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New Species Groups of *Pseudanophthalmus* from the Central Basin of Tennessee (Coleoptera: Carabidae: Trechinae)

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ABSTRACT.—Two new species groups of *Pseudanophthalmus* are proposed. The *simplex* group includes *P. simplex* n. sp. and *P. fowlerae* n. sp. The *cumberlandus* group includes *P. cumberlandus* Valentine, *P. productus* n. sp., and *P. inquisitor* n. sp.; the following are full species and also belong to the *cumberlandus* group: *tiresias, catherinae, insularis, occidentalis, acherontis, tullahoma,* and *bendermani.* All species discussed occupy caves in the Central Basin of Tennessee.

Cave carabids of the very large genus *Pseudanophthalmus* Jeannel (about 200 species) have traditionally been arranged in "species groups" — neutral categories of supposedly monophyletic species assemblages which are of lower rank than subgenera. The comparative homogeneity of the genus does not readily permit division into clearly distinguishable subgenera, but within certain limits there is substantial diversity at the species group level. In preparing a new classification of *Pseudanophthalmus* I was unable to assign two undescribed species from Jackson and Clay counties, in the upper Cumberland River basin, Tennessee, to an existing group. These species are described in the present paper and placed in the new *simplex* group. Two other species with which they are sympatric are close to *P. cumberlandus* Valentine, which I have made the type species of a widely distributed new group, the *cumberlandus* group. This group, occurring throughout the Central Basin of Tennessee and with species in southwestern and southeastern Kentucky, the western Tennessee River valley in Tennessee, and one county in north Alabama, is the largest species group in the genus, including about 30 species.

simplex group (new group)

Size medium (4.0-5.1 mm); robust, depressed; moderately pubescent to nearly glabrous; elytral microsculpture a fine, transverse meshwork, with hint of pruinosity in one species. Pronotum transverse, hind angles right or nearly right. Labrum doubly emarginate. Anterior discal puncture at level of 4th umbilicate; apical groove subparallel or slightly oblique to suture, connected obliquely to 3rd stria in advance of anterior apical puncture, or running to this puncture via prominent crosier; humeri finely serrulate. Mentum tooth broad, emarginate. Mesosternum

declivous. Last abdominal sternite of males with apical margin entire. Aedeagus scarcely arcuate, basal bulb not conspicuously enlarged nor deflexed, apex gradually attenuate and bluntly rounded at tip, only feebly produced; transfer apparatus with rather heavily sclerotized right piece, medially concave, apex knobbed or not, and broadly triangular, membranous, spiny left piece with apex spatulate and twisted 90°, or right piece as described and left piece absent; parameres moderately slender, bearing 4 long setae at their apexes. Type species: *P. simplex*, new species.

Discussion.—This group consists of only two known species that occur in caves of Jackson and Clay counties, Tennessee, at the northeast edge of the Central Basin, in Ordovician limestones of the upper Cumberland River drainage, on the south (left) side of the river. The somewhat isolated troglobitic crayfish species *Orconectes incomptus* (Hobbs and Barr 1972) also occurs in caves of this region.

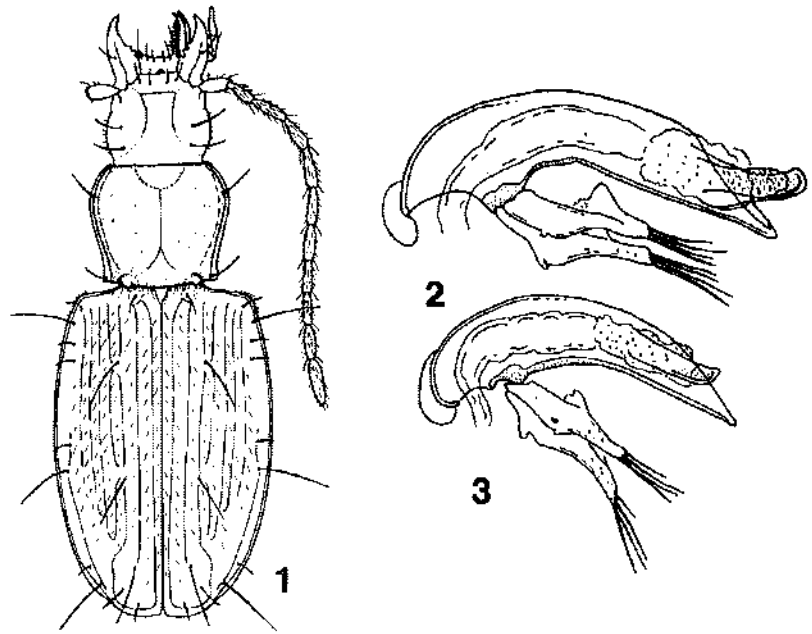
The form of the copulatory sclerites and the serrulate humeri suggest a close relationship with the *pubescens* group (see Barr 1979); very faint pruinose microsculpture on the elytra of one species is additional evidence favoring this view. Different features, however, require the establishment of a distinct group: depressed, robust form; more posterior position of the anterior discal puncture (pleomorphic); reduced pubescense and reduced pruinose microsculpture (probably apomorphic); and the general form of the aedeagus. The transfer apparatus in *simplex* itself is similar in basic pattern to that of the *pubescens* group.

One can speculate that the *simplex* group may be a link between the *pubescens* and *menetriesi* groups on the one hand and the numerous, small to medium species of the *cumberlandus* group on the other. In the *cumberlandus* group there is a single copulatory piece, presumably the left one; its simple structure, together with the apparent loss of the right piece, deprive the phylogenist of a key character in inferring relationships of the group to other *Pseudanophthalmus* species groups. The left copulatory piece in *simplex* is close enough to the *cumberlandus* transfer apparatus that a relationship is at least feasible. Habitus and geographic distribution of the *simplex* group, although weaker evidence supporting a relationship to the *cumberlandus* group, are at least consonant with an hypothesis that the two groups are phylogenetically close.

Pseudanophthalmus simplex, new species
Figs. 1, 2

Etymology.—Latin *simplex*, "simple."

Diagnosis.—With the characters of the group as defined above; two copulatory pieces present; elytral striae deeper, impunctate; elytral microsculpture with a few pruinose patches near center of disc, which is moderately pubescent; apical groove longer.



Figs. 1-3. *Pseudanophthalmus simplex* group. 1. *P. simplex*, n. sp. (4.6 mm). 2. Aedeagus, *P. simplex* n. sp. (0.86 mm). 3. Aedeagus, *P. fowlerae*, n. sp. (0.68 mm).

Description.—Length 4.2-5.1, mean 4.6 mm. Form robust and depressed; elytral microsculpture finely transverse, forming meshes, with trace of pruinose microsculpture near middle of disc, scarcely discernible (50X). Head rounded, as wide as long; labrum distinctly trilobed. Pronotum transverse, 0.8 as long as wide, disc feebly convex and very sparsely pubescent; sides strongly arcuate in apical 0.8, subparallel in basal 0.2; front angles rounded, apex about 0.85 maximum width, which occurs at apical 0.20-0.22, base width nearly equal to maximum width, hind angles large and more or less right or slightly acute, depending on development of lateral emargination of base and secondary angles, which are variably developed but always present in some form. Elytra more than 1.5 times as long as wide, depressed, moderately pubescent; humeri angular, somewhat obsoletely serrulate, prehumeral border not quite perpendicular to midline; inner 4 longitudinal striae moderately impressed, intervals convex, outer striae obsolete; apical groove subparallel or slightly oblique to suture, running to third stria in advance of anterior apical puncture or running to anterior apical puncture via prominent crosier. Aedeagus 0.78-0.89, mean 0.83 mm long; feebly arcuate, basal bulb not appreciably expanded and not deflexed, apex gradually attenuate, scarcely produced, rounded at tip; right copulatory piece a more or

less hyaline hemisheath, its apex a bluntly rounded knob, left piece a little shorter, broadly triangular, densely but minutely spiny, with apex twisted 90° to right and thus appearing as narrow, nipplelike or broadly spatulate, depending on orientation; parameres rather slender, with 4 apical setae.

Type series.—Holotype male (American Museum of Natural History) and one female paratype, Carter Cave, 5.5 km ssw of Flynns Lick, Jackson Co., Tennessee, 23 October 1960, T. C. Barr. Two additional paratypes from same cave, 9 June 1955 and 20 July 1957, T. C. Barr. Three paratypes from Hailes Cave, 0.5 km n of Flynns Licks, 6 May 1959, T. C. Barr, and 19 October 1948, J. M. Valentine and W. B. Jones. (See Barr 1961 for detailed locations and descriptions of these and other caves mentioned in this paper.)

Measurements (in mm).—Holotype male, total length 4.60, head 0.80 long X 0.80 wide, pronotum 0.90 long X 1.10 wide, elytra 2.66 long X 1.72 wide, antenna 3.06, aedeagus 0.86 long.

Distribution.—The material seen of this species includes the type series of 7 specimens and one specimen (not a paratype) from Cherry Cave, northeast Jackson County, Tennessee. The three caves from which the species is known are located at the northeast edge of the Central Basin in the upper Cumberland River drainage; all of the caves are on the south (left) side of Cumberland River.

Discussion.—In Carter Cave the species occurs sympatrically and syntopically with a more abundant species, *P. productus*, of the *cumberlandus* group, under rocks and on silt banks by the cave stream. Females and undissected males can be distinguished by the more robust and more depressed form and by the deeper elytral striation. The aedeagus of *simplex* has a shorter and less produced apex than that of *productus*, and the transfer apparatus consists of two prominent sclerites instead of the small, single, very slender sclerite characteristic of the *cumberlandus* group.

Pseudanophthalmus fowlerae, new species
Fig. 3

Etymology.—Patronymic honoring Mrs. Otia Fowler, owner of the type locality cave.

Diagnosis.—Differs from *simplex* in shallow, irregularly punctate elytral striae, glabrous and non-pruinose elytral disc, microsculpture with denser, transverse meshes; apical groove a little shorter; left copulatory piece absent.

Description.—Length 4.0-4.6, mean 4.3 mm. Form as in *simplex* but paler, slightly more depressed, virtually glabrous, elytral disc highly polished, transverse meshworks of microsculpture denser, and no trace of pruinose microsculpture. Head slightly transverse, labrum doubly emarginate. Pronotum as in *simplex*. Elytra with longitudinal striae more shallowly impressed, feebly punctulate, inner 3 striae regular, fourth stria irregular, outer striae obsolete. Aedeagus 0.66-0.70, mean 0.68 mm, of same form as that of *simplex* but a little smaller and apex even less produced; transfer apparatus a single sclerite, apparently homologous to right piece of *simplex*: large, rather heavily sclerotized, margins parallel, concave to left, apex bluntly rounded but scarcely knobbed.

Type series.—Holotype male (American Museum of Natural History) and 4 paratypes, Sheals Cave, 0.8 km e of Celina, Clay Co., Tennessee, 3 December 1960, T. C. Barr. Six additional paratypes, Sheals Cave, 28 February 1959, 7 April 1960, and 11 August 1965, T. C. Barr and J. R. Holsinger.

Measurements (in mm).—Holotype, total length 4.04, head 0.70 long X 0.74 wide, pronotum 0.76 long X 0.90 wide, elytra 2.20 long X 1.48 wide, antenna 2.80, aedeagus 0.68.

Distribution.—Known only from the type locality cave, from which 11 specimens are available.

Discussion: Two beetles collected in August, 1965, are late tenerals, suggesting midsummer eclosion. Most of the specimens were taken under rocks in a depression in the floor of the entrance room, well within the twilight zone, in an area kept moist by a constant drip from the ceiling, or from the damp silt floor in a small domepit or along the cave stream not far from the entrance. The entrance room is approximately 75 m long, and the cave extends another 180 m along a narrow stream channel. The species is sympatric with *P. inquisitor*, which is noticeably smaller and belongs to the *cumberlandus* group. Both species are about equally abundant, judging from the size of the type series (11 *fowlerae*, 10 *inquisitor*), which were obtained on four separate visits to the cave.

cumberlandus group (new group)

Size small to medium (3-5 mm); moderately pubescent, form variable, usually rather slender and depressed, robust and convex in a few

larger species; elytral microsculpture a fine, tranverse meshwork, pruinose only in species from Rockcastle, Pulaski, and Wayne counties, Kentucky. Labrum doubly emarginate, the median lobe varying from weak to moderately prominent. Anterior discal at level of 4th umbilicate; apical groove typically short and very rounded, joining 3rd stria at or slightly anterior to anterior apical puncture; humeri weakly serrulate or not serrulate. Mentum tooth broad, short, emarginate. Mesosternum declivous. Last abdominal sternite of males with apical margin entire. Aedeagus weakly and evenly arcuate, basal bulb not conspicuously enlarged nor deflexed, aedeagal apex usually slender, more or less produced, not very attenuate, bluntly rounded at tip; transfer apparatus consisting of a single slender, small, elongate-triangular copulatory sclerite; parameres rather short, with 4 setae at their apexes. Type species: *P. cumberlandus* Valentine.

Discussion.—*Pseudanophthalmus cumberlandus* was placed in the *pubescens* group by Jeannel (1949). Barr (1959) previously relegated 7 taxa described as polytypic *P. tiresias* to a section of the *engelhardti* group, where they do not belong; they are small, mostly slender and depressed species, but all have the typical *cumberlandus* group transfer apparatus. Further study of the *tiresias* complex indicates that all 7 taxa are full species.

The group is widely distributed in the Central Basin of Tennessee but also extends into north Alabama (Limestone County), western Kentucky (Christian, Caldwell, and Livingston counties), eastern Kentucky (Rockcastle, Pulaski, and Wayne counties), the eastern Highland Rim of Tennessee (Coffee County), and the western Highland Rim and western valley of the Tennessee River in Tennessee (Montgomery, Dickson, Hickman, and Lewis counties). In numbers of species (approximately 30) the group exceeds the *engelhardti* group. The aedeagal form and simple copulatory sclerite are highly diagnostic; the single sclerite is probably homologous with the left piece of other groups. Some of the component species, especially those at the periphery of the group's collective range, are sympatric with species of the *pubescens, menetriesi,* and *simplex* groups. Some of the species in the southeastern and western parts of Middle Tennessee are geographically close to species of the *engelhardti* group (*P. loedingi humeralis* Valentine and *P. hesperus* Barr, respectively), but no sympatry has been demonstrated. In the case of the sympatric species pair *P. productus/P. simplex* the body size is approximately the same (4.2-5.4 mm and 4.2-5.1 mm respectively), and in the pair *P. inquisitor/P. fowlerae* the former species is much smaller (3.1-3.9 vs. 4.0-4.6 mm, respectively). The species of the *pubescens* and *menetriesi* groups are invariably conspicuously larger than species of the *cumberlandus* group with which they coexist.

Pseudanophthalmus cumberlandus Valentine

Valentine 1937:96. Type locality, Piper Cave, Smith Co., TN.

The species is seasonally abundant in damp areas of Piper Cave, especially on previously flooded muddy floors and around rimstone pools and bat guano, but it is usually rare or absent in winter. Unlike the majority of the species in the group, *P. cumberlandus* is unusually robust and convex, with prominent humeri and nearly perpendicular prehumeral borders, the elytral striae very shallow. I have also taken it in Skeleton Cave, Smith County, and Ann White Cave, Macon County, Tennessee.

Pseudanophthalmus productus, new species
Fig. 5

Etymology.—Latin *productus,* "produced."

Diagnosis.—Closely similar in the robust, convex body form and nearly perpendicular prehumeral borders to *P. cumberlandus* Valentine, differing in denser pubescence, wider pronotum base, deeper elytral striae, and long, produced, aedeagal apex.

Description.—Length 4.2-5.4, mean 4.9 ± S.E. 0.3 mm (N = 35). Form robust and convex, pubescent, rufotestaceous. Head about 0.1 longer than wide; labrum doubly emarginate; antenna 0.7 body length. Pronotum 0.87 as long as wide, transverse-subquadrate; base wider than apex and 0.8 maximum width, which occurs in apical third; sides sinuate in basal sixth, but very shallowly so, hind angles about right, sometimes slightly acute or slightly obtuse, feebly emarginate behind, secondary angles present but rather subdued. Elytra 1.6 times longer than wide, prehumeral borders nearly perpendicular to midline, humeri prominent and serrulate, inner 6 striae moderately impressed, intervals subconvex, apical groove short and very rounded, joining third stria at level of anterior apical puncture. Aedeagus 0.62-0.77, mean 0.70 ± S.E. 0.04 mm long (N = 30), moderately and evenly arcuate, apex elongate, slender, and much produced; copulatory sclerite elongate.

Type series.—Holotype male (American Museum of Natural History) and 27 paratypes, Neil Fisher Cave (=Rip Van Winkle Cave), Smith Co., Tennessee, 25 March 1961, T. C. Barr; 33 paratypes, same cave, 18 October 1948, J. M. Valentine and W. B. Jones.

Measurements (in mm).—Holotype, total length 4.80, head 0.92 long

X 0.84 wide, pronotum 0.92 long X 1.06 wide, elytra 2.85 long X 1.79 wide, antenna 3.32 long.

Distribution.—One hundred seven specimens seen as follows. TENNESSEE: *Smith County.*—Neil Fisher Cave (type locality), New Salem Cave. *Putnam County.*—Bartlett, Bowen, Hargis, Jared Hollow, Petty, and Sadler caves. *Jackson County.*—Burial, Harris, Mahaney, Medley, and Carter caves (see Barr 1961 for cave locations).

Discussion.—This moderately large, robust, convex species is closely similar to *P. cumberlandus* but occurs on the opposite (south, left) side of Cumberland River. It is readily differentiated by characters given in the diagnosis. In the northern part of its range, *P. productus* is sympatric and syntopic with *P. simplex*, and at the southern margin of its range it is conjunct with *P. farrelli* Barr (*robustus* group), which occurs in nearby John Fisher Cave (Barr 1962). Superficially both *P. cumberlandus* and *P. productus* resemble species of the *robustus* group, but their distinctive aedeagi readily differentiate them as members of different groups.

Although a few other species of the *cumberlandus* group are rather robust, they are less convex and do not have the prominent humeri of *P. cumberlandus* and *P. productus*. Neither species is obligatorily riparian, although both are hygrophilous and somewhat seasonal in caves influenced by cold air flowing into large entrances. The niche filled appears to be much like that of *P. robustus* and its allies (other than *P. valentinei* Jeannel, which is riparian), and this ecological similarity may explain the conjunct, nonoverlapping ranges of *P. farrelli* and *P. productus*.

Pseudanophthalmus tiresias Barr, new status

Pseudanophthalmus tiresias tiresias Barr 1959:16. Type locality, Indian Grave Point Cave, Dekalb Co., TN.

This is a species found in mesic cave microhabitats, occurring on wet rotting wood and muddy floors rich in organic matter in the type locality cave and in nearby Fox Cave. It is sympatric with *P. farrelli*, which is conspicuously larger (see Barr 1962).

Pseudanophthalmus catherinae Barr, new status

Pseudanophthalmus tiresias catherinae Barr 1959:17. Type locality, Petty Cave, Marshall Co., TN.

Known only from the type locality along the banks of the cave stream, where it is moderately abundant. The species is rather robust but more depressed than *P. cumberlandus*.

Pseudanophthalmus insularis Barr, new status

Pseudanophthalmus tiresias insularis Barr 1959:18. Type locality, Baker Station Cave, Davidson Co., TN.

The type locality is a small stream cave in Silurian limestones of the Highland Rim margin north of Nashville; known only from the type locality, where it is rare. The species is small, slender, and depressed.

Pseudanophthalmus occidentalis Barr, new status

Pseudanophthalmus tiresias occidentalis Barr 1959:18. Type locality, DePriest Branch Cave, Lewis Co., TN.

Known only from the type locality cave and nearby Cave Branch Cave, Hickman County, Tennessee, this small, slender, depressed species is rare in both caves. It is potentially sympatric with *P. hespertus* Barr (*engelhardti* group), which occurs in the Blowing Caves, Perry County, Tennessee, but the two species have not yet been shown to coexist.

Pseudanophthalmus acherontis Barr, new status

Pseudanophthalmus tiresias acherontis Barr 1959:20. Type locality, Echo Cave, Rutherford Co., TN.

Known only from the type locality cave, apparently a branch of the extensive Snail Shell Cave system (in the main trunk of which it has not yet been collected), this small, slender, depressed species is found in riparian microhabitats. All available specimens are unusually pale, rufotestaceous.

Pseudanophthalmus tullahoma Barr, new status

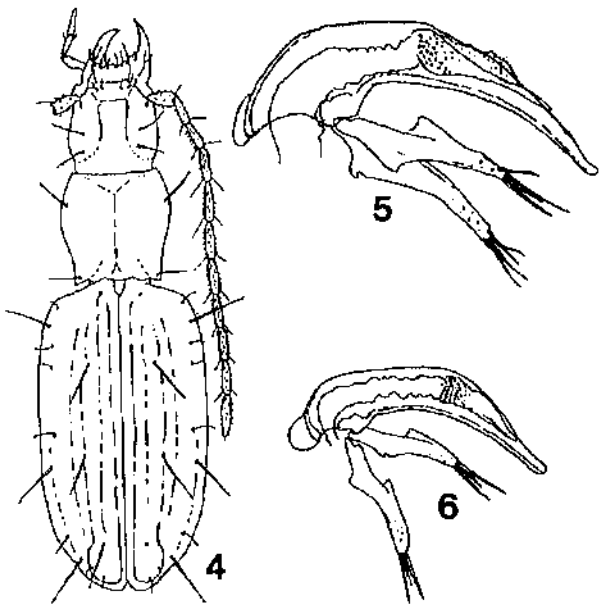
Pseudanophthalmus tiresias tullahoma Barr 1959:20. Type locality, Carroll Cave, Coffee Co., TN.

The species is known only from Carroll and Riley Creek caves, Coffee County, Tennessee, both of which have been flooded by the Tennessee Valley Authority's Normandy Dam on Duck River. In Carroll Cave this small, slender, depressed species occurred on rotting wood in a wet area, and in Riley Creek Cave it occurred in a muddy, periodically flooded area on rotting wood in which large numbers of *Onychiurus* collembolans were found.

Pseudanophthalmus bendermani Barr, new status

Pseudanophthalmus tiresias bendermani Barr 1959:21. Type locality, Benderman Cave, Maury Co., TN.

At the present time this species is known only from the type locality, an extensive stream cave containing much bat guano. The small, slender, depressed beetles are rather abundant in riparian microhabitats.



Figs. 4-6. *Pseudanophthalmus: cumberlandus* group. 4. *P. inquisitor*, n. sp. (3.4 mm). 5. Aedeagus, *P. productus*, n. sp. (0.75 mm). 6. Aedeagus, *P. inquisitor*, n. sp. (0.53 mm).

Pseudanophthalmus inquisitor, new species
Figs. 4, 6

Etymology.—Latin *inquisitor*, "searcher, inquirer."

Diagnosis.—A slender and depressed species characterized by very small size, non-pruinose elytral microsculpture, and the small, scarcely arcuate aedeagus with deflexed apex.

(±S.E.)

Description.—Length 3.1-3.9, mean 3.5±S.E.0.3 mm. Head rounded; labrum feebly trilobed; antenna 0.7 body length. Pronotum transverse, 0.87 as long as wide, margins arcuate in apical two-thirds, then oblique and scarcely sinuate at all to approximately right (or slightly acute or slightly obtuse) hind angles; widths at apex and base subequal and three-fourths greatest width, which occurs in apical third; base emarginate behind angles, secondary angles present; disc with rather long pubescence. Elytra elongate-oval, strongly depressed, 1.6 times longer than wide; microsculpture a fine, very tight, transverse meshwork; humeri angular, prehumeral borders almost perpendicular to midline; longitudinal striae 1-5 more or less complete and moderately impressed, intervals subconvex; apical groove short and widely rounded or (as in holotype) subparallel, joining third stria at anterior apical puncture. Aedeagus 0.48-0.52 mm long, basal bulb large but not sharply set off from median lobe, which is narrow and straight, its apex deflexed, produced, and bluntly rounded at tip; transfer apparatus a single, slender, elongate sclerite; parameres slender, with 3 apical setae.

Type series.—Holotype male (American Museum of Natural History) and one paratype, Sheals Cave, Clay Co., Tennessee, 7 April 1960, T. C. Barr. Three additional paratypes, same cave, 3 December 1960, T. C. Barr, and 5 paratypes, same cave, 11 August 1965, T. C. Barr and J. R. Holsinger. Known only from the type locality.

Measurements (in mm).—Holotype, total length 3.10, head 0.60 long X 0.62 wide, pronotum 0.65 long X 0.77 wide, elytra 1.85 long X 1.15 wide, antenna 2.18 long.

Distribution.—Sheals Cave is 0.8 km e of Celina, Tennessee, near the juncture of Obey and Cumberland rivers at the northeast margin of the Central Basin.

Discussion.—The species is sympatric and syntopic with *P. fowlerae* but is noticeably smaller. It is more readily collected in summer at the back of the entrance room, but a few specimens occur throughout the year along the stream in the back of the cave.

ACKNOWLEDGMENTS.—I thank Dr. John R. Holsinger for assistance in the field, and Drs. J. Manson Valentine and the late Walter B. Jones for contribution of specimens. The encouragement and cooperation of Mrs. Otia Fowler, owner of Sheals Cave at the time of my visits, is greatly appreciated.

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Breeding Migrations, Population Size Structure, and Reproduction of the Dwarf Salamander, *Eurycea quadridigitata*, in South Carolina

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ABSTRACT.—Life history parameters of *Eurycea quadridigitata* from two populations on the upper Coastal Plain of South Carolina were examined. Breeding migrations into Carolina bays occurred during September and October in 1978 and July through October in 1979. The initiation of breeding migrations was associated with a drop in air temperature during late summer or early autumn. The sex ratio of *E. quadridigitata* entering the breeding sites was 1:1. Egg deposition probably occurs during November and early December. Sexual dimorphism in snout-vent lenth (SVL) was not present, but there was significant local variation in SVL of adults ($\bar{x}$ = 26 and 29 mm). The number of ovarian eggs was positively correlated with SVL and varied between populations ($\bar{x}$ = 21 and 33).

INTRODUCTION

Although the dwarf salamander, *Eurycea quadridigitata*, is a widely distributed species in the southeastern United States (Dunn 1926; Mittleman 1947), life history information in most parts of its range is based on anecdotal observations (Bishop 1947; Dunn 1926; Neill 1949; Noble 1927). Sever (1975), in a more complete report, described seasonal variation of the nasolabial glands and included data on the male reproductive cycle. Harrison (1973) and Semlitsch (in press) provided ecological information on habitat, and reproductive and larval characteristics. Taxonomic accounts, distributional records, and other pertinent literature on the species were reviewed by Mittleman (1967).

As previously shown, the drift fence and pitfall trap technique provides an ideal sampling method for monitoring populations of fossorial amphibians (Gibbons and Bennett 1974; Gill 1978; Shoop 1965). Since lack of an adequate sampling technique has hindered the study of *E. quadridigitata*, this study was initiated to provide quanititative information on life history parameters of dwarf salamander populations from the upper Coastal Plain of South Carolina.