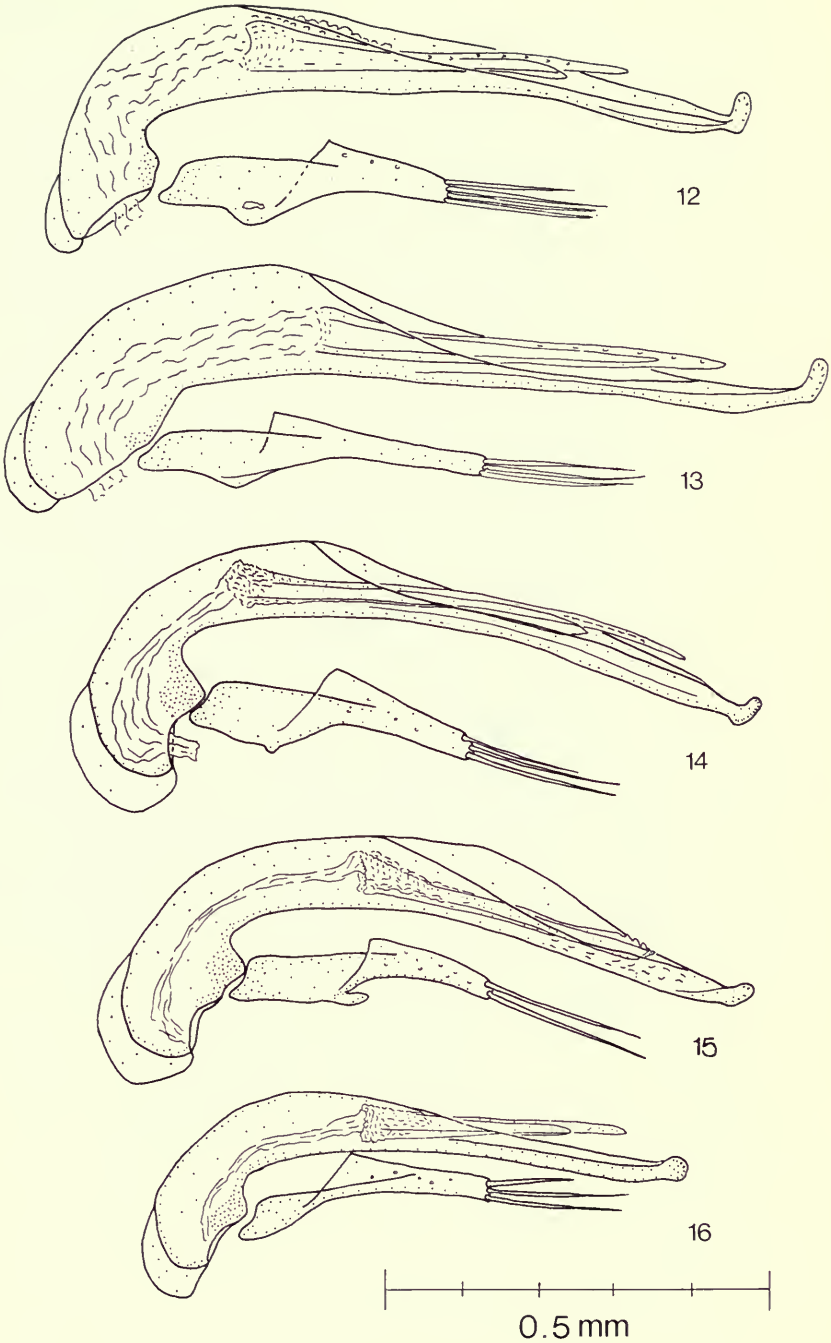
Barr (1967a), in reviewing the characteristics of *P. inexpectatus* Barr of Mammoth Cave, pointed out the similarities of this species to *P. gracilis* Valentine and *P. hadenoecus* Barr of the Appalachian Valley. The similarities which are particularly striking are: 1) all three species have an indentation in the last abdominal sternite of the males (the only other species in which this is found are included in the *horni* group; as discussed above, the indentation in those species is not well developed); 2) the aedeagi of these species are unusually long and slender and contain two long and slender copulatory pieces.

On the other hand, the Appalachian Valley species differ from *inexpectatus* in the following respects: 1) the labrum lacks a tooth; 2) the humeri lack serrations; 3) the striae are very indistinct, even on the disc; 4) the parameres bear four setae.

Though it may eventually be desirable to include the Kentucky forms and the eastern forms in a single group, two distinct subgroups would have to be recognized. For convenience, therefore, the Kentucky forms are here considered as the *inexpectatus* group, a group related to but separate from the *gracilis* group.

Key to the Species and Subspecies of the *inexpectatus* Group

1	One of the copulatory pieces denticulate 2
1′	Neither copulatory piece denticulate . . . . . *umbratilis* n. sp.
2 (1)	Copulatory pieces subequal in length . . . . . *parvus* n. sp.
2′	Copulatory pieces distinctly unequal in length 3
3 (2′)	Longer copulatory piece at least two-thirds length of aedeagus. *cnephosus* n. sp.
3′	Longer copulatory piece 0.5 to 0.6 length of aedeagus 4
4 (3′)	Small (3.4–3.6 mm. long), narrow (width index 0.31–0.34) form from the Bluegrass . . . . . *puteanus* n. sp.


12
13
14
15
16
0.5 mm

4′ Forms from the region south and west of the Bluegrass. *inexpectatus* Barr 5

5 (4′) Smaller (3.3–3.8 mm. long) and proportionately wider (width index 0.34–0.35) form from the Mammoth Cave Plateau... *inexpectatus* s. str.

5′ Larger (3.6–4.2 mm. long) and proportionately narrower (width index 0.30–0.34) form from the Pennroyal Plateau. *inexpectatus orientalis* n. ssp.

Pseudanophthalmus inexpectatus inexpectatus Barr, new status

Pseudanophthalmus inexpectatus Barr, 1959, p. 10. figs. 3A and 7 (3). Type locality: White Cave, Edmonson Co., Ky. Barr, 1962b, p. 281. Barr, 1967a, p. 24.

P. inexpectatus inexpectatus is small in size (the five specimens of which I have measurements average 3.52 ± 0.08 mm. in length). The chaetotaxial index is high (range 0.82–0.93, mean 0.86). The two aedeagi I have measured are 0.98 and 1.01 mm. in length. The copulatory pieces of the aedeagi of both *i. inexpectatus* and *i. orientalis* are 50–60 per cent the length of the aedeagus, and in both forms the right copulatory piece is distinctly longer than the left and is denticulate.

P. i. inexpectatus has been taken in small numbers from White Cave and adjoining Mammoth Cave and from Great Onyx Cave of the Flint Ridge cave system northeast of Mammoth Cave (Barr, 1962b). These are caves of the Mammoth Cave Plateau southwest of the Bluegrass which lie in the Green River drainage.

Pseudanophthalmus inexpectatus orientalis, new subspecies

Type series.—Holotype, allotype, and 8 paratypes from Wilson Cave, 1 mile southeast of Black Gnat, Green Co., Ky., Aug. 21, 1963 (T. C. Barr); 4 paratypes from Phillips Cave, 4 miles northwest of Campbellsville, Taylor Co., Ky., June 23, 1957 (C. H. K. and J. Rittman).

Holotype male (FMNH). Fig. 12. TL 4.03, HL 1.07, HW 0.67, PL 0.73, PW 0.87, EL 2.23, EW 1.30, DE 0.77, ANT 2.33, AED 0.93, c 0.74.

Allotype female (FMNH). TL 4.00, HL 1.13, HW 0.67, PL 0.73, PW 0.83, EL 2.13, EW 1.27, DE 0.73, ANT 2.50, c 0.84.

FIGS. 12–16. Aedeagi of *Pseudanophthalmus* species of *inexpectatus* group. **12.** *P. inexpectatus orientalis* n. ssp. **13.** *P. puteanus* n. sp. **14.** *P. cnephosus* n. sp. **15.** *P. parvus* n. sp. **16.** *P. umbratilis* n. sp.

P. i. orientalis is slightly greater in length (3.87 ± 0.04 mm.) than the nominate subspecies. The average width of the two forms, however, is identical (1.25 ± 0.02 mm.); hence *orientalis* is proportionately narrower (range of width index 0.30–0.34, mean 0.32; range of elytral index 0.57–0.61, mean 0.59) than the nominate form (range of width index 0.35–0.36, mean 0.36; range of elytral index 0.60–0.64, mean 0.63). The chaetotaxial index of *orientalis,* like that of the nominate form, is high (range 0.74–0.96, mean 0.84).

The aedeagus of *orientalis* is slightly shorter (the four measured range from 0.90–0.98 mm., average 0.94 mm.) than that of *inexpectatus* s. str. The genital index of *orientalis* is somewhat smaller (range 0.22–0.26, mean 0.24), therefore, than that of the nominate form (range 0.27–0.29, mean 0.28). In form and in the nature of the copulatory apparatus, however, the aedeagi of these two forms are indistinguishable. Because of their great similarity these two forms are judged to be at most subspecifically distinct.

Wilson Cave and Phillips Cave lie near tributaries of Green River about 40 miles east of the caves in which *inexpectatus* s. str. is found. These caves are in the Pennyroyal Plateau southwest of the Bluegrass in Mississippian limestones of an older age (Osagian series) than those in which Mammoth Cave is formed (Meramecian series).

Pseudanophthalmus puteanus, new species

Type series.—Holotype and 1 paratype from Old Well Cave, 0.6 mile southeast of Nevada, Mercer Co., Ky., June 26, 1965 (J. R. Holsinger).

Holotype male (FMNH). Fig. 13. TL 3.47, HL 0.90, HW 0.57, PL 0.63, PW 0.77, EL 1.93, EW 1.17, DE 0.67, ANT 2.23, AED 1.06, c 0.75.

P. puteanus has a body length (3.46 ± 0.04 mm.) comparable to that of *inexpectatus* s. str. It is considerably narrower than that form in width (1.12 ± 0.04 mm.), however, hence is comparable to *i. orientalis* in width index (range 0.31–0.34, mean 0.32) and elytral index (range 0.58–0.60, mean 0.59). The aedeagus of the single specimen measured is slightly larger in length (1.06 mm.) than the aedeagi of the *inexpectatus* forms. The aedeagal index (0.31) is therefore distinctly higher than that of *i. orientalis* and somewhat higher than that of *i. inexpectatus.* The chaetotaxial index of this species (range 0.70–0.75, mean 0.72) is a bit lower than that of the *inexpectatus* forms. The overall form of the aedeagus of this species and the

shape and proportion of the copulatory pieces are very similar to those of *inexpectatus*.

On the basis of morphology alone this form could be considered another subspecies of *inexpectatus*. The following facts, however, indicate that there is little, if any, possibility of gene exchange between *inexpectatus* and this form: 1) Old Well Cave is 35 miles distant from the nearest cave (Phillips) from which a form of *inexpectatus* is known; 2) Old Well Cave is near a stream whose waters eventually drain north and west via Beech Fork and Rolling Fork to the Ohio River whereas the caves in which *inexpectatus* is found are in the Green River drainage basin; 3) Old Well Cave is in rocks of the Bluegrass which are separated from the limestones of the Pennyroyal Plateau and the Mammoth Cave Plateau in which the *inexpectatus* forms are found by a series of non-caverniferous rocks which comprise Muldraugh's Hill.

Pseudanophthalmus cnephosus, new species

Type series.—Holotype, allotype, and 28 paratypes from Eli Reed Cave, 6.5 miles east-southeast of Hodgenville, Larue Co., Ky., Aug. 17, 1957 (C. H. K. and J. Rittman).

Holotype male (FMNH). Fig. 14. TL 3.50, HL 0.90, HW 0.60, PL 0.65, PW 0.75, EL 1.95, EW 1.15, DE 0.80, ANT 2.15, AED 0.91, c 0.79.

Allotype female (FMNH). TL 3.65, HL 1.00, HW 0.65, PL 0.70, PW 0.80, EL 1.95, EW 1.25, DE 0.70, ANT 2.20, c 0.86.

The body length of *P. cnephosus* (3.77 $\pm$ 0.03 mm.) is intermediate in the range of the *inexpectatus* group, as are the length of the aedeagus (mean of four measured is 0.94 mm.) and genital index (mean is 0.25). The chaetotaxial index (range 0.73–0.93, mean 0.85) also is not unusual. What is most distinctive of this species is that the longer of the two copulatory pieces (the right one) is more than two-thirds the length of the aedeagus (the four measured range from 0.67 to 0.69, average 0.68, the length of the aedeagus). This is in contrast to the other species of the *inexpectatus* group in which the proportion for individual aedeagi ranges from 0.45 to 0.57. In addition, the apex of the elytra is distinctly truncate, or at least obliquely truncate, in *cnephosus* whereas in the other species of the group it tends to be more rounded.

Eli Reed Cave is formed in Mississippian limestones near the eastern margin of the Pennyroyal Plateau. It is on the divide be-

tween Rolling Fork immediately to the east and McDougal Creek which drains westward via Nolin River into Green River.

Pseudanophthalmus parvus, new species

Type series.—Holotype, allotype, and 20 paratypes from Tatum Cave, 1.8 miles west-southwest of Riley, Marion Co., Ky., holotype, allotype, and 18 paratypes, Aug. 17, 1957 (C. H. K. and J. Rittman); 2 paratypes, Oct. 9, 1965 (T. C. Barr).

Holotype male (FMNH). Fig. 15. TL 3.45, HL 0.90, HW 0.60, PL 0.65, PW 0.80, EL 1.90, EW 1.15, DE 0.70, ANT 2.10, AED 0.86, c 1.00.

Allotype female. TL 3.40, HL 1.00, HW 0.60, PL 0.60, PW 0.75, EL 1.80, EW 1.05, DE 0.65, ANT 1.90, c 1.16.

P. parvus, with a length of 3.49 ± 0.03 mm., is one of the smaller species of the *inexpectatus* group. The aedeagus of this species is of intermediate length (the three measured range from 0.82–0.86 mm., average 0.84 mm.) and the resultant genital index (range 0.24–0.25, mean 0.25) is also intermediate for the group. The copulatory pieces are slightly less than half the length of the aedeagus (range 0.46–0.48, mean 0.47). The chaetotaxial index of *parvus* (range 0.85–1.18, mean 0.99) is the highest in the *inexpectatus* group. The pronotum is somewhat more wide in comparison to its length in this species than in the other species of this group. (The average pronotal index values are: *parvus* 1.22, *cnephosus* 1.15, *puteanus* 1.20, *inexpectus* s. str. 1.19, *i. orientalis* 1.15, *umbratilis* 1.18; there is so much overlapping in range between forms, however, that this characteristic is of little value).

The most distinctive characteristics of this species are that the two copulatory pieces are only slightly different in length and that the right one is clearly denticulate. In the forms of the *inexpectatus* group described above the right copulatory piece is toothed and considerably longer than the left; in *umbratilis,* described below, the right copulatory piece is longer than the left but is not denticulate.

Tatum Cave is near the southwest margin of the Bluegrass, adjacent to Muldraugh's Hill which bounds this section to the south and west. Followell Creek on which the cave lies drains into the North Rolling Fork.

Pseudanophthalmus umbratilis, new species

Type series.—Holotype, allotype, and 27 paratypes from Robinson Cave, 4.5 miles west-northwest of Lancaster, Garrard Co., Ky.,

Aug. 16, 1957 (C. H. K. and J. Rittman); 6 paratypes from Dix Dam Cave, 2 miles northwest of Buena Vista, Garrard Co., Ky., 4 on July 2, 1957 (C. H. K. and J. Rittman), 2 on Dec. 16, 1962 (M. D. Hassel); 1 paratype from Arnold's Cave, 1.2 miles west-northwest of Bryantsville, Garrard Co., Ky., July 2, 1957 (C. H. K. and J. Rittman); 1 paratype from Reid's (=Picadome) Cave, 2 miles southwest of Lexington courthouse, Fayette Co., Ky., July 1, 1957 (C. H. K. and J. Rittman); 1 paratype from Swope Cave, 4.5 miles north of Versailles, Woodford Co., Ky., July 3, 1957 (C. H. K. and J. Rittman); 5 paratypes from Clifton Cave, 0.6 mile east-southeast of Clifton, Woodford Co., Ky., 1 on Jan. 19, 1963 (T. C. Barr), 4 on June 24, 1963 (T. C. Barr); 2 paratypes from Hayden Cave, 0.5 mile south-southeast of Gratz, Owen Co., Ky., July 9, 1966 (R. Norton).

Holotype male (FMNH). Fig. 16. TL 3.90, HL 1.05, HW 0.65, PL 0.75, PW 0.85, EL 2.10, EW 1.25, DE 0.90, ANT 2.35, AED 0.72, c 0.74.

Allotype female. TL 4.05, HL 1.15, HW 0.70, PL 0.75, PW 0.90, EL 2.15, EW 1.35, DE 0.80, ANT 2.40, c 0.80.

There is a great deal of variation in the body length of *P. umbratilis* (from 3.20–4.20 mm.) so that a small sample of specimens from a given cave may appear quite different than that from another. But the total range in size variation of the species is displayed in the one cave, Robinson Cave, in which this form has been taken in any number. The average length of the specimens from Robinson Cave (3.86 $\pm$ 0.04 mm.) is very close to that of all the specimens included in this species (3.75 $\pm$ 0.04 mm.). The aedeagi of this species range from 0.68–0.78 mm. and average 0.74 mm. in length, a size considerably smaller than that of the other species of the group. The aedeagal index (range 0.18–0.22, mean 0.20) is the lowest in the group, though not sharply separated from that of *inexpectatus orientalis*. The chaetotaxial index, which ranges from 0.62–1.00, averages 0.78.

The aedeagus of *P. umbratilis* terminates with a small knob just beyond the elongate aperture. The right copulatory piece is distinctly longer than the left and about half (range 0.45–0.51, mean 0.48) the length of the aedeagus. In contrast to the other species of the *inexpectatus* group, neither copulatory piece is toothed.

All the caves in which *P. umbratilis* is found are in Ordovician limestones which form the bedrock of the Inner Bluegrass. More-

over, all these caves are in the drainage basin of the Kentucky River and two of its major tributaries, Dix River and Elkhorn Creek. Interestingly, all the specimens taken of this species are from caves in which forms of the *horni* group are present. But whereas this single form of the *inexpectatus* group is found, several distinct forms of the *horni* group are represented: *horni* s. str. in Reid's Cave; *h. abditus* in Swope Cave; *h. caecus* in Clifton Cave; *elongatus* in Dix Dam Cave, Arnold's Cave, and Robinson Cave; and *desertus desertus* in Hayden Cave. In all but Reid's Cave and Swope Cave *umbratilis* is distinctly smaller than the form of the *horni* group. Though we noted in our field notes that we thought that beetles of two different sizes were present in these caves, we were unable to detect any difference in habitat preference between the larger and smaller forms. The only cave in which we found *P. umbratilis* to be clearly more abundant than the *horni* group form is in Robinson Cave.

BARRI GROUP

Length 3.9–4.9 mm. Microsculpture of body pruinose, especially conspicuous on elytra. Labrum with poorly defined median tooth. Posterior angles of pronotum rectangular with straight or slightly concave lateral margins; basal margin straight or slightly concave, with a rather distinct median ridge extending anteriorly from it to disc; disc pubescent. Elytra convex, covered with short pubescence; reflexed margin rather wide, ciliated throughout length, feebly serrate at humeri; humeri rounded; striae fairly well impressed on disc, less distinct laterally; 1st discal seta approximately at level of 4th marginal humeral papilla; chaetotaxial index intermediate and quite variable; apex truncate to rounded, slightly dehiscent; recurved portion of apical stria well impressed, clearly joining the 3rd stria. Inner margin of femora of anterior legs distinctly angulate (rather than broadly rounded) about one-third the distance from the base of the femora.

Aedeagus moderately elongate, arcuate; basal plate well developed, terminal; apex produced. Transfer apparatus about two-fifths the length of the aedeagus, consisting of a single spatulate or twisted, scoop-shaped element covered with minute acute tubercles. Parameres relatively long, bearing 3 or 4 setae.

Pseudanophthalmus barri, new species

Type series.— Holotype, allotype, and 34 paratypes from Indian Cave, 0.5 mile southwest of Charlestown, Clark Co., Ind., holotype allotype, and 30 paratypes, Aug. 2, 1959 (C. H. K. and W. Bloom), 4 paratypes, Jan. 26, 1957 (L. Hubricht); 6 paratypes from Peyton Beechwood Cave, 3 miles southwest of Charlestown, Clark Co., Ind., Aug. 2, 1959 (C. H. K. and W. Bloom).

Holotype male (FMNH). Figs. 17, 17a. TL 3.94, HL 1.03, HW 0.67, PL 0.77, PW 0.90, EL 2.13, EW 1.27, DE 0.83, ANT 2.47, AED 0.99, c 0.79.

Allotype female (FMNH). TL 4.21, HL 1.07, HW 0.73, PL 0.83, PW 0.97, EL 2.30, EW 1.33, DE 0.97, ANT 2.57, c 0.58.

The two species of the *barri* group, *barri* and *troglodytes*, are virtually identical in length (*barri* 4.36 ± 0.03 mm., *troglodytes* 4.28 ± 0.05 mm.) and width (*barri* 1.39 ± 0.01 mm., *troglodytes* 1.40 ± 0.02 mm.). Moreover, the elytral index of the two forms is comparable (*barri* averaging 0.60, *troglodytes* averaging 0.62). *P. barri* ranges from testaceous to dark ferrugino-testaceous in color. It has a mean chaetotaxial index of 0.65 (range 0.52–0.79). The apex of the elytra is truncate or obliquely truncate. The recurrent apical stria extends anteriorly some distance in a straight line or a weak curve subparallel to the suture then curves inward rather sharply to join the 3rd stria.

The length of the aedeagus of *barri* (the four measured range from 0.99–1.11 mm., average 1.04 mm.) is about one-fourth the body length (range of genital index is 0.24–0.26). The median lobe of the aedeagus is very distinctive in shape. There is a large bulge on the left side of the median lobe just beyond half its length; this is seen most readily in a dorsal view of the aedeagus (fig. 17a). The aperture is on the right side of the lobe opposite the bulge rather than in the usual dorsal position. The apex, which is moderately extended, curves gently downward to a blunt point. The transfer apparatus consists of a single twisted, scoop-shaped element covered with minute acute tubercles.

The caves in which *P. barri* is found lie near Pleasant Run which drains via Silver Creek to the Ohio River. The caves are developed in limestones which are characteristic of the Outer Bluegrass. But inasmuch as these limestones are covered in this portion of Indiana with glacial till of Illinoian age, geomorphologists include this area within the Central Lowlands province.

It gives me great pleasure to name this species in honor of Dr. Thomas C. Barr, Jr., by whose courtesy this form first came to my attention and whose work with the anophthalmids the last decade has set standards worthy of emulation.

Pseudanophthalmus troglodytes, new species

Type series.—Holotype, allotype, and 21 paratypes from High-

baugh Cave, 4.5 miles northwest of Jeffersontown, Jefferson Co., Ky., Oct. 7, 1964 (N. Whitehead).

Holotype male (FMNH). Fig. 18. TL 4.47, HL 1.17, HW 0.77, PL 0.87, PW 1.00, EL 2.43, EW 1.50, DE 1.10, ANT 2.77, AED 1.19, c 0.62.

Allotype female (FMNH). TL 4.24, HL 1.17, HW 0.77, PL 0.83, PW 1.00, EL 2.23, EW 1.37, DE 0.93, ANT 2.50, c 0.70.

It is practically impossible to distinguish *P. troglodytes* from *barri* on the basis of external features. As indicated above, they are virtually identical in length, width, and elytral index. *P. troglodytes* tends to be darker in color, ranging from ferrugino-testaceous to fusco-testaceous. The chaetotaxial index of *troglodytes* (mean 0.72, range 0.59–0.88) is slightly higher than that of *barri*. The apex of the elytra tends to be more rounded in *troglodytes* than *barri*. The variability and wide overlapping of these several traits is so great, however, that they are of little diagnostic value. Of somewhat more value in distinguishing between these two species is the form of the recurrent apical stria. In *troglodytes* it curves gently throughout its length to join the 3rd stria whereas in *barri* it extends some distance subparallel to the suture before curving inward.

P. troglodytes is readily distinguished from *barri* on the basis of aedeagal characters. The aedeagus of *troglodytes* is longer (the five measured range from 1.19–1.26 mm., average 1.24 mm.) than that of *barri*. Inasmuch as the body length of the two species is the same, this means that the genital index of *troglodytes* (range 0.27–0.29) is higher than that of *barri*. The median lobe of the aedeagus of *troglodytes* lacks the peculiar post-median bulge of *barri* and the associated lateral aperture; in *troglodytes* the aperture of the aedeagus is in the usual dorsal position. The transfer apparatus consists of a single spatulate element covered with minute acute tubercles. The apex of the median lobe is moderately extended and curves gently upward and terminates in a small but distinct knob. The parameres of *troglodytes* are more attenuate than those of *barri*.

Highbaugh Cave is less than 15 miles distant from the caves in which *P. barri* is found, but it is separated from them by the Ohio River. The Middle Fork of Beargrass Creek near which Highbaugh Cave lies drains into the Ohio River. The cave is located in the Outer Bluegrass, in rocks of Silurian or Devonian age, just beyond the reach of Illinoian glaciation.

FIGS. 17–22. Aedeagi of *Pseudanophthalmus* species of *barri* and *rittmani* groups. **17.** *P. barri*, n. sp.; **17a**, dorsal view of terminal half of median lobe. **18.** *P. troglodytes*, n. sp. **19.** *P. exiguus exiguus*, n. sp. and ssp. **20.** *P. exiguus furtivus*, n. ssp., terminal half of median lobe. **21.** *P. catoryctos*, n. sp. **22.** *P. conditus*, n. sp.

RITTMANI GROUP

Length 3.5–6.6 mm. Microsculpture of body pruinose, especially conspicuous on elytra. Labrum with weakly or well defined median tooth. Posterior angles of pronotum rectangular with straight lateral margins; basal margin nearly straight; disc convex, sparsely pubescent, with several long hairs on either side of midline. Elytra convex, covered with short, sparse pubescence; reflexed margin of moderate width, ciliated throughout length but most regularly at humeri; humeri rounded or sloping, lacking serrations; striae of disc evident to weakly impressed, lateral striae indistinct or absent; 1st discal seta approximately at level of 4th marginal humeral papilla; chaetotaxial index low, averages ranging from 0.49 to 0.66; apex truncate to somewhat pointed, slightly dehiscent; recurved portion of apical stria distinctly to weakly impressed, distinctly to vaguely joining the 3rd stria.

Aedeagus relatively short; median lobe relatively broad and short, relatively flat ventrally, moderately arched dorsally; basal plate well developed, terminal; apex produced. Copulatory pieces from less than one-fourth to more than one-half the length of aedeagus; composed of two elements, each the extension from a basal cylinder; one element is semicylindrical and partially ensheaths the other. Parameres moderately long, bearing 3 or 4 setae.

Pseudanophthalmus rittmani, new species

Type series.—Holotype, allotype, and 13 paratypes from Baker Cave, 1.7 miles east of Cobhill, Estill Co., Ky., Aug. 15, 1957 (C. H. K. and J. Rittman); 15 paratypes from Watson Cave, 0.8 mile north-northeast of Cobhill, Estill Co., Ky., June 30, 1957 (C. H. K. and J. Rittman); 10 paratypes from Betsy Cave, 4 miles south-south east of Bowen, Powell Co., Ky., July 1, 1957 (C. H. K. and J. Rittman); 1 paratype from Townsend Cave, 4.5 miles east of Cobhill, Estill Co., Ky., Aug. 15, 1957 (C. H. K. and J. Rittman).

Holotype male (FMNH). Fig. 11. TL 6.05, HL 1.75, HW 0.95, PL 1.00, PW 1.20, EL 3.30, EW 2.05, DE 1.40, ANT 3.90, AED 1.42, c 0.42.

Allotype female (FMNH). TL 5.30, HL 1.50, HW 0.85, PL 0.95, PW 1.05, EL 2.85, EW 1.65, DE 1.15, ANT 3.30, c 0.48.

P. rittmani is a large (5.74 ± 0.06 mm.), moderately convex anophthalmid. The pronotum, with sides gently sinuate the entire length, is widest at one-fifth its length. The elytra are moderately wide and have relatively sloping humeri. The striae of the disc are evident though quite broad, shallow, and irregular, but the lateral striae are indistinct; the striae are vaguely and irregularly punctured. The chaetotaxial index is low (range 0.42–0.56, mean 0.49). The apex of the elytra is rounded or somewhat pointed. The recurved portion of the apical stria is distinct; it is gently bowed

except anteriorly where it curves inward rather sharply to join the 3rd stria which is very feebly impressed at this level.

The aedeagus of *rittmani* is relatively large, the six measured ranging from 1.26–1.42 mm., averaging 1.34 mm. in length. It is not large in proportion to the body, however; the genital index ranges from 0.21–0.24, averages 0.22. The median lobe is quite broad. The produced apex forms an open trough which is slightly expanded at its terminus. The copulatory pieces are half or more (0.49–0.56) the length of the aedeagus. The two elements are extensions from two concentric basal cylinders. The ventral part of the outer cylinder develops as a broad, trough-shaped, hyaline element. The ventral portion of the inner cylinder develops as a semicylindrical element, toothed apically, which lies within but extends a bit beyond the other element. The parameres bear 3 or 4 setae.

The caves in which *rittmani* is found lie immediately east of the Bluegrass in the Cumberland Plateau section of the Appalachian Plateaus province, in rocks of Mississippian and/or Pennsylvanian age. Baker, Watson, and Townsend caves are in uplands about 300–500 ft. above the Kentucky River, which are drained by deeply incised tributaries of Miller's Creek which flows into the Kentucky River. Betsy Cave, only some 5 miles distant, is on the other side of a divide; it is on the side of a hollow cut by a branch of the deeply cut South Fork of the Red River which drains by way of the Red River to the Kentucky River.

Interestingly, in all four caves from which *P. rittmani* has been taken is also found another, and clearly smaller, species of this group, *P. exiguus*. In three of these caves a good series was taken of both species. In these cases our field notes show that we recognized two size classes and observed that they occupy two distinct microhabitats. The smaller beetles were found under rocks and in wet sandy mud near the water's edge and scurried quickly when disturbed. The larger beetles were found crawling on moist sandy mud and under rocks some distance away from the water and moved less rapidly than the smaller form when disturbed.

It is my great pleasure to name this species in honor of John Rittman who so capably assisted me in collecting in the summer of 1957 and who has been a frequent and proficient collecting companion since that time.

Pseudanophthalmus exiguus exiguus, new species and subspecies

Type series.—Holotype, allotype, and 13 paratypes from Watson Cave, 0.8 mile north-northeast of Cobhill, Estill Co., Ky., June 30, 1957 (C. H. K. and J. Rittman); 13 paratypes from Baker Cave, 1.7 miles east of Cobhill, Estill Co., Ky., Aug. 15, 1957 (C. H. K. and J. Rittman); 13 paratypes from Betsy Cave, 4 miles south-southeast of Bowen, Powell Co., Ky., July 1, 1957 (C. H. K. and J. Rittman); 2 paratypes from Townsend Cave, 4.5 miles east of Cobhill, Estill Co., Ky., Aug. 15, 1957 (C. H. K. and J. Rittman); 4 paratypes from Natural Bridge Cave, 2 miles southeast of Slade, Powell Co., Ky., 3 on June 28, 1957 (C. H. K. and J. Rittman), 1 on May 27, 1962 (T. C. Barr); 14 paratypes from Pinnacle Cave, 5.5 miles north-northwest of Heidelberg, Lee Co., Ky., Dec. 1, 1962 (T. C. Barr); 6 paratypes from Cave Hollow Cave, 2.5 miles southeast of Crystal, Lee Co., Ky., Dec. 1, 1962 (T. C. Barr); 1 paratype from Stillhouse Cave, 2.5 miles east-southeast of Crystal, Lee Co., Ky., June 29, 1963 (T. C. Barr and R. Kuehne); 1 paratype from Ash Cave, 4 miles east-southeast of Crystal, Lee Co., Ky., Feb. 17, 1963 (P. Dickson).

Holotype male (FMNH). Fig. 19. TL 4.25, HL 1.20, HW 0.70, PL 0.80, PW 0.90, EL 2.25, EW 1.40, DE 1.05, ANT 3.00, AED 0.90, c 0.60.

Allotype female (FMNH). TL 3.75, HL 1.00, HW 0.65, PL 0.70, PW 0.85, EL 2.05, EW 1.30, DE 0.90, ANT 2.45, c 0.62.

P. exiguus exiguus is significantly smaller (3.98 $\pm$ 0.03 mm.) than *rittmani;* the largest *exiguus* specimen is 4.73 mm., the smallest *rittmani* is 4.85. The pronotum, with sides gently sinuate the entire length, is widest at one-third its length. The humeri of the elytra are rounded. The 1st and 2nd striae are feebly impressed and impunctate; the 3rd stria and those beyond it are very indistinct or absent. The chaetotaxial index, though low (range 0.56–0.75, mean 0.65), is somewhat higher than that of *rittmani.* The apex of the elytra is truncate or obtusely angled. The recurrent portion of the apical stria is rather distinct; it extends anteriorly subparallel to the internal margin toward the 4th stria then curves sharply but indistinctly inward to the level of the indistinct 3rd stria.

The aedeagus of *exiguus* s. str. is significantly smaller (the 16 measured range from 0.82–0.96 mm., average 0.88 mm., in length) than that of *rittmani.* The genital index (range 0.20–0.24, mean 0.22), however, is comparable to that of *rittmani.* The median lobe

is of moderate width. The elongate apex curves gently upward and ends in a slightly swollen knob. The copulatory pieces are one-third to two-fifths the length of the aedeagus. As in *rittmani* the two elements are extensions from two concentric basal cylinders, but the form of the elements and their relation to one another are quite different in the two species. In *exiguus* the ventral portion of the inner cylinder develops as a long, spatulate, hyaline element. The dorsal portion of the outer cylinder develops as a semicylindrical, partially chitinized membrane which partially ensheaths and extends a short distance beyond the other element. The parameres bear 3 or 4 setae.

In the series of specimens on the basis of which this form is described there is considerable variation in size, amount of pubescence on pronotum and elytra, distinctness and form of recurrent apical stria, shape of produced apex of aedeagus, width of spatulate transfer element, and relative length of sheathing and spatulate elements. Some of the variation, particularly of the aedeagi, seems attributable to differences in preparation and orientation. No pattern of variation has been recognized which would warrant division of this series into several forms.

As indicated above, *exiguus* s. str. is associated with *rittmani* in all four caves where that form has been found. In these caves *exiguus* is recognizably smaller, occupies a different subhabitat, and moves more quickly than *rittmani*.

The caves in which only *exiguus* s. str. is found are, like those in which it is associated with *rittmani*, located in the Cumberland Plateau in rocks of Mississippian and/or Pennsylvanian age. They are in uplands from nearly 200 to almost 400 ft. above the Kentucky and Red rivers. A small stream near Pinnacle Cave drains directly into the Kentucky River. Stillhouse, Ash, and Cave Hollow caves are along Big Sinking Creek, or its tributaries, which drains by way of Millers Creek into the Kentucky River. Natural Bridge Cave lies near the Middle Fork of Red River which drains by way of the Red River into the Kentucky River.

Pseudanophthalmus exiguus furtivus, new subspecies

Type series.—Holotype and allotype from California Cave, 1.5 miles north-northeast of Ravenna, Estill Co., Ky., Aug. 16, 1957 (C. H. K. and J. Rittman).

Holotype male (FMNH). Fig. 20. TL 3.70, HL 0.95, HW 0.65, PL 0.70, PW 0.80, EL 2.05, EW 1.30, DE 0.85, ANT 2.30, AED 0.85, c 0.73.

Allotype female (FMNH). TL 3.95, HL 1.05, HW 0.70, PL 0.75, PW 0.85, EL 2.15, EW 1.35, DE 1.00, ANT 2.40, c 0.60.

P. exiguus furtivus falls within the range of the variation expressed in *exiguus* s. str. with one exception. The apex of the ensheathing element is distinctly denticulate in *e. furtivus* whereas such denticulations are not present in any of the specimens of the nominate form. This peculiarity seems sufficiently important to warrant considering this a form sub-specifically distinct from the nominate form.

California Cave, 7 miles distant from the nearest cave in which the nominate form is found, is about 600 ft. above the Kentucky River on a ridge of the Cumberland Plateau. The several small streams draining this ridge are tributaries of creeks flowing into the Kentucky River.

Pseudanophthalmus catoryctos, new species

Type series.—Holotype, allotype, and 7 paratypes from Adams Cave, 5 miles south-southwest of Richmond, Madison Co., Ky., Aug. 15, 1964 (T. C. Barr and S. Peck).

Holotype male (FMNH). Fig. 21. TL 3.54, HL 0.90, HW 0.67, PL 0.67, PW 0.83, EL 1.97, EW 1.23, DE 0.73, ANT 2.37, AED 0.68, c 0.70.

Allotype female (FMNH). TL 3.67, HL 0.97, HW 0.70, PL 0.70, PW 0.90, EL 2.00, EW 1.17, DE 0.80, ANT 2.40, c 0.66.

P. catoryctos, with a length of 3.53 ± 0.07 mm., is the smallest species of this group. As in *exiguus*, the pronotum is widest at one-third its length and has gently sinuate sides, the humeri of the elytra are rounded, and the 1st and 2nd striae are feebly impressed and impunctate while the 3rd stria and those beyond it are very indistinct. The chaetotaxial index (range 0.58–0.78, mean 0.66) is like that of *exiguus*. The apex of the elytra is obtusely angled. The recurrent portion of the apical stria is well impressed; it follows a gently rounded course, eventually curving inward to the indistinct 3rd stria.

The aedeagus of *catoryctos* is distinctly shorter than that of *exiguus*, each of the three measured being 0.68 mm. in length. Moreover the genital index (range 0.18–0.19, mean 0.19) is lower than that of *exiguus* and *rittmani*. The median lobe is of moderate width. The apex, which extends only a short distance beyond the aperture, is quite thick and ends in a blunt angle. The copulatory pieces are

just less than one-fourth the length of the aedeagus. The two elements may well be, as is more clearly the case in the other species of this group, extensions from two concentric basal cylinders. An elongate hyaline element which lies above and to the left of and partially encloses the second element may be interpreted as the extension of an outer cylinder. The second element, a short triangular piece, may be interpreted as the extension of an inner cylinder. The parameres bear 3 setae.

P. catoryctos occupies the same cave in the Outer Bluegrass southeast of Lexington as *pholeter* of the *horni* group. It is readily distinguished from that species by its smaller size, lack of humeral serrations, lack of angulate mesosternum, and its aedeagal characteristics. Though *catoryctos* is thus found in a different physiographic province than *rittmani* and *exiguus*, it is from that part of the Bluegrass immediately adjacent to the Cumberland Plateau and the caves lie separated only by a distance of just over 20 miles. The gross morphology of the aedeagus of these three species is so different that it is not immediately apparent that they may be included in a single group. As described above, however, these forms are quite similar in many features of their external morphology. That feature which most strongly supports their inclusion in a single group is the apparent development of the two copulatory pieces of each species as extensions from two concentric basal cylinders. I have recognized the possibility of this interpretation of the copulatory apparatus of *catoryctos* after having been informed by Barr (*pers. comm,*) that he has species from Jackson, Rockcastle, and Fayette counties linking *cartoryctos* to *exiguus*.

INCERTAE SEDIS

Pseudanophthalmus conditus, new species

Type series.—Holotype, allotype, and 1 paratype from Lawrence Cave, 0.5 mile south-southwest of Perryville, Boyle Co., Ky., Aug. 16, 1957 (C. H. K. and J. Rittman).

Holotype male (FMNH). Fig. 22. TL 4.60, HL 1.20, HW 0.85, PL 0.85, PW 1.10, EL 2.55, EW 1.60, DE 0.95, ANT 2.75, AED 1.01, c 0.62.

Allotype female (FMNH). TL 4.50, HL 1.30, HW 0.80, PL 0.80, PW 1.10, EL 2.40, EW 1.50, DE 0.95, ANT 2.65, c 0.61.

P. conditus is a species of moderate length (4.46 ± 0.09 mm.). Its microsculpture is pruinose, in contrast to all the other forms in the

southwestern part of the geographic range considered in this paper. The inner margin of the profemora is broadly rounded. The mesosternum follows a broad convex curve to the anterior narrowing of the mesothorax. The last abdominal sternite of the male is weakly indented.

The head, pronotum, and elytra are pubescent, with the pubescence of the head being more sparse than elsewhere. The labrum possesses a low, broad median tooth. The pronotum, which is widest at about one-fourth its length, has rectangular posterior angles with straight lateral margins. The humeri of the elytra are broadly rounded; they possess more closely spaced setae than the remainder of the reflexed margin, but are not serrulate. The striae of the disc are weakly impressed and not punctate; only traces of striae beyond the 3rd are distinguishable. The elytral apex is broadly rounded. The distinct recurrent portion of the apical stria after paralleling the suture a short distance curves gently inward to join the 3rd stria.

The single aedeagus of *conditus* measured is of moderate length, 1.01 mm. The median lobe is relatively slender; it is flattened ventrally, weakly arched dorsally. The basal bulb is of moderate size, but the basal plate is quite large. The distal aperture extends over half the length of the median lobe. The apex extends a short distance beyond the aperture; it is straight and thin and ends in a blunt point. The parameres bear 4 setae. The transfer apparatus includes an elongate, heavily chitinized element which has a weakly bilobate tip. This element lies dorsally in the median lobe. Ventral to this element, and so closely associated with it that the limits of each are impossible to distinguish, is an extensively developed membranous sac. This sac extends some distance beyond the chitinized element to the tip of the aperture; it is so densely packed there that it almost appears as another element.

Lawrence Cave is near the southern margin of the Bluegrass, close to Muldraugh's Hill. A small stream nearby flows into Chaplin River whose waters drain north and west via Beech Fork and Rolling Fork to the Ohio River.

P. conditus does not appear to be closely related to any other of the species described above. In its external features, notably in its possession of pruinose microsculpture and lack of serrulate humeri, it is most similar to species of the *rittmani* group. But its transfer apparatus cannot, as in that group, be interpreted as extensions from two basal concentric cylinders. Similarly, the transfer apparatus of *conditus* shows no similarity to the characteristics of the

horni and *inexpectatus* groups. Its structure is sufficiently unclear that it could not be ruled out as being similar to that of the *barri* group species. But certain of the external characteristics of *conditus*, specifically its lack of angulate profemora and serrulate humeri, would seem to rule out the possibility of its inclusion in that group.

DISCUSSION

1

Twenty-six forms of anophthalmids are considered above, 24 of them new, from the Kentucky Bluegrass and nearby areas. Nineteen of the new forms are described as species, five as subspecies. In my study of Indiana anophthalmids (Krekeler, 1958) I considered all distinguishable forms as species. This was done on the assumption that caves are typically isolated habitats and that cavernicoles do not move between caves unless caves are known to be interconnected. Forms in different cave systems, it was then argued, would not be exchanging genes; these forms are thus reproductively isolated; and reproductively isolated and distinguishable forms, whether this isolation is extrinsically or intrinsically determined, are species. When I reviewed the dispersal of anophthalmids in further detail (Krekeler, 1959), I decided for reasons outlined in that paper that the burden of proof should be reversed and that cavernicoles should be assumed to be able to move between caves unless there is evidence of a probable barrier to dispersal. Under these circumstances the subspecific rank is a useful tool in the description of anophthalmids, and is accordingly used in this paper. Those forms which are judged by morphological criteria as probably exchanging genes are designated subspecies, while those judged by these criteria as probably not exchanging genes or for which there is evidence that extrinsic factors probably prevent gene exchange are designated species.

The forms described above as subspecies have a geographic distribution such that, and are from caves found in strata related to one another in such a way that, some gene exchange appears to be possible. The several subspecies of *P. horni* are from the Inner Bluegrass where the limestone beds are nearly horizontal so that dispersal between caves may occur by way of underground crevices from time to time. But each subspecies is found in caves which are relatively close to one another and/or of a limited drainage basin so that gene exchange is presumably much more regular. Though *inexpectatus*

s. str. and *i. orientalis* are from caves in limestone beds of different ages, there are not extensive non-caverniferous beds intervening which would serve as a barrier; but the caves are sufficiently far apart (some 40 miles) that gene exchange would not be regular. In the case of *P. desertus*, it is not clear how regular gene exchange is possible between the populations listed as comprising the nominate subspecies. All the caves seem to be formed in Ordovician limestones of the Inner Bluegrass, but there are intervening patches of Eden Shale. It is consistent with the general pattern being considered, however, that the only population which can be distinguished as a distinctive form, *d. major*, is that which is most widely separated from the others so that gene exchange would be the least regular. On the other hand, as described above, *P. puteanus* is so similar morphologically to *inexpectatus* that using such criteria alone it would be considered a subspecies of that form. But since the geographic and physiographic facts indicate little possibility of gene exchange between these forms *puteanus* is considered a species.

2

The distribution of the anophthalmids considered in this paper (see fig. 23) is of great interest for several other reasons. First of all, as I have pointed out previously (Krekeler, 1959), the fact that some of the *inexpectatus* group forms are from the Bluegrass northeast of Muldraugh's Hill (and outliers of it called the Knobs) and others are from the Pennyroyal Plateau and the Mammoth Cave Plateau southwest of Muldraugh's Hill gives us some definite information concerning the dispersal of anophthalmids. Inasmuch as the Muldraugh's Hill cuesta is composed of rocks in which caves are seldom found and the strata dip in such a way that caves completely traversing Muldraugh's Hill are virtually impossible, one can essentially rule out the possibility of the dispersal of anophthalmids between the Bluegrass and the Pennyroyal Plateau by way of caves. Dispersal must rather be or have been overland, possibly in leaf litter or in crevices of the soil. Inasmuch as the single American anophthalmid known from an epigaean environment (Barr, 1967c) and the nearest epigaean relatives of the anophthalmids are inhabitants of cool moist habitats, it seems quite likely, as Jeannel (1949) and Barr (1967c) have suggested, that conditions prevailing during and immediately following the glacial advances of the Pleistocene would have been favorable to overland movement in this region.

Secondly, three of the species described are from caves lying within the boundaries of the Illinoian glacial advance: *chthonius* and *barri* from southeastern Indiana and *krameri* from southwestern Ohio. These are the first American anophthalmids of well over a hundred known forms to be taken from glaciated areas. It does not seem possible that these anophthalmids could have survived in the caves in which they are now found when the area was covered by glacial ice sheets. Even if the channels were not filled with icy water it seems quite improbable that food necessary for their survival would have been available. It thus appears that the anophthalmids entered these caves sometime since the maximum Illinoian glacial advance.

Interestingly, the three species found north of the Ohio River within the Illinoian glacial boundaries are of groups (*horni* and *barri*) in which other species come from caves south of the Ohio River in Kentucky. In the *tenuis* group which I considered in a previous paper (Krekeler, 1958—at that time the species and group was thought to be *eremita*, but it was pointed out by Barr in 1960 that this was in error) the same situation exists: *barberi* is in Kentucky, *tenuis* and other species are in Indiana. In that case I suggested that a stream the size of the present day Ohio River would be a barrier to dispersal of anophthalmids and that movement between Indiana and Kentucky must have occurred when the Ohio River was a much smaller and shorter stream. This would have been prior to the glacial advance (probably Kansan) which diverted waters carried by the preglacial Teays River to the Ohio River basin. If forms of the *horni* and *barri* groups have, by the same reasoning, not crossed the Ohio River since the Kansan advance and have entered the caves in which they are currently found subsequent to the Illinoian advance, for the reasons mentioned in the preceding paragraph, how is their present distribution to be accounted for? The present forms

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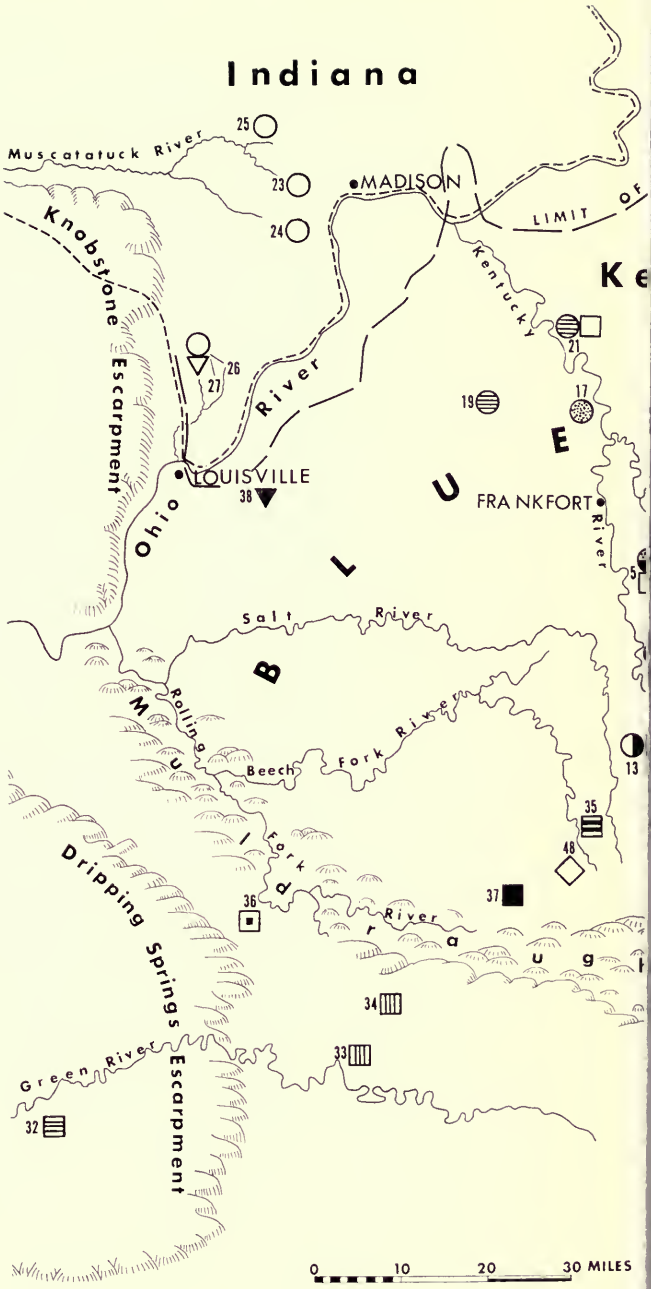
FIG. 23. (*See pp. 78–79*). Distribution of *Pseudanophthalmus* species of the Kentucky Bluegrass and vicinity. The species inhabiting a cave are shown by the symbols for which the code is given at lower right. The numbers designate the position of the caves as follows: **1.** Reid's=Picadome; **2.** Phelps; **3.** Russell; **4.** Church; **5.** Clifton; **6.** Swope; **7.** Weber #2; **8.** Meece; **9.** Weber; **10.** Nonesuch; **11.** Britton; **12.** Keene; **13.** Old Fort; **14.** Dix Dam; **15.** Robinson; **16.** Arnold; **17.** Stevens Creek; **18.** Jones; **19.** Price; **20.** Slack's; **21.** Hayden; **22.** Beaver; **23.** Wilson; **24.** Morris; **25.** Lowry; **26.** Indian; **27.** Peyton Beechwood; **28.** Freeland; **29.** Townsend; **30.** Cave Hill; **31.** Adams; **32.** White; **33.** Wilson; **34.** Phillips; **35.** Old Well; **36.** Eli Reed; **37.** Tatum; **38.** Highbaugh; **39.** Baker; **40.** Watson; **41.** Betsy; **42.** Natural Bridge; **43.** Pinnacle; **44.** Cave Hollow; **45.** Stillhouse; **46.** Ash; **47.** California; **48.** Lawrence.


Indiana
Muscatatuck River
MADISON
LIMIT OF
Ke
Kentucky
Knobstone Escarpment
Ohio River
LOUISVILLE
FRANKFORT
River
BLUE
Salt River
Rolling Fork
Beech Fork River
MULDRAUGH
Dripping Springs Escarpment
Green River
River
25
23
24
26
27
38
21
17
19
5
13
35
48
37
36
34
33
32
0 10 20 30 MILES

h. horni	chthonius	i. inexpectatus
h. caecus	ohioensis	i. orientalis
h. abditus	exoticus	puteanus
solivagus	krameri	cnephosus
elongatus	pholeter	parvus
tenebrosus	rittmani	umbratilis
d. desertus	e. exiguus	barri
d. major	e. furtivus	troglodytes
	catoryctos	conditus

and/or their ancestors must have moved between Kentucky and Indiana-Ohio prior to the Kansan glacial advance. Such movement could have been across the small pre-Kansan Ohio River and/or by way of the divide between the headwaters of the pre-Kansan Ohio (probably just east of Madison, Ind.) and the Teays River. During the Illinoian glacial advance some of the forms already in Indiana and Ohio could have found refuge in areas there beyond the glacial limits. Conditions following the withdrawal of the Illinoian ice sheet could well have been, according to the reasoning used above, favorable to their dispersal overland to the caves where they are now found.

3

In a number of caves from which the anophthalmids considered above have been taken two or three species coexist. In fact, this is almost the rule rather than the exception. As I have previously argued (Krekeler, 1958) and as Barr (1967d) more recently concludes, it seems most likely that speciation was allopatric and that as species have extended their ranges they have become sympatric. Interestingly, as noted above, where *horni* and *inexpectatus* group forms coexist only one *inexpectatus* form (*umbratilis*) can be recognized, whereas five *horni* group forms are recognizable. This may be because the *horni* group forms are the earlier occupants and have diversified in longer isolation while *umbratilis* is a more recent invader. Or this may be because the *horni* group forms are more labile in an evolutionary sense. There is no evidence to support one alternative in preference to the other.

In the case of the coexisting *inexpectatus* and *horni* group forms we did not observe any habitat preference though we did suspect while collecting that more than one species was present because of size differences. In the caves where *barri* and *chthonius* coexist we did not suspect that more than one species was present. We did note, however, that many beetles in these caves (and all but two of them were *barri*) were found rather close to the entrance and in drier places than Indiana anophthalmids are typically found—in fact, there are no streams in either of the two caves. *P. chthonius*, on the other hand, was found on wet mud banks at the type locality and was regularly taken from under rocks on wet gravel banks in Morris Cave. These two species thus seem to have distinct habitat preferences. In the case of *rittmani* and *exiguus* we recognized in the field that a larger and a smaller form exhibited habitat and behavioral

differences as described above. Of particular interest here is that these two species are so similar in many respects that they are included within the same species group. Still there is no need to postulate sympatric speciation. Whether coexisting forms are of the same or different species groups, range extensions following allopatric speciation would appear to be the most likely explanation for present sympatry. The distinct differences in the aedeagi of the two species would seem to assure reproductive isolation. Niche differences, probably related to differences in size and habitat preferences, undoubtedly exist to account for the continued coexistence of the two species in all these cases of sympatry. It so happens that in the case where two forms of the same group coexist such differences in size and habitat preference are readily distinguished.

SUMMARY

Nineteen new species and five new subspecies of *Pseudanophthalmus* are described from the Kentucky Bluegrass and vicinity. They are divisible into four species groups. The majority of the *horni* group forms (*horni* s. str., *horni* **caecus**, *horni* **abditus, solivagus, elongatus, tenebrosus, desertus** s. str., **desertus major, pholeter**) are from the Bluegrass; **chthonius** is from caves in the glaciated portion of southeastern Indiana in the same limestone beds as are included in the Bluegrass; **krameri** is from a cave in the glaciated portion of southwestern Ohio in the same limestone beds as are included in the Bluegrass; **ohioensis** is from the Highland Rim which extends into southwestern Ohio; **exoticus** is from the Cumberland Plateau immediately to the east of the Bluegrass. The majority of the *inexpectatus* group species (**umbratilis, parvus, puteanus**) are similarly from the Bluegrass; *inexpectatus* s. str. is from the Mammoth Cave Plateau southwest of the Bluegrass; *inexpectatus* **orientalis** and **cnephosus** are from the Pennyroyal Plateau southwest of the Bluegrass. Of the *barri* group, one species (**barri**) is from caves in the glaciated portion of southeastern Indiana in the same limestone beds as are included in the Bluegrass, while the other species (**troglodytes**) is from a cave some 20 miles south in the Bluegrass of Kentucky. Three *rittmani* group forms (**rittmani, exiguus** s. str., and **exiguus furtivus**) are from caves in Kentucky on the Cumberland Plateau immediately east of the Bluegrass, while **catoryctos** is from the eastern portion of the Bluegrass some 20 miles

distant. An additional species, *P.* **conditus,** not assigned to a species group, is from the southwestern portion of the Bluegrass.

Forms are described as species which are judged by morphological criteria as probably not exchanging genes or which are probably separated from the form most similar to it by a barrier to dispersal.

From the fact that the range of the *inexpectatus* group forms is divided by the non-caverniferous strata of Muldraugh's Hill it can be concluded that dispersal of these forms or their ancestors was overland. *P.* **chthonius, krameri,** and **barri** are from caves covered by the Illinoian glacial advance and they must have entered them after its withdrawal. These three species, found north of the Ohio River, are of groups with other species in Kentucky south of that river. Movement between Kentucky and Indiana-Ohio must have occurred prior to Kansan glaciation, for at that time the Ohio River probably became the large stream it now is and likely a barrier to dispersal. It is postulated that forms of these groups north of the Ohio River found refuge there beyond the limits of Illinoian glacial boundaries and after this glacier's withdrawal moved into the caves they now occupy.

Two and three anophthalmid species of the same or different species groups coexist in a number of caves. Range extension of species following allopatric speciation appears to be the best explanation for such sympatry. Differences in habitat preference were not observed where *inexpectatus* and *horni* group forms were sympatric. But where **chthonius** of the *horni* group and **barri** of the *barri* group, and where **rittmani** and **exiguus** of the *rittmani* group, were sympatric, definite habitat and/or behavioral differences were observed which may account for their continued coexistence.

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