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Four new species of the genus *Anillinus* Casey (Coleoptera, Carabidae, Anillini) from Alabama, U.S.A., with a revised key to the Alabama species

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Abstract

Four new species of anilline ground beetles are described from Alabama. Two species from Jackson County, *Anillinus clinei* **new species**, and *Anillinus folkertsioides* **new species**, are troglobitic and litter species, respectively. *Anillinus hildebrandti* **new species**, is a troglobitic species from a cave in Morgan County. *Anillinus humicolus* **new species**, from Jefferson County is supposedly an endogean species. All new species are illustrated with images and drawings; a distribution map and a modified key to the Alabama species are provided. With these new discoveries, the known fauna of *Anillinus* of Alabama now includes twelve species. Species compositions of *Anillinus* based on habitat preferences of taxa satisfactorily explain the variations in total species numbers and number of endemics among Alabama and other eastern American states.

Key words: *Anillinus*, Anillini, distribution, eastern USA, identification key, habitat preference

Introduction

The genus *Anillinus* Casey, as currently composed, includes more than 50 species distributed mainly in the eastern part of the USA from Maryland and Indiana in the north to Florida and Texas in the south (Bousquet 2012; Sokolov 2012; Sokolov *et al.* 2014). All of the species in the genus are small (mostly 1–2 mm in length), depigmented, light to medium brown in color, and lack eyes and wings. Species identifications within the genus are largely based on differences in the median lobes and internal sac armatures of male genitalia, while species lineages are largely based on differences in the microsculpture of integuments and the proportions of various body regions.

Habitats of the representatives of the genus segregate into three main categories: moist forest leaf and wood litter, interstitial spaces in soils, and caves or other deep rock crevices. The external morphology of species varies in accordance with the type of habitat in which they live. Within specific lineages, species are often characterized by similar habitat preferences, and sister species are typically allopatric. Many species are extremely restricted in their geographic distribution, especially troglobitic forms which are almost always confined to a single cave or cave system. Within the genus range, topographically complex areas, such as mountains or karst landscapes, are rich in species, with distributions that reflect local and regional patterns of endemism (Sokolov *et al.* 2004).

The last paper focused on the *Anillinus* of Alabama was published almost a decade ago (Sokolov 2012), and was based on the material borrowed from the Carnegie Museum of Natural History (CMNH). In that paper the fauna of *Anillinus* of Alabama was reviewed and illustrated, and a key to the species was provided. As a result, this research effectively tripled the known species diversity of the state. Several considerations discussed there suggested that additional new species remained to be discovered in the state. Some time ago, through the kind courtesy of Robert L. Davidson (Collection Manager, Section of Invertebrate Zoology, CMNH), I received new material of the Alabama Anillini originating from the collection of the late Thomas C. Barr, Jr. Examination of the material resulted in the discovery of four new species in the genus, thus proving the above-mentioned assumption. Descriptions of the new species together with corresponding modifications of a key to the Alabama species of *Anillinus* serve as the basis for this paper.

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Material and methods

This study is based on examination of 91 specimens of *Anillinus* from Alabama, originating from the late Tom C. Barr's collection of Anillini (now in the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA - CMNH). All type material of newly described species is deposited in the CMNH. Verbatim label data are given for the type specimens of all newly described taxa, with label breaks indicated by a backslash ("\").

All specimens were measured electronically using a Leica Z16 APO microscope equipped with a Syncroscopy AutoMontage photomicroscopy system (Syncroscopy, Synoptics Ltd.). Measurements for various body parts are encoded as follows: ABL = apparent body length, from clypeus to apex of elytra; WH = width of head, at level of first orbital setae; WPm = maximal width across pronotum; WPa = width across anterior angles of pronotum; WPp = width across posterior angles of pronotum; LP = length of pronotum from base to apex along midline; WE = width of elytra, at level of 2nd discal setae; LE = length of the elytra, from apex of scutellum to apex of left elytron. ABL measurements are given in mm; others are presented as nine ratios: mean widths –WH/WPm and WPm/WE; and body parts—WPa/WPp, WPm/WPp, WPm/LP, WE/LE, LP/LE, LE/ABL and WE/ABL. All values are given as mean ± standard deviation.

Extractions and processing of genitalia were made using standard techniques as described by Sokolov & Kavanaugh (2014). Photographs of the dorsal habitus of new species were taken with an automontage system on a Leica Z16 microscope. Line drawings of selected body parts were prepared with the help of a camera lucida attached to an Olympus BX 50 compound microscope.

In order to compare the species compositions of *Anillinus* in Alabama and other states a numerical matrix was created in which the state endemics and common species (i.e., species recorded in more than one state) were represented by groups of taxa with similar habitat preferences. The matrix was examined using Principal Component Analysis (PCA) (McGarigal *et al.* 2000) with the help of PAST 3.17 software with default settings (Hammer *et al.* 2001).

Taxonomic Part

Order Coleoptera Linnaeus, 1758

Family Carabidae Latreille, 1802

Subfamily Trechinae Bonelli, 1810

Tribe Anillini Jeannel, 1937

Genus Anillinus Casey, 1918

Anillinus Casey 1918: 167. Type species: *Anillus (Anillinus) carolinae* Casey, 1918, by original designation.
Micranillodes Jeannel 1963a: 57. Synonymy established by Bousquet (2012: 699) and confirmed by Sokolov *et al.* (2014: 83). Type species: *Micranillodes depressus* Jeannel, 1963a, by original designation.
Troglanillus Jeannel 1963b: 147. Synonymy established by Barr (1995: 240). Type species: *Troglanillus valentinei* Jeannel, 1963b, by original designation.

Anillinus clinei Sokolov, sp. n.

(Figs. 1A, 2A, 3A, 4A–C, 5)

Type material. Holotype, one male (CMNH), dissected, labeled: \ Stewart Cave, Ala. nr Paint Rock, Jackson Co., 5.VII.58, under rocks \ H.R. Steeves, Jr. Collector \ [handwritten]. Paratypes, two females, labeled same as holotype [handwritten].

Specific epithet. This species is named after Andrew R. Cline (CDFA-Plant Pest Diagnostic Center, Sacramento, California), a specialist in Nitidulidae, for his friendly help in the author's investigations on Carabidae.

Type locality. USA, Alabama, Jackson County, Stewart Cave.

Differential Diagnosis. Males of *A. clinei* can be distinguished from those of the other congeners by the large size, and the structure of the median lobe having copulatory sclerites of distinctive shape and lacking spines in the internal sac.

Description. Large-sized for genus (ABL 2.33–2.48 mm, mean 2.38±0.084 mm, n=3).

Habitus: Body form (Fig. 1A) moderately convex, slightly ovate, elongate (WE/ABL 0.37±0.007), head of average proportions for genus (WH/WPm 0.68±0.014), pronotum moderately narrow in comparison to elytra (WPm/WE 0.77±0.014).

Integument: Body color brunneo-rufous, appendages testaceous. Microsculpture (Fig. 2A) present along frontal sulci and vertex of head, base of pronotum, and elytra, where it is represented by isodiametric polygonal sculpticells; and absent from clypeus, most of frons, and disc of pronotum. Body surface shiny, surface sparsely and finely punctate, covered with sparse, yellowish, short setae. Vestiture of elytra moderately long (0.3–0.4 length of discal setae).

Prothorax: Pronotum (Fig. 3A) moderately convex, of moderate size (LP/LE 0.41±0.009) and of almost equal length and width (WPm/LP 1.19±0.015), with lateral margins almost rectilinearly and slightly constricted posteriorly (WPm/WPp 1.19±0.014). Anterior angles indistinct, posterior angles nearly rectangular (95–100°). Width between posterior angles much greater than between anterior angles (WPa/WPp 0.82±0.029). Basal margin slightly concave in middle.

Scutellum: Externally visible, triangular, with rounded apex.

Elytra: Narrowly depressed along suture, of average length (LE/ABL 0.59±0.006) and width (WE/LE 0.64±0.011) for genus, with traces of 1–2 striae. Humeri distinct, rounded, in outline forming right angle with longitudinal axis of body. Lateral margins subparallel in middle, slightly divergent at basal fifth, evenly rounded to apex at apical third, with shallow subapical sinuation. Basal margination distinct.

Legs: Protarsi of male with moderately dilated tarsomere 1. Profemora moderately swollen. Metafemora unmodified.

Male genitalia: Median lobe (Fig. 4A) of aedeagus anopic, slightly arcuate and moderately twisted. Shaft greatly dilated in apical half, with moderately elongate apex, conically tapered to subparallel rounded tip. Ventral margin of median lobe moderately enlarged, with many poriferous canals. Dorsal copulatory sclerites fused to form slightly curved, almost symmetrically organized, dorsal and ventral blade-like structures of moderate length, which are more heavily sclerotized dorsally. Spines and scaled membranous folds of internal sac absent. Left paramere (Fig. 4B) of shape common in genus, paramere apex without setae. Right paramere (Fig. 4C) short, bearing many (>5) long setae, which are much longer than the length of paramere.

Geographic Distribution. This species is known only from the type locality in Jackson County, Alabama (Fig. 5, black cross).

Habitat. According to the label, the small series of specimens of this species was collected under rocks in the cave.

Relationships. Presumably the species belongs to the group of local species characterized by a distinctive shape of the shaft of median lobe, which is getting wider towards its apical half. In addition to *A. clinei*, this group includes *A. cavicola* Sokolov, *A. hirsutus* Sokolov, and *A. hildebrandti*, new species, described below.

Anillinus folkertsioides Sokolov, sp. n.

(Figs. 1B, 2B, 3B, 4D–F, 5)

Type material. Holotype, one male (CMNH), dissected, labeled: \ nr. Stewart Cave, Ala. Jackson Co. 5-VII-58 Hollow beech debris \ H.R. Steeves, Jr. Collector \ [handwritten]. Paratypes, three specimens, one male labeled: \ Creek Cave nr Grant, Marshall Co. 25.V.58—Berlesed from cave debris \ H.R. Steeves, Jr. Collector \ [handwritten]; one female labeled: \ Creek Cave nr Grant, Marshall Co., Ala. 2.V.58—Berlesed from cave debris \ H.R. Steeves, Jr. Collector \ [handwritten]; one female labeled: \ nr. Creek Cave, Grant, Marshall Co. 25.V.58 Hollow beech debris \ H.R. Steeves, Jr. Collector \ [handwritten].

Specific epithet. The name of this species originates from the species name "*folkertsi*" and the Greek suffix *–oides* (similar to), alluding to the similarity in male genitalia between the new species and *A. folkertsi* Sokolov & Carlton (in Sokolov *et al.* 2004).

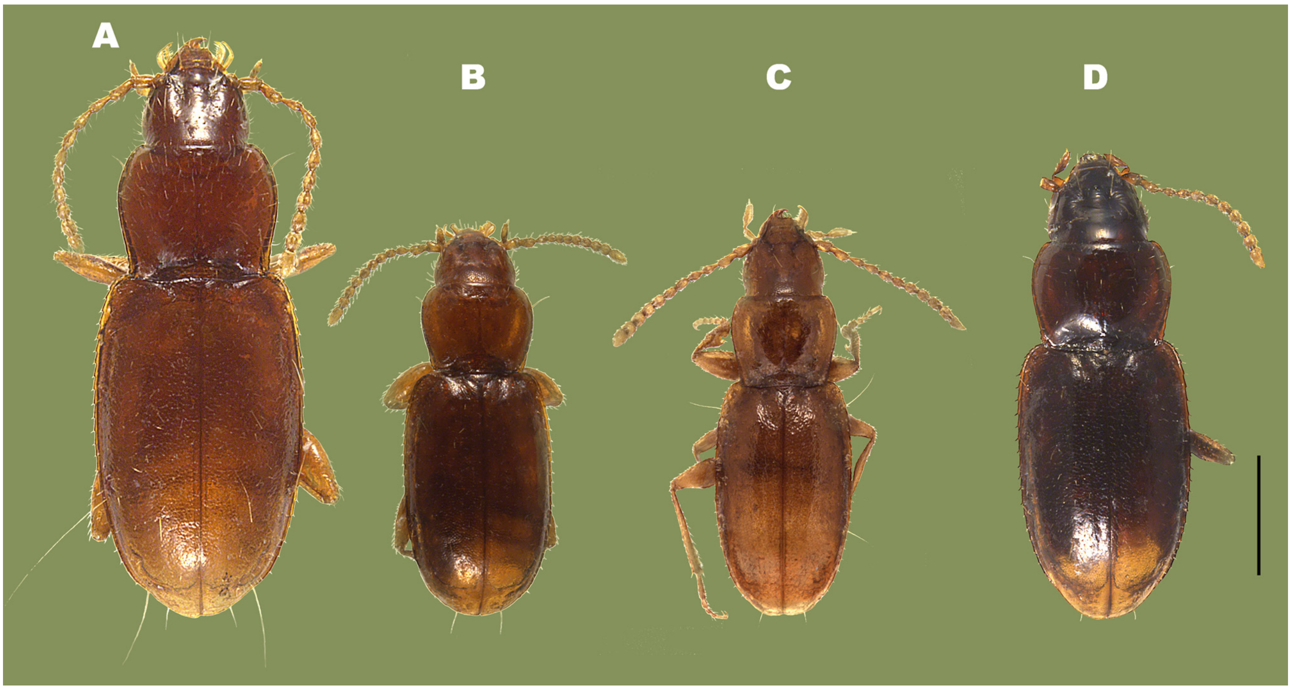


FIGURE 1. Digital images of habitus of *Anillinus* species, dorsal aspect. **A**—*A. clinei* (Stewart Cave, Jackson County, Alabama), **B**—*A. folkertsioides* (Creek Cave, Marshall County, Alabama), **C**—*A. hildebrandti* (Cave Springs Cave, Morgan County, Alabama), **D**—*A. humicolus* (Mountain Brook, Jefferson County, Alabama). Scale bar 0.5mm.

Type locality. USA, Alabama, Jackson County, near Stewart Cave.

Differential Diagnosis. Males of *A. folkertsioides* can be distinguished from those of the other congeners by the structure of the median lobe with strongly enlarged apex and very long flagellum-like copulatory sclerite in the internal sac.

Description. Medium-sized for genus (ABL 1.55–1.69 mm, mean 1.64±0.063 mm, n=4).

Habitus: Body form (Fig. 1B) moderately convex, elongate ovoid (WE/ABL 0.38±0.008), head wide relative to pronotum (WH/WPm 0.76±0.020), pronotum moderately narrow in comparison to elytra (WPm/WE 0.78±0.023).

Integument: Body color brunneo-rufous, appendages testaceous. Microsculpture distinct (Fig. 2B), with isodiametric mesh pattern of polygonal sculpticells over all dorsal surfaces of head, pronotum, and elytra. Body surface shiny, surface sparsely and finely punctate, covered with sparse, yellowish, short setae. Vestiture of elytra moderately long (0.3–0.4 length of discal setae).

Prothorax: Pronotum (Fig. 3B) moderately convex, of moderate size (LP/LE 0.40±0.015), moderately transverse (WPm/LP 1.27±0.023), with lateral margins rectilinearly and moderately constricted posteriorly (WPm/WPp 1.24±0.028). Anterior angles indistinct, posterior angles slightly obtuse (105–110°). Width between posterior angles slightly greater than between anterior angles (WPa/WPp 0.95±0.024). Basal margin straight in middle, slightly oblique at sides.

Scutellum: Externally visible, triangular, with narrowly rounded apex.

Elytra: Narrowly depressed along suture, with traces of 1–2 striae, of average length (LE/ABL 0.59±0.011) and width (WE/LE 0.65±0.016) for genus. Humeri distinct, rounded, in outline forming right angle with longitudinal axis of body. Lateral margins subparallel in middle, slightly divergent at basal fifth, evenly rounded to apex in apical third, without subapical sinuation. Basal margination distinct.

Legs: Protarsi of male with moderately dilated tarsomere 1. Profemora moderately swollen. Metafemora unmodified.

Male genitalia: Median lobe of aedeagus (Fig. 4D) anopic, slightly arcuate, with moderately short and subparallel shaft, with greatly enlarged ovoid apex, widely rounded at tip. The membranous wall of apical ostium is attached to the middle of apical tip thus dividing apex into dorsal and ventral portions. Ventral margin of median lobe moderately enlarged, convex, without poriferous canals. Dorsal copulatory sclerites in form of filament-like structure, apically swirled in short spiral, much longer than aedeagal length. Ventral copulatory sclerites and spines lacking.

Sclerotized membranous folds of internal sac present at the middle of shaft. Left paramere (Fig. 4E) of shape common in genus, paramere apex without setae. Right paramere (Fig. 4F) strongly elongate, bearing a tuft of long setae basally and many (>5) long setae apically; length of basal setae similar to the length of paramere, apical setae shorter than half of the length of paramere.

Geographic Distribution. This species is known from two localities in Jackson and Marshall Counties, Alabama (Fig. 5, red stars).

Habitat. According to the label, the small series of specimens of this species was collected in a hollow with beech debris and sifted out from the debris in a cave. Two collections made outside a cave suggest that this is not a true cavernicolous species.

Relationships. The species is a sister species to *A. folkertsi* Sokolov & Carlton, and the two form a small distinctive group within the genus.

Anillinus hildebrandti Sokolov, sp. n.

(Figs. 1C, 2C, 3C, 4G–I, 5)

Type material. Holotype, one male (CMNH), dissected, labeled: \ Cave Spring Cave, 9mis. E of Decatur, Morgan Co., Ala., June 19, 1939 Coll. A.B. Flanagan \ videt J.M. Valentine 1939 \ [handwritten]. Paratype, one male labeled: \ Cave Spring Cave, S. 4-6-3 W. 9mi. e. s. e. Decatur, Morgan Co., Ala., Coll. W.B. Jones 6-16-'39 \ [handwritten].

Specific epithet. This species is named after Drew Hildebrandt, an Associate Professor of the Department of Surgery at the University of Mississippi Medical Center, Jackson, Mississippi, and an amateur carabidologist, recognizing his valuable input in investigation of biodiversity of the North American Bembidiini and Anillini.

Type locality. USA, Alabama, Morgan County, Cave Springs Cave.

Differential Diagnosis. Males of *A. hildebrandti* can be distinguished from those of the other congeners by the elongate, subparallel habitus together with the structure of the median lobe having copulatory sclerites of the distinctive shape and specific scaly field in the internal sac.

Description. Medium-sized for genus (ABL 1.61–1.68 mm, mean 1.64±0.044 mm, n=2).

Habitus: Body form (Fig. 1C) moderately convex, elongate (WE/ABL 0.35±0.002), head wide relative to pronotum (WH/WPm 0.79±0.012), pronotum moderately narrow in comparison to elytra (WPm/WE 0.80±0.027).

Integument: Body color rufo-testaceous, appendages testaceous. Microsculpture (Fig. 2C) present over all dorsal surfaces: more pronounced on head and elytra, slightly weakened on pronotum, with isodiametric mesh pattern of polygonal sculpticells. Body surface shiny, surface sparsely and finely punctate, covered with sparse, yellowish, short setae. Vestiture of elytra moderately long (0.3–0.4 length of discal setae).

Prothorax: Pronotum (Fig. 3C) moderately convex, of moderate size (LP/LE 0.43±0.030), slightly transverse (WPm/LP 1.14±0.023), with lateral margins moderately constricted posteriorly (WPm/WPp 1.25±0.005), with shallow sinuation before posterior angles. Anterior angles indistinct, posterior angles almost rectangular (95–100°). Width between posterior angles equals the width between anterior angles (WPa/WPp 0.99±0.021). Basal margin slightly concave in middle, slightly oblique at sides.

Scutellum: Externally visible, triangular, with narrowly rounded apex.

Elytra: Narrowly depressed along suture, with traces of 1–2 striae, of average length (LE/ABL 0.57±0.012) for genus, and slightly narrower than average width (WE/LE 0.61±0.010). Humeri distinct, rounded, in outline forming right angle with longitudinal axis of body. Lateral margins subparallel in middle, slightly divergent at basal forth, evenly rounded to apex in apical third, without subapical sinuation. Basal margination distinct.

Legs: Protarsi of male with moderately dilated tarsomere 1. Profemora moderately swollen. Metafemora unmodified.

Male genitalia: Median lobe (Fig. 4G) of aedeagus anopic, slightly arcuate and slightly twisted. Shaft greatly dilated in apical half, with moderately elongate apex, conically tapered to rounded tip. Ventral margin of median lobe slightly enlarged, with many poriferous canals. Dorsal copulatory sclerites fused to form straight, subparallel blade-like sclerite, bifurcated basally and acute apically. Internal sac has a small scaly membranous field overlapping the blade-like sclerite in its apical half, and with scales oriented in dorsal direction. Spines of internal sac absent. Left paramere (Fig. 4H) of shape common in genus, paramere apex with one seta. Right paramere (Fig. 4I) elongate, with many (>10) long setae apically, which are equal to the length of paramere.

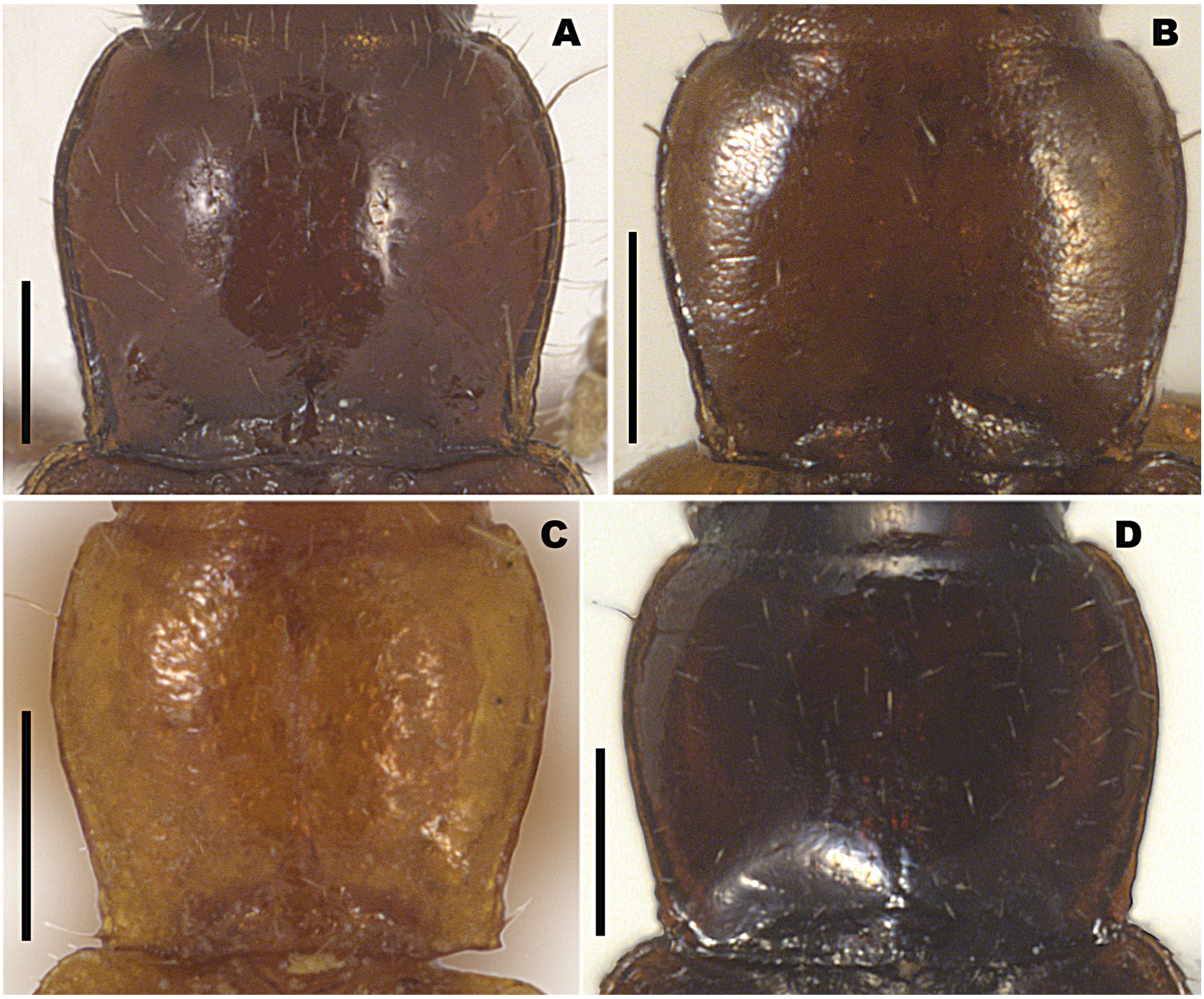


FIGURE 2. Digital images of pronota of *Anillinus* species, dorsal aspect. **A**—*A. clinei* (Stewart Cave, Jackson County, Alabama), **B**—*A. folkertsioides* (Creek Cave, Marshall County, Alabama), **C**—*A. hildebrandti* (Cave Spring Cave, Morgan County, Alabama), **D**—*A. humicolus* (Mountain Brook, Jefferson County, Alabama). Scale bar 0.2mm.

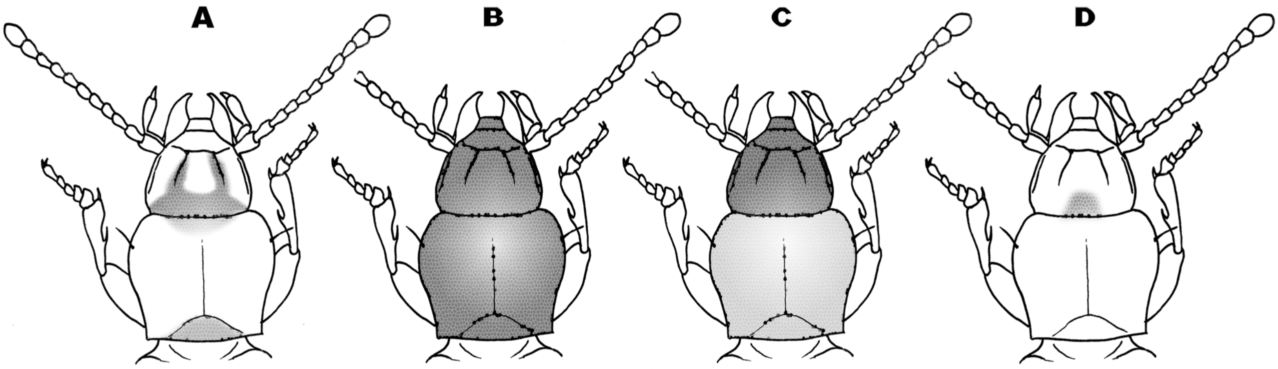


FIGURE 3. Variation of microsculpture patterns among the Alabama *Anillinus*. **A**—*A. clinei* (Stewart Cave, Jackson County, Alabama), **B**—*A. folkertsioides* (Creek Cave, Marshall County, Alabama), **C**—*A. hildebrandti* (Cave Spring Cave, Morgan County, Alabama), **D**—*A. humicolus* (Mountain Brook, Jefferson County, Alabama). Areas with microsculpture are shaded.

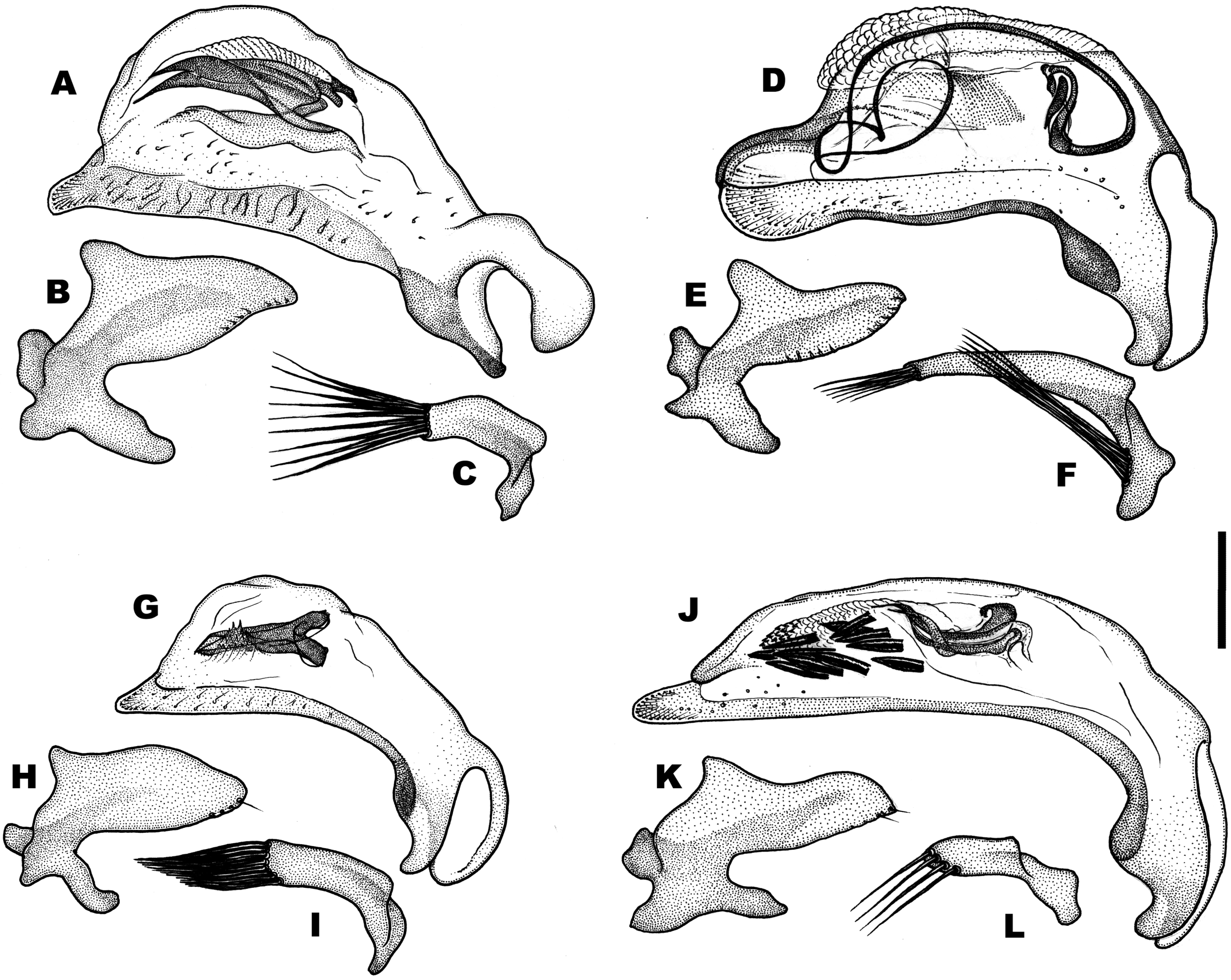


FIGURE 4. Line drawings of male genitalia of *Anillinus* species. *A. clinei* (Stewart Cave, Jackson County, Alabama): **A**—median lobe, right lateral aspect, **B**—left paramere, left lateral aspect, **C**—right paramere, right lateral aspect. *A. folkertsioides* (Creek Cave, Marshall County, Alabama): **D**—median lobe, right lateral aspect, **E**—left paramere, left lateral aspect, **F**—right paramere, right lateral aspect. *A. hildebrandti* (Cave Spring Cave, Morgan County, Alabama): **G**—median lobe, right lateral aspect, **H**—left paramere, left lateral aspect, **I**—right paramere, right lateral aspect. *A. humicolus* (Mountain Brook, Jefferson County, Alabama): **J**—median lobe, right lateral aspect, **K**—left paramere, left lateral aspect, **L**—right paramere, right lateral aspect. Scale bar 0.1mm.

Geographic Distribution. This species is known only from one cave in the Morgan County, Alabama (Fig. 5, yellow circle).

Habitat. According to the label, both specimens of this species were collected in the same cave within an interval of 5 years. Presumably it is a true cavernicolous species.

Relationships. It seems reasonable to place *A. hildebrandti* in one group with the species demonstrating similar shape of the median lobe, i.e., with the shaft dilated in the apical half, enlarged ventral margin, and conically tapered apex. Besides *A. hildebrandti,* this group includes *A. clinei,* new species, described above, *A. cavicola* Sokolov, and *A. hirsutus* Sokolov. The group has a compact range which is limited to four neighboring counties: Morgan, Marshall, Jackson, and Maddison, in the most north-central and northeastern parts of Alabama.

***Anillinus humicolus* Sokolov, sp. n.**

(Figs. 1D, 2D, 3D, 4J–L, 5)

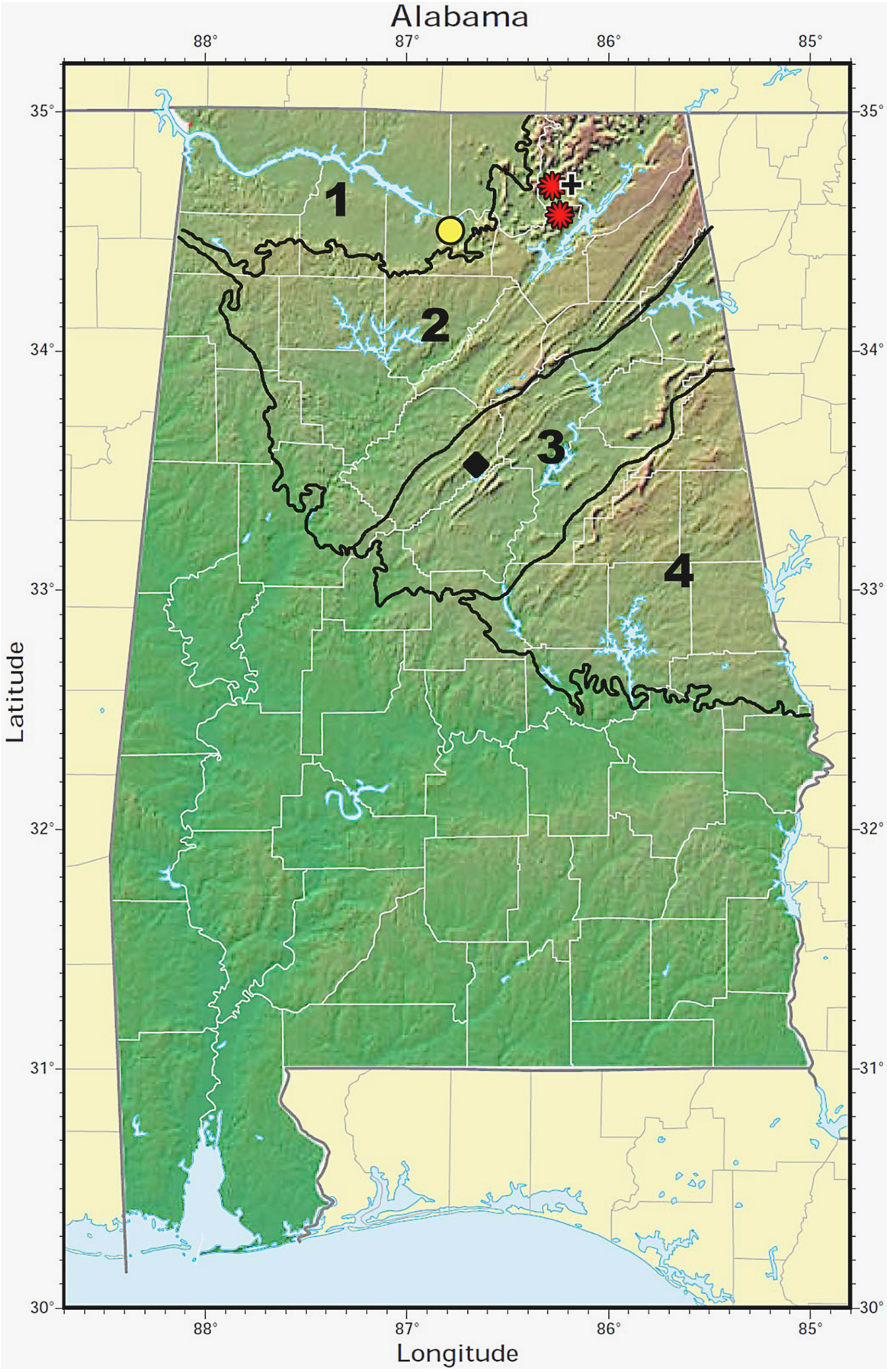


FIGURE 5. Locality records for the newly described species of *Anillinus*: *A. clinei*, black cross; *A. folkertsioides*, red stars; *A. hildebrandti*, yellow circle; *A. humicolus*, black diamond. Physiographic regions of Alabama (Fenneman 1938) numbered as follows: 1—Highland Rim; 2—Cumberland Plateau; 3—Alabama Valley and Ridge; 4—Piedmont Upland.

Type material. Holotype, one male (CMNH), dissected, labeled: \ ALABAMA: Jefferson Co. Cherokee Bend, Mountain Brook nr Birmingham, T.N.King, July 10 1971 \ [computer printed] \ THOMAS C. BARR COLLECTION 2001 ACC. No. 38,014 \ [computer printed] \ 7/10/71 M B \ [handwritten].

Specific epithet. Species name originates from the Latin adjective "*humicolus*" meaning "soil-dwelling", and refers to the presumable habitat of the new species.

Type locality. USA, Alabama, Jefferson County, Mountain Brook (suburb of Birmingham).

Differential Diagnosis. Males of *A. humicolus* can be distinguished from those of the other congeners by the effaced microsculpture on the head and pronotum, and the structure of the median lobe with numerous big spines in the internal sac.

Description. Medium-sized for genus (ABL 1.88 mm).

Habitus: Body form (Fig. 1D) moderately convex, elongate ovoid (WE/ABL 0.38), head wide relative to pronotum (WH/WPm 0.74), pronotum moderately narrow in comparison to elytra (WPm/WE 0.81).

Integument: Body color brunneo-piceous, appendages testaceous. Microsculpture greatly reduced; head and pronotum without microsculpture except small triangular area at the middle of vertex with several polygonal meshes (Fig. 2D); elytra with well-developed polygonal microsculpture. Body surface shiny, surface sparsely and finely punctate, covered with sparse, yellowish, short setae. Vestiture of elytra moderately long (0.3–0.4 length of discal setae).

Prothorax: Pronotum (Fig. 2D) moderately convex, of moderate size (LP/LE 0.40), moderately transverse (WPm/LP 1.32), with lateral margins slightly and rectilinearly constricted posteriorly (WPm/WPp 1.18). Anterior angles indistinct, posterior angles slightly obtuse (110°). Width between posterior angles much greater than between anterior angles (WPa/WPp 0.88). Basal margin slightly concave in middle.

Scutellum: Externally visible, triangular, with narrowly rounded apex.

Elytra: Narrowly depressed along suture, with traces of 1–2 striae, of length (LE/ABL 0.58) and width (WE/LE 0.66) average for genus. Humeri distinct, rounded, in outline forming right angle with longitudinal axis of body. Lateral margins subparallel in middle, slightly divergent at basal fifth, evenly rounded to apex in apical third, without subapical sinuation. Basal margination distinct.

Legs: Protarsi of male with moderately dilated tarsomere 1. Profemora moderately swollen. Metafemora unmodified.

Male genitalia: Median lobe (Fig. 4J) of aedeagus anopic, slightly arcuate and slightly twisted. Shaft elongate, subparallel, with elongate subparallel apex, with rounded tip. Ventral margin of median lobe straight, not enlarged, without poriferous canals. Dorsal copulatory sclerites in form of fused, intertwining blade-like structures slightly widening basally, shaped like an arc with ends facing dorsally, and situated at the middle of shaft. Between dorsal sclerites and apical orifice internal sac has a scaly membranous field with a group of eleven big spines. Left paramere (Fig. 4K) of shape common in genus, paramere apex with two short setae. Right paramere (Fig. 4L) short, with four long setae apically, which are equal to the length of paramere.

Geographic Distribution. This species is known only from Jefferson County, Alabama (Fig. 5, black diamond).

Habitat. The label does not contain any information about subterranean habitat or about any other habitat. Presumably this species is not a cavernicolous species.

Relationships. Based on the structure of the median lobe, *A. humicolus* is a sister species to the cavernicolous *A. valentinei* Barr (cf. Fig. 6G, page 68 in Sokolov 2012). The latter is known to occur in Jefferson County, where it was documented from Crystal Caverns (Peck 1995; Sokolov 2012) situated approximately 16 miles to the NE of the type locality of *A. humicolus*.

Key for identification of the Alabama species of *Anillinus* Casey

The following key is a modification of my old key of the Alabama *Anillinus* (Sokolov 2012) with addition of newly described species. Similarly to the previous key it is mainly based on characters of male genitalia, and to a lesser degree on external features, like the pattern of microsculpture of various body parts, apparent body length, etc. Thus, at present, females of the Alabama *Anillinus* can be identified only tentatively with the limited external features and/or by association with co-occurring males.

1. Large-sized beetles (ABL>2.20 mm) 2
1'. Medium and small-sized beetles (ABL<2.15 mm) 5
2(1). Ventral parts of the body (meso- and metathorax, abdominal sterna) covered with numerous setae. Spines of internal sac

clustered together in a robust plate (Fig. 5G in Sokolov 2012, p.67) . . . . *A. hirsutus* Sokolov

2'. Ventral parts of the body without unusual vestiture. Spines of internal sac either lacking or if present then scattered inside median lobe and separate from each other. 3

3(2'). Internal sac of median lobe with numerous spines separate from each other (like in Fig. 4J 3

3'. Internal sac of median lobe without spines (Fig. 4A) . . . . *A. clinei* Sokolov **sp. nov.**

4(3). Male metafemora modified, with a bifurcate spine near the trochanter. Median lobe with strongly enlarged apex and small spines (Fig. 6A in Sokolov 2012, p. 68) . . . .*A. tombarri* Sokolov

4'. Male metafemora unmodified. Median lobe with narrow apex and numerous large spines (Fig. 6G in Sokolov 2012, p. 68 . . . . *A. valentinei* (Jeannel)

5(1'). Ventral margin of median lobe with a patch of setae (Fig. 6D in Sokolov 2012). Arc of copulative sclerite of median lobe with ends facing ventrally. A litter species with elytral striae obvious only mediad discal setae . . . . *A. steevesi* Barr

5'. Ventral margin of median lobe without a patch of setae. Copulative sclerites of median lobe variable. Species of different habitats and with various elytral striae 6

6(5'). Median lobe with strongly enlarged apex (Fig. 4D and Fig. 27 in Sokolov *et al.* 2004, p. 194). Frons and pronotum with distinct microsculpture of unbroken polygonal sculpticells (Fig. 2D). 7

6'. Median lobe with narrow apex (Figs. 4A, 4G, 4J). At least disc of pronotum with partly obliterated microsculpture seen as a net of partly broken polygonal sculpticells (Figs. 3C and Fig. 2A in Sokolov 2012, p.64) or frons and/or pronotum largely smooth 8

7(6). Internal sac of median lobe with two sclerites. Flagellum-like sclerite shorter, approximately equal to the length of shaft, its apical part not swirled (Fig. 27 in Sokolov *et al.* 2004, p. 194) . . . .*A. folkertsi* Sokolov & Carlton

7'. Internal sac of median lobe with one sclerite. Flagellum-like sclerite long, much longer than the length of shaft, swirled in apical part (Fig. 4D). . . . . *A. folkertsioides* Sokolov **sp. nov.**

8(6'). Frons with distinct microsculpture with isodiametric mesh pattern (Fig. 2C) 9

8'. Frons smooth, without microsculpture (Fig. 2D) 10

9(8). From lateral aspect sclerites of the internal sac of median lobe elongate (Fig. 4G). Right paramere with more than 5 setae (Fig. 4I). . . . . *A. hildebrandti* Sokolov **sp. nov.**

9'. From lateral aspect sclerites of the internal sac of median lobe of approximately equal length and height (Figs. 5A in Sokolov 2012, p. 67). Right paramere with four setae (Figs. 5C in Sokolov 2012, p. 67) . . . .*A. cavicola* Sokolov

10(8'). Pronotum more constricted posteriorly: ratio WPa/WPp>1.00 (Fig. 2B in Sokolov 2012, p. 64), and elytra subdepressed with striae obvious laterad discal setae. Entire vertex and basal part of pronotum with microsculpture. Arc of copulative sclerite of median lobe with ends facing ventrally. Right paramere with more than five setae (Fig. 5F) . . . . *A. davidsoni* Sokolov

10'. Pronotum less constricted posteriorly: ratio WPa/WPp<1.00 (Fig. 3D), and elytra slightly convex with striae obvious only mediad discal setae. Microsculpture of head and pronotum effaced except small triangular area at the middle of vertex (Fig. 2D). Arc of copulative sclerite of median lobe with ends facing dorsally. Right paramere with fewer than five setae (Fig. 4L) 11

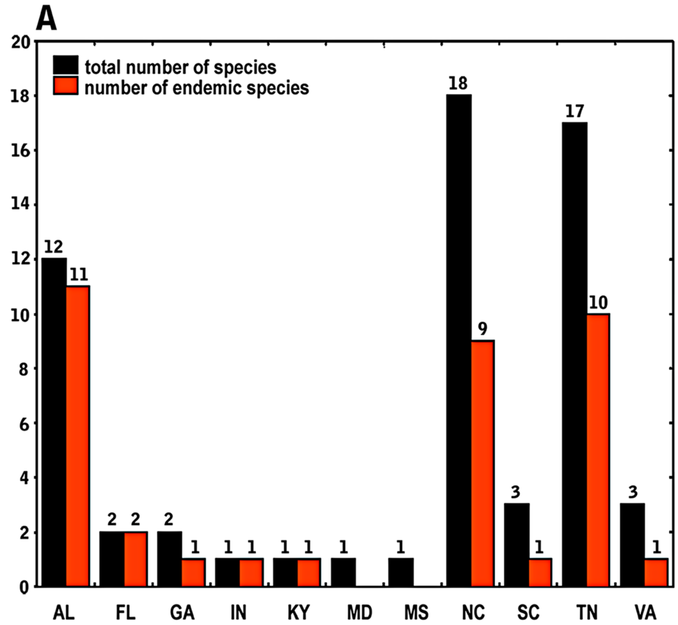
11(10'). Median lobe with apex bent ventrally, forming distinct angle with ventral margin of shaft. Internal sac without spines (Fig 5J in Sokolov 2012, p. 67) . . . .*A. kingi* Sokolov

11'. Median lobe with apex not bent, forming a straight line with ventral margin of shaft. Internal sac with numerous spines (Fig. 4J). . . . .*A. humicolus* Sokolov **sp. nov.**

Discussion

New findings increase the total number of *Anillinus* species recorded in Alabama to twelve. Two new species originate from the Cumberland Plateau Physiographic Region, one species originates from the Alabama Valley and Ridge Physiographic Region, and one species originates from the Highland Rim Physiographic Region (Fig. 5). The two latter findings represent the first records of the subterranean *Anillinus* for the Alabama parts of the correspondent physiographic regions. Among Alabama physiographic regions, the Cumberland Plateau has the greatest diversity of subterranean representatives of *Anillinus*, harboring six of the eight species recorded in the state. This data is in accord with that on the species richness of other subterranean invertebrates as well (Culver *et al.* 2003; Niemiller & Zigler 2013).

In spite of this faunal enrichment, Alabama still only occupies the third position among the eastern states in regards to diversity of *Anillinus* fauna (Fig. 6A, black bars), being significantly outnumbered by North Carolina (18 species) and Tennessee (17 species). However, if considering only the number of endemic species, Alabama is on a par with North Carolina and Tennessee: 11, 9 and 10 respectively (Fig. 6A, red bars). Such a discrepancy in the ratio between species richness and the number of endemics may reflect peculiarities of the geographical regions in which these states are located, and needs to be examined more thoroughly. Ecologically, the *Anillinus* species can be subdivided into litter, endogean, and troglobitic groups in accordance with the types of habitats they dwell in, so that each state can be characterized by the composition of species with particular habitat preferences. If we com-



B

Habitat preference	Common species			Endemic species		
	NC	TN	AL	NC	TN	AL
litter	8	6	1	7	5	3
endogean	1	1	0	2	3	3
troglobitic	0	0	0	0	2	5

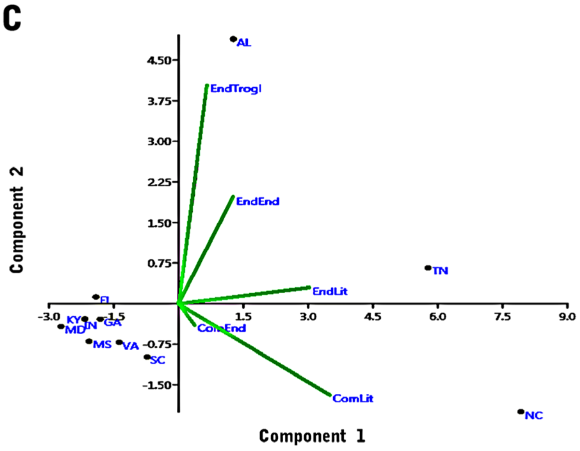


FIGURE 6. Species distribution of *Anillinus* in the eastern USA and factors shaping the genus diversity. **A**—total species number and number of endemics per state in the territory to the east of the Mississippi River (only described species included in Bousquet 2012, Sokolov 2012, 2014). Here and elsewhere state abbreviations follow Federal Information Processing Standards (https://www.nlsinfo.org/content/ cohorts/nlsy79/other-documentation/codebook-supplement/nlsy79-attachment-102-federal); **B**—species compositions in accordance with their habitat preferences in the three most speciose states of the E USA; **C**—biplot graph with clusters of states grouped on the basis of state species compositions using PCA analysis (explanation in the text). Green lines—projections of loadings of the following variables: ComEnd—number of common endogean species, ComLit—number of common litter species, EndEnd—number of endemic endogean species, EndLit—number of endemic litter species, EndTrogl—number of endemic troglobitic species.

pare these state compositions considering two categories: endemics and species common to more than one state, we may get a clue of why Alabama has a higher rate of endemism. Figure 6B demonstrates a part of the numeric matrix compiled on the basis of original and literature data for the three most speciose states. The whole matrix has been analyzed with the help of PCA. The first two components were responsible for more than 96% of the total variance of data, thus pointing out that variations in species numbers among the states were definitely associated with the habitat preferences of the included taxa. The resulting biplot graph of the PCA analysis (Fig. 6C) shows three clusters: the first cluster includes the states with a low diversity of *Anillinus,* whereas the remaining two include the most speciose states. Tennessee and North Carolina form a cluster along the axis of the component 1, while Alabama is associated with the axis of the component 2. The component 1 is maximally influenced by two variables: the number of common litter species and the number of endemic litter species, while the component 2 has high positive associations with other two variables: the number of the endemic troglobytic and endemic endogean species (green lines, Fig. 6C). Accordingly, the component 1 describing the variations of the litter species can be interpreted as a variable reflecting the diversity of the states' terrestrial habitats, while the component 2 describing variations among cave and endogean species can be interpreted as the variable responsible for the diversity of subterranean habitats. These interpretations fit well with the existing natural peculiarities of the topography and geology of Alabama, North Carolina and Tennessee. Analysis of the *Anillinus* fauna of Tennessee and North Carolina reveals the diversity of *Anillinus* in the topographically complex Blue Ridge Mountain Ecoregion (Omernik 1987) of the Southern Appalachians, where both states share a border. Because of the complexity of landscapes, including altitudinal zonation, slope orientations, and vegetation diversity, the group of litter species inhabiting this region is more abundant, while the subterranean fauna of *Anillinus* is less numerous and diverse. In contrast, the terrestrial topography in Alabama is less complex, regional vertical zonation is less pronounced, vegetation is more uniform, etc.; however, the state is famous for the complexity of its subterranean topography, namely for its karst structures. Jackson County, Alabama, for example, is considered to be one of the highest density cave areas in the USA (Christman & Culver 2001). Concordantly, litter species in Alabama are comparatively rare, and the local fauna of *Anillinus* is dominated by representatives of the subterranean lineages, especially those from cave habitats. The dominant role of the troglobitic lineages when compared to other lineages of *Anillinus* is also in accord with the fact that Alabama has one of the highest diversities of troglobitic arthropods in the USA (Peck 1989, 1995, 1998), and is considered to be one of the hotspots of cave endemism (Christman *et al.* 2005; Culver *et al.* 2006). Taking in account that subterranean fauna of *Anillinus* is insufficiently explored and more new species are to be discovered, the proportion of endemics in faunas of Tennessee and North Carolina may grow up in the future. Even in this case, the percentage of endemics in Tennessee and North Carolina still remains less than in Alabama, because of a much higher number of widely distributed litter species in the first two states.

In summary, variations in the species compositions of *Anillinus* considering their habitat preferences satisfactorily explain variations of the regional ratio between species richness and the number of endemics, working as an indicator of differences in the topography and geology of the regions under question.

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References

Barr, T.C. (1995) Notes on some anillines (Coleoptera, Carabidae, Bembidiinae) from southeastern United States, with description of a new genus and two new species. *Special Bulletin Japanese Society of Coleopterology*, 4, 239–248.

Bonelli, F.A. (1810) *Observations entomologiques. Première partie (cicindélètes et portion des carabiques)* [with the "Tabula synoptica exhibens genera carabicorum in sectiones et stirpes disposita"]. Memorie della Reale Accademia della Scienze di Torino, 18, 1–58, 1 tab.

Bousquet, Y. (2012) Catalogue of Geadephaga (Coleoptera, Adephaga) of America, North of Mexico. *ZooKeys*, 245, 1–1722. https://doi.org/10.3897/zookeys.245.3416

Casey, T.L. (1918) *Memoirs on the Coleoptera. VIII*. The New Era Printing Company, Lancaster, Pennsylvania, 727 pp. https://doi.org/10.5962/bhl.title.1159

Christman, M.C. & Culver, D.C. (2001) The relationship between cave biodiversity and available habitat. *Journal of Biogeography*, 28, 367–380. https://doi.org/10.1046/j.1365-2699.2001.00549.x

Christman, M.C., Culver, D.C., Madden, M.K. & White, D. (2005) Patterns of endemism of the eastern North American cave fauna. *Journal of Biogeography*, 32, 1441–1452. https://doi.org/10.1111/j.1365-2699.2005.01263.x

Culver, D.C., Christman, M.C., Elliott, W.R., Hobbs III, H.H. & Reddell, J.R. (2003) The North American obligate cave fauna: regional patterns. *Biodiversity and Conservation*, 12, 441–468. https://doi.org/10.1023/A:1022425908017

Culver, D.C., Deharveng, L., Bedos, A., Lewis, J.J., Madden, M., Reddell, J.R., Sket, B., Trontel, P. & White, D. (2006) The mid-latitude biodiversity ridge in terrestrial cave fauna. *Ecography*, 29, 120–128. https://doi.org/10.1111/j.2005.0906-7590.04435.x

Fenneman, N.M. (1938) *Physiography of eastern United States*. McGraw-Hill Book Co., New York, London, 714 pp.

Jeannel, R. (1963a) Monographie des ''Anillini'', Bembidiides endogés [Coleoptera Trechidae]. *Mémoires du Muséum National d'Histoire Naturelle*, Série A, Zoologie, 28, 33–204.

Jeannel, R. (1963b) Supplément à la monographie des Anillini. Sur quelques espèces nouvelles de l'Amérique du Nord. *Revue Française d'Entomologie*, 30, 145–152.

Hammer, Ø., Harper, D.A.T. & Ryan, P.D. (2001) PAST: Paleontological Statistics software package for education and data analysis. *Palaeontologia Electronica*, 4, 1–9.
Latreille, P.A. (1802) *Histoire naturelle, générale et particulière des crustacés et des insectes. Ouvrage faisant suite à l'histoire naturelle générale et particulière, composée par Leclerc de Buffon, et rédigée par C.S. Sonnini, membre de plusieurs sociétés savantes. Familles naturelles des genres. Tome troisième.* F. Dufart, Paris, 467 pp. [pp. i–xii + pp. 13–467]
https://doi.org/10.5962/bhl.title.15764
Linnaeus, C. (1758) *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. Tomus I.* Laurentii Salvii, Holmiae, [4] + 823 + [1] pp.
https://doi.org/10.5962/bhl.title.542
McGarigal, K., Cushman, S. & Stafford, S. (2000) *Multivariate statistics for wildlife and ecology research*. Springer-Verlag Inc., New York, 283 pp.
https://doi.org/10.1007/978-1-4612-1288-1
Niemiller, M.L. & Zigler, K.S. (2013) Patterns of cave biodiversity and endemism in the Appalachians and Interior Plateau of Tennessee, USA. *PLoS ONE*, 8 (5), e64177.
https://doi.org/10.1371/journal.pone.0064177
Omernik, J.M. (1987) Ecoregions of the conterminous United States. *Annals of the Association of American Geographers*, 77, 118–125.
https://doi.org/10.1111/j.1467-8306.1987.tb00149.x
Peck, S.B. (1989) The cave fauna of Alabama. Part 1. The terrestrial invertebrates (excluding insects). *Bulletin of the National Speleological Society*, 51, 11–33.
Peck, S.B. (1995) The cave fauna of Alabama. Part 2. The insects. *Bulletin of the National Speleological Society*, 57, 1–19.
Peck, S.B. (1998) A summary of diversity and distribution of the obligate cave-inhabiting faunas of the United States and Canada. *Journal of Cave and Karst Studies*, 60 (1), 18–26.
Sokolov, I.M. (2012) Five new species of *Anillinus* Casey from Alabama with a key to the Alabama species (Carabidae: Trechinae: Bembidiini). *Annals of Carnegie Museum*, 81, 61–71.
https://doi.org/10.2992/007.081.0104
Sokolov, I. M. (2014) A new species of *Anillinus* Casey from the Oak Ridge area west of the Appalachian Mountains in Tennessee (Coleoptera: Carabidae: Trechinae: Bembidiini). *Annals of Carnegie Museum*, 82, 225–229.
https://doi.org/10.2992/007.082.0302
Sokolov, I.M., Carlton, C.E. & Cornell, J.F. (2004) Review of *Anillinus* with descriptions of 17 new species and a key to soil and litter species (Coleoptera: Trechinae: Bembidiini). *The Coleopterists Bulletin*, 58, 185–233.
https://doi.org/10.1649/611
Sokolov, I.M. & Kavanaugh, D.H. (2014) The *integripennis* species group of *Geocharidius* Jeannel, 1963 (Carabidae, Bembidiini, Anillina) from nuclear Central America: a taxonomic review with notes about biogeography and speciation. *ZooKeys*, 443, 61–118.
https://doi.org/10.3897/zookeys.443.7880
Sokolov, I.M., Reddell, J.R. & Kavanaugh, D.H. (2014) Life beneath the surface of the central Texan Balcones Escarpment: genus *Anillinus* Casey, 1918 (Coleoptera, Carabidae, Bembidiini): new species, a key to the Texas species, and notes about their way of life and evolution. *ZooKeys*, 417, 71–101.
https://doi.org/10.3897/zookeys.417.7733