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A Classification and Checklist of the
Genus *Pseudanophthalmus* Jeannel
(Coleoptera: Carabidae: Trechinae)

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Cover design: *Pseudanophthalmus delicatus* Valentine, habitus sketch adapted from photograph by David C. Culver.

A Classification and Checklist
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(Coleoptera: Carabidae: Trechinae)

Thomas C. Barr, Jr.¹

Carabid beetles of the subfamily Trechinae are widely distributed in cool, moist microhabitats of all the continents except Antarctica. In North America trechines are most abundant in the Appalachian mountains and Allegheny plateau, the Cordillera, the Sierra Nevada, and the Cascades, as well as the unglaciated cave areas of eastern United States; Mexican species are treated by Barr (1982). *Pseudanophthalmus* Jeannel, with an estimated 225 species, includes about 70 per cent of the known Nearctic species of Trechinae; it is represented in caves of Alabama, Georgia, Illinois, Indiana, Kentucky, Maryland, Ohio, Pennsylvania, Tennessee, Virginia, and West Virginia (Figure 1). A few rare occurrences in forest floor humus and in abandoned coal mines are known (Barr 1967a, 1986). The literature on the genus is scattered, and there has been no recent arrangement of its species into groups. Although preliminary classifications were provided by Valentine (1932) and Jeannel (1949), discovery of much additional material in the past four decades requires a new revision at the species group level.

In this paper I have listed the 175 available trivial names (indexed in Appendix B) that have been proposed for *Pseudanophthalmus*, treating 25 of them as junior synonyms. In the present list 145 species are recognized, of which five are considered polytypic. New status is proposed for 10 taxa, and five new synonymies are proposed. Twenty-six species groups are recognized. A key to species groups is presented, and a detailed listing of the groups' occurrence by states and counties (Appendix A) simplifies the task of determining a *Pseudanophthalmus* specimen by

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limiting the possible choices. Furthermore, the checklist provides a taxonomic framework for future description of approximately 80 undescribed species currently in my collection, which includes the bulk of collections made by J. Manson Valentine and Carl H. Krekeler, who have recently committed this material to my transient care.



Figure 1. Central eastern United States, showing the area in which species of *Pseudanophthalmus* have been found..

World trechines were exhaustively treated by Jeannel in his classic *Monographie des Trechinae* (1926-1930), but only ten Nearctic species of the group were known to him at that time. Subsequent to the *Monographie*, species of *Pseudanophthalmus* were further investigated and described by Barber (1928), Jeannel (1931, 1949), Valentine (1931, 1932, 1937, 1945, 1948), Krekeler (1958, 1973), Barr (1959a, 1959b, 1960a, 1960b, 1962a, 1962b, 1965, 1967a, 1967b, 1979, 1980, 1981, 1982a,

1982b, 1985a), and Barr & Peck (1966). Some of the ecological and evolutionary aspects of cave trechine study in eastern United States were discussed by Valentine (1948, 1952), Krekeler (1959), Barr (1967a, 1968a, 1968b, 1985b), Barr & Crowley (1981), and Barr & Holsinger (1985). Life history studies were published by Keith (1975), Kane et al. (1975), Norton et al. (1975), and McKinney (1975), and allozyme studies on *Neaphænops* were summarized by Kane & Brenner (1988).

Kane et al. (1992) described two extremes in genetic population structure (estimated from allozyme electrophoresis), in the *Pseudanophthalmus tenuis* group and the polytypic cave trechine *Darlingtonia kentuckensis*.

Valentine (1932) and Jeannel (1949) arranged the species of *Pseudanophthalmus* known to them into species groups. New groups were proposed by Krekeler (1958, 1973) and Barr (1959a, 1960b, 1980, 1981). A somewhat different arrangement from that of Valentine or Jeannel is employed in the present paper, in which I have recognized 26 groups, including the ones more recently defined. Although clusters of apparently related groups exist, e.g., what I have called the "engelhardti complex" (Barr 1981), the diagnostic characters thus far employed do not admit the construction of an unequivocal phylogeny of the genus at this time (see Barr 1985b).

Species of *Pseudanophthalmus* are not often confused with other genera. Within the region occupied by the genus are *Neaphænops* Jeannel, *Darlingtonia* Valentine, *Amerodualius* Valentine, and *Nelsonites* Valentine (see Barr 1979 for treatment of *Neaphænops* and Valentine 1952 for descriptions of the other three genera). The rare and taxonomically remote *Xenotrechus* (Barr & Krekeler 1967) is known only from a few caves in southeast Missouri, where *Pseudanophthalmus* is not known to occur. Both *Neaphænops* and *Darlingtonia* are large (about 7 mm), cursorial trechines lacking the anterior apical puncture (++0) and having a vestigial apical recurrent groove. Species in these two genera are very slender, with small pronotum, large and convex elytra, and elongate appendages. Elongation of the head results in abbreviated frontal grooves that end blindly near the occiput, not continued around behind the genae; Jeannel (*Monographie*, op. cit.) called this facies "aphænopsian." *Nelsonites* species are also large (7 mm); the pronotum, elytra, and elongate appendages are "aphænopsian," but the head is quite wide, with large *adductores mandibulae* and massive mandibles; the antennæ are noticeably longer than in other North American cave trechines. *Neaphænops* occurs in the Western Mississippian

plateau (MP-I in Barr 1985b) in Kentucky, from Meade and Breckinridge counties near the Ohio River southward to Mammoth Cave and the Bowling Green-Franklin area. *Darlingtonia*, *Nelsonites*, and *Amerodualius* are known only from the Eastern Mississippian plateau (MP-II in Barr 1985b), in caves along the margin of the Cumberland (Allegheny) plateau. *Nelsonites* ranges as far south as Van Buren County, Tennessee, *Darlingtonia* is known from many Kentucky caves but only a single cave in Tennessee (Fentress County), and *Amerodualius* occurs only in Kentucky, from Jackson County south to northern Wayne and McCreary counties.

Species of *Amerodualius* are difficult to separate from *Pseudanophthalmus*, but in the region where the two genera overlap, most *Pseudanophthalmus* species are smaller, 4.0 mm or less. In northwestern Wayne County, Kentucky (Mill Springs area), where larger species of both genera coexist in the same caves, the distinctive *Amerodualius* aedeagus, with posterolateral "wings" and the subequal, symmetrical copulatory sclerites, is highly diagnostic (see illustrations in Valentine 1952). There is a small gap between the two groups of teeth on the retinaculum of the right mandible in *Amerodualius* species (Valentine 1952), but this character is often difficult to see if the mandibles are closed. In passing it should be noted that *Amerodualius* is no closer taxonomically to the European *Dualius* than *Pseudanophthalmus* is to *Anophthalmus* or *Neaphænopis* is to *Aphænopis* (Jeannel, *in litt.*).

In eastern United States the distributional patterns of cave trechine species reflect the cavernous nature of the limestones and the extent to which continuous limestone outcrops are exposed. The extremes are found in (a) the two Mississippian limestone plateaus on either side of the Cincinnati arch and b) the Appalachian valley and ridge province (Barr 1967, 1968, 1985b), respectively. In (a) geographic ranges of species are more extensive, there are fewer species per unit area of karst, sympatry of species is common, population densities are typically higher with fewer fluctuations, and modal size of species is greater. In (b) species ranges are greatly restricted, there are more species per unit area of karst, sympatry is relatively rare, population densities are lower and often exhibit "flush and crash" fluctuations, and modal size of species is smaller. Intermediate conditions obtain in the Central Basin of Tennessee and the Bluegrass of Kentucky, but the Greenbrier valley in eastern West Virginia, which is underlain by thick Mississippian limestones, has the biogeographic and ecological properties of (a) on a small scale. Karst "islands" – small pockets of exposed

cavernous limestone surrounded by non-limestone strata – resemble the narrow, anticlinal, strike valleys of the Appalachian Ridge & Valley province (b), often harboring one or two endemic species. Such local limestone outcrops occur around the edge of the western Mississippian plateau (Indiana and Kentucky), downdip toward the center of the Interior Coal Basin; in Pine Mountain, a 125-km long fault block within the Allegheny plateau in eastern Kentucky (Barr 1981); and in scattered other areas.

Occurrence of *Pseudanophthalmus* species in habitats other than caves is rare. In eastern West Virginia *P. sylvaticus* (*grandis* group; Barr 1967) inhabits deep soil in birch and spruce forests, and *P. hypolithos* is known from abandoned coal mines in eastern Kentucky (Barr 1986). A very limited dispersal through non-karst terrain is thus possible, but it appears to be much less common in eastern United States than among numerous subterranean trechines in Europe and Japan. No epigean ancestors of *Pseudanophthalmus* inhabit eastern United States, although one species of the predominantly Eurasian genus *Trechoblemus* (a feasible ancestor; see Jeannel 1926-1930) is known from Oregon (Barr 1971), and *Lasiotrechus discus* Ganglbauer, another feasible (but less likely) ancestor, occurs in Canada.

A two-stage process of colonization and speciation in cave trechines of eastern United States was proposed by Barr (1985b and references cited therein); the model postulates an earlier period in which ancestral species adopted a preadaptive, deep-soil mode of life, during Pleistocene glacial maxima or perhaps earlier, followed by a later stage when the soil fauna colonized caves in response to warming and drying climates of interglacial epochs. Varying degrees of troglomorphy among trechine species suggest several episodes of cave colonization in the past (if increase in troglomorphy reflects time since cave colonization). The model is thus relictual, punctuational, and vicariant in nature. Most species groups on the east (Appalachian valley) and west (Interior Low Plateaus) sides of the Allegheny plateau are quite different, and their phylogenetic relationships are not readily determined. Only the *gracilis* (east) and *inexpectatus* (west) groups are clearly related, and only the widespread *engelhardti* group occurs on both the east and west sides of the Allegheny plateau. Barr (1981) proposed that the Allegheny plateau was a major refugium from which cave faunas were derived, but the track of the *petrunkevitchi* group as now recognized is more closely associated with the Blue Ridge in Virginia, which may have served as a minor refugium for ancestors of this group only.

Earlier taxonomic treatments of *Pseudanophthalmus* frequently employed a polytypic species concept (Jeannel op. cit.; Valentine op. cit.; Krekeler 1958 1973; Barr 1959a, 1960b). During the past 40 years, however, extensive sampling of MP species from large numbers of caves has indicated that many alleged "subspecies" within the same polytypic species do not intergrade as anticipated. Although classical hybridization between subspecies of *Pseudanophthalmus* and other genera of North American cave trechines does exist (e.g., see Barr 1979, 1985a), the zone of hybridization is always very narrow and restricted to one cave or a few caves in close proximity. The best studied hybrid zone is that of *Neaphaenops tellkampfi* X *N. meridionalis* (Barr 1979); the two taxa differ in 10 morphological characters, and allozymes show that the hybrid population is polymorphic for alternative alleles fixed in *tellkampfi* and *meridionalis*, respectively (Kane & Brenner 1987). This particular hybrid zone is what might be expected of the interface between semispecies rather than between subspecies. And many taxa that at first blush appeared to be geographic races more commonly are shown (by extensive sampling from many caves) to be parapatric (e.g., see Barr 1962), so that in MP caves the number of morphologically similar taxon pairs that are parapatric actually exceeds the number that can be shown to intergrade (Barr 1985b). All of this suggests that genetic divergence between vicariant populations of cave trechines is quite frequently accompanied by appearance of fortuitous isolating mechanisms, which is at least consistent with Wright's (1931) postulated role of drift and selection in small populations (see also Wright 1982). More than 30 years ago I suggested that troglobite speciation could be explained in terms of Mayr's (1963) founder effect and genetic revolution models (Barr 1967, 1968). I still believe the founder effect may be very significant in cave trechine speciation. However, the close morphological similarity between parapatric species pairs and the biochemical similarity indicated by allozyme-electrophoretic studies that T. C. Kane and I have done on cave and mountain-top trechines suggest that speciation in these beetles is more often accomplished by something less than a "genetic revolution" (Barr 1985b).

The preceding capsule discussion of speciation in cave trechines underscores the need for this checklist – only when the species have been inventoried and described can the systematic data be fully analyzed to illuminate the process of speciation. But cave trechines also offer unique opportunities for the study of predator-prey systems in comparatively simple ecosystems; despite their relatively small size, they are

nevertheless top carnivores in their environment. A simplified means of species determination for non-taxonomists (e.g., behavioral ecologists) would be useful, and I have tried to provide this in Appendix A, where limited geographic distributions of the species are used to facilitate determination.

Pseudanophthalmus Jeannel

Pseudanophthalmus Jeannel, 1920: 154; type species, *Anophthalmus menetriesii* Motschulsky, by original designation.

Divaliopsis Jeannel, 1928: 106; type species, *Anophthalmus bielzi* Miller, by original designation. See Barr 1964.

Tenessarius Valentine (subgenus), 1952: 15; no type species designated, *Neaphaenops intermedius* Valentine here proposed. **New Synonymy!**

Aphanotrechus Barr, 1960a: 65; type species, *Aphanotrechus virginicus* Barr, by original designation. **New Synonymy!**

Anophthalmus of authors prior to 1920, also Barber 1928, NOT Sturm 1844: 131.

Description: Mandible without a premolar tooth; teeth of right mandible not widely separated (i.e., retinaculum not deeply excavated between anterior and posterior groups of tubercles); maxillary palps with last two segments subequal in length; frontal grooves extended onto sides of head (complete), delimiting a more or less distinct neck; two pairs of supraorbital setae (or four pairs in a few species, but never one pair); eyes completely absent or represented by irregular, lunate scar, well-defined, circular areola, or minute pigment spot; mentum fused to submentum; submentum with row of (6-) 8 (-10) prebasilar setae.

Melanin pigments reduced or absent; integuments generally pubescent, glabrous or subglabrous in a few species; metathoracic wings vestigial; abdominal tergites membranous.

Anterior tibia pubescent on external face; male with first two protarsomeres enlarged, dentate, with adhesive setae beneath.

Elytral chaetotaxy usually normal (exceptions noted below), punctures 1 and 2 of umbilicate series in marginal gutter, punctures 3 and 4 displaced onto 8th stria, long whip-like setae in punctures 2, 6, 8; discal punctures on or near 3rd (rarely 4th) stria, normally +++, exceptionally +00, +0+, or ++(2)+(2); recurrent portion of

apical groove usually running into or toward apex of 3rd stria, in a few larger species to 5th or even 7th stria, partly vestigial in one group (*menetriesi* group).

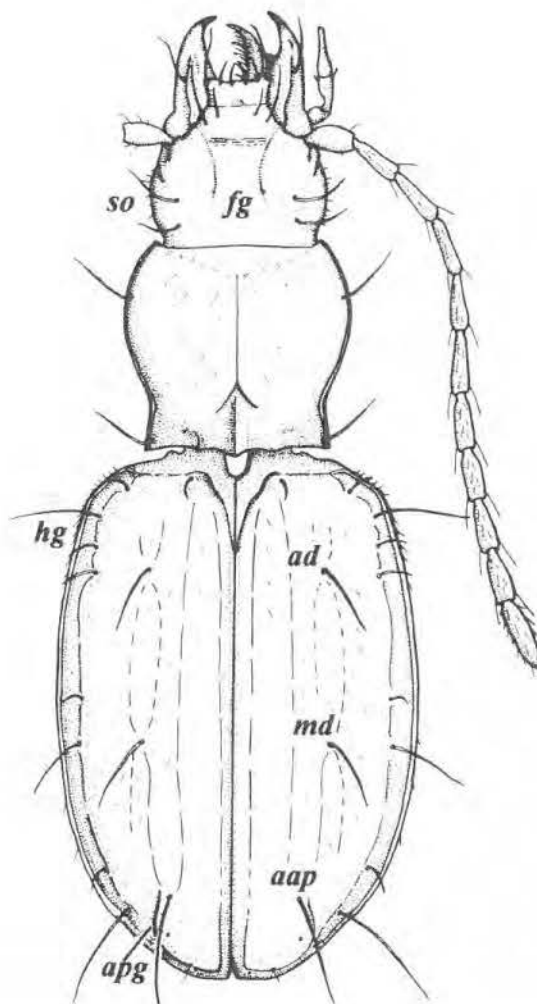


Figure 2. Anatomical terms used in the following key to species groups. The species illustrated is *Pseudanophthalmus emersoni* Krekler; discal setal formula +++).

Abbreviations: *aap*, anterior apical seta; *ad*, anterior discal seta; *apg*, apical recurrent groove; *fg*, frontal groove; *hg*, humeral group of umbilicate punctures; *md*, medial discal seta; *so*, supraorbital seta.

Aedeagus (Figure 3) with basal bulb more or less enlarged, sharply deflexed or not according to species; transfer apparatus (Figure 4) usually of two copulatory sclerites placed on edge and asymmetrical in internal sac (anisotropic); right (dorsal)

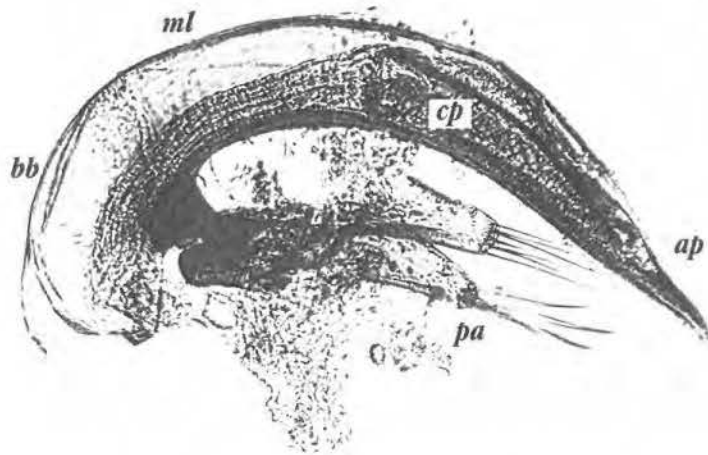


Figure 3. Cleared aedeagus of *Pseudanophthalmus emersoni*, lateral aspect. Abbreviations: *ap*, apex; *bb*, basal bulb; *cp*, copulatory pieces (inside internal sac); *ml*, median lobe; *pa*, parameres.

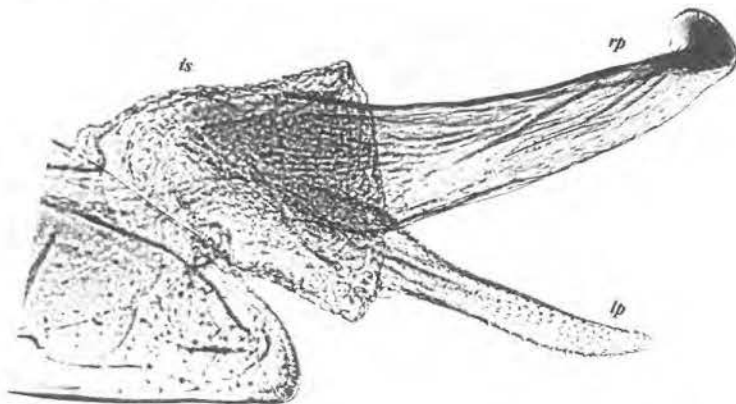


Figure 4. Apex of median lobe of aedeagus showing transfer apparatus of *Pseudanophthalmus ciliaris* with internal sac everted. Abbreviations: *is*, internal sac; *lp*, left copulatory piece; *rp*, right copulatory piece

sclerite usually larger, partially enfolding left (ventral) sclerite; transfer apparatus a single sclerite in certain groups (loss of left or right piece or possibly through basal fusion).

Discussion: Despite its large number of species, *Pseudanophthalmus* is too homogeneous to warrant division into subgenera. Valentine's (1952) concept of *Tenessarius* is the same as my definition of the *intermedius* group in the present paper (see Barr 1962a). *Aphanotrechus virginicus*, from Tazewell County, Virginia, is a somewhat aberrant and peripherally distributed member of the *grandis* group (close to *hypertrichosis* Valentine), other species of which inhabit eastern West Virginia. Its mentum is not actually free, as reported from examination of the female holotype, a late teneral (Barr 1960a), and its proper status has been ascertained by collection of a fully sclerotized male from the type locality. *Duvaliopsis* includes edaphobitic species in the Carpathians and Transylvanian Alps of eastern Europe. The taxon was reviewed by Barr (1964) and is not treated further in the present paper. It was presumably derived independently from the same winged, *Trecho-blemus*-like ancestral stock that gave rise to North American *Pseudanophthalmus* and is not readily separable from the latter on purely morphological grounds. *Xenotrechus* (Missouri) and the taxonomically close genus *Chaetoduvalius* (Carpathians and Transylvanian Alps) share the same sort of curious, bicentric, biogeographical pattern (Barr & Krekeler 1967).

A phylogenetic analysis at the species group level is premature. Diagnostic characters have not been fully analyzed, and additional kinds of characters will probably be required if unequivocal results are to be obtained. The newer, powerful methods of cladistics may ultimately help unravel phylogenetic relationships in this large genus, provided more useful characters are discovered and employed. Three sets of groups appear firmly linked by apomorphic characters, however: 1) *gracilis* - *inexpectatus* (modified last abdominal sternite in males, similar aedeagi), 2) *pubescens* - *menetriesi* (anterior position of anterior discal puncture; see Barr 1979), and 3) *robustus* - *intermedius* (similar aedeagal form and transfer apparatus). The large and apparently monophyletic "*engelhardti* complex," whose species are found predominantly in the Appalachian valley and ridge province (Tennessee and Virginia), is divided into seven groups (Barr 1981). At a lower level of certainty, one might postulate relationships between the *grandis* and *hubbardi* (and possibly *pusio*) groups, the *petrunkevitchi* and *rittmanni* groups, the *inexpectatus* and *horni* groups,

and the *eremita*, *audax*, and *robustus* groups, based on aedeagal pattern and overall similarity of the transfer apparatus (see Barr 1980, 1985b).

Artificial Key to Nearctic Species Groups of *Pseudanophthalmus*

Appendix A, a list of known distribution of groups and species by states and counties, is a useful adjunct to this key, indicating limitations to the number of species groups and species found in a specific geographic region.

"Pruinose microsculpture" as used in the key is easily seen (when present) in dried, mounted specimens that have been cleaned in a grease solvent such as ether. The specimen is viewed at a magnification of about 50X under strong, oblique illumination. Microtrichia projecting up from the posterior margin of the epicuticular polygons reflect light, imparting a frosted appearance to the elytral disc. The chaetotaxial formulas in the first couplet of the key represent presence (+) or absence (0) of the three elytral punctures of the 3rd or 4th stria, respectively called the anterior and posterior discals and the anterior apical by Jeannel (1926-1930). In most species this formula is +++, thus absence of one or two setae from this set is highly diagnostic. The formula ++(2)+(2) indicates that the posterior discal and anterior apical are doubled. The "umbilicate punctures" of couplet 5 are the set of four post-humeral punctures (Fig. 2, *hg*).

The task of identifying the group to which a specimen belongs often requires preparation of a cleared aedeagus. Among several feasible techniques, I prefer mounting in polyvinyl-lactophenol, a mounting medium which is also a clearing agent. A 12 mm #000 cover slip rests over the aedeagus on three glass chips to prevent crushing and distortion. In most species groups the aedeagi are similar in structure, and the transfer apparatus is similar throughout the group; the principal exceptions occur in the *tenuis* and *audax* groups (as here defined). The copulatory sclerites (when both are present) are unequal and asymmetrical, the left piece usually smaller (anisotopic).

1. Mesosternum with median tubercle or vertical shelf AND/OR both pairs of elytral discal setae absent (00+), OR specimen from Ohio 2
- Mesosternum simply declivous; elytra with 1-5 (usually 2) pairs of discal setae [+++, +00, +0+, or ++(2)+(2)]; specimen not from Ohio 3

- 2(1). Aedeagus long and slender, apex much produced and often hooked at tip; transfer apparatus a single sclerite, conical or very slender and elongate, heavily armed with microtrichia; southeast Indiana, southwest Ohio, Bluegrass region of central Kentucky *horni* group
- Aedeagus more or less arcuate and moderately thick, apex not produced; transfer apparatus obviously of two sclerites (left piece may be small but distinct) or clavate with large spines; southern Indiana, central and north-eastern KY *audax* group
- 3(1). Male with median indentation in apical margin of last abdominal sternite; small species with very slender, elongate aedeagus 4
- Male with apical margin of last abdominal sternite entire 5
- 4(3). Range: southwest Pennsylvania, eastern West Virginia, southwest Virginia; copulatory pieces of moderate length *gracilis* group
- Range: central Kentucky, from Mammoth Cave region northeastward to the Bluegrass; copulatory pieces very long and slender ... *inexpectatus* group
- 5(3). Anterior discal puncture of elytron at level of 2nd or 3rd umbilicate puncture; Kentucky and Tennessee 6
- Anterior discal puncture of elytron at or behind level of 4th umbilicate puncture OR specimen from West Virginia, with anterior discal irregularly at level of 2nd or 3rd umbilicate puncture 7
- 6(5). Apical recurrent groove of elytron vestigial, feebly and irregularly impressed, rarely with direct connection to either sutural or 3rd striae; copulatory sclerites of internal sac not conspicuously spiny, right piece not apically knobbed; elytra pruinose or not *menetriesi* group
- Apical groove clearly impressed, continuous with sutural stria and connected with or directed toward 3rd, 5th, or 7th stria; copulatory sclerites spiny, right piece usually knobbed; elytra always with pruinose microsculpture, at least feebly in the striae *pubescens* group
- 7(5). Elytral microsculpture pruinose and isodiametric; Indiana and Kentucky 8
- Elytral microsculpture not pruinose OR scaly-pruinose-transverse and speci-men from West Virginia 13

- 8(7). Profemur normal, not angular at inner base 9
 Profemur sharply angular on inner side near base; aedeagus elongate, apex produced, transfer apparatus a single, long, spiny-tuberculate, scoop-shaped sclerite; opposite sides of Ohio River near Louisville, Kentucky and Indiana *barri* group
- 9(8). Range: Rockcastle, Pulaski, Wayne counties, Kentucky; small species (4 mm or less) aedeagus feebly arcuate, apex blunt, one small copulatory piece *cumberlandus* group (in part)
 — Range or aedeagal characters not as described 10
- 10(9). Humeral margin not serrulate; aedeagal apex not significantly produced OR apex produced and attenuate, usually reflexed or knobbed at tip (eastern Kentucky) 11
 — Humeral margin finely, just perceptibly serrulate; aedeagal apex long, produced, not very attenuate, slightly rounded at tip; copulatory pieces elongate lobes, subequal; form robust, somewhat depressed, length 4.5-5.3 mm; known only from Crawford and Harrison counties, Indiana, and Boyle County, Kentucky *eremita* group
- 11(10). Labrum emarginate, at most feebly trilobed; pronotum sides shallowly sinuate or oblique in basal third, hind angles not produced; if specimen from Indiana, length 3.0-4.5 mm 12
 — Labrum usually prominently trilobed (doubly emarginate); length 4.2-5.9 mm (mean 4.5 mm or more), form slender; pronotum cordiform, sinuate at sides, hind angles sharp and usually produced; range: Mississippian plateaus of southern Indiana and northern Kentucky (west of Louisville), also Hardin County, Illinois *tenuis* group
- 12(11). Range: southern Indiana; aedeagus short and thick, apex blunt; copulatory pieces heavily sclerotized, internal sac spiny *leonae* group
 — Range: central Kentucky along Kentucky River drainage basin, including eastern Bluegrass and edge of Cumberland plateau; aedeagus with apex attenuate and sharp, or produced and more or less knobbed; transfer apparatus typically hyaline and bifid, of two long sclerites apparently fused at base, internal

- sac usually spiny; mostly small species (but one species 4.9-6.3 mm, Estill and Powell counties) *rittmanni* group
- 13(7). Apical recurrent groove of elytron elongate, bisinuate, oblique or subparallel to suture OR subparallel to suture and directed toward 4th or 5th striae (northeast Alabama and northwest Georgia); range: Appalachian valley from New River basin to north Alabama, west along Tennessee River valley and north to Decatur County, Tennessee, also Campbell and Cumberland counties, Tennessee [*engelhardti* complex] 21
- Combination of characters AND/OR range not as described 14
- 14(13). Range: Virginia and West Virginia 15
- Range: Kentucky and Tennessee 18
- 15(14). Length various; eye rudiment present only in species over 4 mm in length, rudiment lunate and somewhat irregular (West Virginia) 16
- Length 3.4-4.0 mm AND distinct, *rounded* eye rudiment present; range: Page, Warren, Smyth, Tazewell, and Wythe counties, Virginia *petrunkevitchi* group
- 16(15). Aedeagus with apex distinctly attenuate, more or less recurved 17
- Aedeagus narrowly tubular, scarcely attenuate at the subtruncate apex (fig. 9); median lobe evenly arcuate; New, Roanoke, Greenbrier, and James river basins *pusio* group
- 17(16). Medium to large species, about 4.5-6.0 mm; usually with few to many long setae on pronotum disc and irregular, lunate eye rudiment; OR (no eye rudiment) anterior margin of labrum with very broad and convex median lobe (*hypertrichosis* series); range: Greenbrier valley of West Virginia, also Randolph and Tucker counties, West Virginia, and Tazewell County, Virginia *grandis* group
- Small species, about 3-4 mm; without discal setae on pronotum, without eye rudiments, labral margin without prominent median lobe, elytra not pruinose; range: upper Shenandoah valley of Virginia, westward to Potomac River basin in Pendleton County, West Virginia *hubbardi* group
- 18(14). Transfer apparatus consisting of single sclerite OR (Jackson and Clay counties, Tennessee) broadly triangular left piece and shoehorn-shaped right piece 19

- Transfer apparatus of two, simple, unmodified, hyaline sclerites with (usually) rounded apex; right piece larger, partially enfolding smaller and rod-like left piece; apex of aedeagus produced and slender, sometimes knobbed; range: Wayne and Adair counties, Kentucky, southwestward along Cumberland plateau margin and Eastern Highland Rim to Jackson County, Alabama . . . 20
- 19(18). Transfer apparatus consisting of one small, triangular or elongate-triangular copulatory sclerite range: Central Basin of Tennessee, also southwestern (Caldwell, Christian, Livingston counties) and southeastern (Rockcastle, Pulaski, Wayne counties) Kentucky, Fentress County, Tennessee, and Limestone County, Alabama *cumberlandus* group
- Transfer apparatus consisting of one or two copulatory sclerites, one of these large, hemicylindrical, rounded or knobbed at apex; range: Jackson and Clay counties, Tennessee *simplex* group
- 20(18). Elytral microsculpture forming densely transverse meshes . . . *robustus* group
- Elytral microsculpture isodiametric *intermedius* group
- 21(13). Aedeagus without subapical constriction (dorsal view) and apex not hatchet-shaped or ventrally sharply cusped (lateral view) 22
- Apex of aedeagus arrow-shaped in dorsal view because of subapical constriction and/or hatchet shaped with sharp ventral cusp in lateral view. *engelhardti* group
- 22(21). Pronotum disc with 1-4 long setae on each side in addition to normal pubescence 23
- Pronotum disc pubescent but without longer setae 25
- 23(22). Small, slender, usually depressed species (3.1-4.5 mm) 24
- Larger (4.4-6.2 mm); slender, often convex species; aedeagal apex produced and slender OR (Rye Cove, Virginia) button-shaped *jonesi* group
- 24(23). Aedeagus with apex slender, moderately produced and attenuate, with very finely truncate knob in lateral view *tennesensis* group
- Aedeagus with apex feebly produced and bluntly rounded at tip, median lobe weakly arcuate, basal bulb rather small, left copulatory piece very small *hirsutus* group

- 25(22). Aedeagus with apex slender and considerably produced and attenuate. 26
- Aedeagus with apex briefly produced, either bluntly rounded or finely truncate, in some species also deflexed *hubrichti* group
- 26(25). Aedeagus with apex strongly deflexed, falciform, slightly knobbed apical groove of elytron subparallel to suture; northwest Georgia, northeast Alabama *alabamae* group
- Aedeagus with apex not knobbed, not or but slightly reflexed at tip; Pine Mountain, Kentucky and Scott County (Hunter Valley), Virginia. *hypolithos* group

Checklist of Described Species and Subspecies of Nearctic *Pseudanophthalmus*

One hundred forty-five species of *Pseudanophthalmus*, five of which are polytypic, are recognized in the present list; 12 taxa have been accorded new status, and seven taxa are newly relegated to synonymy. The group distributions given below reflect known but undescribed species; counties marked with an asterisk (*) harbor undescribed material diagnosed from my collections. The last attempt to treat all known species of the genus was that of Jeannel (1949), a paper invaluable in its day. Jeannel recognized 11 species groups, but I have suggested 26 in the present paper; these groups will eventually include from two to about 30 species, with a mean of eight or nine species per group. Citations have been somewhat abbreviated but include the reference to the original description and the more useful, pertinent subsequent treatments. Annotations have been kept to a minimum. Formal descriptions of species groups have been shortened to include only principal diagnostic characters. "Small" species are about 4 mm long or less; "large" species are between 4-6 mm; "very large" species exceed 6.0 mm. Cave descriptions and locations are given for Alabama by Varnedoe (1973), for Indiana by Powell (1961), for Tennessee by Barr (1961) and Matthews (1975), for Virginia by Douglas (1964) and Holsinger (1975), and for West Virginia by Davies (1958, 1965). No comparable compendium exists for Kentucky caves.

1. *grandis* group

Large, conspicuously setose and pubescent species with a lunate eye rudiment

OR (no eye rudiment) a broad, convex median lobe in the labral margin. Eastern West Virginia (Greenbrier valley north to Elkins and Tucker County); one very rare species in Tazewell County, Virginia (*virginicus*).

Includes the *grandis* and *fuscus* groups of Valentine (1932), the *grandis* and part of the *pusio* groups of Jeannel (1949), and part of the *hubbardi* group of Barr (1965).

- 1.1a. *grandis grandis* Valentine 1931:254. Type locality, Higginbotham Cave No. 1, Greenbrier County, West Virginia; abundant in many other caves of north of Greenbrier River; very abundant.
- 1.1b. *grandis elevatus* Valentine 1932: 265. Type locality, Organ Cave, Greenbrier Co., West Virginia; prevalent south of Greenbrier River in southern Greenbrier and north-central Monroe counties.
- 1.2. *orthosulcatus* Valentine 1932: 265 (*grandis orthosulcatus*). Greenville Saltpeter (=Head-of-Mill-Pond) Cave (type locality), Laurel Creek, and Crossroad caves, Monroe County, West Virginia. Valentine (1932) and Jeannel (1949) suggested full species status, now confirmed by collection of males; occupies a karst island of Union limestone (Greenbrier series) surrounded by Bluefield member of the Mauch Chunk.
- 1.3a. *fuscus fuscus* Valentine 1931: 254. Coffman Cave (type locality) and many other caves of Greenbrier County, West Virginia, north of Greenbrier River. Syn.: *subaequalis* Valentine 1931: 255.
- 1.3b. *fuscus constrictus* Valentine 1931: 267. Organ Cave (type locality), Greenbrier County, West Virginia, and other caves of Greenbrier and north-central Monroe counties south of Greenbrier River.
- 1.4. *sylvaticus* Barr 1967: 167. Edaphobitic; type locality, birch woods near Cranberry Glades, Pocahontas County, West Virginia, also (NEW RECORD) spruce forest on top of Yew Mountains nearby.
- 1.5. *hypertrichosis* Valentine 1932: 266. Type locality, Martha's (=Martha Clark's =Long's) Cave, Pocahontas County, West Virginia, and other caves of southern Pocahontas County.
- 1.6. *henroti* Jeannel, 1949: 69. Arbuckle's (type locality), General Davis, and other caves of southern Greenbrier County, West Virginia; rare.

- 1.7. *virginicus* (Barr) 1960: 66 (*Aphanotrechus virginicus*). Known only from the type locality, Hugh Young Cave, Maiden Spring, Tazewell County, Virginia;
- 1.8. *krekeleri* Barr, 1965: 52. Known only from type locality, Rich Mountain Cave, Randolph County, West Virginia.
- 1.9. *montanus* Barr, 1965: 52. Bennett (type locality) and Arbogast-Cave Hollow (NEW RECORD) caves, Tucker County, West Virginia.

2. *hubbardi* group

Small, pubescent species with no eye rudiment; elytral microsculpture not pruinose; labrum singly emarginate; last abdominal sternite not emarginate in males. Aedeagus moderately attenuate toward apex, copulatory pieces rather short and subequal. Endemic to the upper Potomac River basin, in Page, Rockingham, Shenandoah, Bath, and Highland counties, Virginia, north and west to Pendleton County, West Virginia.

Includes most of the *hubbardi* group as defined by Valentine (1932) and Jeannel (1949) and part of the *hubbardi* group of Barr (1965), here limited to *hubbardi*, *potomaca*, and similar small species with the characteristics given above.

- 2.1. *hubbardi* (Barber), 1928: 196 (*Anophthalmus*). Known only from the type locality, Luray Caverns, Page County, Virginia, where it has not been retaken for several decades, perhaps because of commercialization of the cave.
- 2.2. *limicola* Jeannel, 1931: 450 (*hubbardi limicola*). Maddens Cave (type locality), Shenandoah Caverns, Shenandoah Wild Cave, Shenandoah County, Virginia.
- 2.3. *parvicollis* Jeannel, 1931: 450 (*hubbardi parvicollis*). Type locality, Battlefield Crystal Caverns, Rockingham County, Virginia; collecting discouraged by cave owner for over 30 years, present status of species unknown.
- 2.4. *avernus* Valentine, 1945: 648 (*hubbardi avernus*). Known only from type locality, Endless Caverns, Rockingham County, Virginia.
- 2.5. *intersectus* Barr, 1965: 57. Known only from type locality, Crossroads Cave, Bath County, Virginia.
- 2.6. *potomaca* Valentine, 1932: 262. Type locality, Kenny Simmons Cave, Pendleton County, West Virginia; also Vandeventer's Cave, Highland County, Virginia.

- 2.7. *senecae* Valentine, 1932: 263 (*potomaca senecae*). NEW STATUS. Stratosphere Balloon (type locality) and Nameless caves, also Seneca Caverns, Pendleton County, West Virginia. Extrinsically isolated from *potomaca* by thick shales and sandstones.

3. *petrunkevitchi* group

Small, pubescent species with a distinct eye rudiment: either a dark pigment spot (*petrunkevitchi*) or a pale, circular areola, sometimes ringed with dark pigment (other species). Aedeagus elongate and slender, transfer apparatus a single, rolled sclerite, possibly fused from two pieces. Bland, Page, Pulaski*, Smyth, Tazewell, Warren, Washington*, and Wythe* counties, Virginia.

Includes part of *hubbardi* group of Jeannel (1949) and part of "*gracilis* subgroup" of Barr (1965).

- 3.1. *petrunkevitchi* Valentine 1945: 652. Type locality, Skyline Caverns, Warren and Page counties, Virginia.
- 3.2. *hoffmani* Barr 1965: 58. Buchanan Saltpeter (type locality) and Marble caves, Smyth County, Virginia; questionable record (Barr 1965: 59) from Hamilton Cave, Bland County, Virginia, confirmed by subsequent collection of male specimen.
- 3.3. *hortulanus* Barr 1965: 60. Known only from Cassells Cave (type locality), Burkes Garden, Tazewell County, Virginia.

4. *pusio* group

Small to medium species without an eye rudiment; males with margin of last ventral entire; aedeagus very distinctive with cylindrical median lobe, apex bluntly truncate. James and New (including Greenbrier) river basins in western Virginia and eastern West Virginia.

Includes *pusio* and *higginbothami* groups of Valentine (1932) and part of *pusio* and *higginbothami* groups of Jeannel (1949); about as defined by Barr (1965) with addition of *higginbothami* and transfer of *fuscus* to the *grandis* group (Barr 1981: 92).

- 4.1 *pusio* (Horn) 1868: 125 (*Anophthalmus*). See Barr 1965: 43 for complete citations. Erhardts (type locality), Thorn Hill, Aunt Nellie's, Agnew caves, Montgomery County, Virginia; NEW RECORD: Goodwin's Cave, Roanoke County, Virginia. Synonym: *pusio bathycola* Valentine 1932: 268 (Aunt Nellie's Cave). Type cave has been destroyed by quarrying.
- 4.2 *nelsoni* Barr 1965: 44. Old Tunnel (type locality) and Blue Spring caves, Alleghany County, Virginia.
- 4.3 *pontis* Barr 1965: 45. Known only from type locality, Buck Hill Cave, Natural Bridge, Rockbridge County, Virginia.
- 4.4 *punctatus* Valentine 1931: 250 (*pusio punctatus*). Tawney's (type locality), Clover Hollow, Spruce Run, Smoke Hole caves, Giles County, Virginia.
- 4.5 *lallemani* Jeannel 1949: 74. Known only from type locality, General Davis Cave, Greenbrier County, West Virginia; smallest species of the genus.
- 4.6 *higginbothami* Valentine 1931: 251. Type locality, Higginbotham caves at Maxwelton, Greenbrier County, West Virginia; widely distributed in Lewisburg and Hillsboro regions, Greenbrier and Pocahontas counties, possibly polytypic. Aedeagus shorter than in other *pusio* group species but similarly cylindrical with bluntly truncate apex.

5. *gracilis* group

Small species in which males have a median indentation in the apical margin of the last abdominal sternite; aedeagus long and slender, copulatory pieces subequal and rather short. Giles and Craig counties, Virginia; Pendleton and Randolph* counties, West Virginia; Fayette* County, Pennsylvania; and Garrett* County, Maryland. At present the only species of *Pseudanophthalmus* known from Maryland and Pennsylvania belong to this group.

Defined by Barr (1981:92); includes part of *grandis* group of Valentine (1932), part of *hubbardi* group of Jeannel (1949), and parts of "*gracilis*" and "*kekeleri* subgroups" of Barr (1965). The *gracilis* group, on the east side of the Allegheny plateau, and the *inexpectatus* group on the west side (Kentucky) share the same aedeagal form and the emarginate male last sternite; this is the only clear affinity between different *Pseudanophthalmus* groups on opposite sides of the Alleghenies.

- 5.1. *gracilis* Valentine, 1931: 253. Tawney's (type locality), Clover Hollow caves, Giles County, and Rufe Caldwell Cave, Craig County, Virginia.
- 5.2. *hadenoeus* Barr, 1965: 53. Known only from the type locality, Mystic Cave, near Onego, Pendleton County, West Virginia.

6. *inexpectatus* group

Small species in which the males have a median indentation in the apical margin of the last abdominal sternite; aedeagus and copulatory sclerites similar to *gracilis* group but much longer and more slender. .

Kentucky, from the inner Bluegrass region southwest to Hardin*, Hart, Larue, Green, Taylor, and Edmonson counties in the western Mississippian plateau.

The group was defined by Krekeler (1973)

- 6.1. *inexpectatus* Barr, 1959a: 10. Mammoth (type locality), White, and Great Onyx caves, Mammoth Cave National Park, Kentucky. Smallest of five *Pseudanophthalmus* species in Mammoth Cave.
- 6.2. *orientalis* Krekeler, 1973: 59 (as *inexpectatus orientalis*). NEW STATUS. Type locality, Wilson Cave, Green County, Kentucky; also known from other caves in northern Green, eastern Hart, and Taylor counties, Kentucky. The species is distinctly allopatric with respect to *inexpectatus*, separated by a definitive distributional gap.
- 6.3. *puteanus* Krekeler, 1973: 60. Old Well Cave (type locality), Mercer County, and nearby Jackson Cave, Boyle County, Kentucky.
- 6.4. *cnephus* Krekeler, 1973: 61. Type locality, Eli Reed Cave, Larue County, Kentucky. NEW RECORD: Murphy Cave, Roanoke Hill, Nelson County, Kentucky. Both caves are at the top of Muldraugh's Hill, the eastern escarpment edge of the western Mississippian plateau.
- 6.5. *parvus* Krekeler, 1973: 62. Known only from the type locality, Tatum Cave, Marion County, Kentucky.
- 6.6. *umbratilis* Krekeler, 1973: 62. Type locality, Robinson Cave, Garrard County, Kentucky; also reported from several other caves in Garrard, Fayette, Woodford, and Owen counties, Kentucky. The Fayette-Woodford and Owen county populations may possibly constitute distinct species (see Krekeler 1973 for discussion of wide variation in this species).

7. *horni* group

Small to medium species with a slender, elongate aedeagus and a single, spiny, triangular copulatory sclerite; a mesosternal protuberance is present except in the Ohio species; some species have a very feeble emargination in the male last abdominal sternite, much less pronounced than in the *gracilis* and *inexpectatus* groups but suggesting affinity with those groups.

Bluegrass region of Kentucky and adjacent southeast Indiana and southwest Ohio; one species from Lee County, Kentucky, tentatively placed here.

The group was defined by Krekeler (1973).

- 7.1. *horni* (Garman) 1892: 241 (*Anophthalmus horni*). Reid (=Picadome) Cave, at Picadome School, Lexington (type locality), Crystal, Russell, and Phelps (=Cave Hill) caves, Fayette County, Kentucky; the type locality cave was closed about 35 years ago. Synonyms: *horni garmani* Jeannel, 1949: 49; *horni minor* Jeannel, 1949:49.
- 7.2. *caecus* Krekeler, 1973: 43 (*horni caecus*). NEW STATUS. Clifton Cave (type locality), Woodford County, Kentucky. The type locality cave was closed about 35 years ago.
- 7.3. *abditus* Krekeler, 1973: 44 (*horni abditus*). NEW STATUS. Swope (type locality), Weber #2 caves, Woodford County; Meece Cave, Jessamine County, Kentucky.
- 7.4. *solivagus* Krekeler, 1973: 44. Weber (type locality), Nonesuch, Britton caves, Woodford County; Keene Cave, Jessamine County, Kentucky.
- 7.5. *elongatus* Krekeler, 1973: 46. Old Fort Cave (type locality), Mercer County; Dix Dam, Arnold, Robinson caves, Garrard county, Kentucky.
- 7.6. *tenebrosus* Krekeler, 1973: 48. Known only from the type locality, Stevens Creek Cave, Henry County, Kentucky.
- 7.7. *desertus* Krekeler, 1973: 49 (*desertus desertus*). Clark, Scott, ?Henry, and ?Owen counties, Kentucky. The Henry and Owen county populations possibly represent a distinct species.
- 7.8. *major* Krekeler, 1973: 50 (*desertus major*). NEW STATUS. Known only from the type locality, Beaver Cave, Harrison County, Kentucky. [This is a

much larger species (4.9-5.3 vs. 3.9-4.8 mm) species than *desertus*, with longer aedeagus (1.29-1.35 vs. 0.91-1.17 mm), rounder head, and broader elytra with more regular striae].

- 7.9. *chthonius* Krekeler, 1973: 50. Wilson (type locality) and Morris caves, Jefferson County; also Jennings and Clark counties, Indiana.
- 7.10. *ohioensis* Krekeler, 1973: 52. Known only from the type locality, Freeland Cave, Adams County, Ohio.
- 7.11. *krameri* Krekeler, 1973: 54. Known only from the type locality, Cave Hill Cave, Adams County, Ohio.
- 7.12. *pholeter* Krekeler, 1973: 55. Known only from the type locality, Adams Farm Cave, Madison County, Kentucky.
- 7.13. *exoticus* Krekeler, 1973: 53. Known only from the type locality, Townsend Cave, Lee County, Kentucky. Described on a unique male and provisionally assigned to the *horni* group. Townsend Cave, at the head of Billey Fork, is not in Estill County as reported by Krekeler (1973), but 150 m over the boundary in Lee County.

8. *rittmani* group

Mostly small species but including one large to very large species (*rittmani*); elytra pruinose; aedeagus with apex attenuate, usually knobbed (except *cataryctos*), one copulatory piece of two unequal lobes fused at base.

Powell, Estill, Lee*, Jackson* and Madison counties, eastern Kentucky.

The group was defined by Krekeler (1973).

- 8.1. *rittmani* Krekeler, 1973: 68. Type locality, Baker Cave (type locality), Powell County; frequent in many other caves between Red and Kentucky rivers in Powell and Estill counties, Kentucky.
- 8.2. *exiguus* Krekeler, 1973: 70 (as *exiguus exiguus*). Watson Cave (type locality), Estill County; common in many other caves of Estill, Lee, and Powell counties, Kentucky. NEW SYNONYMY: *exiguus furtivus* Krekeler, 1973: 72.
- 8.3. *cataryctos* Krekeler, 1973: 72. Known only from the type locality, Adams Farm Cave, Madison County, Kentucky; the only group species outside the Cumberland plateau margin.

9. *audax* group

Mesosternum with median tubercle or sharp, vertical shelf AND/OR both anterior and posterior discal setae absent (00+); medium-small species (under 5 mm), aedeagus moderately arcuate, apex not appreciably produced.

Distribution tricentric: a) Lawrence County, Indiana; b) Carter, Elliott, and Menifee* counties, eastern Kentucky; and c) Adair*, Edmonson, Green*, Hart, and Taylor* counties, western Kentucky.

Includes *audax* group of Jeannel (1949) and Barr (1959b), *emersoni* group of Krekeler (1958), and *packardi* group of Barr (1959a).

- 9.1. *audax* (Horn) 1883: 272 (*Anophthalmus*). Type locality, Ronalds Cave, Hatcher Valley, Hart County, Kentucky; also from White Cave, Edmonson County; very rare (Barr 1959b, 1966-67).
- 9.2. *emersoni* Krekeler, 1958: 176. Donnehue's (type locality) and Buddha (NEW RECORD) caves, Lawrence County, Indiana.
- 9.3. *packardi* Barr, 1959a: 22. Type locality, Bat Cave, Carter County, Kentucky, also (NEW RECORDS) Cattle, Counterfeiters', Horn Hollow, Jarvie Roark, Iolanthe, Ollegemuk caves, Carter County, and Tar Kiln Cave, Elliott County. *Anophthalmus pusio*: Packard 1888, NOT Horn 1868.

10. *barri* group

Medium-small species with profemora sharply angular on inner side near base; aedeagus elongate, apex produced, transfer apparatus a single, spiny-tuberculate, scoop-like sclerite.

The group includes a pair of vicar species on opposite sides of Ohio River, near Louisville, in Clark County, Indiana, and Jefferson County, Kentucky.

The *barri* group was defined by Krekeler (1973).

- 10.1. *barri* Krekeler, 1973: 64. Indian (type locality) and several other caves in southern Clark County, Indiana.
- 11.1. *troglydites* Krekeler, 1973: 65. Known only from the type locality, Highbaugh Cave, and Eleven Jones Cave, Jefferson County, Kentucky; the type cave has been destroyed by construction of a subdivision and is concreted shut.

11. *tenuis* group

Large, slender species with distinctly cordiform pronotum, its sides deeply sinuate before acute, sharp, more or less produced hind angles; labrum doubly emarginate; elytra more or less pruinose, at least in striae; aedeagal apex attenuate-truncate.

Southern Indiana in the Mitchell plain-Crawford upland, northern Kentucky in the Pennyroyal plateau and eastern edge of the Interior Coalfield, south to Grayson and Hart counties, also one cave in Hardin County, Illinois.

Includes the *eremita* group of Valentine (1932) and Jeannel (1949), the *eremita*, *youngi*, and *shilohensis* groups of Krekeler (1958), and the *tenuis*, *youngi*, and *shilohensis* groups of Barr (1960b). There are three distinctive types of transfer apparatus in the group (corresponding to the three groups of Krekeler and Barr), but they are probably derivable from one ancestral type, and it seems preferable to emphasize the species' distinctive habitus. Geographically the group's track includes the lower basin of the preglacial Teays River. Considerable confusion in the literature resulted from the erroneous notion that *eremita* (Horn) and *tenuis* (Horn) were synonymous; between 1920 and 1960 the species now correctly known as *tenuis* was called *eremita* (see Barr 1960b). *Pseudanophthalmus eremita* is a rare species assigned to another group (*eremita* group, new sense), and the species of the *tenuis* group are often rather abundant.

11.1. *tenuis* (Horn) 1871: 327 (*Anophthalmus*). Type locality, Wyandotte Cave, Crawford County, Indiana, and many other caves in Crawford, Harrison, and southern Washington counties, Indiana. Synonymy: *eremita* of authors, NOT Horn 1871 (see Barr 1960b: 308, 312); *eremita longicollis* Jeannel, 1949: 57; *bloomi* Krekeler, 1958: 172.

11.2. *stricticollis* Jeannel 1931: 450 (*eremita stricticollis*). NEW STATUS. Type locality, Marengo Cave, Crawford County, Indiana, and numerous caves in northeast Crawford, southwest Washington, the eastern 2/3rds of Orange, and southern Lawrence County south of East Fork of White River; differs from *P. tenuis* in larger body size and aedeagal length; geographic ranges of *tenuis* and *stricticollis* are contiguous but non-overlapping in southern Washington and northern Crawford counties. NEW SYNONYMY: *morrisoni* Jeannel, 1931: 451 (Donaldson Cave, Lawrence County); *jeanneli* Krekeler, 1958: 171

(Elrod's Cave, Orange County); *blatchleyi* Barr, 1960b: 316 (Truett's Cave, Monroe County). The Truett's Cave specimen, collected by H. Wickham, is judged to have been mislabeled, and all *stricticollis* appear to range south of East Fork of White River. Keith's (1975) seasonal study of an Orange County population pertains to *stricticollis*, not *tenuis* (as stated).

- 11.3. *barberi* Jeannel 1928: 133 (*eremita barberi*). Type locality, Otter Creek (=Rockhaven) Cave, Meade County, Kentucky. NEW RECORDS: species is present and often very abundant in many caves of Meade, Breckinridge, and Hardin counties, Kentucky, becoming rare in northern Hart and Larue counties at the southern limit of its range.
- 11.4. *illinoisensis* Barr and Peck 1966: 519. Type locality, Cave Spring Cave, Hardin County, Illinois. The only species of cave trechine known from Illinois and is restricted to the type locality.
- 11.5. *youngi* Krekeler, 1958: 175 (*youngi youngi*). Type locality, Clifty Caves (= "Cave River Valley"), Washington County, Indiana. NEW RECORDS: many caves in Crawford, Orange, Lawrence, and Washington counties, Indiana; species is much more widely distributed than previously recorded, with almost the same geographic range as *stricticollis*. NEW SYNONYMY: *donaldsoni* Krekeler, 1958: 175 (Donaldson's Cave).
- 11.6a. *shilohensis shilohensis* Krekeler, 1958: 178 (*shilohensis*). Type locality, Shiloh Cave, Lawrence County, Indiana; occurs in caves of central Lawrence County north of East Fork of White River.
- 11.6b. *shilohensis mayfieldensis* Krekeler, 1958: 178 (*mayfieldensis*). Type locality, Mayfield's Cave, Monroe County, Indiana; occurs in numerous caves in southwest Monroe, northwest Lawrence, and southeast Owen counties, Indiana, intergrading with *shilohensis shilohensis* in Sullivan's Cave and vicinity, Lawrence County. Misidentified as *Anopthalmus tenuis* by Banta (1907). NEW SYNONYMY: *boonensis* Krekeler, 1958: 180 (Boone's Cave, Owen County). Owen County specimens fall well within the range of variability of the *shilohensis mayfieldensis* populations in caves of the Whitehall region.

12. *leonae* group

Small to medium-sized species lacking the slender habitus of the *tenuis* group,

the mesosternal protuberance of *P. emersoni*, and the slender, elongate aedeagus of the *horni* or *barri* groups; elytra pruinose; aedeagus short and thick, apex blunt, two heavily sclerotized copulatory pieces, internal sac spiny.

Northwest Lawrence and southern Monroe counties, Indiana.

The group was defined by Barr (1960b), but the definition must now be expanded to include two species (Monroe County, * undescribed) attaining a length of about 4.0 mm.

- 12.1. *leoniae* Barr, 1960b: 310. Known only from the type locality, Hert Farm Cave, near Springville, Lawrence County, Indiana.

13. *eremita* group

Medium-small to large species with pruinose elytra, the striae obsolescent, form robust and rather depressed; aedeagal apex long and not sharply attenuate, copulatory pieces elongate, subequal, lobate (reminiscent of *robustus* group).

Two rare species from Crawford and Harrison counties, Indiana, and Boyle County, Kentucky, respectively.

The group was defined for *eremita* only by Barr (1960b), but *conditus* (listed as "Incertae sedis" by Krekeler 1973), though smaller, has the same group characteristics.

- 13.1. *eremita* (Horn) 1871: 325 (*Anophthalmus*). Wyandotte Cave (type locality), Crawford County, and Langdon Cave, Harrison County, Indiana. A rare species, NOT *eremita* of authors other than Horn before 1960 (Barr 1960b: 308).
- 13.2. *conditus* Krekeler, 1973: 73. Lawrence (type locality) and Crawford (NEW RECORD) caves, near Perryville, Boyle County, Kentucky.

14. *robustus* group

Mostly large species (one aberrant species about 4 mm), form robust, rather depressed, elytra not pruinose, at least inner striae well impressed, elytral microsculpture of dense, transverse meshes; aedeagus with apex produced, right copulatory piece hemicylindrical, usually longer, partially enfolding smaller, slender, elongate, cylindrical left piece, both pieces unarmed.

Western margin of Cumberland plateau and adjacent Highland Rim from Wayne and McCreary counties, Kentucky, to Grundy County, Tennessee, with westernmost species in Adair* County, Kentucky, and Smith and Dekalb counties, Tennessee. See Barr 1962a (distribution maps and species key).

The group is the same as the *robustus* group of Valentine (1932) and Barr (1962), but Jeannel's (1949) *robustus* group also included *P. horni* (*horni* group) as well as species of the *intermedius* group. The latter are closely similar but distinguished (i.a.) by isodiametric microsculpture of the elytra.

- 14.1. *robustus* Valentine 1931: 250. Type locality, Johnson Saltpeter Cave, Putnam County, Tennessee; abundant in caves of Dekalb, Grundy, southern Overton, Putnam, Warren, and White counties, Tennessee. SYNONYMS: *neglectus* Jeannel 1949: 50; *megosteus* Barr 1959a: 12.
- 14.2. *farrelli* Barr 1959a: 12. Type locality, Indian Grave Point Cave, Dekalb County, Tennessee; common in caves of Smith Fork drainage in Dekalb and southern Smith counties, Tennessee.
- 14.3. *beakleyi* Valentine 1937: 97 (emendation of *beaklei*). Type locality, Bunkum Cave, Pickett County, Tennessee; frequent in caves of Fentress, Overton, Pickett counties, Tennessee, and southern Wayne and McCreary counties, Kentucky. Syn.: *lupus* Barr 1959a: 14.
- 14.4. *valentinei* Jeannel 1949: 51. Type locality, Johnson Saltpeter Cave, Putnam County, Tennessee; caves of southern Overton and eastern Putnam counties, Tennessee.

15. *intermedius* group

Large to very large (7.0 mm) species with aedeagus and transfer apparatus as described for *robustus* group, to which it appears taxonomically close; elytral microsculpture, however, is isodiametric, not transverse; some larger species semiaphænopsian in habitus.

Western margin of Cumberland plateau from Overton County, Tennessee, to Jackson and Marshall counties*, Alabama.

The group is the same as the *intermedius* group of Valentine (1932) and Barr (1962) but was part of Jeannel's (1949) *robustus* group. It is equivalent to subgenus *Tennessarius* Valentine (1952), which was made a synonym of *Pseudanophthalmus*

by Barr (1962). The obliquely sloping prehumeral borders and deplanate areas around the scutellum emphasized by Valentine (1952) also apply to some species of the *robustus* group (as defined here) from Wayne County, Kentucky, and these traits are less marked in smaller species of the *intermedius* group, such as *macradyi*. The elytral microsculpture is a more reliable group character, if the two groups are to be separated at all. *Nelsonites* Valentine (1952) was probably derived from this section of *Pseudanophthalmus*: the elongate body form, oblique prehumeral borders, large size, and elongate appendages are indeed similar, but *Nelsonites* has much longer antennae, longer last segments of the maxillary palps, and a comparatively huge head and mandibles; the anterior discal seta of the elytra is displaced forward to the level of the second umbilicate puncture (as in the *menetriesi* and *pubescens* groups; see Barr, 1979).

- 15.1. *intermedius* (Valentine) 1931: 249 (*Neaphænops*). Type locality, Wonder Cave, Grundy County, Tennessee; several caves in Grundy and Franklin counties, Tennessee, at the west base of the Cumberland plateau.
- 15.2. *templetoni* Valentine 1948: 7 (*intermedius templetoni*). Type locality, Cumberland Caverns (=Higginbotham Cave), Warren County, Tennessee; several caves in Collins River drainage in southern Warren and northern Grundy counties, Tennessee. Largest species of the genus, 7 mm or more.
- 15.3. *vanburenensis* Barr 1959a: 15 (*templetoni vanburenensis*; see Barr 1962: 111). Type locality, McElroy Cave, Van Buren County, Tennessee; limited to caves of Van Buren County at the west base of the Cumberland plateau escarpment.
- 15.4. *macradyi* Valentine 1948: 9 (emendation of *macradei*). Type locality, Cumberland Caverns (=Higginbotham Cave), Warren County, Tennessee; several caves in eastern Warren and northern Grundy counties, Tennessee.

16. *pubescens* group

Medium-large to very large species, elytra more or less pruinose, anterior discal puncture at level of 2nd or 3rd umbilicate puncture, apical recurrent groove well developed; apex of ædeagal median lobe often obliquely truncate, right copulatory sclerite partially enfolding rod-like, very knobby left piece.

Pennyroyal plateau of western Kentucky from Hart and Metcalfe counties southwestward to Caldwell* and Crittenden* counties; also northern Sumner* Robertson, Cheatham, Montgomery, and eastern Stewart* counties, Tennessee.

Pseudanophthalmus pubescens was included in the *menetriesi* group by Valentine (1932); the group as constituted here is the same as that of Jeannel (1949 with the exclusion of *cumberlandus*; see also Barr 1979, 1980.

- 16.1a. *pubescens pubescens* (Horn) 1868: 126 (*Anophthalmus*). Type locality Cave City (=Railroad) Cave, Barren County, Kentucky; abundant in Kentucky caves from Hart and Metcalfe counties westward to eastern Warren County; see Barr & Crowley 1981, Barr 1985a.
- 16.1b. *pubescens intrepidus* Barr 1985a: 127. Buchanan Cave (type locality) Allen County, and Bryant Edmonds Cave, Barren County, Kentucky. Intergrades with nominate *pubescens* in Beckton Cave, Barren County.
- 16.2. *princeps* Barr 1979: 17. Type locality, Hoy Cave, Simpson County Kentucky; caves in West Fork of Drakes Creek drainage in eastern Warren and Simpson counties, Kentucky, also Whiteoak Cave, northern Sumner County Tennessee.
- 16.3a. *ciliaris ciliaris* Valentine 1937: 95 (monotypic). Type locality, Dunbar Cave, Montgomery County, Tennessee; abundant in several caves of eastern Montgomery, northern Cheatham, and western Robertson counties, Tennessee also southern edge of Christian, Todd, and western Logan counties, Kentucky (close to Tennessee state line only).
- 16.3b. *ciliaris orlindae* Barr 1959a: 7 (as full species). Type locality, Jesse James Cave, Robertson County, Kentucky; caves of southern Logan and southwestern Simpson counties, Kentucky, also eastern Robertson county, Tennessee. Intergrades with nominate *ciliaris* in Bell Witch Cave, Robertson County Tennessee (Barr 1979).
- 16.4. *loganensis* Barr 1959a: 7 (*ciliaris loganensis*). Type locality, Coopers (=Savage) Cave, Logan County, Kentucky; abundant in caves of southern Warren, Simpson, and Logan counties, Kentucky, also northwest Sumner and northeast Robertson counties, Tennessee.

- 16.5. *colemanensis* Barr 1959a: 6 (*ciliaris colemanensis*). NEW STATUS.
Coleman Cave (type locality) and other caves in Blooming Grove Creek valley,
western Montgomery County, Tennessee.

17. *menetriesi* group

Large species, elytra pruinose or not, anterior discal puncture at level of 2nd or 3rd umbilicate puncture, apical recurrent groove vestigial. Transfer apparatus of two subequal copulatory sclerites.

Pennyroyal plateau of western Kentucky from Hardin to Warren counties, southeastward through Adair, Cumberland, Metcalfe, and Monroe counties, Kentucky, to northern Clay* and Jackson* counties, Tennessee, with one isolated species in Wilson* County, Tennessee.

Same as the *menetriesi* group of Jeannel (1949), including part of Valentine's (1932) *menetriesi* group.

- 17.1a. *menetriesi menetriesi* (Motschulsky) 1862: 41 (*Anophthalmus*). Type locality, Mammoth Cave, Edmonson County, Kentucky; abundant in caves of southern Hart, Edmonson, Barren, and eastern Warren counties, Kentucky (see Barr and Crowley 1981, Barr 1985a). Syn.: *ventricosus* Motschulsky 1862: 42; *angulatus* LeConte 1863: 18 (Mammoth Cave type locality for both names).
- 17.1b. *menetriesi campestris* Barr 1985a: 119. Type locality, Walnut Hill Cave, Barren County, Kentucky; several caves of central Barren and southeast Warren counties, Kentucky. Intergrades with nominate *menetriesi* in caves near Park City and Cave City, Warren County.
- 17.2. *simulans* Barr 1985a: 120. Known only from Cub Run Cave, Hart County, Kentucky.
- 17.3. *transfluvialis* Barr 1985a: 123. Lost River (= "Big Bertha" Entrance = McGinnis) Cave, Warren County, Kentucky; caves of west-central Warren County from Bowling Green to easternmost tip of Logan County, Kentucky.
- 17.4. *pilosus* Barr 1985a: 120. Type locality, Bland Cave, Hardin County, Kentucky; caves of southwest Hardin (Star Mills area) and northwest Hart counties, Kentucky.
- 17.5. *globiceps* Barr 1985a: 122. Type locality, Barnes Smith (= "Blind Snail") Cave, northeast Hart County, Kentucky; known only from the type locality.

- 17.6a. *cerberus cerberus* Barr 1985a: 123. Type locality, Rhoton Cave, Monroe County, Kentucky; many caves of southeast Barren, southern Adair, northwest Cumberland, southwest and most of Monroe counties, Kentucky.
- 17.6b. *cerberus completus* Barr 1985a: 124. Type locality, Cole Cave, and six other caves in central Barren County, Kentucky. Intergrades with nominate *cerberus* in Bowles Branch Cave, Barren County.
- 17.7. *striatus* (Motschulsky) 1862: 41 (*Anophthalmus*). Type locality, Mammoth Cave, Edmonson County, Kentucky; many caves of Hart, Edmonson, Metcalfe, eastern Warren counties, Kentucky. Syn.: *interstitialis* Hubbard 1880: 52.
- 17.8a. *darlingtoni darlingtoni* Barr 1985a: 125. Type locality, Jones Cave, Adair County, Kentucky; caves south of Green River in northern Adair, northeast Metcalfe, and southern Green counties, Kentucky (see Barr 1985b for distribution map and discussion of variation among local populations).
- 17.8b. *darlingtoni persimilis* Barr 1985a: 126. Type locality, Woodard Cave, Green County, Kentucky; caves north of Green River in central Green and eastern Hart counties, Kentucky (see Barr 1985b for distribution map and sites of intergradation with nominate *darlingtoni*).

18. *simplex* group

Medium-small species, aedeagus weakly arcuate, apex attenuate but scarcely produced, transfer apparatus a spiny, triangular left piece and a hemicylindrical, slightly knobbed or apically rounded right piece, or only the right piece as described.

Cumberland River valley in Jackson and Clay counties, Tennessee, on left (south) side of the river.

The group was defined by Barr (1980) and includes only two known species.

- 18.1. *simplex* Barr 1980: 86. Carter (type locality), Haile's, and Cherry caves, Jackson County, Tennessee.
- 18.2. *fowlerae* Barr 1980: 88. Known only from the type locality, Sheal's Cave, Clay County, Tennessee.

19. *cumberlandus* group

Small to medium-large species; aedeagus weakly arcuate, transfer apparatus of

a single small, elongate-triangular sclerite; aedeagal apex usually not very attenuate, briefly produced, rather blunt at tip (a few exceptions).

Central Basin (where it is the dominant group) and northwest Highland Rim, and western Tennessee River valley of Tennessee; Limestone County, Alabama; and Christian, Caldwell, Livingston, Rockcastle, Pulaski, and Wayne counties, Kentucky, and north Fentress County, Tennessee..

The group was defined by Barr (1980). *Pseudanophthalmus cumberlandus* was placed in the *pubescens* group by Jeannel (1949); Barr (1959a) previously relegated seven taxa described as polytypic *P. tiresias* to the *engelhardti* group, where they do not belong.

- 19.1. *cumberlandus* Valentine 1937: 96. Type locality, Piper Cave, Smith County, Tennessee; other nearby Smith County caves and (NEW RECORD) Ann White Cave, Macon County, Tennessee.
- 19.2. *productus* Barr 1980: 91. Type locality, Neil Fisher (=Rip Van Winkle) Cave, Smith County, Tennessee; known from a dozen other caves in Smith, Jackson, and western Putnam counties, Tennessee.
- 19.3. *tiresias* Barr 1959a: 16 (*tiresias tiresias*). Indian Grave Point (type locality) and nearby Fox caves, Dekalb County, Tennessee.
- 19.4. *catherinae* Barr 1959a: 17 (*tiresias catherinae*). Known only from the type locality, Petty Cave, Marshall County, Tennessee.
- 19.5. *insularis* Barr 1959a: 18 (*tiresias insularis*). Known only from the type locality, Baker Station Cave, northern Davidson County, Tennessee.
- 19.6. *occidentalis* Barr 1959a: 18 (*tiresias occidentalis*). DePriest Branch Cave, Lewis County (type locality), and nearby Cave Branch Cave, Hickman County, Tennessee.
- 19.7. *acherontis* Barr 1959a: 20 (*tiresias acherontis*). Echo Cave section of Snail Shell Cave system (type locality), Patton, Patterson, Cave of the Medallions, Doctor Mays, and Herron caves, Rutherford County; and Blowhole, Mary Williams, and Jackson caves, Wilson County, Tennessee.
- 19.8. *tullahoma* Barr 1959a: 20 (*tiresias tullahoma*). Carroll (type locality) and Riley Creek caves, Coffee County, Tennessee; both caves are now flooded by Normandy Reservoir.

- 19.9. *bendermani* Barr 1959a: 21 (*tiresias bendermani*). Known only from the type locality, Benderman Cave and two other caves in Maury County, Tennessee.
- 19.10. *inquisitor* Barr 1980: 94. Known only from the type locality, Sheal's Cave, Clay County, Tennessee.

20. *engelhardti* group

Medium-small species with bisinuate apical recurrent groove and without long setae on pronotum disc (in addition to usual pubescence; except west-central Tennessee); apex of aedeagus constricted before apex, which is arrow-shaped in dorsal view; in lateral view apex is typically hatchet-shaped OR more or less attenuate, with or without a terminal knob.

Widely distributed from extreme southwest Virginia (Lee County) through the Appalachian valley of east Tennessee (Anderson, Campbell, Claiborne, Hamilton, Marion, Hancock, and Rhea counties) and Georgia (Dade and Walker counties), then west along the Tennessee River valley into northern Alabama (Blount, Colbert*, Dekalb, Jackson, Lauderdale*, Lawrence*, Madison, Marshall, and Morgan counties), finally northward along the western Tennessee River valley in Decatur*, Perry, and Wayne counties, Tennessee.

Barr (1981) reorganized the "*engelhardti* complex," recognizing seven species groups among the primarily Appalachian valley species with an elongate, bisinuate apical recurrent groove, resurrecting Valentine's (1932) *engelhardti*, *alabamae*, and *hirsutus* groups. Jeannel (1949) also recognized a separate *hirsutus* group, but included *jonesi* and *alabamae* with his *engelhardti* group. The seven taxa described by Barr (1959a) as polytypic *P. tiresias* are now assigned to the *cumberlandus* group.

- 20.1. *engelhardti* (Barber) 1928: 195 (*Anophthalmus*). Known only from the type locality, English Cave, Claiborne County, Tennessee.
- 20.2. *deceptivus* Barr 1981: 43. Known only from the type locality, Fisher Cave, Lee County, Virginia.
- 20.3. *wallacei* Barr 1981: 46. Known only from the type locality, Weaver Cave, Anderson County, Tennessee.

- 20.4. *rotundatus* Valentine 1932: 71. Type locality, English Cave, Claiborne County, Tennessee; known also from Parkeys (Jeannel 1949) and Subers caves, Hancock County, Tennessee, and Smith Cave, Lee County, Virginia.
- 20.5. *sidus* Barr 1965: 64. Known only from the type locality, Meredith Cave, Campbell County, Tennessee.
- 20.6. *holsingeri* Barr 1965: 63. Known only from the type locality, Young-Fugate's cave system, Lee County, Virginia.
- 20.7. *nortoni* Barr 1981: 48. Known only from the type locality, Grassy Creek Cave, Rhea County, Tennessee.
- 20.8. *fulleri* Valentine 1932: 272. Type locality, Tennessee Caverns, Hamilton County, Tennessee; occurs in six other caves in Lookout Valley west of Lookout Mountain, Dade County, Georgia (Barr 1981).
- 20.9. *fastigatus* Barr 1981: 50. Known only from the type locality, Horseshoe Cave, Walker County, Georgia, on the east side of Lookout Mountain.
- 20.10. *nickajackensis* Barr 1981: 51. Known only from the type locality, Nickajack Cave, Marion County, Tennessee; cave was flooded in 1967 by waters of Nickajack Reservoir.
- 20.11. *sequoyah* Barr 1981: 52. Known only from the type locality, Sequoyah Caverns (=Ellis Cave), Dekalb County, Alabama.
- 20.12. *steevesi* Barr 1981: 53. Randolph (type locality), Rickwood, Bryant, and Horse caves, Blount County, Alabama.
- 20.13. *lædingi* Valentine 1931: 252 (emendation of *lodingi*). Shelta (type locality), Barclay, Canoe, Hoopers Well, Matthews, Sinks, and Spook caves, Madison County, Alabama. Closely similar to 20.14, 20.15, and 20.16.
- 20.14. *profundus* Valentine 1945: 637. NEW STATUS. Natural Well (type locality), Cave Spring, Rousseau, and Hering caves, Madison County, Alabama; occurs in caves of the Flint River drainage east of Monte Sano Mountain. NEW SYNONYMY: *lodingi aquaticus* Valentine 1945: 638.
- 20.15. *alladini* Valentine 1945: 637. NEW STATUS. Alladin (type locality), Scott, and McFarland caves, Madison County, Alabama.
- 20.16. *humeralis* Valentine 1931: 253. Crystal (type locality) and Wonder caves, Grundy County, also Dry and Caroline Cove caves, Franklin County, Tennessee. Syn.: *humeralis brevis* Valentine 1932: 273.

- 20.17. *meridionalis* Valentine 1945: 639 (*lodingi meridionalis*). NEW STATUS. Type locality, Saltpeter (=Nyman=Guntersville Caverns) Cave, also (NEW RECORDS) Beech Spring, Bishop, Davidson, Hampton, Old Blowing, Warrenton, and Campbell caves, Morgan County, Alabama, near Guntersville Dam. Closely similar to 20.18 and 20.19.
- 20.18. *fluviatilis* Valentine 1948: 12 (*lodingi fluviatilis*). NEW STATUS. Rock House Cave, Marshall County, (type locality) and Hughes, Lamons, B & J, Mill Bluff, Shine, Talucah, Turtle, Wolf caves, Morgan County, Alabama. Occurs in drainage basin of Cotaco Creek near Oleander, Morgan City, and Valhermoso Springs, including Newsome Sinks and Lamons Cove.
- 20.19. *distinguens* Valentine 1948: 12 (*lodingi distinguens*). NEW STATUS. Inge (type locality), Anvil, Horseback, and Roper caves, Morgan County, Alabama. Occurs in Trinity-Hartselle region of northwest Morgan County in the Flint Creek basin.
- 20.20. *hesperus* Barr 1959a: 15. Bethel (type locality) and (NEW RECORDS) Blowing caves, Perry County, also Sheep Cave, Wayne County, Tennessee.

21. *tennesseensis* group

Small to medium-small species with bisinuate apical recurrent groove; pronotum with two long setae each side of disc; aedeagus neither constricted before base nor with arrow-shaped apex; hemicylindrical right copulatory piece sheathing a large, spinulose left piece.

The four known species occupy caves of Anderson, Knox, Roane, and Union counties, Tennessee, north and west of Knoxville.

The group was defined by Barr (1981). Previously both Valentine (1937) and Jeannel (1949) included *P. tenneseensis* in the *engelhardti* group. See Barr (1981) for descriptions and cave locations.

- 21.1. *tennesseensis* Valentine 1937: 98 (emendation of *tenesensis*). Grand Caverns (type locality, =Atomic Caverns), George Light, and Rock Hill caves, Knox County, and Eblen Cave, Roane County, Tennessee.
- 21.2. *pusillus* Barr 1981: 56. Known only from the type locality, Martin Cave, Anderson County, Tennessee.

- 21.3. *paynei* Barr 1981: 56. Moores Bridge (type locality), Flowstone, and Norris Quarry No. 2 caves, Anderson County, Tennessee.
- 21.4. *unionis* Barr 1981: 57. Wright (type locality) and Wolf caves, Union County, Tennessee.

22. *hirsutus* group

Small to medium-small species with bisinuate apical recurrent groove; 2-4 long setae either side of pronotum disc; form slender and depressed with elytra subparallel; aedeagus not constricted before base, median lobe weakly arcuate, copulatory sclerites very small, especially left piece.

Distributed along the Appalachian valley from southwest Virginia (Lee and Scott counties) through Tennessee (Hamilton, Marion, and Monroe counties) to northeast Alabama (DeKalb County) and Georgia (Dade County).

The group was proposed by Valentine (1932) and redefined by Jeannel (1949) and Barr (1965, 1981). Jeannel (1949) included *hubrichti* in the group, and Barr (1965) originally included *hubrichti*, *egberti*, and *vicarius*, which more appropriately belong in the *hubrichti* group.

- 22.1. *hirsutus* Valentine 1931: 252. Cudjo's (type locality) and Cumberland Mountain Saltpeter caves, in Cumberland Gap National Park, Lee County, Virginia.
- 22.2. *delicatus* Valentine 1932: 270 (*hirsutus delicatus*). Gilly (type locality) and twelve other caves in central Lee County, Virginia (see Barr 1981 for cave list).
- 22.3. *sericus* Barr 1981: 62. Known only from the type locality, Lane Cave, Scott County, Virginia.
- 22.4. *paulus* Barr 1981: 63. Known only from the type locality, Nobletts Cave, Monroe County, Tennessee.
- 22.5. *digitus* Valentine 1932: 67. Tennessee Caverns (type locality, =Crystal Cave), Hamilton County, Tennessee, and Johnson's Crook and Byers caves, Dade County, Georgia.
- 22.6. *ventus* Barr 1981: 64. Known only from the type locality, Blowing Cave, at Sequatchie, Marion County, Tennessee.
- 22.7. *assimilis* Barr 1981: 65. Sequoyah Caverns (type locality, =Ellis Cave) and Kudzu Cave, DeKalb County, Alabama.

23. *hubrichti* group

Small to medium species, form slender and depressed, pronotum disc without supernumerary setae; aedeagal apex not arrow-shaped, bluntly rounded or finely truncate, deflexed in one species.

The group has a limited geographic distribution in the Appalachian valley, from Giles, Russell, Tazewell, and Scott counties, Virginia, to Hawkins County, Tennessee.

The group was defined by Barr (1981). Previously its species had been assigned to the *hirsutus* group by Jeannel (1949) and Barr (1965), although Barr (op. cit.) placed *quadratus* in a far too inclusive "*hubbardi* group."

- 23.1. *hubrichti* Valentine 1948: 13. Known only from the type locality, Dougherty Cave, Russell County, Virginia.
- 23.2. *sanctipauli* Barr 1981: 67. Banners Corner Cave (type locality, =Big Spring Cave), Russell County, and Greears Sweet Potato Cave, Scott County, Virginia.
- 23.3. *egberti* Barr 1965: 49. Starnes Cave (type locality) and Giant Caverns (=Hopkins Cave), Giles County, Virginia.
- 23.4. *quadratus* Barr 1965: 60. Known only from the type locality, Straley's Cave and nearby Spring Run Cave, Giles County, Virginia.
- 23.5. *vicarius* Barr 1965: 48. Hugh Young (type locality), Bowen, Fallen Rock, Gully, and Lost Mill caves, Maiden Spring area, Tazewell County, Virginia.
- 23.6. *paradoxus* Barr 1981: 70. Known only from the type locality, Sensabaugh Saltpeter Cave, Hawkins County, Tennessee.

24. *jonesi* group

Large to medium-large species with bisinuate apical recurrent groove, slender and convex form, appendages elongate; pronotum elongate-cordiform with small hind angles and 1-4 long, supernumerary setae each side on disc; aedeagus with apex produced and not arrow-shaped.

Distributed in the Appalachian valley from Lee, Scott, and Wise counties, Virginia, to Claiborne and Hancock counties, Tennessee, also in the Pine Mountain

fault block (Harlan County, Kentucky; Campbell County, Tennessee) and in Grassy Cove (Cumberland County, Tennessee).

Prior to 1981, when Barr defined the group, the only known species (*jonesi*) had been included in the *engelhardti* group by Jeannel (1949), and Valentine (1945) speculated that it belonged to a little-known, more widely distributed stock.

- 24.1. *jonesi* Valentine 1945: 645. Known only from Grassy Cove, Cumberland County, Tennessee, from Grassy Cove Saltpeter (type locality), Mill, and Blowhole caves.
- 24.2. *scutillus* Barr 1981: 73. Known only from the type locality, New Mammoth Cave, in Pine Mountain, Campbell County, Tennessee.
- 24.3. *rogersae* Barr 1981: 75. Known only from the type locality, Sawmill Hollow Cave, in Pine Mountain, Harlan County, Kentucky.
- 24.4. *seclusus* Barr 1981: 76. Flannery Cave (type locality) and six other caves, all in Rye Cove, Scott County, Virginia.
- 24.5. *pallidus* Barr 1981: 78. Chadwell (type locality), Buis Saltpeter, and English caves, Claiborne County, Tennessee.
- 24.6. *longiceps* Barr 1981: 79. Fisher Cave (type locality), Lee County, Virginia, and Panther Creek Cave, Hancock County, Tennessee; both caves are high on Newman Ridge.
- 24.7. *thomasi* Barr 1981: 80. Blair-Collins (type locality) and Coley No. 2 caves, Scott County, Virginia.
- 24.8. *cordicollis* Barr 1981: 82. Known only from the type locality, Little Kennedy Cave, Wildcat Caves, and the Omega cave system, Wise County, Virginia.

25. *hypolithos* group

Small, slender and depressed species with bisinuate apical recurrent groove; pronotum without supernumerary setae on disc; aedeagal spex slender and attenuate, not arrow-shaped.

Four of five known species inhabit caves of Pine Mountain, eastern Kentucky (Pike, Harlan, Bell, and Whitley counties), and the fifth species occupies a cave at the base of the Allegheny front in Scott County, Virginia. *P. hypolithos* was subsequently discovered in abandoned coal mines (Barr 1986).

The group was defined by Barr (1981).

- 25.1. *hypolithos* Barr 1981: 83. Type locality, Old Quarry Cave, near Ashcamp, Pike County, Kentucky; also known from two abandoned coal mines approximately 15-25 km southwest of the type cave, in Floyd County, Kentucky (Barr 1986).
- 25.2. *scholasticus* Barr 1981: 84. Known only from the type locality, Sawmill Hollow Cave, in Pine Mountain, Harlan County, Kentucky.
- 25.3. *calcareus* Barr 1981: 85. Known only from the type locality, Limestone Cave, in Pine Mountain, Whitley County, Kentucky.
- 25.4. *frigidus* Barr 1981: 86. Known only from the type locality, Icebox Cave, in Pine Mountain, Bell County, Kentucky.
- 25.5. *praetermissus* Barr 1981: 87. Known only from the type locality, Kern's Cave No. 1, Scott County, Virginia.

26. *alabamae* group

Medium-large species with apical recurrent groove subparallel to suture, its apex directed toward 4th or 5th longitudinal striae; pronotum irregularly with 1-4 supernumerary setae each side; aedeagal apex slender, produced, briefly but distinctly deflexed at tip, not arrow-shaped.

The two known species occur at the western edge of the Appalachian valley in Dekalb County, Alabama, and Chattooga and Walker counties, Georgia, on opposite sides of Lookout Mountain.

Although Valentine (1932) suggested group status for *alabamae*, Jeannel (1949) and Barr (1965) relegated it to the *engelhardti* group. Barr (1981) restored it to group standing and added the related species *P. georgiae*.

- 26.1. *alabamae* Valentine 1932: 273. Manitou Cave (type locality) and six other caves in Little Wills Valley, Dekalb County, Alabama (Barr 1981).
- 26.2. *georgiae* Barr 1981: 90. Blowing Spring Cave (type locality), Chattooga County, also Pettijohn and Mountain Cove Farm caves, Walker County, Georgia.

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Appendix A

Distribution of *Pseudanophthalmus* Species Groups by States and Counties

In practice the exact provenance of a specimen is very helpful in its determination since most species have very local geographic ranges. Although additional, previously unknown species will surely be found in the future, the major cave regions of eastern United States have been extensively collected, so that the ranges of all but the rarest species are rather well known. The following information, arranged by states and counties, is useful in conjunction with the artificial key. An asterisk (*) indicates the existence of one or more undescribed taxa represented in my collection from the geographic areas in the list. Recent taxonomic references are cited where pertinent. Species of *Pseudanophthalmus* are known from 11 states – Alabama, Georgia, Illinois, Indiana, Kentucky, Maryland, Ohio, Pennsylvania, Tennessee, Virginia, and West Virginia.

Approximately 80 unnamed species in my private collection of *Pseudanophthalmus* have been diagnosed, and these will be described in future papers. The major groups most in need of further study at this writing are the *cumberlandus*, *engelhardti*, *grandis*, *intermedius*, *pubescens*, *robustus*, and *tenuis* groups, but one to three undescribed species are represented in each of the *audax*., *gracilis*, *leonae*, *menetriesi*, *petrunkevitchi*, *pusio*, and *rittmani* groups.

Alabama

alabamae group – Dekalb County (*alabamae* Barr 1981)

cumberlandus group – Limestone County*

engelhardti group – widespread across northern Alabama* (Jeannel 1949; Valentine 1948; see checklist for rearrangements)

hirsutus group – Dekalb County (*assimilis* Barr 1981)

intermedius group – Jackson* and Marshall* counties

Georgia

alabamae group – Chattooga County (*georgiae* Barr 1981)

engelhardti group – Dade (*fulleri*) and Walker (*fastigatus*) counties (Barr 1981)

hirsutus group – Dade County (*digitus* Barr 1981)

Illinois

tenuis group – Hardin County (*illinoisensis* Barr & Peck 1966)

Indiana

audax group – Lawrence County (*emersoni* Krekeler 1958)

barri group – Clark County (*barri* Krekeler 1973)

eremita group – Crawford and Harrison counties (*eremita* Barr 1960b)

horni group – Clark, Jefferson, Jennings counties (*chthonius* Krekeler 1973)

leona group – Monroe*, Orange*, and Lawrence (*leona*) counties (Barr 1960b)

tenuis group – widespread in Mitchell plain and Crawford upland in Crawford (*tenuis*, *stricticollis*, *youngi*), Dubois*, Greene*, Harrison (*tenuis*), Lawrence* (*stricticollis*, *shilohensis*, *youngi*, et al.), Monroe* (*shiloensis* et al.), Orange (*stricticollis*, *youngi*), Owen (*shilohensis*), Washington (*tenuis*, *stricticollis*, *youngi*) counties (Krekeler 1958, Barr 1960b; see rearrangement in checklist)

Kentucky

audax group – Adair*, Edmonson-Hart (*audax*), Carter-Elliott (*packardi*), Green*, Russell*, and Menifee* counties

barri group – Jefferson County (*troglodytes* Krekeler 1973)

cumberlandus group – Caldwell*, Christian*, Livingston*, Pulaski*, Rockcastle*, and Wayne* counties

eremita group – Boyle County (*conditus*; Krekeler 1973)

gracilis group – Boyle-Fayette-Garrard-Owen-Woodford (*umbratilis*), Edmonson (*inexpectatus*), Green-Hart-Taylor (*orientalis*), Hardin*, Larue-Nelson (*cnephus*), Marion (*parvus*), and Mercer and Boyle (*puteanus*) counties (Krekeler 1973)

horni group – Boyle-Garrard-Mercer (*elongatus*), Clark-?Franklin-Owen-Scott (*desertus*), Fayette (*horni*), Harrison (*major*), Henry (*desertus*, *tenebrosus*), Jessamine (*solivagus*), (*exoticus*), Madison (*pholetor*), Woodford (*cæcus*, *abditus*, *solivagus*) counties (Krekeler 1973)

hypolithos group – Bell (*frigidus*), Harlan (*scholasticus*), Pike and Floyd (*hypolithos*), and Whitley (*calcareus*) counties (Barr 1981)

jonesi group – Harlan County (*rogersae* Barr 1981)

- menetriesi* group – Hardin (*pilosus*), Hart (*pilosus, simulans, menetriesi, striatus*), Edmonson (*menetriesi, striatus*), Barren (*menetriesi, striatus, cerberus*), Warren (*menetriesi, striatus, cerberus, transfluvialis*), Green-Taylor (*darlingtoni*), Adair* (*darlingtoni, cerberus*), Metcalfe* (*darlingtoni, cerberus, striatus*), Monroe (*cerberus, striatus*), and Cumberland (*cerberus*) counties (Barr 1985a, 1985b)
- pubescens* group – Hart-Metcalfe-Edmonson-Barren (*pubescens*), Warren* (*pubescens, loganensis, princeps*), Allen* (*pubescens, princeps*), Simpson (*princeps, loganensis, ciliaris*), Logan-Russell (*ciliaris, loganensis*), Todd*, Christian* (*ciliaris et al.*), Trigg*, Caldwell*, Lyon*, and Crittenden* counties (Barr 1979, 1985a; Barr & Crowley 1981)
- rittmanni* group – Estill-Lee-Powell (*exiguus, rittmani*) and Madison (*cataryctos*) counties (Krekeler 1973); Jackson* County
- robustus* group – Adair*, Clinton -McCreary- Wayne (*beakleyi*) counties (Barr 1962)
- tenuis* group – Breckinridge-Hardin-Hart-Larue-Meade (*barberi*) and Grayson* counties

Maryland

- gracilis* group – Garrett County*

Ohio

- horni* group – Adams County (*ohioensis, krameri*; Krekeler 1973)

Pennsylvania

- gracilis* group – Fayette County*

Tennessee

- cumberlandus* group – Widely distributed in Central Basin and western Tennessee River valley, known from following counties: Bedford*, Cannon*, Cheatham*, Clay (*inquisitor*), Coffee* (*tullahoma et al.*), Davidson* (*insularis et al.*), Dekalb (*tiresias*), Dickson*, Fentress*, Hickman* (*occidentalis*), Jackson (*productus*), Lawrence*, Lewis (*occidentalis*), Macon (*cumberlandus*), Marshall (*catherinae*), Maury

(*bendermani*), Moore*, Putnam (*productus*), Rutherford*-Wilson
(*acherontis* et al.), Smith (*cumberlandus*), Sumner* ; see Barr (1980)

- menetriesi* group – Clay-Jackson (*cerberus*; Barr 1985a) and Wilson* counties
simplex group – Clay (*fowlerae*) and Jackson (*simplex*) counties (Barr 1980)
pubescens group – Sumner (*princeps*, *loganensis*), Robertson (*ciliaris*,
loganensis), Montgomery (*ciliaris*, *colemanensis*), Cheatham (*ciliaris*),
Stewart* (Barr 1979)
robustus group – Fentress-Pickett (*beakleyi*), Overton* (*beakleyi*, *robustus*,
valentinei), Putnam (*robustus*, *valentinei*), Dekalb (*farrelli*, *robustus*),
Smith (*farrelli*), and Warren-White-Vanburen-Grundy (*robustus*)
counties (Barr 1962)
intermedius group – Franklin (*intermedus*), Overton*, Putnam (*vanburenensis*),
Van Buren (*macradyi*, *vanburenensis*), Warren (*macradyi*, *templetoni*),
Grundy (*templetoni*, *intermedius*); see Barr (1980)
engelhardti group – Campbell* (*sidus* et al.), Claiborne (*engelhardti*,
rotundatus), Hancock (*rotundatus*), Hamilton (*fulleri*), Anderson
(*wallacei*), Marion (*nickajackensis*), Rhea (*nortoni*), Union (*unionis*),
Decatur*, Perry (*hesperus*), and Wayne (*hesperus*) counties (Barr 1981)
tennesseensis group – Anderson (*pusillus*, *paynei*), Knox-Roane (*tennesseensis*),
and Union (*unionis*) counties (Barr 1981)
hirsutus group – Hamilton (*digitus*), Marion (*ventus*), and Monroe (*paulus*)
counties (Barr 1981)
hubrichti group – Hawkins County (*paradoxus*; Barr 1981)
jonesi group – Campbell (*scutilus*), Claiborne (*pallidus*), Cumberland (*jonesi*),
and Hancock (*longiceps*) counties (Barr 1981)

Virginia

- hubbardi* group – Bath* (*intersectus*), Highland (*potomaca*), Page (*hubbardi*),
Rockingham* (*avernus*, *parvicollis*), Shenandoah (*limicola*) counties
(Barr 1965)
grandis group – Tazewell County (*virginicus*)
pusio group – Alleghany (*nelsoni*), Botetourt*, Giles (*punctatus*), Montgomery
-Roanoke (*pusio*), and Rockbridge* (*pontis*) counties (Barr 1965)
gracilis group – Giles and Craig counties (*gracilis*; Barr 1965)

petrunkevitchi group – Warren-Page (*petrunkevitchi*), Bland-Smyth (*hoffmani*), Tazewell (*hortulanus*), Pulaski*, Washington*, and Wythe* counties (Valentine 1945, Barr 1965)

engelhardti group – Lee County (*deceptivus*, *holsingeri*, *rotundatus*) (Barr 1981)

hirsutus group – Lee (*hirsutus*, *delicatus*) and Scott counties (*sericus*) (Barr 1981)

hubrichti group – Giles (*egberti*, *quadratus*), Russell (*hubrichti*), Scott (*sanctipauli*), and Tazewell (*vicarius*) counties (Barr 1981)

jonesi group – Lee (*longiceps*), Scott (*seclusus*, *thomasi*), and Wise (*cordicollis*) counties (Barr 1981)

hypolithos group – Scott County (*praetermissus*; Barr 1981)

West Virginia

grandis group – Greenbrier* (*grandis*, *fuscus*, *henroti*), Monroe* (*grandis*, *orthosulcatus*, *fuscus*, *henroti*), Pocahontas* (*grandis*, *fuscus*, *hypertrichosis*, *sylvaticus*), Randolph (*krekeleri*), and Tucker (*montanus*) counties (Jeannel 1949, Barr 1965)

hubbardi group – Pendleton County (*potomaca*, *senecae*; Barr 1965)

gracilis group – Pendleton (*hadenoeus* Barr 1965), and Randolph* counties

pusio group – Greenbrier and Pocahontas counties (*lallemani*, *higginbothami*; Jeannel 1949), Mercer*, and Monroe* counties

Appendix B

Available Trivial Names in *Pseudanophthalmus*

Proposed available names in North American *Pseudanophthalmus* are alphabetized and indexed to the checklist numbered taxa. Junior synonyms and emended names are italicized.

<i>abditus</i> 7.3	<i>campestris</i> 17.1b	<i>donaldsoni</i> 11.5	<i>gracilis</i> 5.1
<i>acherontis</i> 19.7	<i>cataryctos</i> 8.3	<i>egberti</i> 23.3	<i>grandis</i> 1.1a
<i>alabamae</i> 26.1	<i>catherinae</i> 19.4	<i>elevatus</i> 1.1b	<i>hadenoeus</i> 5.2
<i>alladini</i> 20.15	<i>cerberus</i> 17.6a	<i>elongatus</i> 7.5	<i>henroti</i> 1.6
<i>angulatus</i> 17.1a	<i>chthonius</i> 7.9	<i>emersoni</i> 9.2	<i>hesperus</i> 20.20
<i>aquaticus</i> 20.14	<i>ciliaris</i> 16.3a	<i>engelhardti</i> 20.1	<i>higginbothami</i> 4.5
<i>assimilis</i> 22.7	<i>cnephosus</i> 6.4	<i>eremita</i> 13.1	<i>hirsutus</i> 22.1
<i>audax</i> 9.1	<i>colemanensis</i> 16.5	<i>exiguus</i> 8.2	<i>hoffmani</i> 3.2
<i>avernus</i> 2.4	<i>completus</i> 17.6b	<i>exoticus</i> 7.13	<i>holsingeri</i> 20.6
<i>barberi</i> 11.3	<i>conditus</i> 13.2	<i>farrelli</i> 14.2	<i>horni</i> 7.1
<i>barri</i> 10.1	<i>constrictus</i> 1.3b	<i>fastigatus</i> 20.9	<i>hortulanus</i> 3.3
<i>bathycola</i> 4.1	<i>cordicollis</i> 24.8	<i>fluviatilis</i> 20.18	<i>hubbardi</i> 2.1
<i>beaklei</i> 14.3	<i>cumberlandus</i> 19.1	<i>fowlerae</i> 18.2	<i>hubrichti</i> 23.1
<i>beakleyi</i> 14.3	<i>cæcus</i> 7.2	<i>frigidus</i> 25.4	<i>humeralis</i> 20.16
<i>bendermani</i> 19.9	<i>darlingtoni</i> 17.8a	<i>fulleri</i> 20.8	<i>hypertrichosis</i> 1.5
<i>blatchleyi</i> 11.2	<i>deceptivus</i> 20.2	<i>furtivus</i> 8.2	<i>hypolithos</i> 25.1
<i>bloomi</i> 11.1	<i>delicatus</i> 22.2	<i>fuscus</i> 1.3a	<i>illinoisensis</i> 11.4
<i>boonensis</i> 11.6b	<i>desertus</i> 7.7	<i>garmani</i> 7.1	<i>inexpectatus</i> 6.1
<i>brevis</i> 20.16	<i>digitus</i> 22.5	<i>georgiae</i> 26.2	<i>inquisitor</i> 19.10
<i>calcareus</i> 25.3	<i>distinguens</i> 20.19	<i>globiceps</i> 17.5	<i>insularis</i> 19.5

<i>intermedius</i> 15.1	<i>montanus</i> 1.9	<i>productus</i> 19.2	<i>steevesi</i> 20.12
<i>intersectus</i> 2.5	<i>morrisoni</i> 11.2	<i>profundus</i> 20.14	<i>striatus</i> 17.7
<i>interstitialis</i> 17.7	<i>neglectus</i> 14.1	<i>prætermisus</i> 25.5	<i>stricticollis</i> 11.2
<i>intrepidus</i> 16.1b	<i>nelsoni</i> 4.2	<i>pubescens</i> 16.1a	<i>subæqualis</i> 1.3a
<i>jeanneli</i> 11.2	<i>nickajackensis</i> 20.10	<i>punctatus</i> 4.4	<i>sylvaticus</i> 1.4
<i>jonesi</i> 24.1	<i>nortoni</i> 20.7	<i>pusillus</i> 21.2	<i>templetoni</i> 15.2
<i>krameri</i> 7.11	<i>occidentalis</i> 19.6	<i>pusio</i> 4.1	<i>tenebrosus</i> 7.6
<i>krekeleri</i> 1.8	<i>ohioensis</i> 7.10	<i>puteanus</i> 6.3	<i>tenesensis</i> 21.1
<i>lallermanti</i> 4.5	<i>orientalis</i> 6.2	<i>quadratus</i> 23.4	<i>tennesseensis</i> 21.1
<i>leonae</i> 12.1	<i>orlindae</i> 16.3b	<i>rittmani</i> 8.1	<i>tenuis</i> 11.1
<i>limicola</i> 2.2	<i>orthosulcatus</i> 1.2	<i>robustus</i> 14.1	<i>thomasi</i> 24.7
<i>lodingi</i> 20.13	<i>packardi</i> 9.3	<i>rogersae</i> 24.3	<i>tiresias</i> 19.3
<i>loedingi</i> 20.13	<i>pallidus</i> 24.5	<i>rotundatus</i> 20.4	<i>transfluvialis</i> 17.3
<i>loganensis</i> 16.4	<i>paradoxus</i> 23.6	<i>sanctipauli</i> 23.2	<i>troglydites</i> 10.2
<i>longiceps</i> 24.6	<i>parvicollis</i> 2.3	<i>scholasticus</i> 25.2	<i>tullahoma</i> 19.8
<i>longicollis</i> 11.1	<i>parvus</i> 6.5	<i>scutilus</i> 24.2	<i>umbratilis</i> 6.6
<i>lupus</i> 14.3	<i>paulus</i> 22.4	<i>seclusus</i> 24.4	<i>unionis</i> 21.4
<i>macradei</i> 15.4	<i>paynei</i> 21.3	<i>senecae</i> 2.7	<i>valentinei</i> 14.4
<i>macradyi</i> 15.4	<i>persimilis</i> 17.8b	<i>sequoyah</i> 20.11	<i>vanburenensis</i> 15.3
<i>major</i> 7.8	<i>petrunkevitchi</i> 3.1	<i>sericus</i> 22.3	<i>ventricosus</i> 17.1a
<i>mayfieldensis</i> 11.6b	<i>pholeter</i> 7.12	<i>shilohensis</i> 11.6a	<i>ventus</i> 22.6
<i>megosteus</i> 14.1	<i>pilosus</i> 17.4	<i>sidus</i> 20.5	<i>vicarius</i> 23.5
<i>menetriesi</i> 17.1a	<i>pontis</i> 4.3	<i>simplex</i> 18.1	<i>virginicus</i> 1.7
<i>meridionalis</i> 20.17	<i>potomaca</i> 2.6	<i>simulans</i> 17.2	<i>wallacei</i> 20.3
<i>minor</i> 7.1	<i>princeps</i> 16.2	<i>solivagus</i> 7.4	<i>youngi</i> 11.5