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The distribution and evolution of cavernicolous *Ptomaphagus* beetles in the southeastern United States (Coleoptera; Leiodidae; Cholevinae) with new species and records

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New data show the presence of additional full-species taxa of cavernicolous *Ptomaphagus* beetles, bringing to 18 the number of troglobitic species in the southeastern United States.The new species are ***Ptomaphagus chromolithus*** and ***Ptomaphagus torodei***; full species rank is given to *P. solanum*, *P. fecundus*, *P. longicornis*, and *P. julius*; *P. laticornis* is resurrected from synonomy. *Ptomaphagus nicholasi* is placed in synonomy under *P. hirtus*. A phylogeny is proposed. A model of speciation is proposed with cave populations isolated during interglacials, and with probable overland dispersal and interpopulation contact during glacials.

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L'examen de nouvelles récoltes a révélé la présence de nouvelles espèces de coléoptères cavernicoles du genre *Ptomaphagus*, ce qui porte à 18 le nombre d'espèces troglobites dans le Sud-Est américain. Les nouvelles espèces sont ***Ptomaphagus chromolithus*** et ***Ptomaphagus torodei***; *P. solanum*, *P. fecundus*, *P. longicornis* et *P. julius* acquièrent le statut de vraies espèces; l'espèce *P. laticornis* redevient valide après avoir été synonymisée. *Ptomophagus nicholasi* devient synonyme de *P. hirtus*. On trouvera ici la présentation d'une phylogénie de *Ptomophagus* ainsi qu'un modèle de spéciation qui tient compte de l'isolement des populations cavernicoles au cours des périodes interglaciaires et qui démontre les voies probables de dispersion sur terre et les contacts possibles entre les populations durant les glaciations.

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Introduction

The taxonomy of populations that are both geographically variable and allopatrically distributed has long presented a problem to systematic zoologists (Brown 1959; Wilson and Brown 1953). More importantly, such populations are of great interest to biologists in exploring the evolutionary events of genetic differentiation and species origin (Mayr 1963; Dobzhansky 1970; Ayala 1975). This is especially true of highly restricted animals specialized for life in caves, as recently reviewed by Culver (1982) and Howarth (1983).

The troglobitic (obligately cavernicolous, blind, and wingless) *Ptomaphagus* beetles of the southeastern United States, and especially northeastern Alabama, are such a group of populations. Their systematics have been studied by Jeannel (1949), Barr (1963), and Peck (1973). In 1973 I conservatively concluded that about 80 known populations of these beetles in Alabama represented a complex of forms and subspecies of a few polytypic species. Since then, additional field and laboratory work have helped to clarify the morphological and genetic relationships of these "polytypic species" and theoretical aspects of the nature and origin of their geographic separation.

Review and discussion of data

A mixture of laboratory and field observations and experiments have been used to gain direct and indirect information on the "polytypic species," "*P. hatchi*" and "*P. loedingi*" of northeastern Alabama. The background data, procedures, and implications are presented here for each of these "problem" species. Methods and procedures are as in Peck (1973, 1983). A total of over 120 cave-limited populations of *Ptomaphagus* have now been sampled in northeastern Alabama in over 540 visits to over 215 separate caves. Specimens upon which the systematic conclusions are based are deposited in the Canadian National Collection of Insects (Ottawa), Museum of Comparative Zoology (Harvard University), Field Museum of Natural History (Chicago), and in the author's collection.

The problem of the "forms" of "P. hatchi"

Ptomaphagus hatchi occurs in Grundy and Franklin counties, Tennessee, and Jackson and Madison counties, Alabama. One peripheral isolate was called a subspecies, *P. hatchi fecundus* Barr. Within the center of the range of what was called form I, two distinct forms of female spermathecae were recognized and called forms II and III (Figs. 4, 8, 10). The frequency of these forms and the amount of intrapopulational variation were not known.

Dissections have now been made on all available females and their spermathecal morphology was examined. These represent 61 separate cave populations. Variation in spermathecal form was found to occur within populations in various minor structural proportions, but the variation did not overlap and blur the distinct limits of the categories of the forms. Totals were 490 females for the typical form I, 164 for form II, and 113 for form III. Accompanying these were 851 males which can be separated only with difficulty and low reliability.

The striking finding was that each cave population was found to contain only *one* form of spermatheca. However, there is no discrete and simple pattern in the geographical distribution of the forms (Fig. 1). Within continuous limestones that should be expected to contain abundant subterranean avenues for dispersal, the populations (as characterized by different spermathecal forms) seem to have rigorously segregated themselves. This suggested that the spermathecal forms are actually an indicator of species-level taxonomic categories that have established intrinsic barriers to gene flow and are somehow acting to exclude each other. This strict allopatry of species is known in other Tennessee cave *Ptomaphagus* (Peck 1975) and in cave carabids (Barr 1962), crickets and crayfishes (reviewed in Hubbell and Norton 1978). "Competitive exclusion" is usually

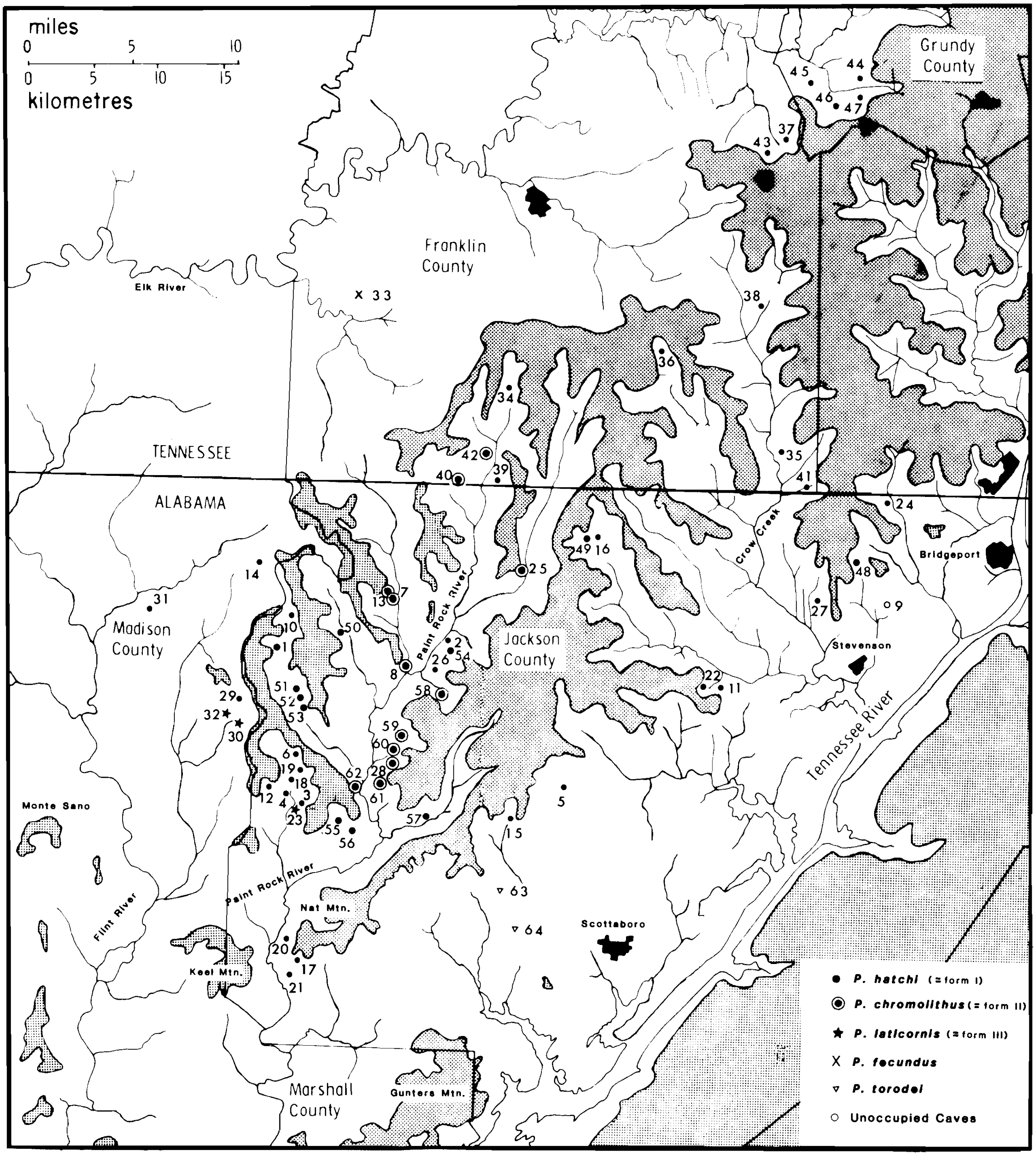


FIG. 1. Distribution of troglobitic (obligately cavernicolous) *Ptomaphagus* beetles in northeastern Alabama and adjacent Tennessee. Stippling represents the Pottsville sandstone remnants of the cap rock of the Cumberland Plateau, locally called the Jackson County Mountains. Caves do not exist under this cap rock. Consequently, plateau remnants, as well as the large rivers and streams and their alluviated valleys, represent barriers to subterranean terrestrial dispersal (after Peck 1973). The names for the cave localities are as follows: 1, Borderline; 2, Bouldin; 3, Cave Stand; 4, Clemmons; 5, Cornellison No. 2; 6, Devils Stairstep and Keel; 7, Doodlebug Pit-Blowing; 8, Doug Green; 9, Edgefield; 10, Hambrick; 11, Happy Hollow; 12, Honey Hollow Saltpeter; 13, Horseshoe; 14, Hurricane; 15, Indian Rocks; 16, Jess Elliott and Tate; 17, Kennamer; 18, McFarland; 19, McFarland Hollow Blowing and McFarland Spring; 20, The Morgue; 21, Nat; 22, Rainbow; 23, Rousseau; 24, Russell; 25, "Section 20"; 26, Swaim; 27, Talley Ditch; 28, Williams Saltpeter; 29, Aladdin; 30, Hutton; 31, Jacks; 32, Scott; 33, Caney Hollow; 34, Caroline Cove; 35, Crownover Saltpeter; 36, Custard Hollow; 37, Dry; 38, Lost Cove; 39, Mill Hollow Head; 40, Putman Spring; 41, Rannie Willis; 42, Round Mountain; 43, Wet; 44, Crystal-Wonder; 45, Partin Spring; 46, Trussell; 47, Wildman; 48, Dry; 49, Haddon Spring; 50, Cagle; 51, Roadside; 52, Crowson and Slippery Pole; 53, Fourth of July; 54, Buds; 55, Dripping Spring; 56, Trenton; 57, Guess Creek; 58, Beanfield; 59, Fortyeight Ten; 60, Little Sink; 61, Putman; 62, Moon Spring; 63, Hall; and 64, Two Way.

invoked as a mechanism but no attempts have been made to experimentally demonstrate this.

Genetic evidence to support the hypothesis that spermathecal forms were indicators of such "species" boundaries was sought in interpopulational hybrid crosses. The data showed that there is a great resistance to gene flow and low apparent fitness for hybrid F_1 and F_2 adult beetles when different "spermathecal forms" are crossed (Peck 1983).

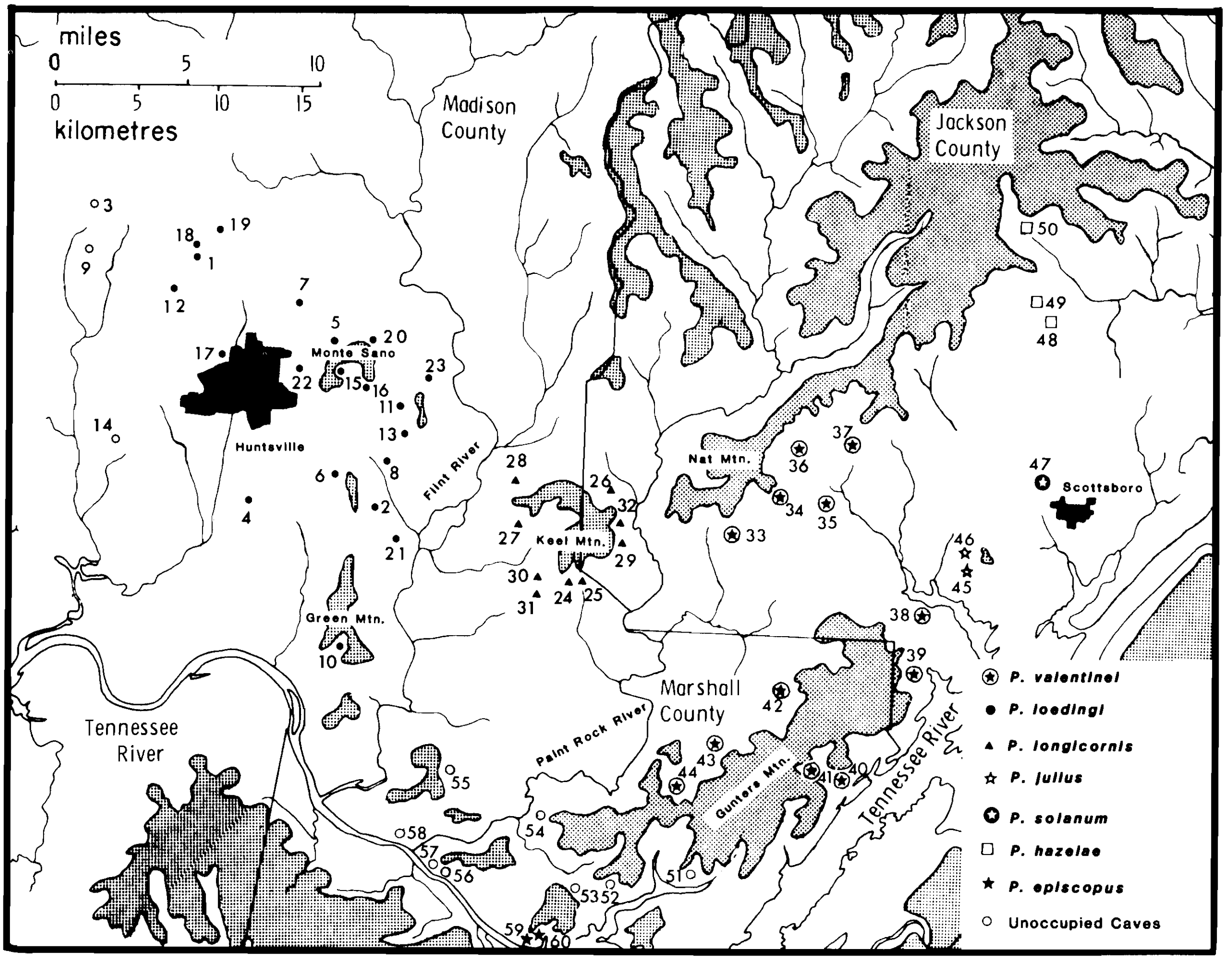


FIG. 2. Distribution of troglobitic *Ptomaphagus* in northeastern Alabama. Stippling as in Fig. 1. The names for the cave localities are as follows: 1, Barclay; 2, Buford; 3, Burwell; 4, Byrd Spring; 5, Cold Spring; 6, Canoe; 7, Cave Spring; 8, Drake; 9, Ellis; 10, Green Grotto; 11, Jett; 12, Kelly Natural Well; 13, Lott and Pitt Sinkhole; 14, Matthews; 15, Natural Well; 16, Sadler Spring; 17, Shelta; 18, Sinks; 19, Spook; 20, The Sinks; 21, Taploe; 22, Toll Gate Natural Well; 23, Twin; 24, Bee Sink and Moon Sink; 25, Butler Sink and Chittimwood; 26, Crossing; 27, Goat; 28, Grayson Spring; 29, Greising; 30, Hering; 31, Labyrinth; 32, Paint Rock; 33, Pig Pen; 34, Lost; 35, Larkin; 36, Schiffman; 37, Limrock Blowing; 38, Sauta; 39, Mink; 40, War Eagle; 41, Royal Shaft; 42, Cathedral; 43, Guffey; 44, Kirkland; 45, House of Happiness; 46, Lindsay Spring; 47, Sheldons; 48, Ivey Bottom; 49, Driftwood; 50, Tumbling Rock; 51, Dunham; 52, Ledbetter; 53, Bishop; 54, Keller; 55, Morring Spring; 56, Painted Bluff; 57, Merrill; 58, Clark Bluff; 59, Honeycomb; and 60, McHardin.

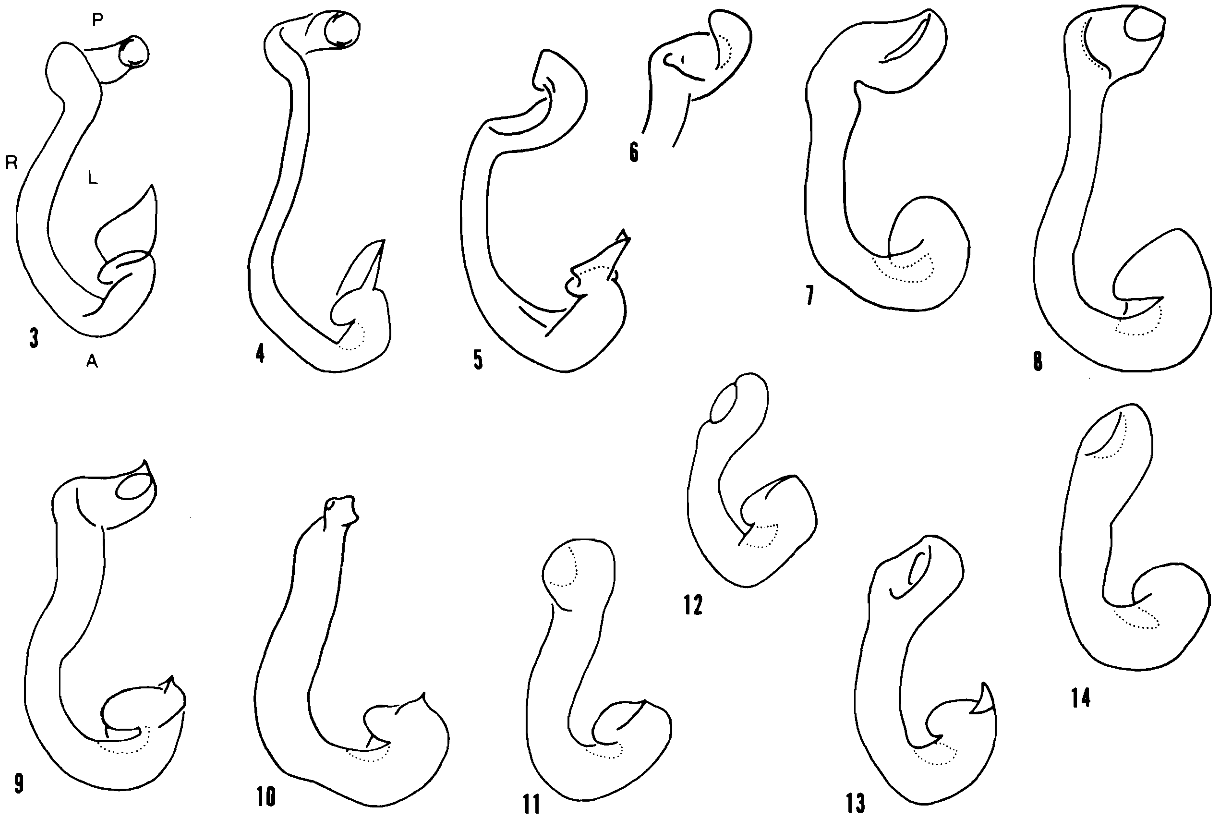
Lastly, preliminary electrophoretic analysis of allozymes was made on forms I (from Roadside Cave) and II (from Doug Green Cave). Enzyme activities were measured for a general protein (Coomassie Blue), glucophosphoisomerase, octanol dehydrogenase, phosphoglucomutase, indophenol oxidase, malate dehydrogenase, hydroxybutyrate dehydrogenase, malic enzyme, and carbonic anhydrase. The banding patterns were found to be the same in all but the carbonic anhydrase in samples of a mean of 8 ($R = 5-12$) individuals per population. At this last locus, all six specimens of form I had a distinct and clearly separated band from that of five specimens of form II (C. Laing, unpublished data). This is statistically significant at the 5% level using Fisher's exact test and demonstrates the absence of interbreeding between these populations. When compared with data on Kentucky cave *Ptomaphagus hirtus* populations (Laing et al. 1976) and other studies (e.g., reviewed in Ayala 1975 and Ferguson 1980) this difference also suggests that the forms may be at the level of differentiation that characterizes full species.

The conclusion of these three mutually reinforcing lines of evidence is that the forms actually have the characteristics of full species and should be so recognized. An implication is that the untested subspecies *P. hatchi fecundus* is also of full species rank.

*The problem of "subspecies" in "*P. loedingi*"*

The above conclusions raised questions about the rank of the allopatrically distributed "subspecies" populations of *P. loedingi* in Madison and Jackson counties, Alabama. These "subspecies" were known to occur (Fig. 2) in discrete and extrinsically isolated limestone regions, separated by major river barriers and alluviated lowlands, and are morphologically more distinct than the forms of *P. hatchi* (Figs. 11–14).

Data bearing on this problem are fewer, but interpopulational hybrid crosses were unsuccessful, thus suggesting substantial genetic differentiation and intrinsic isolation between the tested populations (Peck 1983). Their geographically isolated nature certainly prevents present day subterranean contact and gene flow, so that they are actually isolated biological species (sensu Mayr 1963) by the same criteria applied to some species of cave carabid beetles (Barr and Peck 1966). The conclusion is that these taxa should also be recognized as



FIGS. 3–14. Spermathecae of cavernicolous *Ptomaphagus* in the *loedingi* cluster of species in northeastern Alabama. Fig. 3. *P. valentinei* Jeannel, Schiffmans Cove Cave; letters indicate orientation of right, R; left, L; posterior, P; and anterior, A. Fig. 4. *P. chromolithus* n. sp., Doug Green Cave (formerly *P. hatchi* form II). Fig. 5. *P. torodei* n. sp., Two Way Cave. Fig. 6. *P. torodei* n. sp., Two Way Cave, variation in posterior piece. Fig. 7. *P. solanum*, Sheldons Cave (formerly *P. loedingi solanum* (Peck). Fig. 8. *P. laticornis* Jeannel, Scott Cave (formerly *P. hatchi* form III). Fig. 9. *P. fecundus* Barr, Caney Hollow Cave. Fig. 10. *P. hatchi* Jeannel, Crystal Cave (Tennessee) (formerly *P. hatchi* form I). Fig. 11. *P. loedingi* Jeannel, Shelta Cave. Fig. 12. Variation in *P. loedingi* Jeannel, Pitts Cave (originally *P. valentinei jonesi* Jeannel). Fig. 13. *P. longicornis*, Crossing Cave (formerly *P. loedingi longicornis* Jeannel). Fig. 14. *P. julius*, House of Happiness Cave (formerly *P. loedingi julius* Peck).

full species.

The problem of the species "P. nicholasi"

Ptomaphagus nicholasi was described by Barr in 1963 from five specimens collected by Br. G. Nicholas Sullivan in Fogelpole Cave, Monroe County, Illinois. Later examination of the type series showed it to be morphologically inseparable from populations of *P. hirtus* from the immediate vicinity of Mammoth Cave, Kentucky (Peck 1973). The species validity was accepted and interpreted as being an isolated population of a biological species derived from *P. hirtus*, which dispersed overland during the Wisconsinan glacial some 350 km from central Kentucky to western Illinois (Peck 1973). Extensive fieldwork in caves throughout Illinois has failed to rediscover this beetle either in the type locality or any other Illinois cave. No evidence was found of habitat disruption or other change to suggest that the beetle had recently become extinct (Peck and Lewis 1978). The possibility was suggested that the species was based on erroneously labeled material from Kentucky. The collector had in fact been in caves in Flint Ridge of Mammoth Cave National Park just days before visiting Fogelpole Cave, Illinois.

In the light of the inability to rediscover the species in Illinois, and the unprecedented dispersal event (for a cave-limited beetle) that would be needed to explain the presence of a *P. hirtus*-like population in Illinois, I now suggest that the species does not exist, that it was based on mislabeled Kentucky material of *P. hirtus*, and that *P. nicholasi* should be considered a synonym of *P. hirtus*.

Taxonomic revisions

The above new evidence and conclusions require the following revisions of taxonomic status and descriptions of new species. However, much laboratory and fieldwork yet remains to be done to further test the hypotheses contained in this systematic arrangement.

Ptomaphagus hatchi Jeannel, new restricted status

The species is here recognized as populations formerly called *P. hatchi hatchi* form I (Peck 1973) (Fig. 10) in south-central Tennessee and northeastern Alabama (Fig. 1). New population records and the number of specimens are the following: *Alabama*. Jackson County. Dry Cave (AL 438[1]), 9 mi W Bridgeport,[2] May 1970, R. Graham, 2. Crowson Cave (AL 1025), 6 mi NW Hollytree, 4.VII.69, W. Torode, 10. Cagle Cave (AL 283), 4 mi NNW Princeton, 20.VII.71, S.B. Peck, 37. Slippery Pole Cave (AL 1022), 9.V.73, S.B. Peck, 28. Buds Cave (AL 651), 4 mi NE Princeton, 10–19.V.72, S.B. Peck, 18. Guess Creek Cave (AL 593), 21.VIII.71, S.B. Peck,

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[1] The AL number identifies the cave in the catalogue of the Alabama Cave Survey.

[2] Specimen label data on localities are not converted from imperial to metric units.

16. Cave 50 ft above Haddon Spring (R6E, T1S, Sec. 31, Hytop), 2.II.1980, T. King, 4. Roadside Cave (AL 826), 0.4 mi NW Hollytree, 21.VII.71, S.B. Peck, 20. Dripping Spring Cave (AL 330), 1 mi NW Trenton, 18.VIII.71, S.B. Peck, 5. Trenton Cave (1101), $\frac{3}{4}$ mi WNW Trenton, 18.VIII.71, S.B. Peck, 1. Fourth of July Cave, (AL 967), 3.5 mi NW Hollytree, 23.VIII.71, S.B. Peck, 4.

Ptomaphagus chromolithus **Peck, new species**

HOLOTYPE FEMALE: In Field Museum, Chicago. Type locality: Alabama, Jackson County, Williams Saltpeter Cave (AL 590). Type data: 28.VIII.67, R. Graham.

PARATYPES: 40 females and 25 males with same data; 5 males and 5 females, 5.VIII.67, S. Peck and A. Fiske.

DIAGNOSIS: The species is characterized by a very elongate and thin spermatheca, with a distal twist and large basal crest (Fig. 4). The description otherwise is that of *P. hatchi* (Peck 1973, p. 78).

DISTRIBUTION: The species occurs in caves in the upper Paint Rock River drainage of Jackson County Alabama and Franklin County Tennessee (Fig. 1). Seven of these populations were formerly called form II of *P. hatchi* in these caves as well as Round Mountain, Putman Spring, "Section 20", Horseshoe, Doodlebug Pit-Blowing, and Doug Green caves (Peck 1973). Two hundred fifty-two specimens are known from these localities. The following are new population records: Jackson County. Little Sink Cave (AL 657), 0.5 mi E Hollytree, 21.VIII.71. S.B. Peck, 21. Beanfield Cave (AL 1069), 3 mi E Princeton, 19.VIII.71, S.B. Peck, 3. Fortyeight Ten Cave (AL 604), 2 mi ENE Hollytree, 10.V.72, S.B. Peck, 12. Moon Spring Cave (AL 1067), 9–12.V.1972, S.B. Peck, 2.

ETYMOLOGY: The specific name is used as a noun in apposition. It is from the Greek *chroma* and *lithos* for color and stone, referring to the Paint Rock River.

RELATIONSHIPS: The characters of the spermatheca suggest that the species is derived from a common ancestor with *P. valentinei* and not from *P. hatchi* as previously implied.

Ptomaphagus laticornis Jeannel, new status

This species is known only from Hutton, Rousseau, and Scott caves, near the border of Madison and Jackson counties, Alabama (Figs. 1, 8). It is resurrected from synonymy under *P. hatchi* as form III (Peck 1973). More records should be sought to document the species distribution and how it and *P. hatchi* segregate themselves, especially in the two ends of the same subterranean river system in connected Cave Stand and Rousseau caves. The Hutton population was erroneously called *P. hatchi* form I. No new records are available.

Ptomaphagus fecundus Barr, resurrected status

The species is raised from subspecies status (Figs. 1, 9). Other populations should be sought in Franklin County Tennessee, because the type population seems to have become extinct following the disappearance of the bat colony whose guano apparently supported the beetles.

Ptomaphagus torodei **Peck, new species**

HOLOTYPE FEMALE: In Field Museum, Chicago. Type locality: Alabama. Jackson County. Two Way Cave (AL 1068), 6 mi WNW Scottsboro. Type data: 9.VII.1973, S.B. Peck.

PARATYPES: 18 with same data and one from Hall Cave (AL 763), 7 mi NW Scottsboro, 8.VII.1973, S.B. Peck (Fig. 1).

DIAGNOSIS: The species is characterized by the spermatheca (Figs. 5, 6) with a pronounced but variable cuplike depression in the posterior end, a thin and curved shaft, and anterior bulb with pronounced crest. In all other observed characters the species is similar to *P. valentinei* Jeannel.

ETYMOLOGY: The species is named for Mr. William Torode of Huntsville, Alabama, in recognition of his contributions to my fieldwork and to general speleology through his discovery, exploration, and surveying of many caves in Alabama.

RELATIONSHIPS: The species is judged to have originated as a peripheral isolate of *P. valentinei*, from which it is now separated by no apparent extrinsic barriers to gene flow.

Ptomaphagus loedingi Hatch, new restricted status

The species is here recognized as being limited to populations in Madison County, Alabama, west of the Flint River (Figs. 2, 11, 12). Future workers should try to test the status of the peripheral population in Pitts Sinkhole Cave, described as *P. valentinei jonesi* Jeannel and later synonymyzed under *P. loedingi* (Fig. 12).

Ptomaphagus julius Peck, new status

The status of this taxon (Figs. 2, 14) is raised from a subspecies of *P. loedingi.* A new record is Jackson County, Lindsay Spring Cave (AL 975), 4 mi WSW Scottsboro, Aug. 1969, Graham and Wilson, 3.

Ptomaphagus solanum Peck, new status

The taxon status (Figs. 2, 7) is raised from a subspecies of *P. loedingi*. No new records are available.

Ptomaphagus longicornis Jeannel, new status

The taxon status (Figs. 2, 13) is raised from a subspecies of *P. loedingi*. No new records are available.

Ptomaphagus valentinei Jeannel

The following (see Figs. 2, 3) are new records: Jackson County. Lost Cave (AL 584), NW of Stephens Gap, 8.III.70, R. Graham, 1. Marshall County. Royal Shaft (AL 1188), Feb. 1971, R. Graham, 2. War Eagle Cave (AL 565), 30.VIII.69, R. Graham, 2.

Ptomaphagus hirtus Tellkampf, 1844, p. 313.

Ptomaphagus nicholasi Barr, 1963; p. 53. New synonomy.

This species is here placed as a synonym of *P. hirtus* of the Mammoth Cave region of Kentucky for the reasons given in the above discussion.

These adjustments bring to 18 the number of cave-evolved species of *Ptomaphagus* known from the southeastern United States. These, combined with the edaphophilic (soil-dwelling) *P. shapardi* of the Ozark region make up the *hirtus* species group.

Phylogenetic relationships

The southeastern troglobitic *Ptomaphagus* should be an ideal group for the study of evolutionary dynamics. A sufficient number of species are present, with interpretable characteristics, to allow the construction of a hypothesis of phylogeny following the general methodology of "Hennigian" character analysis (Wiley 1981). The *hirtus* species group is assumed to be monophyletic, based on a combination of characters of gross body shape, male genitalia, habits, habitats, and especially the female spermatheca. However, the morphological characters

TABLE 1. Ancestral and derived character states used in Fig. 15, based on present knowledge of character conditions in *Ptomaphagus*, *Adelopsis*, *Echinocoleus*, *Ptomaphaginus*, and *Proptomaphaginus*, all members of the tribe Ptomaphagini. Character polarities were determined by the "out-group comparison" method (Watrous and Wheeler 1981). Illustrations of character states refer to figures in Peck 1973

No.	Character	Character state: Ancestral	Character state: Derived
1	Spermathecal shaft	Longer, thinner (Figs. 141–157)	Shorter, thicker (Figs. 158–163)
2	Spermathecal orifice	Posteriorly oriented (Figs. 158–163)	Laterally oriented (Figs. 141–157)
3	Aedeagus	Curved (Figs. 19–34)	Straight (Figs. 35, 38)
4	Mesosternal carina*	Lower (Figs. 78, 79)	Higher (Fig. 91)
5	Pronotal strigae	Present	Reduced or absent
6	Eyes*	Cluster of distinct facets (Fig. 5)	Unpigmented reduced facets (Fig. 6)
7	Spermathecal shaft	Thin (Figs. 142–145, 149–151, 153, 157)	Thinner (Figs. 146–148, 152, 154–156)
8	Posterior end of spermatheca	Not or slightly expanded (Figs. 142–145, 149–151, 153, 157)	Greatly deflected (Figs. 146–148, 152, 154–156)
9	Spermathecal crest	Small (Figs. 142, 149, 156)	Large (Figs. 152, 154)
10	Aedeagal tip	Straight (Figs. 24, 25, 30)	Upturned (Fig. 26)
11	Hind pronotal sides	Curved	Straight
12	Body length*	Smaller (2.0–2.8 mm)	Larger (2.6–3.3 mm)
13	Antennal segment III*	Subequal to II	Longer than II
14	Antennae*	Shorter (Fig. 114)	Longer (Fig. 116)

*Cave-dependent characters, potentially appearing convergently in separate lines (see Barr 1967; Christiansen 1961; Peck 1973).

may be symplesiomorphies. Based mainly on the more simple spermathecal configuration, this group is also thought to be the sister group to two more advanced and widespread groups containing over 36 species distributed from Guatemala to Canada, inhabiting forest litter, nests and burrows of vertebrates and invertebrates, and caves. These other groups also contain species with reduced or absent wings and eyes, and which may be cavernicolous.

An analysis of morphological characters within the *hirtus* group provides a set of hypotheses of character transformations from an ancestral to a derived state (Table 1). A hypothesis of phylogeny is proposed (Fig. 15). In such an analysis, care must be given to functional relationships of characters so that a phylogeny is not based on convergence. This is especially true if cave-dependent and cave-independent characters are not recognized and separated (Christiansen 1961). The cave-dependent characters have a higher probability of multiple independent origin and of convergent or parallel evolution as a response to selection by cave environments and are thus less reliable. These characters have been discussed for *Ptomaphagus* by Peck (1973). In cave *Ptomaphagus* regressive evolution is prominent, and character transformation series based on shared, derived complex characters are difficult to find or may be of questionable reliability. For instance, Fig. 15 shows an interpretation of the multiple origin of character states in several cave-dependent characters, such as two separate losses of eyes (character 6), two separate developments of a prominent mesosternal carina (character 4), and three separate developments of longer antennae (character 14). Straight pronotal hind angles (character 11) appears in a derived condition three times, but if this is an adaptive response to cave-selection on body form is not clear.

The most parsimonious use of some of these multiple character occurrences, such as the loss of eyes, would be to place them more basally on the cladogram. Thus eye loss would occur only once, and this character would be reversed (eyes regained) in *P. shapardi*. This is a prime example of how characters have to be weighted and evaluated in their placement in reconstructing phylogeny. That is, loss characters have low weight. There are many separate gene-based developmental patterns involved in the ontogeny of complex characters such as eyes. There are thus many ways to produce blindness or eye regression (reviewed in Culver 1982). Packard (1888) showed histologically that there was a complete degeneration of the optic nerve between the brain and the pigmentless eye facet remnants in *P. hirtus*. While eyelessness and eye polymorphism is known in many separate groups of beetles (e.g., Cornell 1972; Dybas 1977), I know of no case where it is suggested that a species has regained eyes after they were lost in an ancestor. "Dollo's Law" of the irreversibility of evolution would be violated by the reappearance of such a complex character as eyes after their loss. Characters 4, 11, and 14 are likewise not used more basally to define clades in Fig. 15 because they are interpreted as the multiple products of convergence. Greatest weight has thus been given to cave-independent characters.

An additional difficulty with the cladogram is that several species or species groups such as the *hazelae* group, the *hatchi–longicornis–whiteselli* group, and the large *hatchi* group itself have no derived characters to define them. Thus, the groups are paraphyletic, being based only on shared ancestral characters. Additional study and analysis by alternative methods may or may not find characters to substantiate the groups as they are presented. The methods I have employed may be at the limits of their utility or reliability for understanding speciation in a group where characters are most frequently lost, reduced, or subject to convergence because of uniformly extreme environmental selective pressures.

Lastly, some aedeagal and spermathecal characters seem to be correlated, such as in characters 2 and 3, and 9 and 10. This suggests that there may be some functional relationship between them. These may partially represent the actual intrinsic isolating mechanisms between the species. If this is so, it could also imply that the species were sympatric or parapatric

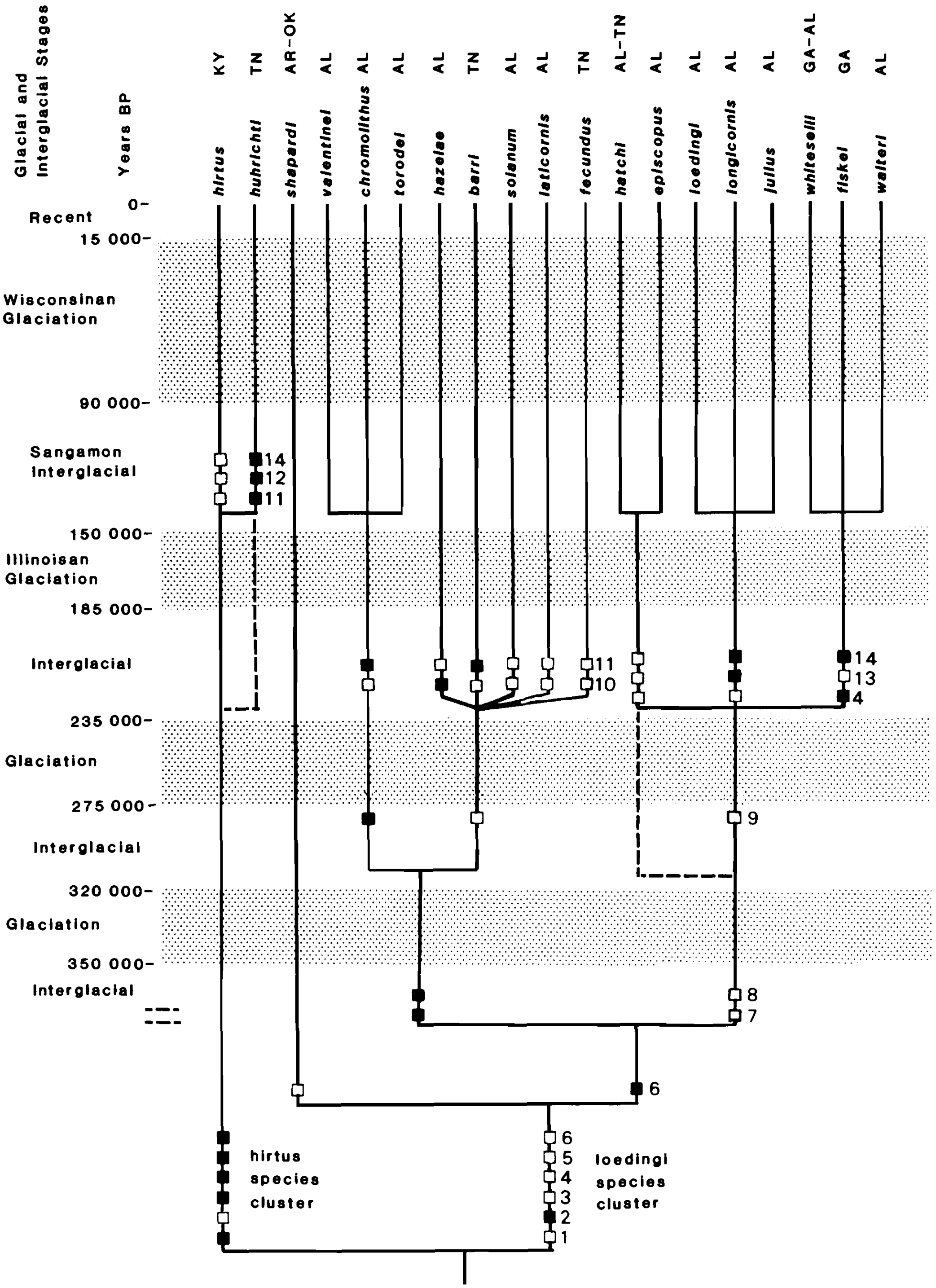

FIG. 15. Phylogenetic hypothesis of evolution in the monophyletic, cavernicolous *hirtus* species group of *Ptomaphagus (Adelops)* of the southeastern United States. Numbers refer to characters in Table 1, transforming from ancestral (☐) to derived (■) states. State abbreviations with species names indicate distribution. Lineage splits and character origin are shown for the latest likely times for the events (giving comparatively rapid evolution). If the events were earlier, diversification was slower. The model for differentiation is one of small allopatric populations isolated (virtually instantaneously) in caves during the beginnings of repeated interglacial cycles because of an inability to tolerate the initiation of epigean habitat warming and drying. Low-level troglobites (or cave-limited troglophiles) formed during one interglacial were probably capable of overland dispersal as troglophiles in the next glacial. Increasing specialization incrementally limited the capacity for overland dispersal in following glacials. The timing of cycles of glacials and interglacials is from Harmon *et al.* 1977, based on the use of geochemical isotope techniques to determine the time and temperature of deposition of cave stalagmites (see also Harmon, Thompson *et al.* 1978, Harmon, Schwarz, and Ford 1978). Interglacials are shown of greater duration than generally indicated by marine cores. The actual picture (including the effects of interstadial climate changes) may be more complex, suggesting greater difficulty in matching biotic and climatic events. If there was a "great interglacial" from 280 000 to 400 000 years BP (Harmon *et al.* 1977), it would have been a period of pronounced cave restriction and adaptation (or extinction). Unresolved difficulties with the diagram include clades which are not defined by shared derived characters. The horizontal clade lines are intended to indicate time of hypothesized population isolation and possible initiation of character divergence.

in the past, as I suggest they were during phases of overland dispersal and population contact during glacial climatic conditions.

The ease of obtaining large population samples, of rearing them, of making hybrid crosses, and of performing electrophoretic analyses gives abundant opportunity to others to independently test the phylogeny.

Timing of speciation events

A favored model of speciation of terrestrial arthropods in caves is the allopatric isolation of populations in cave habitats in interglacials, because of intolerance to epigean conditions of warmth and dryness (see Barr 1967, 1968; Chapman 1982; and Howarth 1983 for background on speciation in caves). These occupations and isolations could have been repeated as cycles through the many climate changes of the Pleistocene (Peck 1978*a*, 1980; Peck and Lewis 1978). The effects of the climatic changes on vegetation are well known (Watts 1979, 1980).

With such a model of dynamic cyclic population isolation and dispersal, the phylogeny can be put on a time scale, where the appearance of derived character states can be coordinated with times of interglacial cave isolation. It should be realized that a paleoenvironmental understanding of all but the late Pleistocene is still lacking. Most Pleistocene temperature curves have been based on ocean sediment cores (Broecker and Van Donk 1970; Shackleton and Opdyke 1973). While the use of geochemical techniques to date the time and temperatures of deposition of cave stalagmite deposits seems a powerful tool by which we can hope to understand the changes in cave environments through the Pleistocene (Harmon *et al.* 1977), there is still too much variation from site to site to give more than a rough framework upon which to hang biological events (see also Harmon, Thompson *et al.* 1978; Harmon, Schwarz, and Ford 1978).

The proposed timing of isolation events in Fig. 15 is consistent with other data. Within the present interglacial period, genetic differentiation is interpreted to have accumulated in *P. hirtus* in Kentucky caves, but it is not morphologically detectable nor has it affected the hybridization potential of the populations sampled from throughout the range (Laing *et al.* 1976). This probably holds true for the other taxa of cavernicolous *Ptomaphagus*. Therefore, differentiation that is morphologically detectable probably dates from at least the next earlier interglacial period of subterranean isolation, and this probably represents the last time of species differentiation. The earlier divergences in lineages (Fig. 15) are probably minimum times for the appearance of the derived character states.

The timing and number of cave occupations and isolations remain theoretical but are certainly more than the four recognized in the "classic" sequences of the central United States. A stabilized system of terms for time intervals and events is yet to be achieved for terrestrial deposits in North America (Boellstorff 1978). Also, the Pleistocene is now being seen by some (Beaty 1978; Cooke 1973; Emiliani 1972; Wright 1976) as a sequence of long-lasting glacials of 80 000 to 100 000 years punctuated by significantly shorter interglacials of 10 000 to 15 000 years. An alternative possibility is that interstadials, such as the mid-Wisconsinan interstadial from about 36 000 to 23 000 years BP, could have had climates with the same effects on populations as full interglacials. Either of these would give comparatively short periods for population isolation and genetic differentiation and much longer periods for possible overland (as well as underground) dispersal and the biotic "testing" of the new genotypes. Thus, only comparatively short time spans may have been available for the evolution of "troglobites," which were thus probably not highly specialized and therefore had a better opportunity to reoccupy epigean habitats in the succeeding glacial. Recent work in France (Juberthie *et al.* 1980) has shown many "cave" taxa to be present in deep soils in noncave regions.

The genetic attributes and structures of cavernicolous *Ptomaphagus* populations are poorly known (Laing *et al.* 1976). However, they may have the characteristics that would help explain their seemingly rapid diversification and speciation in Alabama caves via the founder principle and genetic revolutions, as explained by Barr (1968). Selection in multilocus systems controlling developmental, behavioral, and other integrated traits is particularly sensitive to founder effects (Templeton 1980). Cavernicolous *Ptomaphagus* do have the population attributes (where known) listed by Templeton (1980, p. 1029) which increase their susceptibility to speciation by the founder effect. Thus, depending on genetic and population structure (Templeton 1980), the ancestral cave-colonizing populations of *Ptomaphagus*, under the effects of changing climate and restriction to caves, could have experienced a rapid increase in inbreeding at the time of cave isolation without necessarily experiencing a reduction of genetic variability. If the number of loci involved in the genetic revolution (or genetic transilience) was only in the order of magnitude of 10, this in itself could have actually *caused* the speciation event (Templeton 1980, 1981, 1982). Additional genetic discussion relevant to cave speciation theory is that of Lande (1980, 1981).

However, while the above theory argues that periods of change may be *interpreted* as possibly having been very rapid, there is no direct evidence to show that they actually were in the cavernicolous *Ptomaphagus*. The problem of rate of genetic change in cavernicoles in both neutralist and selectionist hypotheses is reviewed by Culver (1982).

Rapid speciation events, allowed by the above population genetics theories, are portrayed as such in Fig. 15 and appear to support the much discussed punctuated equilibrium model of speciation (see Kirkpatrick 1982). However, I see these processes as working within a microevolutionary framework, and follow the critique of the punctuated equilibrium model of Levinton and Simmons (1980).

Origin and dispersal of "troglobites"

The species ancestral to modern cave-evolved species of terrestrial arthropods are generally considered to have been deep soil and litter inhabitants; i.e., edaphophiles that had potential for becoming troglophiles (Barr 1968). The edaphophilic *Adelopsis* of the southeastern United States (Peck 1978*b*) may be ecologically analogous to these ancestral species. Epigean species that can occupy caves and maintain populations in them are called troglophiles. When interglacial climatic change eliminates the adjacent epigean populations of the troglophilic species, the population in a cave becomes genetically isolated and may begin a separate path of genetic differentiation. Such a cave-limited population, especially when it displays cave-selected features, is called a troglobite.

With the return of suitable epigean climatic conditions in the next glacial, the nascent troglobite may still be generalized enough to have potential for reoccupation of some epigean habitats and for overland dispersal through deep litter, or moss mats, talus, etc.

This is likely in populations that had not proceeded too far along the path of cave specialization. Their degree of restriction to cave habitats was probably related to the severity of change of epigean climatic conditions. Thus, a population that was a nascent troglobite in an interglacial might have been able to again become a troglophile in the next glacial.

I suggest this as a mechanism by which populations that had already experienced some cave isolation and differentiation could later reach unoccupied limestone mountains, such as Keel Mountain (Fig. 2) surrounded by deeply alluviated lowlands. I assume that underground dispersal of terrestrial troglobites is possible at any time if there are subaerially continuous limestones. However, there are several geologically isolated limestone mountains in Alabama with cave-specialized species of *Ptomaphagus*. The question is whether or not the ancestors of these populations had experienced character divergence through cave isolation at a time previous to their dispersal to the isolated cave-containing mountains in which they now occur. The cladogram (Fig. 15) does suggest a sequence of character changes which may have occurred in earlier cycles of interglacial cave isolation, followed by later overland dispersal in glacials.

Origin of a species swarm

The picture of evolution of cave *Ptomaphagus* presented here and in Fig. 15 is very different from one presented earlier (Peck 1973). It is seen now that there is a more elaborate hierarchy of lineage origin over a greater span of time. Even though the rate of beetle evolution as documented by fossils (Coope 1979) shows no evidence for Pleistocene speciation, it could have occurred in small and immobile populations under extreme selective pressures (populations such as in caves and those least likely to leave a fossil record). It is likewise true that even in cave areas, the peripheral isolates, with less possibility of maintaining subterranean gene flow, were those most likely to diverge or to go extinct. Pleistocene climatic changes are seen to have coordinated "pulses" of cave colonization and the vicariance fragmentation of epigean distributions.

From this series of considerations, a scenario of historical zoogeography can be constructed. Two main lineages are present, representing two ancestral species. One of these, to become the *hirtus* species cluster, was more northern in distribution, and the other, to become *P. shapardi* and the *loedingi* species cluster, was more southern. A microphthalmic and micropterous condition and a deep litter or soil habitat was a preadaptive stage for both lineages. This ancestral condition has survived only in *P. shapardi* of the Ozarks. The presence of this lowland species, the absence of montane survivors in the upper elevations of the Appalachians, and the general distribution patterns shown by other edaphophilic cholevines (i.e., *Adelopsis*, Peck 1978*b*) in the southeast suggests that the early lineages may have been lowland, and not necessarily montane as earlier stressed (Peck 1973).

What followed the initial cave colonization in an interglacial was a series of successes and failures in the survival of populations in the face of repeated environmental changes. Epigean glacial conditions were more rigorous in the north and fewer lineages either originated or survived in the *hirtus* cluster. To the south, where glacial conditions were less rigorous, more lineages survived and more differentiation occurred. Circumstantial evidence suggests that these processes occurred primarily in the latter half of the Pleistocene, and involved few ancestors of rather limited distribution. Otherwise we should expect more species over a wider area (such as in the thousands of unoccupied caves of the Appalachian Valley region of West Virginia, Virginia, eastern Tennessee, and east-central Alabama) and more occurrences of sympatry, as found in the large troglobitic carabid beetle genus *Pseudanophthalmus*. The sympatry of *Pseudanophthalmus* may be because there was a larger number of ancestral lineages or they had more time to develop ways to divide niche resources and to adopt different modal body sizes (Barr and Crowley 1981), or for other reasons such as greater dispersal potential in broadly continuous karst regions (Barr 1967).

Epigean cholevines may achieve sympatry and an apparent lessening of competitive intraction by differences in body size and seasonality, as demonstrated by Topp and Engler (1980). Generally it has been found that closely related species with similar "niche" requirements can coexist successfully if none of their populations is resource limited (Ayala 1972; Pielou 1975; Schoener 1974, 1982). We have shown that the cavernicolous *Ptomaphagus* populations have genetically diverged to a point where they are reproductively isolated and should be treated as species. However, these species probably still have niche requirements which are so similar that they are actual competitors for resources, such as food, which are probably limited in caves (even if their population sizes are also regulated by factors other than shortages of shared resources). The species are thus ecologically incompatible and this is shown in their mutually exclusive populations.

The occupation of any particular cave probably had a large random (historical) component to it, whether dispersal to the cave was by either underground or overland means. But once a cave site was occupied by one taxon, it prevented the colonization of another (unless some taxa are competitively superior and are able to evict the first occupants). In any event, these possible processes of epigean population interaction were probably much more frequent during glacials, when overland dispersal and sympatry was more likely. Isolating mechanisms may have been reinforced or improved by such epigean interactions. Minor range alterations may have occurred in the Recent through subterranean dispersal to previously unoccupied caves, or through competitive replacement by more dominant species. Population cage studies, such as those done with *Drosophila*, can experimentally examine this question (reviewed in Ricklefs 1973, p. 519).

Conclusion

In conclusion, I suggest that the model I have presented for the dynamics of population isolation and genetic differentiation in cave *Ptomaphagus* is one that should be generally applicable to other groups of terrestrial cavernicoles, such as to other beetles, millipeds, and crickets. If several species components of cave communities have had the same set of geograhic distributions and experienced the same population fragmentations through several cycles, their species−area cladograms should be similar. This outcome would show that not only species but cave communities can have species distributional patterns formed by processes of what has come to be called vicariance biogeography (Rosen 1978; Wiley 1981).

The above data and hypotheses are offered as a contribution to understanding the evolutionary dynamics of terrestrial cave invertebrates. Much additional field and laboratory work yet remains to be done to fully document the details of the geographic distribution, systematics, and evolution of these rich faunas in the southeastern United States, where over 2000 caves and over 80 species of cave-limited arthropods are known to occur in Alabama alone.

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