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Author(s): Thomas C. Barr, Jr.

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THE ROBUSTUS GROUP IN THE GENUS
PSEUDANOPHTHALMUS (COLEOPTERA: CARABIDAE:
TRECHINI)¹

By THOMAS C. BARR, JR.²

The blind carabid beetles of the cavernicole genus *Pseudanopthalmus* Jeannel are wingless, rufous or testaceous, usually pubescent, and for the most part completely eyeless. Like most carabids, they are predatory, feeding on small millipedes, enchytraeid annelids, and other cave animals. Like most representatives of the tribe Trechini, to which they belong, they are found in cool, moist microhabitats. In the caves, therefore, they are most often encountered in wet or humid areas near a source of food.

A feature of special biological interest is the pronounced local endemism exhibited by the genus, each cave region having its own peculiar assemblage of species. In a recent checklist of troglobites of the United States, Nicholas (1960) listed 82 described species and subspecies of *Pseudanopthalmus*. This number will be greatly increased as many additional species already collected from the extensive cave regions of the eastern United States are described. Although poorly represented in most museum and private collections because its species are known only from caves, *Pseudanopthalmus* is quite probably the fifth largest genus of Carabidae in the United States, exceeded in number of species only by *Bembidion*, *Pterostichus*, *Agonum*, and *Harpalus*. It is far more homogeneous and geographically less widely distributed than any of these four epigeal genera.

The genus was reviewed by Jeannel (1949), but additional contributions have been made by Krekeler (1958) and Barr (1959a, 1959b, 1960a). An excellent review of problems of dispersal of these beetles was written by Krekeler (1959). Populations from different cave systems in a given region are often distinguished only by slight but constant differences. Even if it were possible to interbreed two such slightly different populations in the laboratory (breeding experiments of this nature have not yet been performed), one would not be justified in assuming that interbreeding occurs in nature, and that the two populations contribute to the same gene pool. Several factors have combined to necessitate an undesirable degree of subjectivity in assigning specific or subspecific rank to different populations from various cave systems. The principal difficulties are rarity of certain species, problems associated with subterranean collecting, and concomitantly, inadequately known range of variation and geographic range. The potential contribution of cavernicole taxonomy to the broader and more general problem of animal speciation is, however, great, and it should be well worth the effort to seek a more objective basis for defining and recognizing a cavernicole species.

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² Department of Zoology, University of Kentucky, Lexington.

Emerson (1945) suggested that the subspecies of *Pseudanophthalmus* described by Valentine (1932) are full species because of the "indicated reproductive isolation." However, it is often not possible to know in advance whether closely similar populations from two different caves in the same region are reproductively isolated or not (Barr 1959a, 1960a, 1960b). The beetles are probably capable of ranging rather widely through subterranean openings inaccessible to man. There is ample geological evidence that such openings are abundant and extensive in limestone terrains, especially in stream valleys (Barr 1961a). Just as an oil pool may be tapped by various wells at different locations, so may the species population of a widely dispersed cavernicole be sampled throughout its geographic range. The sampling localities are the individual, accessible caves.

As with epigeal populations, extensive distributional data and large series of specimens would be most useful in clarifying some of the problems of cavernicole taxonomy. Some species of *Pseudanophthalmus* are either so rare or so difficult to obtain that it is not feasible to acquire large series from numerous caves. But certain species groups inhabiting karst regions with hundreds of known caves are characteristically rather abundant. A detailed analysis of one or more of these groups should provide evidence of possible application to the less common groups. Such an analysis has been attempted in the present paper.

The *robustus* species group of *Pseudanophthalmus*, as defined below, is distributed (Fig. 5) throughout much of the upper Cumberland River drainage in Tennessee and a small part of Kentucky. It inhabits cave systems in the valleys of the Wolf, Obey, Roaring, and Caney Fork rivers, all east tributaries of the Cumberland. Physiographically, the range of the group includes the western margin of the Cumberland plateau, the undulating surface of the Eastern Highland Rim, and a small portion of the east margin of the Central Basin of Tennessee. In this paper, four species are recognized. Conclusions are based on examination of approximately 1500 specimens from 75 different caves in 9 Tennessee counties and 2 Kentucky counties.

The material examined in the present study was collected between 1956 and 1961. Male genitalia were cleared and mounted in polyvinyl-lactophenol by the method I have described previously (Barr 1961b).

Jeannel (1949) included *P. horni* (Garman 1892), *P. macradei* Valentine 1948, *P. intermedius* Valentine 1931, and *P. templetoni* Valentine 1948 in his "groupe *robustus*." *P. horni* and its relatives, found in central Kentucky and northward, are morphologically and geographically distinct (Krekeler 1959) and are more naturally included in the *horni* species group. Valentine (1952: page 15) proposed the subgeneric category *Tennessarius* for the large, slender, glabrous species *intermedius* and *templetoni*, although the proposal was not treated in detail and a type species (presumably *intermedius*) was not designated. In 1959 I followed Jeannel and placed *robustus*, *macradei*, and *templetoni* together in the "*robustus* group." Further study and collection of much additional material have convinced me that *intermedius*, *templetoni*, *macradei*, and *vanburenensis* Barr 1959 are sufficiently distinct to merit inclusion in an *intermedius*

group (new group), but not different enough from other members of *Pseudanophthalmus* to warrant setting them apart as a subgenus. *P. macradei* and *P. vanburenensis* (see below) bridge the gap between *intermedius* and *templetoni* and the other members of the genus. These four species, plus other undescribed species of the *intermedius* group from Kentucky, Alabama, and Tennessee, will be treated in detail in a later paper. *Tenessarius* Valentine is here regarded as a synonym of *Pseudanophthalmus* Jeannel.

Pseudanophthalmus vanburenensis Barr [NEW STATUS]

Pseudanophthalmus templetoni vanburenensis Barr 1959a: page 15; type: McElroy Cave, Van Buren Co., Tennessee (American Mus. Nat. Hist., New York).

Since writing the original description of *P. vanburenensis*, I have taken additional material both of this species and of *P. templetoni*, and am convinced that the two forms are distinct species. From both *intermedius* and *templetoni*, *P. vanburenensis* differs in the proportionately more robust form, the rounded (not deplanate) humeri, the less obliquely inclined prehumeral borders, and the enlarged, boot-shaped apex of the aedeagus. These same characters and the larger size serve to distinguish it from *P. macradei*.

ROBUSTUS GROUP

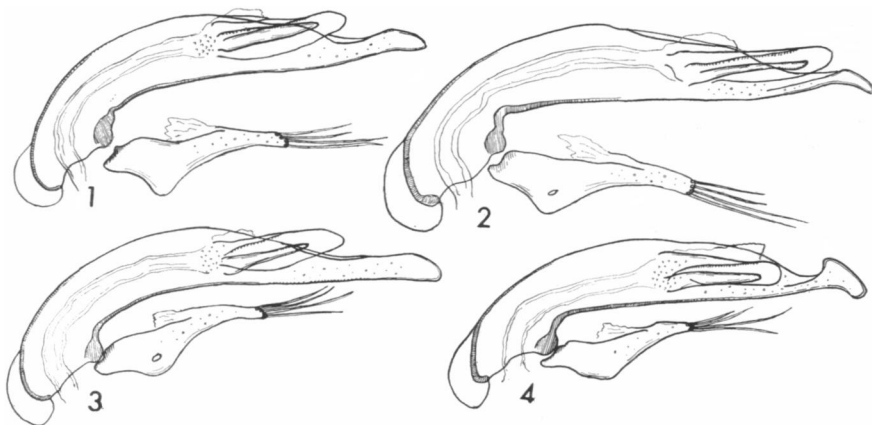
Length 3.8-5.6 mm. Pronotum glabrous; elytra with sparse, very short pubescence when observed with oblique illumination. Labrum doubly emarginate, median lobe usually rather low. Pronotum transverse, usually 15-20% wider than long; margins feebly sinuate; hind angles large and right. Elytra oblong-elliptical; humeri angulate and serrulate, prehumeral borders nearly perpendicular to median line; longitudinal striae deep, conspicuously punctate (except in *valentinei*); apical groove short and rounded, its recurrent portion connected with 3rd longitudinal stria (or rarely 5th in *farrelli*) at level of apical discal seta; anterior discal seta behind level of 4th marginal humeral seta. Aedeagus elongate, rather slender; apex variously modified into a blunt, deflexed spout or a knob; transfer apparatus of two pieces, the left a slender, hollow rod nested in the broad, curved lamina of the right piece; internal sac feebly armed with small scales; parameres with 4 setae. Type species: *P. robustus* Valentine 1931.

The affinities of the *robustus* group lie with the *menetriesi* and *eremita* (sensu Barr 1960a) groups on the one hand, and with members of the *intermedius* group on the other. All four species groups are closely linked by the form of the copulatory apparatus, which consists of a large, lamellar, medially concave right piece, within which is nested a smaller, rod-like left piece; both copulatory pieces are simple, unmodified, and have blunt, rounded apices.

In listing caves from which members of the *robustus* group are known, I have made use of the county numbers assigned in *Caves of Tennessee* (Barr 1961a). By referring to this book, the reader can find the exact location and a brief description of each cave. Unnumbered caves are not described in the book. The location of holotypes is given in parentheses after citation of the original description.

KEY TO SPECIES OF THE ROBUSTUS GROUP (MALES ONLY)

1. Apex of aedeagus boot-shaped (Fig. 4); longitudinal striae of elytra very feeble, punctuation obsolete; Putnam and Overton Counties, Tennessee-----**P. VALENTINEI** Jeannel
Apex of aedeagus produced but not boot-shaped; longitudinal striae well defined, usually strongly punctate ----- 2
- 2(1). Apex of aedeagus not deflexed (Fig. 3); Overton, Pickett, and Fentress Counties, Tennessee, to Clinton and Wayne Counties, Kentucky-----**P. BEAKLEI** Valentine
Apex of aedeagus narrower in lateral view, slightly but clearly deflexed ----- 3
- 3(2). Aedeagus smaller (0.88-1.02 mm), more slender, apex thicker in lateral view; (Fig. 1); central Overton to northern Grundy County, Tennessee--**P. ROBUSTUS** Valentine
Aedeagus larger (1.01-1.12 mm), apex narrower in lateral view (Fig. 2); caves of Smith Fork drainage, DeKalb and Smith Counties, Tennessee-----**P. FARRELLI** Barr



FIGURES 1-4. Aedeagi of *Pseudanopthalmus* of the *robustus* group. 1—*P. robustus* Val., Dairyhouse Cave, White Co., Tenn. 2—*P. farrelli* Barr, Indian Grave Point Cave, DeKalb Co., Tenn. 3—*P. beaklei* Val., Sells Cave, Fentress Co., Tenn. 4—*P. valentinei* Jeannel, Blind Fish Cave, Putnam Co., Tenn.

Pseudanopthalmus robustus Valentine

FIG. 1

Pseudanopthalmus robustus Valentine 1931: page 250, pl. 20, Fig. 2; type: Johnson Cave, Putnam Co., Tennessee (U. S. Nat. Mus.). Valentine 1932: 274, pl. 23, Fig. 1. Jeannel 1949: page 49, Figs. 28, 31. Barr 1959a: page 10.

Pseudanopthalmus robustus neglectus Jeannel 1949: page 50, Fig. 33; type: Cumberland Caverns, Warren Co., Tennessee (Mus. Nat. Hist. Nat., Paris). Barr 1959a: page 12. [NEW SYNONYMY].

Pseudanopthalmus robustus megosteus Barr 1959a: page 12, Fig. 4(2); type: Big Bone Cave, Van Buren Co., Tennessee (American Mus. Nat. Hist., New York). [NEW SYNONYMY].

The type species of the group is also the most widely distributed, ranging along the Eastern Highland Rim, between the western margin of the Cumberland plateau and the eastern margin of the Central Basin in an area

some 65 miles long and 6 to 25 miles wide. The northern limit is in central Overton County about 3 miles southwest of Livingston and the southern limit is in northern Grundy County near Viola. From the distribution map (Fig. 5) it may be seen that the Overton County populations are apparently isolated from the populations in the rest of the range, the intervening caves being inhabited by *P. valentinei* (drainage basin of Spring Creek, a tributary of Roaring River).

In various parts of its range, *P. robustus* is sympatric with *P. valentinei*, *P. macradei*, *P. templetoni*, *P. vanburenensis*, and *Nelsonites walteri* Val. In no known localities is it sympatric with its closest relatives, *P. beaklei* or *P. farrelli*. From *P. farrelli*, *P. robustus* is separated by the Caney Fork River, although there is no reason to suppose that the river constitutes a physical barrier to dispersal. *P. beaklei* approaches within 4 miles of the northernmost limit of the range of *P. robustus*, but no clinal variations indicating potential intergradation in the inaccessible, intermediate, subterranean areas have been detected.

P. robustus was collected from the following caves: TENNESSEE. *Overton County*: Carr Saltpeter, 2 Bear, 8 Crawford, 14 Mill, 22 Russell. *Putnam County*: 1 Ament, 5 Blind Fish, 8 Bridge Creek, 9 Buckner Sink, 10 Calkiller Saltpeter, 18 Johnson (type loc.), 19 Kuykendall, Mine Lick Creek, 35 Wall. *DeKalb County*: 7 Clemons. *White County*: 1 Baker, 2 Blue Spring, 7 Haskell Sims, 8 Indian, 9 Lost Creek, 11 Moore, 12 Mott Cove, 15 Pollard Saltpeter, 17 Quebeck, 19 Rockhouse, 22 Selby, 23 Sparkman, 24 Stonehead, 25 Walling, 26 Ward. *Van Buren County*: 1 Big Bone, 10 McElroy, 12 Rice. *Warren County*: 2 Blowing, 3 Cumberland, 4 Grissom Quarry, 6 Hobbs, 8 John Green, 19 Solomon Saltpeter. *Grundy County*: 5 Boyd Hollow, 9 Dry, 19 Skull, 20 Tom Campbell, 22 Wanamaker.

Pseudanophthalmus farrelli Barr [NEW STATUS]

FIG. 2

Pseudanophthalmus robustus farrelli Barr 1959a: page 12, Fig. 4(3); type: Indian Grave Point Cave, DeKalb Co., Tennessee (American Mus. Nat. Hist., New York).

The range of this species is limited to caves in the valley of Smith Fork (a tributary of Caney Fork River, which flows into the Cumberland), on the west (left) side of the Caney Fork in Smith and DeKalb counties, Tennessee. All of the caves are developed in Ordovician limestones of the Nashville group at Central Basin level. At the type locality, *P. farrelli* is sympatric with *Pseudanophthalmus tiresias* Barr.

P. farrelli was collected from the following caves: TENNESSEE. *DeKalb County*: 1 Avant, 9 Cripps Mill, 12 Fox, 17 Hall, 19 Indian Grave Point (type loc.), 20 Jim, 25 Snow Hill. *Smith County*: 4 John Fisher.

Pseudanophthalmus beaklei Valentine [NEW STATUS]

FIG. 3

Pseudanophthalmus robustus beaklei Valentine 1937: page 97, pl. 8, Fig. 3; type: Bunkum Cave, Pickett Co., Tennessee (U. S. Nat. Mus.).

Pseudanophthalmus robustus subsp. *Beakleyi*: Jeannel 1949: page 51, Fig. 32 (emendation).

Pseudanophthalmus robustus lupus Barr 1959a: page 14, Fig. 4(4); type: Wolf River Cave, Fentress Co., Tennessee (American Mus. Nat. Hist., New York) [NEW SYNONYMY].

North of Livingston, Overton County, Tennessee, *P. beaklei* replaces *P. robustus* as the dominant *Pseudanophthalmus* in the caves along the western margin of the Cumberland plateau. Its range extends northeastward through Pickett and Fentress Counties, Tennessee, into adjacent portions of Clinton and Wayne Counties, Kentucky. It is sympatric in various caves with *P. valentinei*, *Nelsonites jonesei* Val., *Darlingtonia kentuckensis* Val., and with 3 other, undescribed species of *Pseudanophthalmus* (belonging to the *intermedius* and *menetriesi* groups).

P. beaklei was collected from the following caves: TENNESSEE. *Overton County*: 6 Coleman, 10 Falling Springs, 17 Parrott, 27 Wash Lee. *Pickett County*: 3 Bunkum (type loc.), 6 Massengill, 8 Pratt. *Fentress County*: 2 Copley Saltpeter, 4 Gwinn Cove, 5 Manson Saltpeter, 10 Sells, 12 Tater, 13 Wolf River. KENTUCKY. *Clinton County*: Copperas Saltpeter Cave, 1.4 mi. south of Savage, in the Port-au-Grace Community. *Wayne County*: Blowing Cave, 0.75 mi. southeast of Sunnybrook, at the head of Carpenter Fork; Wind Cave, 3.5 mi. south-southwest of Slickford, at the base of Horse Pound Ridge.

Pseudanophthalmus valentinei Jeannel

FIG. 4

Pseudanophthalmus Valentinei Jeannel 1949: page 51, Figs. 24, 29; type: Johnson Cave, Putnam Co., Tennessee (Mus. Nat. Hist. Nat., Paris).

P. valentinei occupies certain caves of the Eastern Highland Rim near the western base of the Cumberland plateau in Putnam and Overton Counties, Tennessee. It is sympatric with both *P. robustus* and *P. beaklei*, as well as with *Nelsonites walteri* and at least one undescribed species of *Pseudanophthalmus* (*intermedius* group). In the middle portion of its range (fig. 5) it appears to occupy exclusively the caves of the Spring Creek drainage north of Cookeville, separating the northernmost colonies of *P. robustus* from populations in the rest of the range of that species.

P. valentinei was collected from the following caves: TENNESSEE. *Putnam County*: Algood School, 5 Blind Fish, 18 Johnson (type loc.), Webb. *Overton County*: 3 Bilbrey, 7 Copeland Saltpeter, 10 Falling Springs, 11 Fancher (both cave and pits), 16 Obe Lee, 25 Swift, 27 Wash Lee.

DISCUSSION

The taxonomic picture revealed by examination of the wealth of material available in this group is one of three closely similar, allopatric forms, and one markedly dissimilar form (*P. valentinei*) which is sympatric with two of the others. In all probability, *robustus*, *farrelli*, and *beaklei* are comparatively recent descendants from a common ancestor. It is conceivable that one might wish to emphasize this recency of descent by

treating them as a polytypic species, as has been done in the past. I prefer to regard them as full species for the following reasons: (1) The three do not interbreed in nature. Although it is possible that they might interbreed in the laboratory (and such desirable data are not yet available), the distributional data indicate that they do not do so in their natural habitats. (2) There is no evidence of clinal variation toward the limits of the ranges, which might be expected if intergradation occurred.

In arriving at this interpretation, I have been influenced by the arguments of Krekeler (1958, 1959) on the practicability of extrinsically determined isolation of species populations, but believe that the degree of isolation of a population in any given cave system is not determinable *a priori*. In extensive karst areas underlain by predominantly horizontal limestone strata, the geographic limits of a cavernicole species are probably decided by selective factors, not by the physical inability of the species to penetrate beyond the area in which it occurs. *P. valentinei* is quite rare in the Calfkiller Valley, at the southernmost limit of its range. *P. robustus* becomes relatively uncommon near the southern limit of its range, where it is sympatric with *P. macraderi* (*intermedius* group), a species of similar size and apparently similar ecological preferences. *P. macraderi* is very abundant where *P. robustus* is rare, but itself is extremely rare in the Calfkiller Valley. There is apparently no extrinsic deterrent to prevent dispersal of *P. robustus* and *P. macraderi* within the limits of their respective ranges, but, if abundance is any index of adaptation to a particular set of environmental circumstances, the two species are responsive to different selection pressure complements.

One might suppose that *P. robustus* would be extrinsically isolated from *P. farrelli* by stratigraphic barriers. The bulk of the caves inhabited by *robustus* are developed in the Mississippian limestones of the Chester and Meramac series. Between the Meramac rocks and the Ordovician limestones of the Nashville group in which the *P. farrelli* caves are developed there is an unbroken sequence of Osage rocks (predominantly Fort Payne chert) and the Chattanooga shale. The Fort Payne and the Chattanooga apparently do not prevent dispersal of *P. robustus* across the entire Eastern Highland Rim to Central Basin level, where it has been taken in caves along Mine Lick Creek, in western Putnam County, and in a cave near Caney Fork River, in a nearby portion of DeKalb County.

It is believed that the ranges of the four species and of the group as a whole are rather accurately delineated. The *robustus* group is replaced (geographically though not necessarily ecologically) by the *engelhardti* group (*P. tiresias* and relatives) of *Pseudanophthalmus* to the west and south; by the *cumberlandus* and *menetriesi* groups to the northwest; and by *Ameroduvallius jeanneli* Valentine to the northeast. The *intermedius* group occurs in the same area as the *robustus* group but extends farther northeast and southwest along the western base of the Cumberland plateau, although it does not extend out into the Mississippian plateau or into the Central Basin.

The present interpretation of *P. robustus*, *P. farrelli*, and *P. beaklei* as full, strictly allopatric species raises questions about the status of the various "subspecies" of such wide-ranging polytypes as *P. loedingi* Valen-

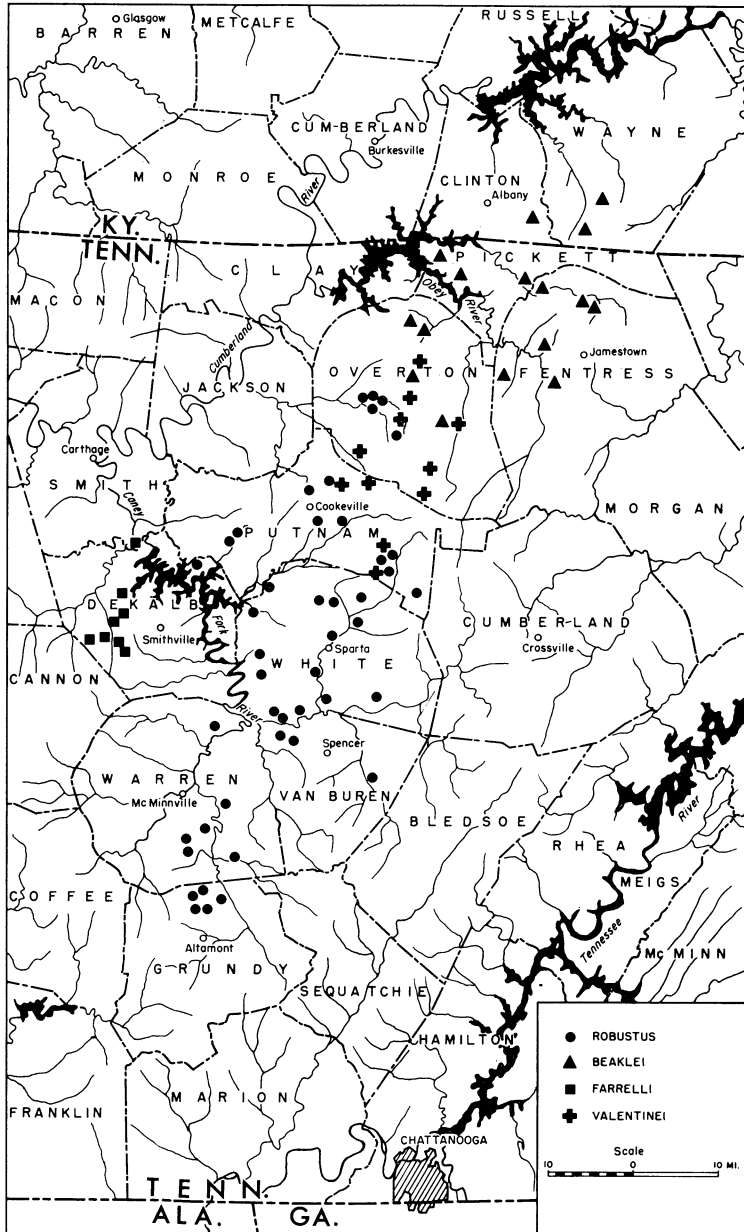


FIGURE 5. Geographic distribution of the *robustus* group of *Pseudanophthalmus* (drafted by R. Potts).

tine (emendation of *P. lödingi* Valentine 1931: page 252; *P. lödingi* of authors), *P. tirsias* Barr, and *P. tenuis* (Horn). Each of these polytypes requires reexamination and reevaluation, especially if larger series and better distributional data can be obtained. I made a partial attempt to do this for *P. tenuis* (Barr 1960a) and still believe that *P. eremita longicollis* Jeannel and *P. bloomi* Krekeler are synonyms of *P. tenuis*. Many more caves must be sampled before the status of the other supposed subspecies of this polytype can be clarified.

The geographic range of the *robustus* group (and to a lesser extent, of the *intermedius* group) coincides rather closely with the known range of *Trechus* (*T.*) *cumberlandus* Barr 1962, distributed along the Cumberland plateau from Grundy County, Tennessee, to Wayne County, Kentucky. *T. cumberlandus* is a member of the *carolinae* group, allied to *T. schwarzi* Jeannel. The *carolinae* group (Barr 1962) has four known species, three of which occur in the mountains of western North Carolina (Mt. Mitchell and vicinity). The fourth species, *T. cumberlandus*, is known from caves, sinkholes, and from gravelly areas near cold springs.

Jeannel (1949) suggested that the epigeal ancestors of *Pseudanophthalmus* may have lived in the southern Appalachians during the Pleistocene, spreading outward into the Appalachian valley and Interior Low Plateaus in periods of glacial advance and retreating into caves or becoming extinct at the surface during the warmer, drier, interglacial periods. At the present time the only living surface Trechini in the eastern United States belong the genus *Trechus* (and to *Lasiotrechus*, introduced in the northeast), most of the species of which inhabit the southern Appalachians. A few wide-ranging species of *Trechus* are found in the extreme northern United States and Canada. We can only conjecture about the geographic distribution of ancestral *Pseudanophthalmus*, but in all probability the Appalachians served then, as now, as a center of trechine dispersal and speciation. The present distribution of the *carolinae* group demonstrates that at least one group of trechines centered in the Appalachians has been able to colonize wet, cool microhabitats along the western front of the Cumberland plateau. In view of the close morphological similarity of *T. cumberlandus* to *T. schwarzi*, this colonization must have been a comparatively recent event. Perhaps it took place during Wisconsin time, when a common ancestor of the two species ranged freely across the Cumberland plateau, becoming restricted to cool, moist areas as the Wisconsin ice sheet retreated northward. Such an event is possibly a pattern of trechine dispersal in the eastern United States. The epigeal, ancestral species of *Pseudanophthalmus* which gave rise to *P. robustus*, *P. beaklei*, and *P. farrelli* could have colonized cave systems along the edge of the Cumberland plateau in a similar manner. It is suggested that the colonization of the plateau by the *carolinae* group may be repeating the pattern of similar colonization by the *robustus* group and possibly also the *intermedius* group during the Pleistocene.

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BOOK REVIEW

A HANDBOOK OF BIOLOGICAL ILLUSTRATION, by Frances W. Zweitel, Phoenix Science Series, The University of Chicago Press. Price \$1.95.

This handbook is a welcome guide to "the biologist who is not an artist and the artist who is not a biologist." It is intended for the guidance of the student or professional biologist who is unfamiliar with the materials and techniques of illustrating and who may find it necessary to prepare his own illustrations for classroom assignments or scientific publications. The text is well written and clearly illustrated. The author discusses printing processes, size and preparation of graphs and maps, lettering, illustrations from photographs, mounting and handling illustrations. Each chapter has a list of selected references for those who wish to delve deeper into the subject. Every biologist who expects to publish and illustrate his publication will find this handbook a worthwhile investment.—Eugene J. Gerberg, Insect Control & Research, Inc., Baltimore 28, Maryland.