

THE STATUS AND AFFINITIES OF
DUVALIOPSIS JEANNEL (COLEOPTERA: CARABIDAE)¹

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The genus *Duvaliopsis* was established by Jeannel (1928) for a small group of endogenous, anophthalmous trechines from the Carpathian Mountains and the Transylvanian Alps of Romania, Czechoslovakia, and Poland. Although earlier authors had classified them with *Anophthalmus* Sturm, *Trechus* Clairville, or *Duvalius* Delarou-zée (formerly considered a subgenus of *Trechus*), Jeannel (1928) clearly demonstrated their morphological similarity to *Trechoblemus* Ganglbauer and to North American cavernicole trechines of the genera *Pseudanophthalmus* and *Neaphaenops*. *Trechoblemus*, *Duvaliopsis*, *Pseudanophthalmus*, and *Neaphaenops* were placed in a "série phylétique de *Trechoblemus*", united by the common possession of certain characters: (1) the mentum is fused to the prementum; (2) the recurrent portion of the apical groove of the elytron is usually connected to or directed toward the 3rd longitudinal stria; (3) the copulatory sclerites (of which there are one or two) are placed laterally (anisotopic), rather than ventrally (isotopic), in the internal sac; and (4) the anterior tibiae are pubescent on the outer side.

Subsequent to 1928, additional genera in North America and Japan have been described which should probably be allied with this series (Valentine 1952, Yoshida and Namura 1952, Uéno 1956 and 1958, Barr 1960).

In the eastern United States, the largest and most widely distributed genus of cave beetles is *Pseudanophthalmus*, species of which are now known from Indiana, Kentucky, Tennessee, Alabama, Georgia, Ohio, Virginia, West Virginia, and Pennsylvania. Although found only in caves up to the present time, a few Virginia species have rudimentary eyespots, suggesting comparative recency of adopting a wholly subterranean mode of life. The absence of epigeal trechines from North America which seem to share a relatively recent ancestry with *Pseudanophthalmus* and other cave genera has provoked considerable speculation on the history and evolution of the group. *Trechoides fasciatus* Motschulsky, from the Oligocene Baltic amber, could belong either to *Lasiotrechus* or *Trechoblemus* (Jeannel, 1928). This fossil demon-

¹This investigation was supported in part by a grant from the National Science Foundation, no. G-18765.

Manuscript received by the editor February 25, 1964.

strates the presence of the series in Europe in the mid-Tertiary, but reveals nothing about the North American representatives. Morphologically, the closest known relative of *Pseudanophthalmus* is *Duvaliopsis*.

The Museum of Comparative Zoology, Harvard University, recently obtained part of the collection of Dr. Eduard Knirsch, Kolín, Czechoslovakia, which contains 44 specimens of *Duvaliopsis*, including all 8 forms treated by Jeannel in his monumental *Monographie des Trechinae* (1928). I am indebted to Dr. Philip J. Darlington, Jr., curator of entomology at the Museum of Comparative Zoology, for permission to undertake a study of these beetles.

When Jeannel (1928) established the genus *Duvaliopsis*, only 10 species of the North American *Pseudanophthalmus* were known, presenting a far narrower conception of the limits of the latter genus than is held today. The chief diagnostic characters of *Duvaliopsis* were said to be (Jeannel 1928): (1) punctures 3 and 4 of the marginal series ("fouets huméraux de la série ombiliquée") are closely applied to the marginal gutter; and (2) the transfer apparatus consists of a single copulatory piece in the form of a very long, concave spoon, bifid at the apex, the convex side facing the right side of the internal sac. *Pseudanophthalmus* differed in having: (1) punctures 3 and 4 of the marginal series farther from the marginal gutter than punctures 1 and 2; and (2) the transfer apparatus consisting of 2 pieces, not bifid.

In examining all 8 forms of *Duvaliopsis* known to Jeannel when he established the genus and in comparing them with most of the known species of *Pseudanophthalmus*, I am unable to find any consistently significant difference in the chaetotaxy of the humeral marginal set. In larger species of *Pseudanophthalmus*, especially those with moderately convex elytra, the 3rd and 4th punctures do appear farther from the gutter than the 1st and 2nd. As Jeannel himself very clearly explained (*Monographie*, III, p. 18), the relative positions of the umbilicate series are far from absolute, and are related to the hypertrophic enlargement of the external interstriae. Thus the alleged generic character would appear valid when a large, convex *Pseudanophthalmus* (e.g. *P. menetriesii* Motsch., the generotype) is compared with a *Duvaliopsis* (all of which are small and rather depressed), but would break down when the comparison is made with a small species of *Pseudanophthalmus* with depressed elytra.

The transfer apparatus of *Duvaliopsis* is indeed distinctive, but so are the many transfer apparatus types of the twenty-odd species groups of *Pseudanophthalmus*. The unusual length of the copulatory piece in

itself is not diagnostic, since certain species of *Pseudanophthalmus*, e.g. the *gracilis* section of the *hubbardi* group, have equally long transfer apparatuses. Even the single copulatory piece is not peculiar, since *P. cumberlandus* Val. and its allies have but a single copulatory piece.

In conclusion, there appears to be no reason why *Duvaliopsis* should be maintained as a genus distinct from *Pseudanophthalmus*. Its distinctiveness is on the order of magnitude of the difference between various species groups of *Pseudanophthalmus*, and it is to this status which I propose it be relegated.

The study of the Knirsch material has suggested certain changes in the taxonomic arrangement proposed by Jeannel (1928). A revision is given below.

Pseudanophthalmus Jeannel

Jeannel 1920: p. 154; type species: *Anophthalmus menetriesii* Motschulsky.

SYNONYM: *Duvaliopsis* Jeannel 1928: p. 106; type species: *Anophthalmus bielzi* Miller.

bielzi group

(= *Duvaliopsis* Jeannel)

Size small (3.3-4.0 mm.), integument pubescent. Head rounded or slightly wider than long; eyes absent, their site indicated in some species by a small, oblique cicatrix; antennae about half the body length (except in *rybinskii*). Pronotum transverse, $1/5$ to $1/3$ wider than long; margins arcuate in apical $1/2$ to $2/3$, then sloping evenly back to the hind angles with little or a very brief sinuosity; hind angles rather small, variable; disc with sparse, long pubescence. Elytra $3/5$ as wide as long, subconvex or depressed; striae regular or irregular, deeply or shallowly impressed, finely punctulate (except in *bielzi*); first discal puncture at the level of the 4th marginal puncture, slightly anterior to it, or slightly posterior; apical recurrent groove highly variable, parallel or oblique to the suture, connecting with either the 3rd or 5th longitudinal stria, with or without a crochet, but always terminating well in advance of the apical puncture. Aedeagus usually arcuate and moderately slender, the basal bulb set off from the median lobe by a slight constriction, the apex attenuate with the tip reflexed (produced into the shape of a boot in *meliki*); transfer apparatus a single, elongate, spoon-shaped copulatory piece with its concave side facing the left side of the internal sac, its dorsal and ventral edges rolled and sclerotized and apically produced to give a bifid appearance; internal sac with moderate armature of small, blunt scales; parameres with 3 or 4 setae at their apices. Type species: *Anophthalmus bielzi* Seidlitz.

KEY TO SPECIES OF THE BIELZI GROUP²

- 1 Elytra with internal longitudinal striae deeply impressed, all striae more or less irregular; labrum with a rather deep, V-shaped emargination 2
 Elytra with the internal longitudinal striae shallowly impressed and regular, finely punctulate; labrum shallowly emarginate 3
- 2(1) Elytra subconvex, striae deep and fairly regular, with little or no punctulation; humeri rounded, the prehumeral borders oblique to the median line (Romania: Transylvanian Alps) *bielzi* (Seidlitz)
 Elytra depressed, internal striae moderately impressed, slightly irregular, and finely punctulate; humeri more angular, the prehumeral border nearly perpendicular to the median line (Czechoslovakia: Carpathians) *pilosellus* (Miller)
- 3(1) Antennae half as long as the total body length; segments VII-X thick, more than half as wide as long 4
 Antennae $\frac{2}{3}$ as long as total body length; segments VII-X slender, less than half as wide as long (Poland: Carpathians) *rybinskii* (Knirsch)
- 4(3) Humeral margin distinctly serrulate; head as long as wide 5
 Humeral margin with serrulations obsolete; head slightly but distinctly wider than long (Romania: eastern Carpathians) *calimanensis* (Knirsch)
- 5(4) Aedeagus long and slender, the apex reflexed then curved downward in the shape of a boot (Romania: eastern Carpathians) *meliki* (Csiki)
 Aedeagus robust, with a slender and briefly produced apex (Romania: Transylvanian Alps) *transylvanicus* (Csiki)
- Most of the species are figured by Knirsch (1924) or Jeannel (1928), who also list the precise localities from which each is known.

Pseudanophthalmus bielzi (Seidlitz) new combination*Anophthalmus Bielzi* Seidlitz 1867: p. 45.*Trechus (Duvallius) Bielzi*: Knirsch 1925: p. 90.*Duvallhopsis Bielzi*: Jeannel 1928: p. 109, figs. 1349-1352.*Pseudanophthalmus pilosellus* (Miller) new combination*Anophthalmus pilosellus* Miller 1868: p. 11.*Trechus (Duvallius) Bielzi pilosellus*: Knirsch 1924: p. 65, figs. 3 and 8; Knirsch 1925: p. 91.

²Includes only the Knirsch material; I have not seen *D. pilosellus beskidensis* Hliskowski 1942 (Ent. Listy 5: 17).

Duvaliopsis pilosellus: Jeannel 1928: p. 110, figs. 1354, 1346, and 1347.

Anophthalmus Bielzi Stobieckii Csiki: 1907: p. 574.

Trechus (Duvalius) Bielzi Stobieckii: Knirsch 1925: p. 91.

Duvaliopsis pilosellus Stobieckii: Jeannel 1928: p. 111.

Jeannel's key to species (*Monographie*, III, p. 108) is erroneous because *bielzi* is said to have angular humeri with the prehumeral border perpendicular to the median line. However, only in *pilosellus* are the humeri sharply angular and the prehumeral borders perpendicular. This is amply confirmed by Knirsch's long series of both *pilosellus* and *stobieckii*. I can find no taxonomically significant differences between these two supposed subspecies. The male genitalia are identical.

Pseudanophthalmus rybinskii (Knirsch) new combination

Trechus (Duvalius) Bielzi Rybinskii Knirsch 1924: p. 63; figs. 5 and 6;
Knirsch 1925: p. 91.

Duvaliopsis pilosellus Rybinskii: Jeannel 1928: p. 111.

Pseudanophthalmus calimanensis (Knirsch) new combination

Trechus (Duvalius) Bielzi calimanensis Knirsch 1924: p. 65, figs. 4 and 7.

Duvaliopsis pilosellus calimanensis: Jeannel 1928: p. 111, fig. 1353.

These two species, *P. rybinskii* and *P. calimanensis*, are quite distinct from *pilosellus* in characters given in the key as well as in genitalic differences. Judging from strictly morphological criteria, they are probably more closely related to *meliki* and *transylvanicus* than they are to either *bielzi* or *pilosellus*.

Pseudanophthalmus meliki (Csiki) new combination

Anophthalmus Bielzi Meliki Csiki 1912: p. 537.

Duvaliopsis Meliki: Jeannel 1928: p. 114, figs. 1355, 1356, and 1357.

Trechus (Duvalius) pauperculus Knirsch 1925: p. 91.

Duvaliopsis Meliki pauperculus: Jeannel 1928: p. 114.

In the distinctive boot-shaped enlargement of the apex of the aedeagus, this species recalls a similar feature in *P. valentinei* Jeannel and *P. vanburenensis* Barr (Tennessee, U. S. A.). The other species of the *bielzi* group are possibly more closely related to each other than to *P. meliki*, but the transfer apparatus confirms their affinity with the latter species.

Pseudanophthalmus transylvanicus (Csiki) new combination

Anophthalmus Bielzi transylvanicus Csiki 1902: p. 52.

Trechus (Duvalius) transylvanicus: Knirsch 1925: p. 91.

Duvaliopsis transylvanicus: Jeannel 1928: p. 113.

In this species the head is as long as wide; the labral emargination is very shallow; the pronotum is $1 \frac{1}{4}$ times as wide as long; the hind angles of the pronotum are acute, with a deep and very brief marginal sinuosity before them; the elytral humeri are clearly serrulate; the first discal puncture is at or behind the 4th humeral marginal puncture; and the apical recurrent groove is long and parallel to the suture, variably connected with the 5th or the 3rd longitudinal stria. The aedeagus of a topotype (Schuler Gebirge, Transylvanian Alps, Romania) in the Knirsch collection measures 0.86 mm. long, much larger and more robust than that of *pilosellus*. The apex narrows abruptly and is briefly produced. The copulatory piece measures about $\frac{1}{3}$ of the total length of the aedeagus.

DISCUSSION

The realization that the *Pseudanophthalmus* found in caves of the eastern United States have their endogenous counterparts in the mountains of eastern Europe is primarily of zoogeographic interest. Like many disjunct distributions, this one suggests an earlier, broader distribution followed by intermediate extinction. Certainly the geographic extent of compatible trechine microenvironments would have been considerably broadened under the influence of a periglacial climate. The species of the *bielzi* group are now as closely restricted to the higher elevations (1200 meters and above, according to Jeannel, op. cit.) of the Carpathians and Transylvanian Alps as the American *Pseudanophthalmus* are restricted to caves. Both American and European species are presumably descended from winged, *Trechoblemus*-like ancestors.

Although the species of the *bielzi* group are not primarily cavernicolous, they are probably similar to forms which colonized North American caves during the Pleistocene interglacials. Endogenous *Pseudanophthalmus* have not been discovered in the eastern United States. I made a careful search of the high mountains of North Carolina and Tennessee in the summer of 1960, finding many *Trechus* (Barr 1962) but no *Pseudanophthalmus*. If we were to seek a close environmental parallel to the Carpathians and Transylvanian Alps in North America, however, we would have to look farther north, nearer to the terminal moraines of the Pleistocene glaciers. The few scattered peaks 4000 feet or higher in Virginia and West Virginia would bear careful search. A recent study of the *Pseudanophthalmus* of the Appalachian valley (Barr, in press) suggests that the cave species of that area have descended, with slight modification, from a smaller number of endogenous species. Each ancestral endogenous species is presumed to

have occurred in the geographic area in which the caves are at present inhabited by closely similar, allopatric species or subspecies.

Similar patterns of speciation occur among *Pseudanophthalmus* of the *horni* group in the Bluegrass of Kentucky, where apparently two ancestral species colonized the caves. One species had a short aedeagus similar to that of *P. horni* Garman, while the other had a long, hooked aedeagus similar to that of *P. inexpectatus* Barr. A single ancestral species is postulated for the *tiresias* section of the *engelhardti* group, which occupies the Central Basin of Tennessee. Cave colonization and speciation does not seem to have been radically different in the Appalachian valley, the Bluegrass, and the Central Basin.

Patterns of trechine speciation are more difficult to explain in cave systems of the karst plains developed on Meramac and Chester limestones of the Interior Low Plateaus — specifically, the Mitchell plain of Indiana, the Pennyroyal plateau of Kentucky, and the Eastern Highland Rim of Tennessee. Here the networks of subterranean solutional openings are more extensive, and dispersal from one cave system to another takes place more readily. Here it is possible for abundant, mobile species to have (for cave trechines) fantastically extensive ranges, up to 75 miles long in *Darlingtonia kentuckensis* Valentine and 110 miles long in *Neaphaenops tellkampfi* Erichson. Here it is not uncommon for 3, 4, or even 5 species of troglotic trechines to inhabit the same cave, a phenomenon best explained by multiple invasion.

But despite the special interest that American coleopterists may have in speculating that American *Pseudanophthalmus* descended from preadapted, montane, endogenous species like those of eastern Europe, the *bielzi* group itself deserves further careful study. With the possible exception of *P. pilosellus*, all the species are quite rare, so that morphological variation cannot be adequately subjected to statistical analysis. No useful taxonomic purpose is served by naming each local population a different subspecies, as has been done for certain European carabids (hundreds of names have been applied to *Carabus granulatus* and *C. cancellatus*, for example). It appears premature to apply the polytypic species concept to the *bielzi* group. However, extensive collecting, especially in Romania, would make possible a sound study of alpine speciation in the *bielzi* group, involving analysis of variation and comparison of existing geographic ranges with Pleistocene glacial patterns and inferred Pleistocene climatology. Few detailed studies of the flightless insects of the Carpathians have been made (Kaszab 1961). Such an investigation, while increasing the store of information on the role of the Carpathians and Transylvanian Alps as a

Pleistocene refugium, would also significantly broaden the base of our knowledge of cave colonization and speciation among trechines.

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