

SYSTEMATICS AND EVOLUTION OF
FOREST LITTER *ADELOPSIS*
IN THE SOUTHERN APPALACHIANS*
(COLEOPTERA: LEIODIDAE; CATOPINAE)

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The beetle genus *Adelopsis* was described by Portevin in 1907, and was proposed for a microphthalmic soil-inhabiting species from Bolivia. Since then, some 20 additional species have been described, and the genus is known to be distributed through the Neotropics from Mexico to southern Brazil and adjacent Argentina. The species are generally large-eyed and winged, and are probably all scavengers of decaying organic matter in mesic tropical lowland and montane forests. They may occasionally occur in caves. The beetles are seldom represented in collections, but they may be frequently collected by sifting forest litter, or by using dung or carrion-baited pitfall traps. My field program of such collecting in the Neotropics since 1966 shows the genus to be far more diverse, abundant, and widespread than indicated in the present literature (Peck, 1977).

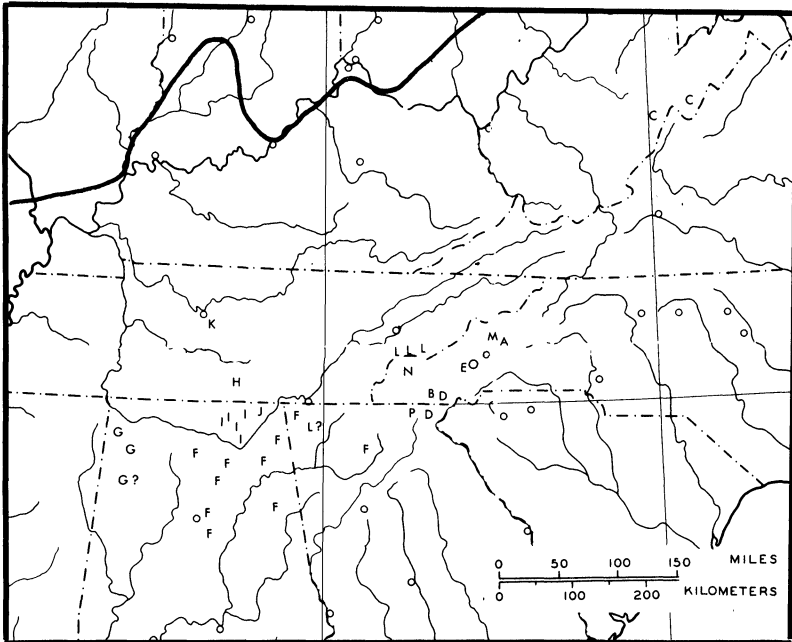
Adelopsis was first found to occur outside the Neotropics when I (Peck, 1973) realized that *Adelops mitchellensis* (Hatch, 1933) from Mt. Mitchell, North Carolina, actually belonged in the genus *Adelopsis*. Some authors had placed the species in the genus *Ptomaphagus*. At that time I noted that I also had material of other species from North Carolina, Georgia, Tennessee, Alabama and West Virginia. My indication that they were also in New Mexico was in error (Peck, 1978). The purpose of this paper is to describe these species which occur in forest litter and soil habitats in the southeastern United States, and to consider their distributional and evolutionary history.

Generic diagnosis. The characters are those of Leiodidae, Catopinae, Ptomaphagini (as given in Peck, 1973). As such they are small beetles with a loose antennal club, with segment 8 always smaller than 7 and 9. They have transverse pronotal and oblique

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elytral strigae, and the summits of their tibiae are armed with a comb of many short and equal spines, as well as by two longer spurs (see Peck, 1973, 1977 and their cited references).

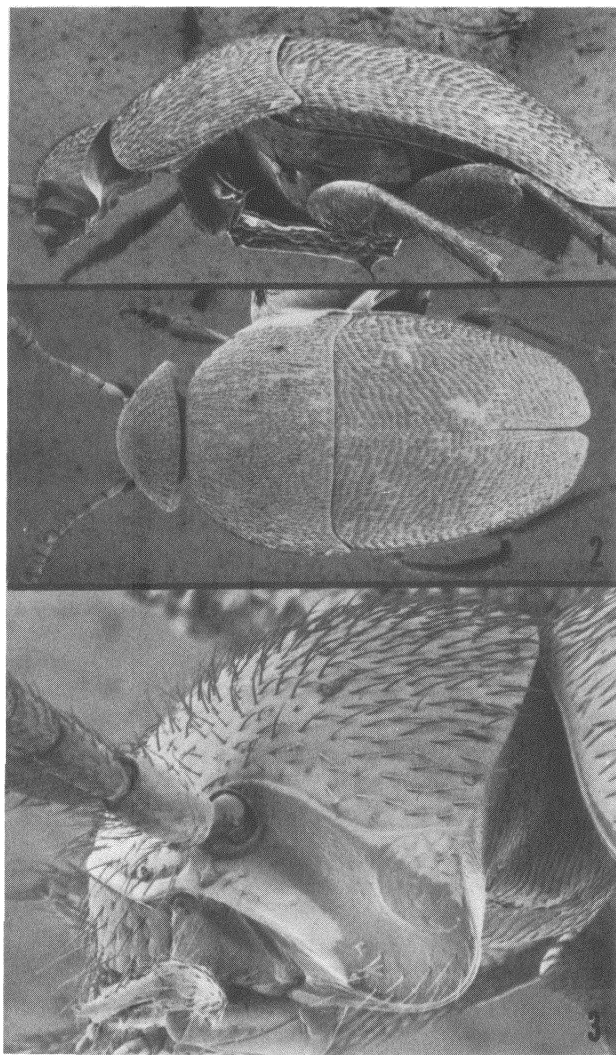
Adelopsis is generally difficult to separate from its nearest neighbor, the genus *Ptomaphagus*, using only external characters. Tropical species of *Adelopsis* (but not those of the U.S.) usually differ by being smaller (length 2.6 mm or under) and in having the antennal club more loosely composed of gradually larger segments, of which the last two are often conspicuously lighter in color. The genera are more reliably separated by the chitinized internal reproductive structures of the aedeagus and spermatheca. In *Adelopsis* the spermatheca (as far as is known) is a more simple curved tube, and the aedeagus has a tip which is more elaborately sculptured, or



Map 1. Distribution of known species of *Adelopsis* in the southeastern United States. Heavy irregular line indicates maximum extent of Pleistocene glaciations. A, *A. mitchellensis*. B, *A. steevesi*. C, *A. alleghenyensis*. D, *A. suteri*. E, *A. richlandensis*. F, *A. appalachiana*. G, *A. jonesi*. H, *A. bedfordensis*. I, *A. cumberlandia*. J, *A. scottsboroensis*. K, *A. nashvillensis*. L, *A. fumosa*. M, *A. alta*. N, *A. joanna*. O, *A. pisgahensis*. P, *A. orichalcum*.

is broader and more blunt. The orifice is dorsally sub-terminal and cuts the left side of the aedeagus as in *Ptomaphagus*. The southeastern U.S. *Adelopsis* species are all forest litter and soil inhabitants. They are all wingless and have eyes reduced to a collection of about 20 pigmented facets. These structural features will help to distinguish them from most *Ptomaphagus*, which are either winged and with larger eyes, or are more subterraneanly adapted (for life in caves) and have more-reduced eyes.

Description. The following applies only to the range of variation known in the species in the southeastern U.S. Additional details on Neotropical species may be found in Jeannel (1936) and Szymczakowski (1964, 1968, 1969, 1975). Length 2.3 to 2.6 mm, width 1.2 to 1.3 mm. Form elongate oval, compact, convex (Figs. 1, 2). Color light to dark reddish brown. Pubescent, with numerous short recumbent hairs. Head finely punctured; eyes reduced to collection of about 20 pigmented facets (Fig. 3); eye width $1/3$ width of space from antennal base to head margin across eye. Antennae short, compact; club darker, somewhat flattened; reaching from middle to hind margin of pronotum when laid back; segment 3 shorter than 2, segment 6–10 wider than long; 8 over twice as wide as long (segments usually longer and thinner in upper elevation deep-litter species than in lower elevation litter-soil species). Last article of maxillary palp slightly shorter than preceding; conical, thinner. Pronotum widest $1/3$ before base, 1.4 to 1.5 times as wide as long; hind angles acute, hind margin straight; sides arcuate; covered with seta-bearing punctures strongly to faintly organized into striae. Elytra fused, sides gradually tapering to apex in both sexes; external apical angles broadly rounded; sutural angles rounded; apex oblique; strigae distinct, oblique, composed of seta-bearing punctures. Metathoracic (flight) wings reduced to tiny scales. Mesosternal carina low, its notch distinct. Legs not noticeably short and compact (seemingly adapted for running and not digging); protibiae bowed-in, mesotibiae bowed-out, metatibiae straight; comb of spines limited to tibial apex; protibial apex oblique and rounded in both sexes; sexual dimorphism only in protarsi, males with first 4 protarsal segments expanded and spongy-pubescent beneath. Aedeagus curved, stout, blunt, with orifice cutting to dorsal surface through left side; internal sac with curled, short, terminal stylet with surface ridges on one side of tip; about 6 sensory hairs on under



Figures 1-3. SEM photomicrographs of *Adelopsis mitchellensis* (Hatch). 1. Lateral view, left proleg removed. 2. Dorsal view. 3. Lateral view of head showing eye reduced to collection of about 20 poorly defined facets.

surface of each side of tip. Parameres fused to aedeagus at base; with three terminal hairs. Spiculum gastrale short, thick, less than $\frac{1}{4}$ its length projecting beyond anterior end of genital plates. Spermatheca thin and curved; anterior recurved and often with flattened crest; posterior end often laterally curved-back on itself.

Bionomics. The known United States species are all inhabitants of moist moss, litter, and soil of forests in the Appalachian Mountain Chain, south of the limits of glaciation, from the lowlands inside the Fall-line to the summits of the highest mountains. They are occasionally found in soil-filled rock crevices or under large rocks deeply embedded in forest soils, but are more usually captured by sifting litter and moss and by extracting them with Tulgren-Berlese funnels. The litter at the sides of rotting logs seems to be a favored habitat. They may be locally abundant in association with decomposing fleshy fungi or material richly impregnated with fungal hyphae, but some may be taken at dung or carrion baits in forests, or in caves. The frequency with which they have been collected in caves reflects only that this is a way by which a collector can gain easy access to the faunas of deep soils. In caves, the beetles are found near cave entrances only and not in the deep regions of caves. The beetles are not morphologically adapted for caves as such. This is evident when they are compared to cave-evolved species of *Ptomaphagus* (Peck, 1973), so they should be termed edaphophiles (or endogeans or edaphobites), rather than troglaphiles, or troglobites. In litter, they seem to be more frequently encountered in the springtime and early summer, probably because they are more commonly present in the upper layers of litter and soil which are cool and moist at these seasons. They probably retreat downwards with the increasing warmth and dryness of summer. Records do not indicate it, but I think they would be active and accessible to the collector in the late fall and at certain times of the winter as well.

Life cycle characteristics have been determined only from specimens captured on several occasions in Morrison's Cave, Dade County, Georgia, and kept in laboratory culture at 15°C. The techniques are those used in culturing *Ptomaphagus* beetles (Peck, 1973, 1975). Eggs are laid singly by the females on the soil surface of the culture vessel. These hatch in a mean time of 12 days (range 9–15, $n = 7$). There seem to be three larval instars, and these feed for about 20 days before constructing a mud igloo or pre-pupation cell,

in which the larvae spend a mean of 14 days (range 12–16, $n = 7$) before pupating. The total larval duration then has a mean time of 34 days (range 23–40, $n = 7$). The pupal stage lasts for a mean of 20 days (range 14–24, $n = 6$), and pupal darkening is evident for the last two days before eclosion. The newly emerged adult remains in the pupal chamber for 5 days ($n = 3$) before emerging. The cycle is similar to that of several litter and cave species of *Ptomaphagus* at the same temperature (Peck, 1973, 1975, and unpubl.). Total longevity of adults is unknown. Adults of unknown age collected in April lived in culture for up to 10 months. Oviposition frequency could be determined for only one paired female which laid 9 eggs in 30 days at intervals of from 1 to 10 days.

The larvae are very similar to those of *Ptomaphagus* and I am unable to confidently distinguish the two. There is no strong evidence for seasonality in reproduction. In caves (and deep soil?) it may occur whenever moisture and food conditions are suitable and this probably holds for forest litter situations with cool-moist seasons being better than warm-dry ones.

Systematics

Methods and Materials. Specimens were borrowed from the following collections and curators: American Museum of Natural History (AMNH), Lee Herman; Field Museum of Natural History (FMNH), Henry Dybas; Illinois Natural History Survey (INHS), Milton W. Sanderson; United States National Museum (USNM), John Kingsolver; Museum of Natural History, University of Alabama (UANH), Herbert Boschung; Museum of Comparative Zoology (MCZ), John Lawrence and Alfred Newton. Specimens not attributed to these collections are in that of the author. Types are deposited in the Canadian National Collection (CNC) unless otherwise indicated. Initials of collectors who frequently found material are as follows: SBP, Stewart B. Peck, often helped by Alan Fiske, James Peck, and Jarmila Peck; WBJ, the late Walter B. Jones, often helped by A. Flannagan, J. M. Valentine, and others; HRS, Harrison R. Steeves, Jr., often helped by J. Patrick. WRS, Walter R. Suter. All HRS and WRS material is in the FMNH.

My collecting methods are described in sufficient detail elsewhere (1973, 1977, and Newton and Peck, 1975) and need not be repeated. This is also true for the methodology of specimen preparation, with one major exception. A scanning electron microscope (SEM) was

found to be of great help in viewing and understanding the three-dimensional structure of the tips of the minute aedeagi. With this understanding, they can be more easily interpreted in the usual slide or glycerine jelly mounts and preparations. SEM photomicrographs were used to make the drawings of the aedeagal tips. A set of three views is usually necessary to interpret and understand the geometry of the aedeagal tip. Although a set of about 6 hairs occurs on each side of the undersurface of the aedeagal tip in all species, these have little value in helping to characterize the species. These hairs have been shown on only a few drawings. Internal sacs were fully seen only in polyvinyl-lactophenol slide mounts.

Variation. Little variation is evident in these species, and little is known of variation within the other species of the genus. Variation over the geographic range of a species is known and illustrated only for *A. simoni* (Portevin), known from Brazil, Venezuela and Mexico (Szymczakowski, 1968) and in *A. brunneus* Jeannel, from cave and forest sites from Columbia through Venezuela to Trinidad (Szymczakowski, 1975). Apparent variation in spermathecae is partly due to the difficulty in preparing these fragile structures. When material is limited and the normal spermathecal shape is not known with certainty, several may be illustrated.

Individual diagnoses are not given in the following species accounts. In all cases it would indicate that the species are characterized by the combination of characters of their geographic ranges, and of the aedeagal tips, and possibly of the spermathecae.

The gender of the genus is treated as feminine, following the use of its author.

The *mitchellensis* species group

This group is probably not a closely related assemblage, and is used as a grouping of convenience. Each of the five species is clearly defined, and each may be as phylogenetically old as the cluster of 11 species placed in the following *appalachiana* species group.

1. *Adelopsis mitchellensis* (Hatch) Figs. 1-5, 50

Adelops mitchellensis Hatch, 1933: 208. Synonymy given in Peck 1973: 55.

Material seen. North Carolina. Yancey County. Mt. Mitchell, no other data, holotype male, allotype female, and paratype male 50133, USNM. Mt. Mitchell 4500-6000' (=1475-1967 m); 17-24.VI.

1939, E. D. Quirsfeld, 1 male, MCZ. Mt. Mitchell, 6400' (2098 m), 3-10.IV.1967, S. Peck, carrion trap 214 in summit hemlock and moss forest, 1 female. Black Mountains, no other data, 1 female, USNM; 1 female, FMNH. Black Mts., 8.VIII.1911, 2 females, AMNH.

Description. Aedeagus (figs. 4-5) with dorsal section of tip flattened and projecting posteriorly over orifice on upper left side. Ventral section broad with central ogival point. Spermatheca fishhook-like (fig. 50) with simple posterior portion, and prominent crest on anterior end.

Distribution. The species is probably limited to the Black Mountains of Yancey County, containing Mt. Mitchell, the highest point in the eastern United States (2191 m). This is the only locality known to have two species of *Adelopsis*, for here *A. mitchellensis* is sympatric with *A. alta*. Some early collection records confused these two.

Notes. The species is probably most common in the upper elevation forests of spruce-fir or birch-maple. Adults have been collected in April, July, August, and September.

2. *Adelopsis steevesi* n. sp.

Figs. 6, 7

Holotype male and allotype female in CNC. Type data: North Carolina. Macon County. Norton, Coweeta Hydrological Laboratory, 24.X.1965, 4,000' (1311 m), log-litter, HRS. Paratypes: 17 with same data; 12 with same data but 22.V.1965, 4100' (1344 m) rot wood debris.

Description. Dorsal section of aedeagus tip (figs. 6-7) incised, upraised as knob on left, and as flattened vertical blade on right. Ventral section deeply emarginate, nearly same length as dorsal section. Spermatheca similar to that of *A. joanna*, *A. alta*, *A. fumosa*, *A. richlandensis*, and *A. suteri*.

Etymology. Named for Mr. Harrison R. Steeves, Jr., of Birmingham, Alabama, in recognition of his extensive field collecting of litter beetles in the southeastern United States (collection deposited in FMNH).

Distribution. The species should be expected in other sites in the vicinity of Highlands, North Carolina.

3. *Adelopsis alleghenyensis* n. sp.

Figs. 8–10, 51, 52

Holotype male and allotype female in CNC. Type data: West Virginia. Pendleton County. 5 mi (8 km) S Witmer, 3000' (915 m), 16.VII.1971, SBP, litter Ber. 217. Paratypes: 11 with same data; Spruce Knob, 3500' (1148 m), 8.VI.1967, SBP. Ber. 58, 1 male and 1 female; Pocahontas County, Hills Creek Falls, 19.VI.1971, W. Shear, Berlese, 2 males and 2 females.

Description. Dorsal section of aedeagal tip low and simple (figs. 8–10), with recurved flange on left; ventral section broadly pointed, with tip downcurved, extending far beyond dorsal section. Spermatheca (figs. 51–52) thick and gently curved, anterior crest large.

Etymology. The name refers to the northwestern flank of the Appalachians called the Allegheny Mountains, lying along the border of Virginia and West Virginia and extending into Pennsylvania.

Distribution. The species probably has a wider range than the known 60 mile (100 km) long NE-SW line along the Allegheny Mountains of West Virginia.

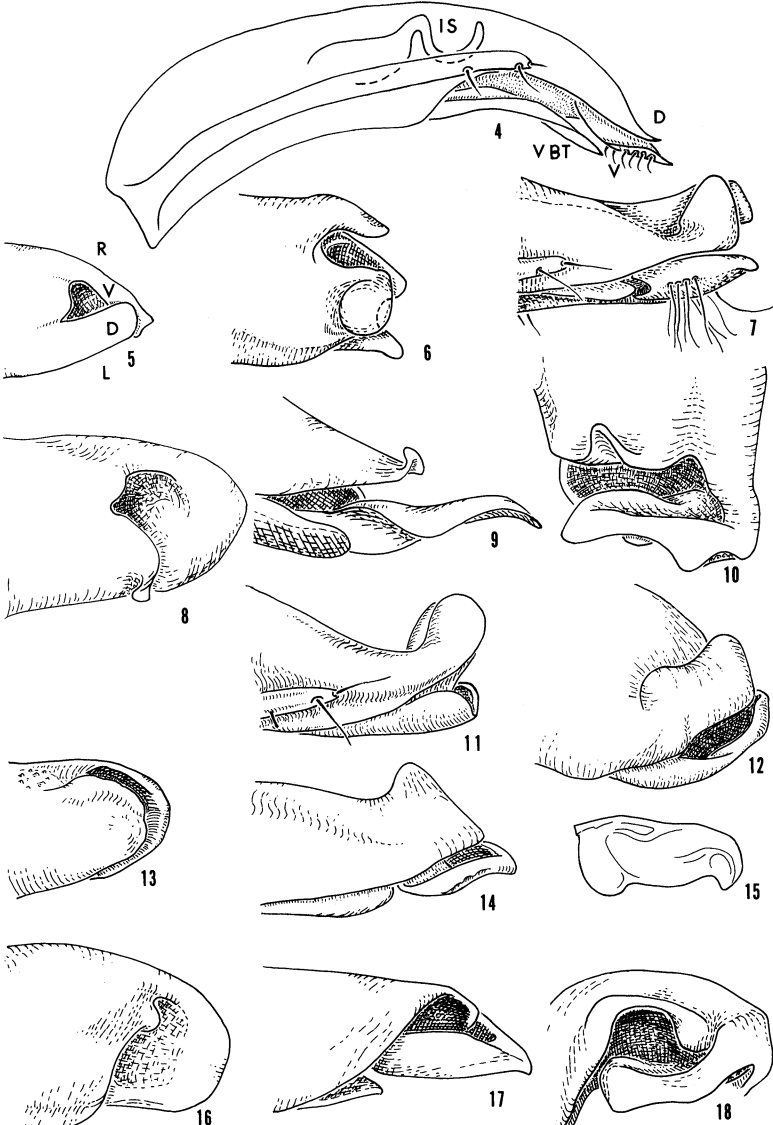
4. *Adelopsis suteri* n. sp.

Figs. 11, 12, 53, 54

Holotype male and allotype female in CNC. Type data. Georgia. Rabun County. Mountain City, Black Rock Mountain State Park, 15.VI.1973, W. R. Suter, litter at log under *Rhododendron*. Paratypes: 1 with same data; Black Rock Mountain State Park, 3000' (915 m), 21.VII.1967, 2 males. North Carolina. Macon County. 5 mi (8 km) NE Highlands, 27.X.1969, W. Shear, *Rhododendron* litter, 1 male. Jackson County, 7 mi (11 km) S Cashiers, 11.VI.1973, White-water Falls, elm-maple pseudofork, WRS, 1 female.

Description. Dorsal section of aedeagal tip (figs. 11–12) inflated, upturned, with broad and shallow depression in middle, equal in length to uniformly emarginate ventral section. Spermatheca (figs. 53–54) with sharp bend in posterior end, which projects strongly above plane of central curved section, anterior crest high.

Etymology. Named for Dr. Walter R. Suter of Carthage College, Kenosha, Wisconsin, in recognition of his extensive collecting



of litter beetles in the southeastern United States (collections deposited in FMNH).

Distribution. The species is to be expected in other localities in the Coweea Mountains in the vicinity of Highlands, North Carolina, which has been found to be a region rich in species of ground dwelling beetles.

5. *Adelopsis richlandensis* n. sp.

Figs. 13, 14, 55, 56

Holotype male and allotype female in CNC. Type data. North Carolina. Haywood County. Richland Balsam, 6000' (1967 m), 7–26.VIII.1965, S. & J. Peck, carrion trap. Paratypes; three females with same data; and 1 female, Haywood-Jackson Counties, Rinehart Knob, 6000' (1967 m), 1.VIII.1960, T. C. Barr.

Description. Dorsal section of aedeagal tip (figs. 13–14) uniformly rounded, but with slight emargination; sloping downwards from high crest on right to low and flat left side, ventral section uniformly rounded and projecting beyond dorsal section. Spermatheca as in figs. 55–56, characteristic form not known with certainty.

Etymology. The name refers to Richland Balsam, the type locality, and highest point on the Blue Ridge Parkway.

Distribution. There seems little reason to expect only this species on Richland Balsam. Mt. Pisgah, with *A. pisgahensis*, is on the same mountain ridge and there are no intervening lowland barriers to dispersal of these flightless beetles. Soco Gap and Balsam Gap to the northwest, each above 3000' (1000 m) separate Richland Balsam from the Plott Balsams and Balsam Mountains, but these also seem inadequate barriers to isolate Richland Balsam from species inhabiting these other mountain regions. Intensive collecting should resolve the questions of how these species are distributed with regards to each other.

Figs. 4–18. Structures of *Adelopsis*. 4. Left lateral view of entire aedeagus of *A. mitchellensis*, with internal sac (IS), ventral blade of tegmen (VBT), and dorsal (D) and ventral (V) sections of aedeagal tip. 5. Dorsal view of aedeagal tip of *A. mitchellensis* indicating right (R) and left (L) sides, and dorsal (D) and ventral (V) sections of the tip. 6–7. Dorsal and lateral views, aedeagal tip, *A. steevesi*. 8–10. Dorsal, lateral, and posterior view, aedeagus, *A. alleghenyensis*. 11–12. Aedeagal tip. *A. suteri*. 13–14. *A. richlandensis* aedeagal tip. 15. Internal sac *A. appalachiana*. 16–18. *A. appalachiana*, note that parameres and hairs on ventral surface of ventral section of aedeagus are not shown in most drawings.

The *appalachiana* species group

This group is seen as a naturally based and closely related phyletic unit. It is based on *A. appalachiana*, the most widespread species in both lowland and montane regions. Progressive modification of the relatively simple aedeagus (assumed to be generalized and pleisotypic) in the nominate species could readily produce the other aedeagal types known in the group.

6. ***Adelopsis appalachiana* n. sp.**

Figs. 15–18, 57–60

Holotype male and allotype female in CNC. Type data: Alabama. DeKalb County. Fort Payne, Manitou Cave, 1937, W. B. Jones, trap. Paratypes: 49 with same data; 8 with same data except 1939; and the following: *Alabama*. DeKalb County. Kelly Girls Cave, 1 mi (1.6 km) SE Collinsville, 25.VIII.1965, SBP, 2; Cook Cave (Ala 253), 13.VIII.1958, WBJ, 2; Lykes Cave, 27.VIII.1965, SBP, fungus on entrance talus, 22; Cherokee Cave, 4.5 mi (6.5 km) NE Ft. Payne, 15.VIII.1967, SBP, 1. Blount County. Blount Springs, 19.III.1966, SBP, litter in limestone crevice, 1; 7 mi (11 km) S Cleveland, outside Horseshoe-Crump Cave, 28.VI.1967, SBP, litter Ber. 70, 2; outside Bangor Cave, 19.III.1966, SBP, rotten tree roots, 4; outside Bangor Cave, 5.IV.1967, SBP, 1; inside Bangor Cave, 20.XII.1965, SBP, 1; near Inland Lake, 28.IX.1958, HRS, forest floor debris, 4. Shelby County. Helena, 3.I.1959, HRS, treehole, 1. Jefferson County. Near Purdy Cave #1, 13.IX.1958, HRS, forest debris in rock crevice, 1. Morgan County. 3½ mi (6 km) SE Fayette, 21.V.1972, SBP, Ber 241, litter outside cave entrance, 14. *Georgia*. Dade County. Morrisons Cave 13.VII.1967, SBP, 6; 16.IX.1968, SBP, 1; 16–23.VI.1972, SBP, 3; 4 mi (6.5 km) NE Rising Fawn, 15.VII.1967, SBP, forest litter Ber 78, 4; Johnson Crook Cave #2, 4 mi (6.5 km) NE Rising Fawn, 14.VII.1967, SBP, 2 in cave entrance; outside Johnson Crook Cave #2, 14.VII.1967, SBP, 6 in litter.

Tentatively associated material. *Alabama*. Etowah County. Wright Cave, 11.VII.1958, WBJ, 1 male, 1 female. Morgan County. Inge Cave, 2.V.1959, T. C. Barr and HRS, under debris, 2 males. Cleburne County. Cheaha Mountain State Park, 330 m, 13.VI.1967, SBP, litter Ber 59, 2. Marshall County. Guntersville, near Griffith Cave, 30.IV.1960, HRS, 1 female; Kelly Ridge Cave, near Warren-town, 23.VIII.1958, HRS, 1 female. *Georgia*. Walker County.

McLemore Cove, 9 mi (15 km) SW LaFayette, 14.VII.1967, forest log litter Ber 79, SBP, 3. Dawson County. Mt. Oglethorpe, 2000' (610 m), 20.VIII.1967, SBP, litter Ber 80, 1 damaged male.

Description. Dorsal section of aedeagus tip (figs. 16–18) regularly curved, unadorned, shortest on left side and longest on right; ventral section regularly curved with downturned tip; posterior view with dorsal section forming a uniformly arched genital orifice, with a uniform border; setae on ventral surface lying in groove rather than separated depressions. Internal sac thick, not narrowed into curved tube at apex (fig. 15). Spermatheca (figs. 57–60) smoothly curved, anterior part broadened and without crest, posterior part recurved off structural plane.

Variation. The Morgan County, Alabama, sample has a lower arch, with a flattened middle to the genital orifice when seen from behind. This opening is most highly arched in the Cheaha Mountain, Alabama, male which also has a differing left margin to the ventral section.

Etymology. The name refers to the Appalachian Mountains, around the southern end of which this species is distributed.

Distribution. This is the most widely distributed species, ranging from north-central Alabama, south of the Tennessee River, eastwards into northwestern Georgia.

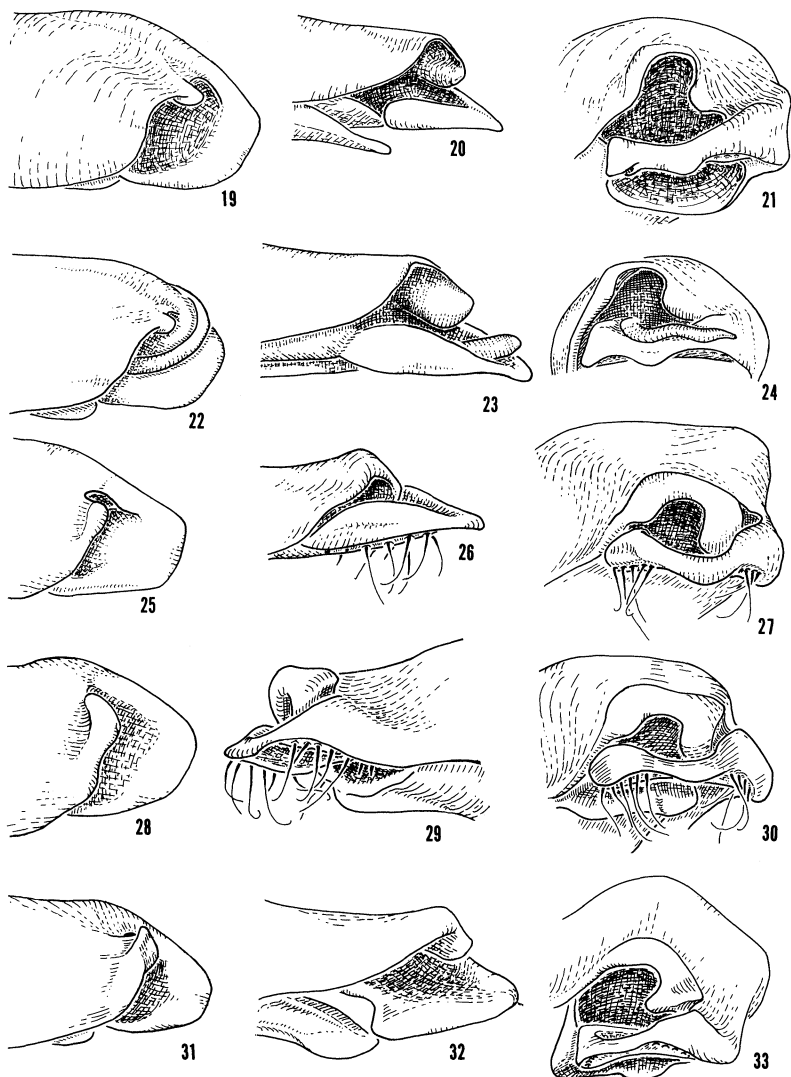
Field Notes. This is the most frequently collected species because it has a wide range, and occurs in a region which has received much collecting attention. It has been found in forest litter and in the entrance zone of caves, in the months of January, March, May, June, July, August and September. It is probably active throughout the year.

7. *Adelopsis jonesi* n. sp.

Figs. 19–21

Holotype male in CNC. Type data. Alabama. Colbert County. Wolf Den Cave (Ala. 83), near Maude, 25.IX.1940, W. B. Jones.

Tentatively associated material. Alabama. Colbert County. McClusky Cave, near Maude, 15.IX.1940, WBJ, 1 male missing aedeagus; Gist Cave, 13.V.1940, WBJ, 2 females. Franklin County, The Dismals, 30.VIII.1958, HRS, forest floor debris, 1 female. Hale County. Moundville State Park, 7.VII.1967, SBP, log litter Ber 75, 3 females. Tuscaloosa County. No other locality, VI, Alabama Museum Expedition, 1 female (UANH).



Figs. 19–33. Views of aedeagal tips of *Adelopsis*. 19–21. *A. jonesi*. 22–24. *A. bedfordensis*. 25–27. *A. cumberlandi*. 28–30. *A. scottsboroensis*. 31–33. *A. nashvilensis*. Scale of aedeagal tips approximately equal.

Description. Dorsal section of aedeagal tip with highly raised edge forming large arch over genital orifice (figs. 19–21); ventral section smoothly rounded. Spermatheca of tentatively associated females indistinguishable from those of *A. appalachiana*.

Relationships. This species is easily derived in aedeagal type from *A. appalachiana* by an increased arching of the dorsal section of the genital orifice. It probably represents an isolated and now differentiated peripheral population of the latter.

Etymology. The species is named for the late Dr. Walter B. Jones, of Huntsville and Tuscaloosa, Alabama, who, as former State Geologist and Director of the Alabama State Museum of Natural History, did so much to promote studies of the natural history of the southeast.

8. *Adelopsis bedfordensis* n. sp.

Figs. 22–24

Holotype male in FMNH. Type data. Tennessee. Bedford County. Campbell Cave, 17.I.1960, H. R. Steeves, Jr., under rock in dark zone.

Description. Aedeagal tip (figs. 22–24) with uniformly arching dorsal section without upturned flange in dorsal and lateral views. Genital orifice moderately arched in posterior view and asymmetrical. Internal sac long, thin, and curved.

The aedeagus is difficult to distinguish from that of *A. appalachiana*, except for the striking differences in their internal sacs.

Etymology. The name refers to the county in which the type was collected (and to which it may be approximately restricted in distribution), located in the eastern Highland Rim of south-central Tennessee.

9. *Adelopsis cumberlandia* n. sp.

Figs. 25–27, 61

Holotype male and allotype female in CNC. Type data: Alabama, Jackson County. 5 mi (8 km) N Garth, 19.V.1972, S. Peck, leaf litter Ber 239. Paratypes: 65 with same data; 2 with same date but in dung baited pit traps; and the following: *Alabama*. Jackson County. Paint Rock, Nat Mountain, 15.III.1966, SBP, 3 under log; Keel Cave, Sharp Mt., 11.VI.1940, WBJ, 1; Clemons Cave, Sharp Mt.,

9.VI.1940, WBJ, 1; Rousseau Cave, July, 1968, R. Graham, 1; Rousseau Cave, 12.VII.1973, SBP, 4 baited near entrance; Paint Rock, near Crossing (Stewart) Cave, 5.VII.1958, HRS, 2 in rock crevice debris; 5 mi (8 km) NW Princeton, 19.V.1972, SBP, forest litter Ber 240, 1. Madison County. Monte Sano State Park, 17.V.1972, SBP, log litter Ber 238, 5; Monte Sano, Huntsville, 1936, R. Hopping, 2 (UANH). Monte Sano, VI.1937, Ala. Mus. Exped., 1 (UANH); Tumbling Gap (NE ridge of Monte Sano), June 3–8, 1911, H. P. Loding, 2 (UANH); Sharps Cove, 5.VII.1965, SBP, leaf Ber., 1. Marshall County. Grant, Guffey Cave, 25.V.1958, 1 in floor debris in entrance light zone, HRS; Grant, near River Cave, 25.V.1958, 4 under debris at entrance light zone, HRS; Creek Cave, 25.V.1958, HRS, 1 in cave debris; 1 mi N Guntersville Dam, 26.VI.1967, litter Ber 68, SBP; Hampton Cave, Guntersville, 11.VII.1973, SBP, 1.

Description. Dorsal section of aedeagal tip short (figs. 25–27) thickened and upcurved, especially at right side where small broad tooth exists (best seen from right side); ventral section projecting, tip truncate; posterior view with uniformly broad arch over orifice. Internal sac thick and slightly curved. Spermatheca similar to that in *A. scottsboroensis* (fig. 62) but with more bend in posterior part when seen from right, and with a lower crest on the anterior part.

Etymology. The name refers to the Cumberland Plateau, flanking the NW face of the Appalachian Mountains.

Distribution. The species range is in the forested slopes and valleys of the southern end of the Cumberland Plateau, in northeastern Alabama, north and west of the Tennessee River. This river is a natural boundary of the species range, separating it from that of *A. appalachiana* south of the river.

Notes. The species has been found in moist forest litter and cave entrances in the months of March, April, May, June, July and August.

Relationships. The species is derivable from *A. appalachiana* by an increased arching of the genital orifice, a thickening of the dorsal orifice lip, and an increase in the length of the ventral section.

10. *Adelopsis scottsboroensis* n. sp.

Figs. 28–30, 62, 63

Holotype male and allotype female in CNC. Type data: Alabama. Jackson County. 10 mi (16 km) N Scottsboro, 16.V.1972, SBP,

forest litter Ber 237 (from limestone crevices near Tumbling Rock Cave). Paratypes: 6 with same data.

Description. Dorsal section of aedeagal tip short (figs. 28–30) and upturned, with right side free and reflexed; in posterior view right margin of arch above orifice projecting and deflexed to right. Spermatheca thin and uniformly curved as in figs. 62–63.

Etymology. Named for the city of Scottsboro, which sits at the base of a spur of the Cumberland Plateau, near the margin of the drainage basin probably containing the species range.

Distribution. The species should be expected to occur in additional sites below the Plateau escarpment in the headwaters of Mud and Coon Creeks, Jackson County. Some beetles and other invertebrates are known to be endemic to this area, so some general mechanism may have worked to isolate them in this section of the Cumberland Plateau escarpment. How the species range overlaps or intergrades with that of *A. cumberlanda* (occurring a short distance to the west and south along the same general face of the Plateau, and in the drainage of the Paint Rock River) is not known.

Relationships. The species can be considered a local isolate of *A. cumberlanda*, from which the aedeagal tip is easily derived.

11. *Adelopsis nashvillensis* n. sp.

Figs. 31–33

Holotype male in USNM. Type data: Tennessee. Davidson County near Nashville, 3 November 1937, S. F. Austin, "elm-maple, 562". Tentatively associated material; one female, Tennessee, Warren County, Hubbard Cave at Irving College, 16.X.1948, W. B. Jones and J. M. Valentine.

Description. Aedeagus with dorsal section of tip (figs. 31–33) upturned, and recurved on right side; in posterior view genital orifice deflected up and to the right.

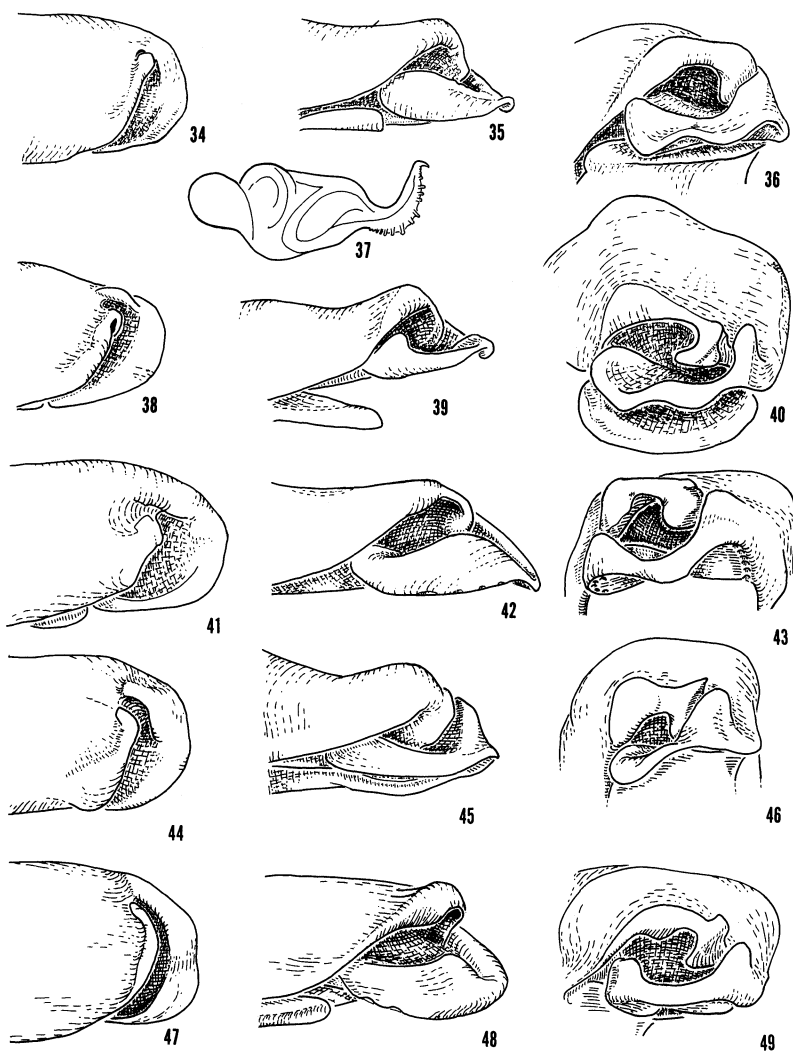
Etymology. The name refers to the city near where the species was collected.

Relationships. The species seems to be closest to *A. cumberlanda*, from which the aedeagal tip can be easily derived.

12. *Adelopsis fumosa* n. sp.

Figs. 34–37, 64, 65

Holotype male and allotype female in FMNH. Type data. Tennessee. Sevier County. Great Smoky Mountains National Park,



Figs. 34-49. Aedeagal structures of *Adelopsis*. 34-36. *A. fumosa*. 37. Internal sac, *A. fumosa*. 38-40. *A. alta*. 41-43. *A. joanna*. 44-46. *A. pisgahensis*. 47-49. *A. orichalcum*.

16.IX.1953, 2.5 road miles (4 km) above Chimney Campground, 3600 ft. alt. (1180 m), H. S. Dybas, leaf litter Berlese. Paratypes: 7 with same data; and the following from Great Smoky Mountains National Park. Cherokee Orchard, 2–3000 ft (610–910 m), 15.IX.1953, H. S. Dybas, 2 in *Tilia* treehole; 3 in forest floor litter; 4 in flood debris (all in FMNH). State road to Newfound Gap, 3500 ft (1147 m), 16.IX.1953, H. S. Dybas, litter, 8 (FMNH). Chimney Campground, 1.IX.1948, Ross and Stannard, 3, (INHS). Gatlinburg, 14.IX.1948, Quirsfeld, 5 (MCZ). Clingman's Dome Summit, 6640 ft (2177 m), 6–26.VIII.1965, SBP, carrion trap; 8 mi (13 km) S Gatlinburg, 3100 ft, 17.V.1972, A. F. Newton, 2 in carrion trap; Buckeye Nature trail, 10.VIII.1974, J. L. Bengtson, maple litter. Georgia. Walker County. Bible Spring Cave, 2 mi (3 km) NE Lookout, 20.VI.1967, SBP), male.

Description. Dorsal section of aedeagal tip (figs. 34–36) uniformly rounded and arched; ventral section on right enlarged to enclose right dorsal section. Internal sac as in fig. 37. Spermatheca (figs. 64–65) with prominent crest.

Variation. The single male from the summit of Clingman's Dome seems to show differences that, with adequate material, could prove to be specifically distinct. The aedeagal tip seems more bilobed on the dorsal section and with a more prominent recurved flange on the right. The internal sac seems more elongate and less curved in its distal half.

Etymology. The name is derived from the Latin for smoke, referring to the species range in the Great Smoky Mountains. However, the Georgia population is a disjunct some 200 km to the southwest.

Relationships. The aedeagal tip shows the closest similarity to, and is most easily derived from that of *A. appalachiana*.

13. *Adelopsis alta* n. sp.

Figs. 38–40, 66

Holotype male in USNM. Type data: North Carolina. Yancey County. Mt. Mitchell, 6500 ft (2131 m), 25.VI.1937, E. Shoemaker. Paratypes: Mt. Mitchell, 4–6000 ft. (1311–1967 m) 17–24.VI.1939, Quirsfeld, 4 (INHS); Mt. Mitchell, 12.VI.1973, litter under *Rhododendron*, WRS, 1.

Description. Dorsal section of aedeagal tip (figs. 38–40) higher and thicker on left, right side with downturned process curving into genital orifice; ventral section thickened and upturned at base on both right and left sides. Spermatheca (fig. 66) with central piece curved inwards like grip of an archer's bow.

Etymology. The name is the Latin adjective for “high” and refers to the species' high elevation habitats in the Black Mountains and Mt. Mitchell.

Notes. This species is sympatric with *A. mitchellensis*, with which it has been confused, but to which it is not at all closely related judging from the dissimilarity of the aedeagal tips.

Relationships. The species is most easily derived from a generalized ancestor like *A. appalachiana* by modification of the aedeagal tip through stages similar to *A. alta*, *A. cumberlandia*, and *A. nashvillensis*, though these may not be direct ancestors.

14. ***Adelopsis joanna* n. sp.**

Figs. 41–43, 67, 68

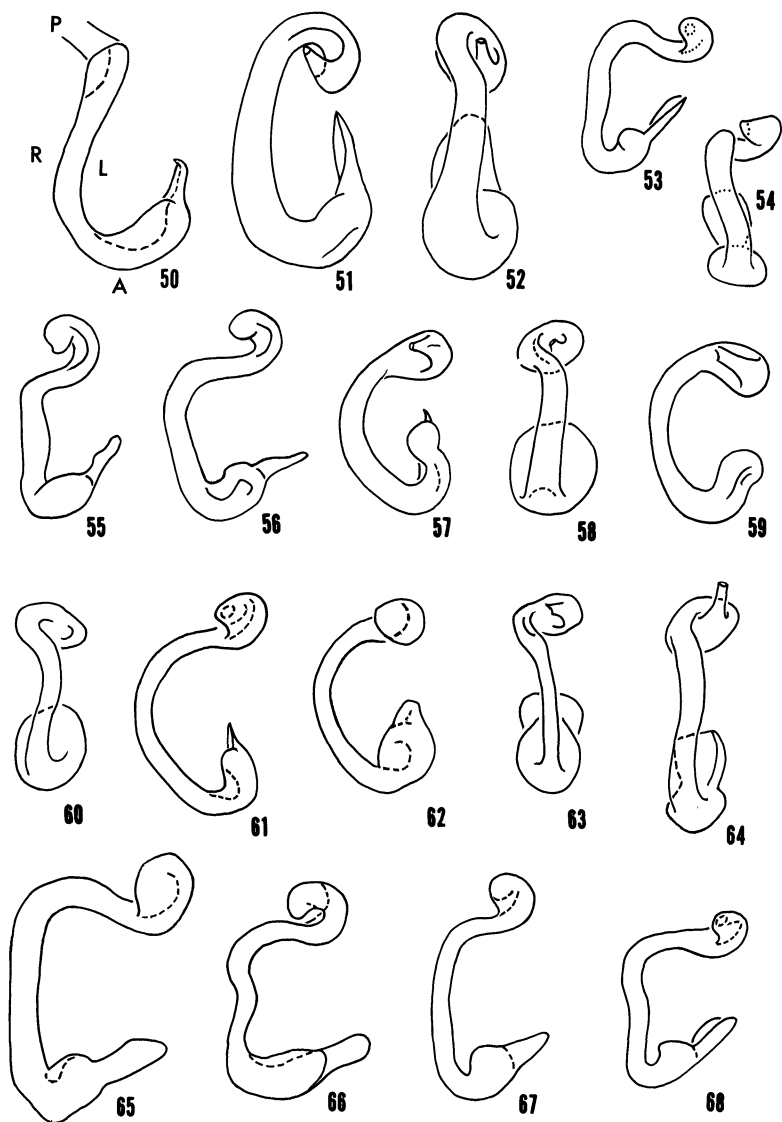
Holotype male and allotype female in CNC. Type data: North Carolina. Cherokee County. Joanna Bald, near Andrews, 4700 ft (1540 m), 26.VII.1967, S. B. Peck, litter Ber. 96. One paratype female with same data.

Description. Dorsal section of aedeagal tip (figs. 41–43) not smoothly curved, but more angular and forming offset arch over genital orifice; ventral section upcurved on left but more so on right, forming prominent notch between it and the dorsal section. Spermatheca thin, irregularly curved (figs. 67, 68).

Etymology. The name refers to the type locality, and is used as a feminine noun in apposition.

Relationships. The species seems to be derived from a *cumberlandia*-like ancestor through a form like that in *A. alta*, and may be an isolate of the ancestor of this species.

Figs. 50–68. Spermathecae of *Adelopsis*. 50. *A. mitchellensis* indicating anterior (A), posterior (P), right (R), and left (L) sides as oriented in the beetle. 51–52. *A. alleghenyensis*. 53–54. *A. suteri*. 55–56. *A. richlandensis*. 57–58. *A. appalachiana*, Morrison Cave, Georgia. 59–60. *A. appalachiana*, outside Bangor Cave, Alabama. 61. *A. cumberlandia*, paratype. 62–63. *A. scottsboroensis*. 64. *A. fumosa*, 8 mi S Gatlinburg, Tennessee. 65. *A. fumosa*, Clingman's Dome, Tennessee. 66. *A. alta*. 67–68. *A. joanna*. All drawn to same scale.



15. ***Adelopsis pisgahensis* n. sp.**

Figs. 44–46

Holotype male, allotype female, and paratype male in MCZ. Type data: North Carolina. Haywood-Transylvania County line, Mt. Pisgah, about 1475 m (on Blue Ridge Parkway), 11–12.IX.1934, Quirsfeld.

Description. Aedeagal tip (figs. 44–46) with dorsal section broadly swollen on left and with sharp point on right; ventral section low and regular on left but on right broadly expanded and upraised along notch between it and dorsal section.

Etymology. The name refers to the type locality. Mt. Pisgah is a section of the mountain ridge continuous with Richland Balsam, inhabited by *A. richlandensis*. There is no evident barrier to dispersal between the two and they must be assumed to be parapatric or sympatric.

Relationship. The species has a highly derived type of aedeagal tip and may be descendant from an ancestor similar to *A. alta*.

16. ***Adelopsis orichalcum* n. sp.**

Figs. 47–49

Holotype male in CNC. Type data: Georgia. Union County. Brasstown Bald, el. 2415 ft (790 m), 24.X.1966, H. R. Steeves, forest debris.

Description. Dorsal section of aedeagal tip (figs. 47–49) uniformly thicker from left to right, ending in upcurved spur; ventral section upcurved on left, depressed and emarginate in middle, and more upcurved on right.

Etymology. The name is Latin for brass, is used as a noun in apposition, and refers to Brasstown Bald, the highest point in Georgia, in the vicinity of which the species is probably restricted.

Relationships. The species is derivable from a generalized stock like *A. appalachiana* through intermediates that were probably also ancestral to *A. pisgahensis*, *A. joanna*, and *A. alta*.

Evolutionary and Distributional History

Jeannel (1936, 1964) considered the evolutionary center of the genus (and the tribe) to be in Colombia and Venezuela. Species here have an aedeagus with a copulatory orifice displaced onto a nearly

sagittal plane. This condition was judged to be a form from which all other aedeagal tips could be derived. He also saw this genus as ancestral to *Ptomaphagus*, which developed a more "successful and harmonious" and less variable aedeagal type, and then spread through North America, and across the proto-Atlantic to Europe in the Eocene. He also saw an earlier connection from South America in the Jurassic to southeast Asia, where another derivative genus, *Ptomaphaginus*, now occurs. Szymczakowski (1964, 1969) agrees with the idea of an American evolutionary origin, but sees little evidence to support arguments for specific dispersal routes. The survival of *Proptomaphaginus* in relictual species in the Caribbean and Mexico supports the idea of an American origin for the stock that became *Ptomaphaginus* in the Oriental Region.

I do not yet have a suitable overview of the genus as a whole to elaborate on or offer alternative hypotheses to those of Jeannel and Szymczakowski. This is best postponed until after my now massive tropical American collections are studied. However, some ideas can be proposed for the collection of species limited to the southeastern United States.

The genus probably originated in tropical America in the late Mesozoic. Whether this was in what we now know as South, Central or North America probably cannot be known with certainty. However, the greatest present generic diversity in the tribe is now known to be in or adjacent to Mexico. This area (and Central America) has been an important evolutionary center in its own right. Savage (1966) suggested that broad, terrestrial, forested connections united these three regions in the Paleocene and permitted north-south faunal movements, so that mesic tropical climates and forests were continuous through South America up to what is now the central United States. The patterns of distribution of forest litter reptiles and amphibians may be informative and related because they occupy environments similar to Catopinae, though their dispersal abilities are probably very different. However, Savage (1974) has reconsidered the evidence and now finds less substantial support for such broad connections, and now thinks there was a significant water gap separating South America from "nuclear Central America" and North America from the Cretaceous up to the Pliocene. This is more consistent with other current ideas of plate tectonic biogeography (Raven and Axelrod, 1975). This gap, however, could have been crossed by island hopping and waif

dispersal, of which winged *Adelopsis* (and *Ptomaphagus*) should have been capable.

These considerations then suggest an origin of *Adelopsis* in "tropical" North or Central America perhaps in the late Cretaceous or early Tertiary, and a movement through forests in the early Tertiary into the Appalachian Region. The continuous distribution of the genus was then broken with the developing xeric climates of the Miocene, forming an effective non-forested barrier across what is now northern Mexico (Axelrod, 1960, Graham, 1973). This disjunction is observed in many groups (see Rosen, 1978). Since this disjunction the assumed large-eyed and winged ancestral stocks have vanished from what became the United States, leaving only the small-eyed and wingless soil species of the Appalachians. Past workers have suggested that the mesic forests of the Appalachians and Mexico were rejoined in Pleistocene glacials, but most recent analyses do not tend to support this (Graham, 1973; Martin and Harrell, 1957; Rosen, 1978).

The comparative uniformity of overall morphology and aedeagal types in the Appalachian species suggests that a single ancestral species became an inhabitant of soil and deep litter. Subsequent (late Tertiary?) isolations perhaps produced the set of less-similar species in the *mitchellensis* species group. Differentiation of these species may have been reinforced by Pleistocene climatic fluctuations and distributional displacements. One of these species may have become something like *A. appalachiana* and it experienced speciation by range expansion, contraction, and population isolation in response to Pleistocene climatic fluctuations. The more cool and wet conditions accompanying glacials (Watts, 1970, 1975; Whitehead, 1965) would allow their spread through the lowlands. Warmer and drier conditions of interglacials would separate populations of these seemingly poorly mobile beetles as they retreated to favorable and more isolated sites at higher elevations or in mesic forest refugia of canyons, gorges, and protected spots below topographic escarpments. By this process, an *A. appalachiana*-like ancestor differentiated into the species of this more closely knit group.

The production of 16 species from one ancestor seems only a modest amount of differentiation if the southeastern *Adelopsis* have truly been isolated from their Neotropical congeners for some 35–40 million years, especially when compared to some examples of

“explosive” species production on islands in 10 million years or less. However, the fossil record shows that other groups with the same Appalachian-Mexican disjunction have undergone very little differentiation in the same time, especially in certain tree genera (Axelrod, 1960, p. 269; Rosen, 1978). It should also be noted that these papers deal more with examples that seem to be northern in origin and which have moved into Mexico and southwards rather than the opposite (Graham, 1973).

It might at first seem puzzling that a Neotropical genus, characteristic of lowland mesic tropical forests should have species isolated on the highest peaks of the southern Appalachians. However, it is not difficult to see the origin of the situation. When they were first colonized the Appalachians seem to have had a tropical or subtropical climate, and to have had a more gentle relief, sometimes called the “Schooley Peneplain”. Their present relief is due to later Tertiary uplift and erosional rejuvenation, a process to which the beetles could undoubtedly adapt as their populations either were slowly elevated, or slowly moved into higher sites.

The broad patterns of species distribution seem similar to those of other flightless beetles inhabiting deep litter and/or soil in the Appalachians (see Darlington, 1943). Close comparisons can be made with the eyeless *Anillinus* carabids (Barr, 1969; pers. comm.), *Arianops* pselaphids (Barr, 1974), and more distant ones with *Trechus* carabids (Barr, 1962, 1969), and *Catopocerus* leioidids (Peck, 1974). These show species to be generally confined to upland areas or in deeper soil (collected in caves) or protected gorges in the lowlands. Some of these groups have species which may be more widespread in the northern end of the unglaciated Appalachians, but most contain more species, but with not much more sympatry, in the vicinity of the junction of North and South Carolina and Georgia (the vicinity of Highlands, North Carolina). The mechanism that acted to generate and then preserve the diversity near Highlands might have worked in a relatively similar manner on these and many other groups of forest litter-inhabiting insects and other arthropods.

Conclusion

The genus *Adelopsis*, otherwise Neotropical in distribution, is found to have 16 species in the southern part of the Appalachian region of the United States. All these species are small-eyed and

wingless, are inhabitants of forest soil and deep litter, and must have limited dispersal abilities. Higher elevation Appalachian localities seem generally to be occupied by distinct, more distantly related, and very localized species. Lower elevation sites are more often occupied by more similar species which are more often of a wider distribution. This last generalization is reflected in the *appalachiana* species group which may have resulted from a more recent series of speciation events. There is not enough evidence to suggest how ranges may have been affected and populations isolated with the changed climatic conditions of the Pleistocene, but these are known to have markedly lowered vegetational zones in the southern Appalachians in the last glacial. Since most of the material reported on in this paper was incidentally gathered by persons in pursuit of other beetles, many more species undoubtedly remain to be discovered. These may possibly more than double those already known, particularly in the poorly collected regions extending for some 260 km (160 mi) along the Appalachian and Blue Ridge crests between the NE corner of North Carolina, through Virginia, to Spruce Knob, West Virginia. A more firmly based interpretation of the evolutionary history of the genus in the southeastern United States will be possible when these taxa and additional distributional data become known. Because of inadequate material, this paper is only a preliminary report. This is a reflection of the still inadequate status of knowledge of the soil and litter faunas of North America in general.

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