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Revision of the *elongatus* and *pecki*
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(Coleoptera: Carabidae: Trechinae: Anillini), with four
new species and notes on *Anillinus turneri* Jeannel, 1963

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Revision of the *elongatus* and *pecki*
species groups of *Anillinus* Casey, 1918
(Coleoptera: Carabidae: Trechinae: Anillini), with four
new species and notes on *Anillinus turneri* Jeannel, 1963

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Abstract. The small, eyeless beetles of the genus *Anillinus* Casey (Coleoptera: Carabidae: Trechinae: Anillini) comprise a diverse, ubiquitous, but poorly known component of insect biodiversity in the southeastern United States. Their limited dispersal capabilities make them ideal subjects for biogeography, but taxonomic problems and undescribed species diversity hamper such studies. In this paper, we redescribe four enigmatic species, *Anillinus docwatsoni* Sokolov and Carlton, *Anillinus elongatus* Jeannel, *Anillinus pecki* Giachino, and *Anillinus turneri* Jeannel, and consider their relationships. The *elongatus* species group is revised, with descriptions of four newly discovered species, *Anillinus arenicollis* Harden and Caterino, **new species**, *Anillinus montrex* Harden and Caterino, **new species**, *Anillinus pittsylvanicus* Harden and Caterino, **new species**, and *Anillinus uwharrie* Harden and Caterino, **new species**. Two species previously considered part of the *elongatus* group are determined to not belong here, *Anillinus cavicola* Sokolov and *Anillinus turneri* Jeannel. The exact placement of *A. turneri* remains uncertain, but it shares some character states with the *sinuaticollis* group. We erect the *pecki* group for *A. docwatsoni* and *A. pecki*, which are likely sister species. We provide a key to the eastern species groups of *Anillinus* and the species of the *elongatus* and *pecki* species groups. *Anillinus pecki* is broadly distributed in the southern Appalachian Mountains northeast of the French Broad River basin, while *A. docwatsoni* is apparently endemic to the Hickory Nut Gorge in western North Carolina. *Anillinus pecki* is reported for the first time from Tennessee and Virginia. All members of the *elongatus* group have small geographic ranges and are difficult to sample without special techniques, hinting that many more species await discovery in the densely populated Piedmont region of North Carolina, where natural habitats are rapidly being lost. Our sampling was not dense enough to test biogeographic hypotheses, but distributions of the *elongatus* group species suggest that hydrochory might have played an important role in passive dispersal and reproductive isolation. These taxonomic contributions will facilitate future studies on the genus and serve to highlight the rich insect biodiversity that remains to be discovered in the southeastern United States.

Key words. Piedmont, endogean fauna, micro-range endemic, biodiversity, Nearctic.

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Introduction

With 66 previously described species, the genus *Anillinus* Casey is one of the most diverse genera of Anillini in the world. Despite being small and eyeless (Fig. 1A,B), with limited dispersal capabilities, *Anillinus* can be found over a broad area of the United States, concentrated in three regions: the Balcones Escarpment of central Texas (Sokolov et al. 2014; Sokolov 2022), the Ozark Plateau and Ouachita Mountains of Missouri, Arkansas and Oklahoma (Sokolov et al. 2004, 2017; Sokolov and Watrous 2008), and the eastern United States from Maryland, Ohio, and Indiana south to Florida, Alabama, Mississippi, and Louisiana (Dury 1902; Sokolov and Carlton 2010;

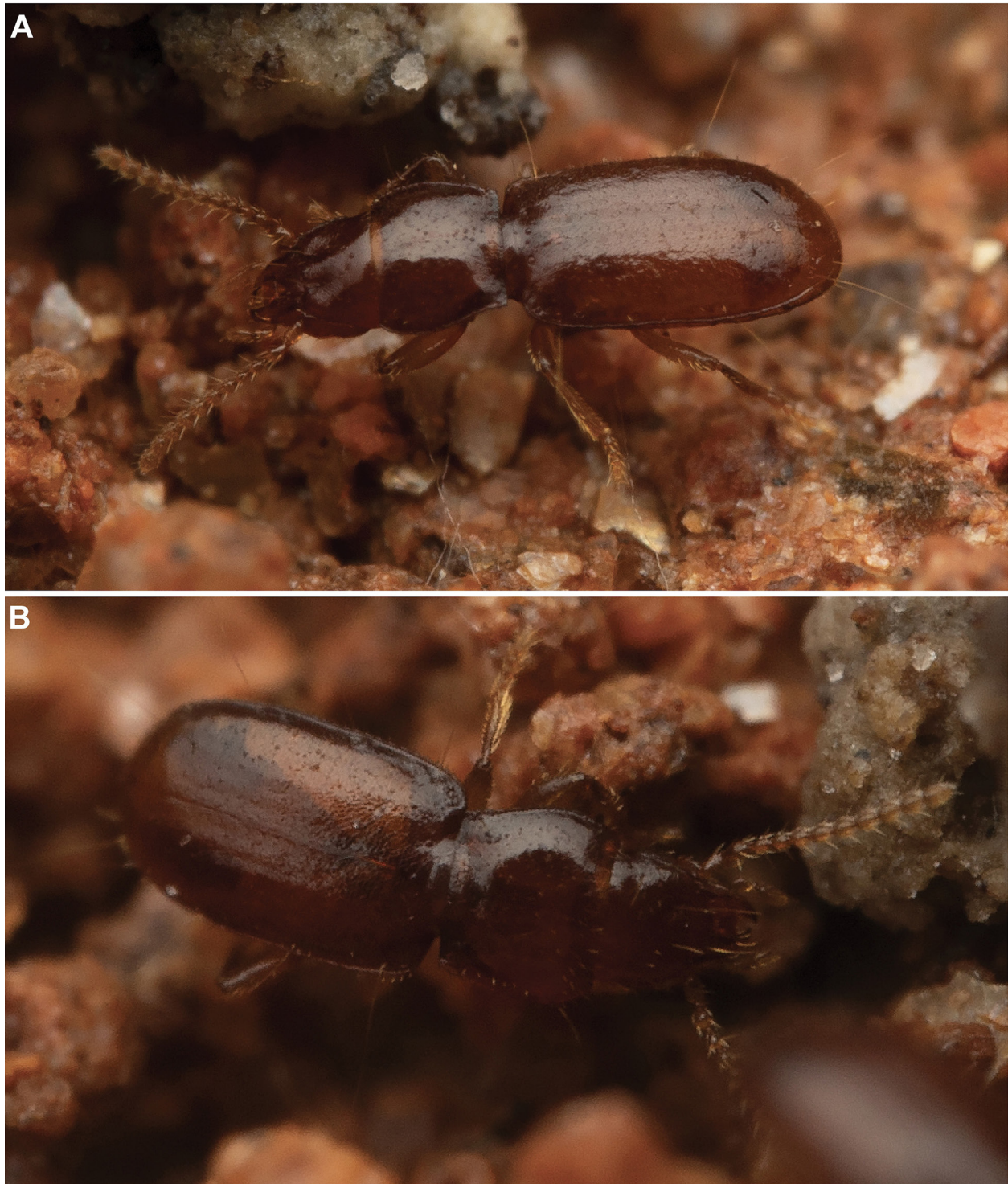


Figure 1. Live individual of *Anillinus uwharrie*. **A)** Left lateral aspect. **B)** Dorsal aspect. Photographed by Adam Haberski. Body length of this species is 1.53–1.83 mm.

Sokolov 2012, 2021; Sokolov and Schnepf 2021). The southeastern United States holds the majority of the species, most of which have been described within the past two decades. Despite recent taxonomic attention, there remain several species in the southeastern United States that are poorly known.

Understanding relationships among species of *Anillinus* has been challenging because some species were described with brevity or based upon inadequate material. In the Piedmont and Blue Ridge foothills, three species remain enigmatic since their descriptions: *Anillinus docwatsoni* Sokolov and Carlton, *Anillinus elongatus* Jeannel, and *Anillinus turneri* Jeannel. The holotype, and only male specimen, of *A. docwatsoni* was slide-mounted and crushed by the coverslip, obscuring important male genitalic structures. The descriptions of *A. elongatus* and *A. turneri* are terse and lack important characters (Jeannel 1963a, b). The holotypes of both *A. elongatus* and *A. turneri* are female, and males of *A. turneri* have not been previously studied and described in detail. *Anillinus elongatus* was redescribed by Sokolov et al. (2004), who adopted a conservative concept that encompassed specimens spanning a large geographic range; recent collections of endogean *Anillinus* in the Piedmont region have revealed numerous short-range endemic species related to *A. elongatus*. Additionally, we found that the specimen labeled as the neotype of *A. elongatus* by Sokolov et al. (2004) is not the specimen designated in the text; it is not from the type locality and is not conspecific with *A. elongatus*.

We redescribe *A. turneri*, including the first description of its male secondary sexual modifications, based on two male topotypic specimens discovered by C. Harden in the Carnegie Museum of Natural History. We also redescribe *A. docwatsoni* based on freshly collected material from the type locality and redescribe its likely sister species *Anillinus pecki* Giachino. The pecki species group is erected for *A. docwatsoni* and *A. pecki*. The known species of the elongatus group are also revised, with a redescription of *A. elongatus* based largely on fresh material, and descriptions of four recently discovered species. The species and species groups relationships are discussed, along with biogeographic patterns.

Materials and Methods

This study is based on examination of three specimens of *A. turneri*, 347 specimens of the pecki group, and 131 specimens of the elongatus group. Specimens cited and/or examined are deposited in the following collections:

- ADC** (Augusto Degiovanni personal collection, Bubano, Italy)
- CMNH** (Carnegie Museum of Natural History, Pittsburgh, PA, USA)
- CNC** (Canadian National Collection, Ottawa, Ontario, Canada)
- CUAC** (Clemson University Arthropod Collection, Clemson, SC, USA)
- CWHC** (Curt W. Harden personal collection, Central, SC, USA)
- FSCA** (Florida State Collection of Arthropods, Gainesville, FL, USA)
- INHS** (Illinois Natural History Survey, Champaign, IL, USA)
- JRLC** (James R. LaBonte personal collection, Salem, OR, USA)
- LSAM** (Louisiana State Arthropod Museum, Baton Rouge, LA, USA)
- NCSU** (North Carolina State University Insect Collection, Raleigh, NC, USA)
- UGCA** (University of Georgia Collection of Arthropods, Athens, GA, USA)
- USNM** (United States National Museum of Natural History, Washington, D.C., USA)
- TLC** (Todd Lawton personal collection, Winnipeg, Manitoba, Canada)
- VMNH** (Virginia Museum of Natural History, Martinsville, VA, USA)

Morphology

Terminology of structures follows that of Slipinski and Lawrence (2013). Designation of right and left parameres follows modern convention, as does the designation of dorsal and ventral faces of the median lobe (Sokolov 2022).

The following measurements of body parts were taken from calibrated images, using Adobe Photoshop (24.1.1 release): apparent body length (**ABL**), measured from anterior margin of clypeus to apex of elytra at midpoint; maximum head width (**HW**); maximum pronotum width (**PW**); basal pronotum width, measured at posterior angles but not including protruding denticles when present (**PbW**); maximum elytral width (**EW**);

elytral length (**EL**), measured from posterior margin of scutellum to apex of elytra at midpoint; and length of the ring sclerite of males (**RL**). Relative sizes and proportions are given as ratios in the descriptions.

The macrosetae on the head that are here referred to as “supraorbital setae” are perhaps not homologous with supraorbital setae of other authors. Two large setae are present on each side of the head in all Nearctic anillines studied, with the posterior ones set more medial than the anterior ones. A third large seta is sometimes present on either side of the head behind the anterior seta and is equidistant from that seta and the posterior seta; this third seta is longer and slightly wider than the scattered background setae, but the associated pore is not always as large as the pores of the other two supraorbital setae. The placement of the third setae is consistent across specimens of a species and when it is present, the head is described as having three supraorbital setae on each side. Most anillines have short setae scattered in this region of the head, and it is possible that this “third seta” is homologous with a seta that is present and shorter in species that we consider to lack it; in the taxa we describe as having three supraorbital setae, the third seta is just as long or nearly so as the other two supraorbital setae and is therefore conspicuous.

Examination of external structures was done using Amscope (sku: SM-1BSL-V331), Leica M80, and Olympus SZX7 stereoscopes, at 7–100× magnifications. Cleared and uncleared mouthparts, legs, male and female genitalia were placed in glycerin on depression slides and examined using a Motic BA300 compound microscope. Abdomens from which DNA had been extracted were largely free of musculature, and genitalia could be easily removed using minuten pins and fine forceps. Male genitalia of other specimens were removed by relaxing the specimen in warm water for 0.5 hours or longer and then pulling the aedeagus out of the abdomen using a bent minuten pin while bracing the specimen with fine forceps; a fingertip placed between the forceps controlled the amount of closure and prevented crushing the specimen. When necessary, genitalia were cleared in 0.5mL centrifuge vials containing either 85% lactic acid or 10% potassium hydroxide (KOH) placed in a warm water bath for 0.5 hours or more (lactic acid) or 5 to 10 minutes (KOH). Some median lobes were further cleared by placing in a drop of clove oil and allowing to sit overnight at room temperature. Pieces were rinsed in 80% ethanol after removing from glycerin and before placing in clearing agents. Most genitalia were stored in glycerin in plastic microvials pinned beneath the specimens. Both male and female genitalia are asymmetrical, so permanent mounting prevents studying their true structure and was for this reason largely avoided. Despite this shortcoming, the male genitalia of holotypes were mounted in Euparal on plastic boards to minimize the risk of their being lost. Some female genitalia were also permanently mounted in the same manner.

Results

Taxonomy

Anillinus Casey, 1918

Anillinus Casey 1918: 167. Type species: *Anillus* (*Anillinus*) *carolinae* Casey, 1918, by original designation (Casey 1918).

Micranillodes Jeannel 1963a: 57. Synonymy established by Bousquet (2012: 699). Type species: *Micranillodes depressus* Jeannel, 1963, by original designation (Jeannel 1963a).

Troglanillus Jeannel 1963b: 147. Synonymy established by Barr (1995: 240). Type species: *Troglanillus valentinei* Jeannel, 1963, by original designation (Jeannel 1963b).

Diagnosis. Male *Anillinus* in the eastern United States can be distinguished most readily from the other eastern anilline genus, *Serranillus* Barr, by the unmodified posterior margin of the last abdominal ventrite, and the well-developed right paramere of the aedeagus with four or more apical setae.

Note. With the exception of *A. turneri*, the species treated in this work are members of the “ESP clade”, which includes the elongatus group, sinuaticollis group, and pecki group. This clade was revealed by DNA sequence data (Harden and Caterino, in prep), and includes montane litter species with a moderately convex and ovoid habitus (pecki group), deep soil species with a somewhat flattened and parallel-sided habitus (sinuaticollis group), and deep soil species with a strongly flattened, narrowed and parallel-sided habitus (elongatus group). The first and

last of these groups are the subject of this work; the *sinuaticollis* group contains several undescribed species in western South Carolina and will be treated in a separate paper on the fauna of that state.

Key to *Anillinus* species groups in Georgia, North Carolina, South Carolina, and Virginia, and species of the *elongatus* and *pecki* groups.

Diagnostic characters have not been found for females of the species treated in this paper. The shape of the spermatheca and its duct probably has some value, but these structures are asymmetrical and appear differently shaped in even slightly different aspects; they have not been studied in sufficient detail to confirm their utility in diagnosing species. Females are best identified by DNA sequence data or by association with males. The latter must be done with caution, since syntopy of two or more closely similar *Anillinus* species is common.

Identifications of males made based only on external characters should be considered tentative; the male genitalia offer the decisive characters for species identification.

1. Protarsomere 1 expanded and bearing conspicuous white adhesive setae ventrally. Last abdominal ventrite with two macrosetae near posterior margin (Males) 2
- Protarsomere 1 not expanded, without adhesive setae ventrally. Last abdominal ventrite with four macrosetae near posterior margin (Females) 18
- 2(1). Metafemur with prominent tooth on posterior margin, either subtriangular or narrow and peg like (Fig. 2C–I) 3
- Metafemur without tooth on posterior margin, at most with medial field of coarse microsculpture (Fig. 2A,B) 13
- 3(2). Ventral adhesive setae present on protarsomere 2 (Fig. 3B–F) 4
- Ventral adhesive setae absent on protarsomere 2 (Fig. 3A) 11
- 4(3). Body moderately convex and ovoid. Hind femora moderately produced posteriorly, with a small blunt tooth. Flagellum of median lobe short. Distribution: north of New River in West Virginia and Virginia **langdoni group (in part; *Anillinus virginiae* Jeannel)**
- Body dorsoventrally flattened and subparallel. Hind femora various, usually with more prominent posterior tooth. Flagellum of median lobe long, filamentous. Distribution: Piedmont of southern Virginia, North Carolina and South Carolina (*elongatus* group) 5
- 5(4). ABL greater than 2 mm 6
- ABL less than 2 mm 7
- 6(5). Profemora with prominent spine on ventral margin **A. sp. “NC, Orange Co. sp. 2”**
- Profemora without spine **A. sp. “NC, Mint Hill”**
- 7(5). Apex of median lobe deflected ventrally in lateral aspect (Fig. 9F,O) 8
- Apex of median lobe not deflected ventrally in lateral aspect 9
- 8(7). Apex of median lobe angulate, blocky (Fig. 9O). Metafemur slightly swollen, tooth on posterior margin prominent (Fig. 2I). Second protarsomere distinctly expanded and dentate on inner margin (Fig. 3H). Disc of pronotum covered with strong microsculpture. Distribution: northeastern South Carolina **A. arenicollis sp. n.**
- Apex of median lobe rounded (Fig. 9F). Metafemur not swollen, tooth on posterior margin small (Fig. 2G). Second protarsomere weakly expanded and minutely dentate on inner margin. Disc of pronotum without traceable microsculpture. Distribution: southern Virginia . . . **A. pittsylvanicus sp. n.**
- 9(7). Median lobe tapered apically in lateral aspect with ventral margin nearly straight (Fig. 7H) **A. uwharrie sp. n.**
- Median lobe not tapered, ventral margin curved or sinuate in lateral aspect (Fig. 7E,J) 10
- 10(9). Apex of median lobe broad, evenly curved (Fig. 9C). Flagellum of internal sac sinuous. Left paramere aetose (Fig. 9A) **A. elongatus Jeannel**

- Apex of median lobe small, abruptly bisected by membranous dorsal margin in dorsolateral aspect (Fig. 9I). Flagellum of internal sac nearly straight beyond basal bend. Left paramere with two or more setae (Fig. 9G) *A. montrex* sp. n.
- 11(3). Profemora with spine on ventral face OR mesotrochanters spinose
 **albrittonorum group (in part), undescribed species group from South Carolina**
- Profemora and mesotrochanters unmodified 12
- 12(11). Dorsal margin of median lobe strongly sclerotized (Fig. 7M). Right paramere narrow and elongate (Fig. 5B). Distribution: Peach County, Georgia *A. turneri* Jeannel
- Dorsal margin of median lobe thin, weakly sclerotized (Fig. 7D,N). Right paramere broad. Distribution: northern South Carolina, northern Alabama, central Tennessee, southern Kentucky, eastern Louisiana **sinuaticollis group**
- 13(2). Right paramere with eight or more setae **barberi group, moseleyae group, hirsutus group**
- Right paramere with four setae 14
- 14(13). Metafemur slightly swollen, produced posteriorly. Second protarsomere without ventral adhesive setae *Anillinus erwini* Sokolov and Carlton
- Metafemur not swollen. Second protarsomere usually with adhesive ventral setae (absent in members of steevesi group and some small valentinei group species) 15
- 15(14). Ventral margin of median lobe in lateral aspect with row of stout, conspicuous setae (Fig. 7A). Flagellum weakly sclerotized and short *A. pecki* Giachino
- Ventral margin of median lobe usually asetose, if setae are present, they are small and visible only in aspects other than lateral. Flagellum various 16
- 16(15). Internal sac in addition to flagellum with spines, plates or fields of small teeth 17
- Internal sac unarmed, without sclerites other than flagellum
 **loweae group (in part), langdoni group (in part), valentinei group (in part)**
- 17(16). Flagellum short, weakly sclerotized (Fig. 7L). Distribution: Henderson and Rutherford Counties, North Carolina *A. docwatsoni* Sokolov and Carlton
- Flagellum longer OR, if short, then dark and strongly sclerotized
 **steevesi group (in part), loweae group (in part), valentinei group (in part)**
- 18(1). Spermathecal duct long, coiled 19
- Spermathecal duct short, not coiled 22
- 19(18). Spermatheca with stem strongly ribbed for at least part of its length (Fig. 8A–E,G)
 **elongatus group (in part)**
- Spermatheca with stem entirely smooth (Fig. 8H,I) 20
- 20(19). Body depressed dorsoventrally, elytra parallel sided 21
- Body moderately convex, elytra more ovoid **steevesi group, valentinei group (in part)**
- 21(20). Head with frontoclypeal horn minute, inconspicuous in lateral aspect
 **undescribed species group from South Carolina**
- Head with frontoclypeal horn conspicuous, visible in lateral aspect **elongatus group (in part)**
- 22(18). Spermathecal duct not apparent **valentinei group (in part)**
- Spermathecal duct visible 23
- 23(22). Spermatheca with stem strongly ribbed for at least part of its length 24
- Spermatheca with stem entirely smooth **erwini group, sinuaticollis group, albrittonorum group, barberi group, langdoni group, loweae group (in part)**
- 24(23). Distribution: north and east of Asheville Basin **pecki group**
- Distribution: south and west of Asheville Basin **moseleyae group and loweae group (in part)**

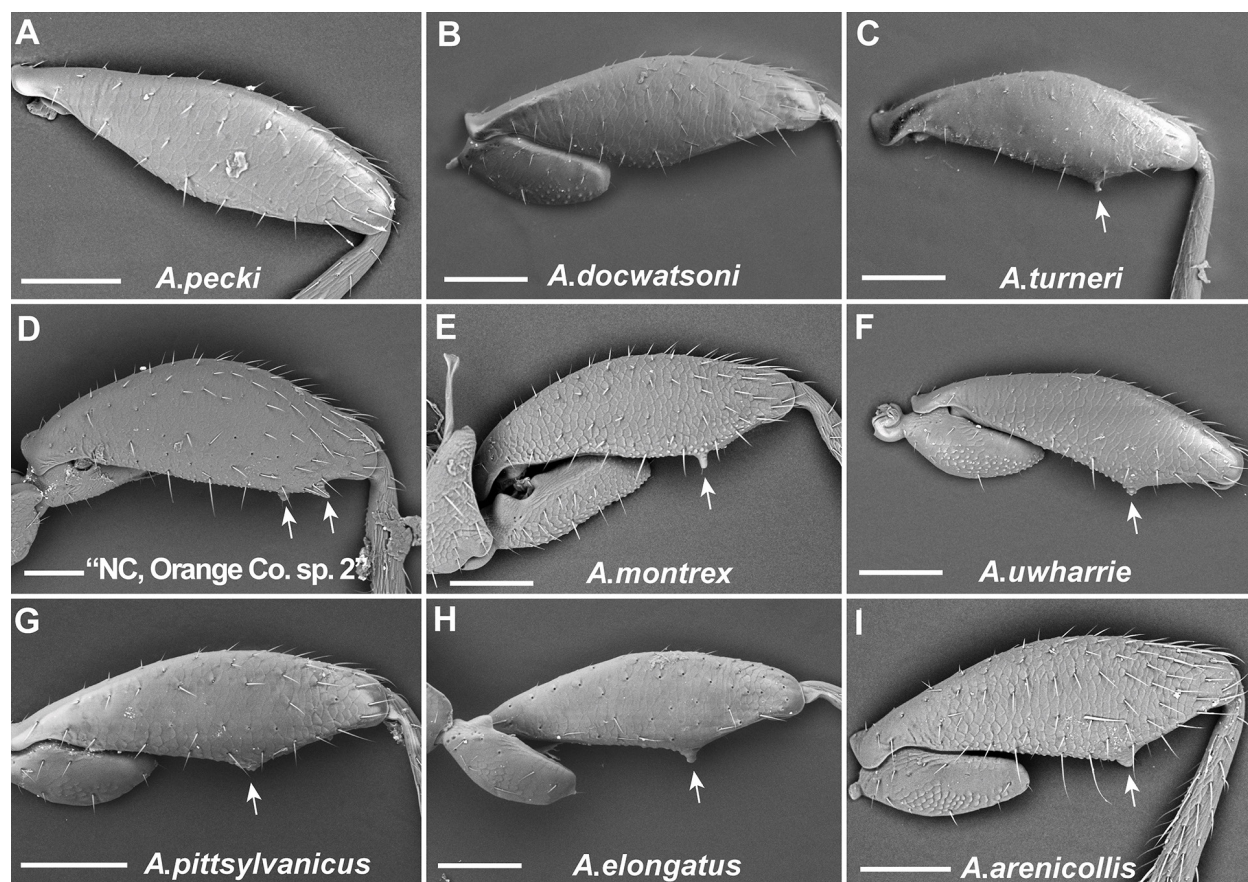


Figure 2. Scanning electron micrographs of male left metafemora of *Anillinus* species, ventral aspect. **A)** *A. pecki*. **B)** *A. docwatsoni*. **C)** *A. turneri*. **D)** *A. sp.* “North Carolina, Orange Co. sp. 2”. **E)** *A. montrex*. **F)** *A. uwharrie*. **G)** *A. pittsylvanicus*. **H)** *A. elongatus*. **I)** *A. arenicollis*. Scale bars = 0.1 mm.

Species Accounts

pecki group, new species group

Diagnosis. Small to medium (ABL = 1.67–1.92 mm) *Anillinus* with a quadrisetose right paramere (Fig. 5A). Submedial setae of mentum positioned posterior to mentum tooth. First and second protarsomeres of males with adhesive vestiture ventrally (Fig. 3B,C). Habitus moderately convex and ovoid, not strongly flattened or parallel sided (Fig. 4A, 6B). Flagellum of median lobe short, weakly sclerotized and “open” laterally, median lobe with or without stout setae on ventral margin (Fig. 7A,B,K,L, 6D). Internal sac with field of sclerotized scales on left side, weakly or strongly sclerotized. Spermatheca with long stem that is strongly ribbed medially, angulate at base (Fig. 8A,B); spermathecal duct short and not coiled.

The two species belonging to this group are most likely to be confused with members of the langdoni group (sensu Sokolov et al. 2007) and loweae group (sensu Sokolov and Carlton 2010), which share many of the character states listed above. The female genitalia provide the best means of separating the two groups: the spermathecal stem is smooth in members of the langdoni group and all loweae group species except *Anillinus cherokee* Sokolov and Carlton (our observations), which has a more evenly curved stem basally.

Distribution. The group consists of two species, *A. docwatsoni* and *A. pecki*. *Anillinus docwatsoni* is apparently restricted to the Hickory Nut Gorge and immediate vicinity in western North Carolina, whereas *A. pecki* is broadly distributed from the Black Mountains in western North Carolina to the Mt. Rogers area of southwest Virginia.

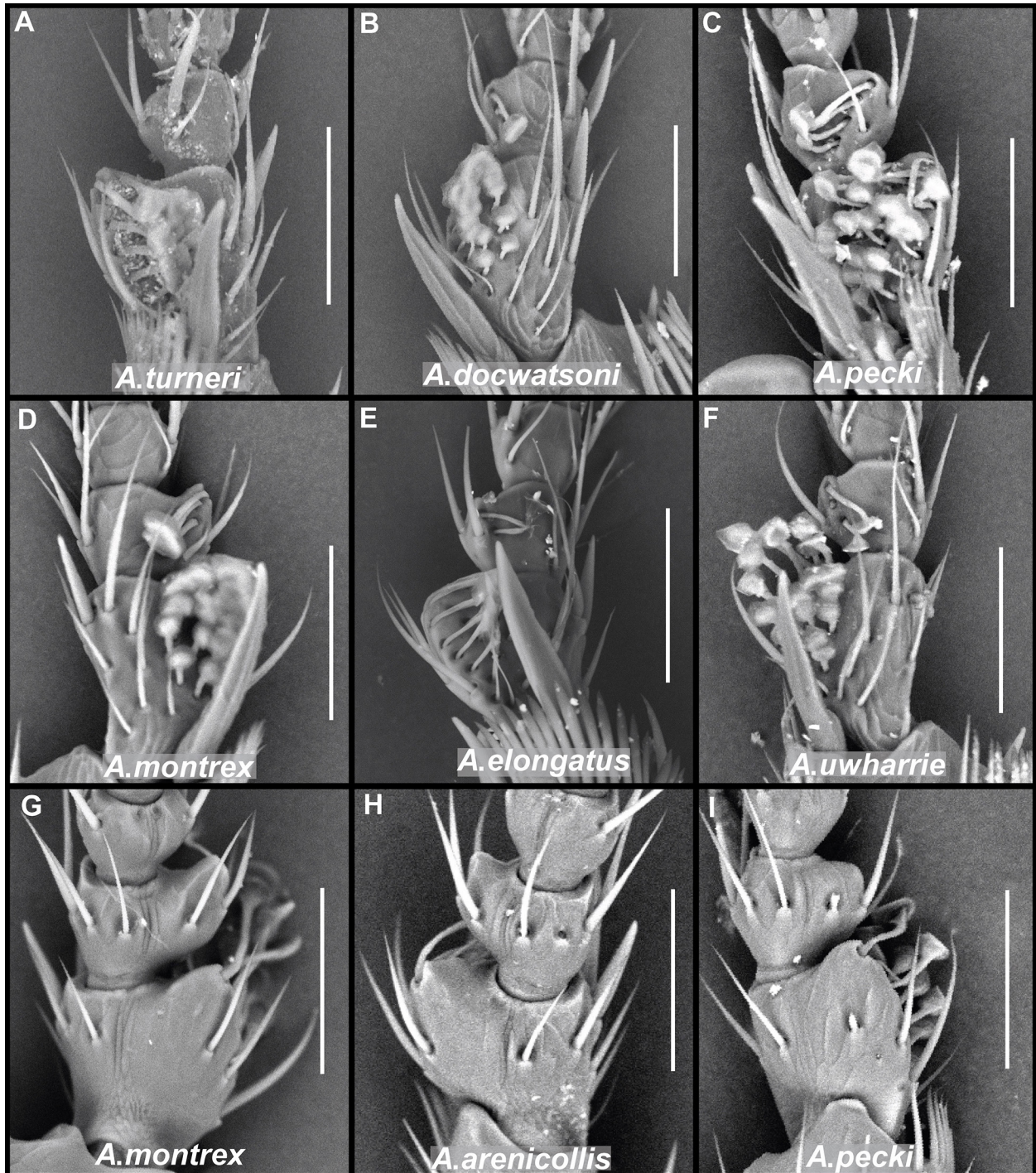


Figure 3. Scanning electron micrographs of left (A,B,E–G,I) and right (C,D,H) male protarsomeres of *Anillinus* species. **A)** *A. turneri*, ventral aspect. **B)** *A. docwatsoni*, ventral aspect. **C)** *A. pecki*, ventral aspect. **D)** *A. montrex*, ventral aspect. **E)** *A. elongatus*, ventral aspect. **F)** *A. uwharrie*, ventral aspect. **G)** *A. montrex*, dorsal aspect. **H)** *A. arenicollis*, dorsal aspect. **I)** *A. pecki*, dorsal aspect. Scale bars = 0.1 mm.



Figure 4. Dorsal habitus of *Anillinus* species. A) *A. pecki*. B) *A. turneri*. C) *A. uwharrie*. D) *A. elongatus*. E) *A. pittsylvanicus*. F) *A. arenicollis*. G) *A. montrex*. H) *A. cavicola*. Scale bars = 1 mm. Abdomen removed for DNA extraction in A, C, and F.

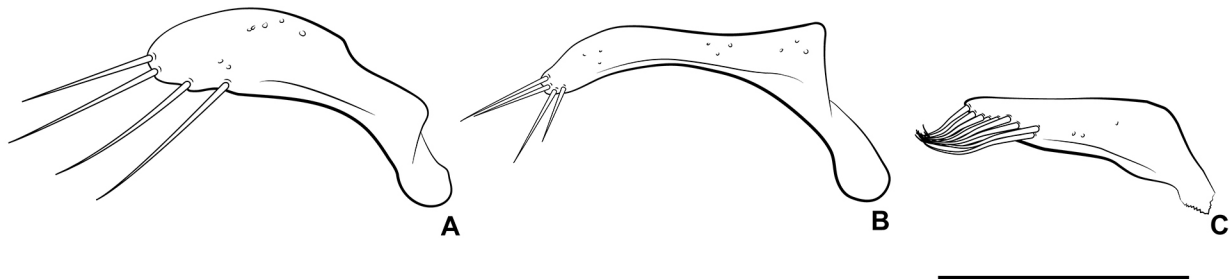


Figure 5. Line drawings of right paramere of *Anillinus* species, right lateral aspect. A) *A. pecki*. B) *A. turneri*. C) *A. cavicola*. Scale bar = 0.1 mm.



Figure 6. *Anillinus docwatsoni*. **A)** Holotype, ventral aspect. **B)** Fresh specimen, dorsal aspect. **C)** Aedeagus of holotype, right lateral aspect. **D)** Median lobe of fresh specimen, right dorsolateral aspect. Scale bars = 1 mm (A, B) and 0.1 mm (C, D). Abdomen removed for DNA extraction in B.

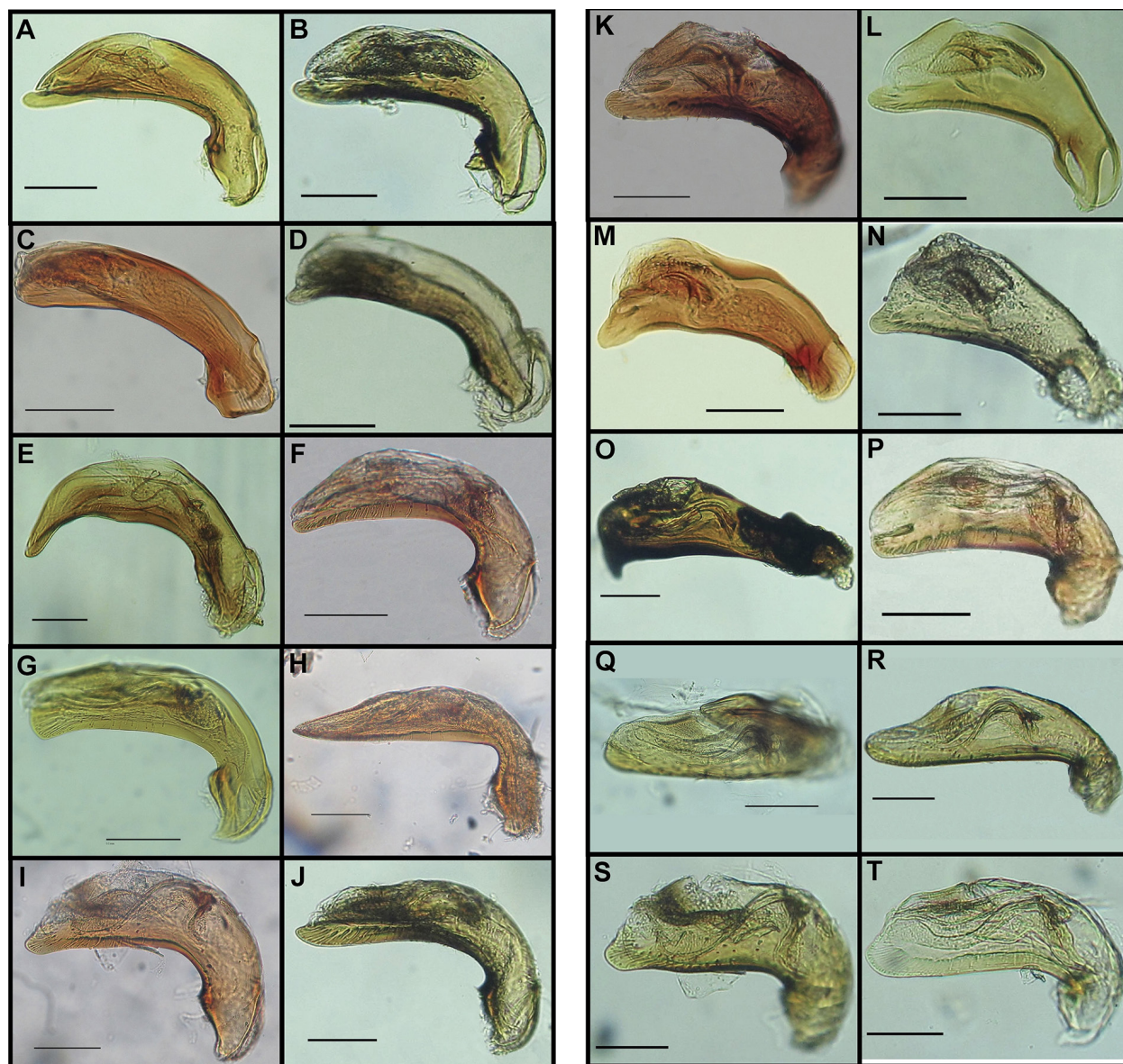


Figure 7. Median lobes of *Anillinus* species in right lateral aspects (A–J) and right dorsolateral aspects (K–T). A,K) *A. pecki*. B,L) *A. docwatsoni*. C,M) *A. turneri*. D,N) *A. cf. felicianus*. E,O) *A. sp.* “North Carolina, Orange Co. sp. 2.” F,P) *A. montrex*. G,Q) *A. arenicollis*. H,R) *A. uwharrie*. I,S) *A. pittsylvanicus*. J,T) *A. elongatus*. Scale bars = 0.1 mm.

Anillinus docwatsoni Sokolov and Carlton, 2004

Fig. 2B, 3B, 6A–D, 7B,L, 8A, 11

Material examined. Holotype male (NCSU): Slide mounted in unknown medium, with genitalia extracted and mounted on same slide (Fig. 6A); labels attached to slide with tape, reading “HOLOTYPE *Anillinus docwatsoni* Sokolov and Carlton: Sokolov et al. 2004 [handwritten on red paper]” “USA, NC Rutherford Co., Chimney Rock, 15 Sept. 1996, J. F. Cornell, Broad R. flood debris.”

Other material (n = 39, ADC, CUAC, CWHC, JRLC): USA: NORTH CAROLINA: Henderson Co.: Bearwallow Mountain, 35.4623, –82.3601, 10 Aug. 2021, M. Caterino leg., sifted flood debris, CUAC000066881, CWH-500 (1♂); Same data as previous (6♂, 4♀). **Rutherford Co.:** Chimney Rock State Park, South Shore of Broad River, 35.4392, –82.2492, 11 Apr. 2023, C.W. Harden leg., under rock, CUAC000066860, CWH-486 (1♂); Chimney

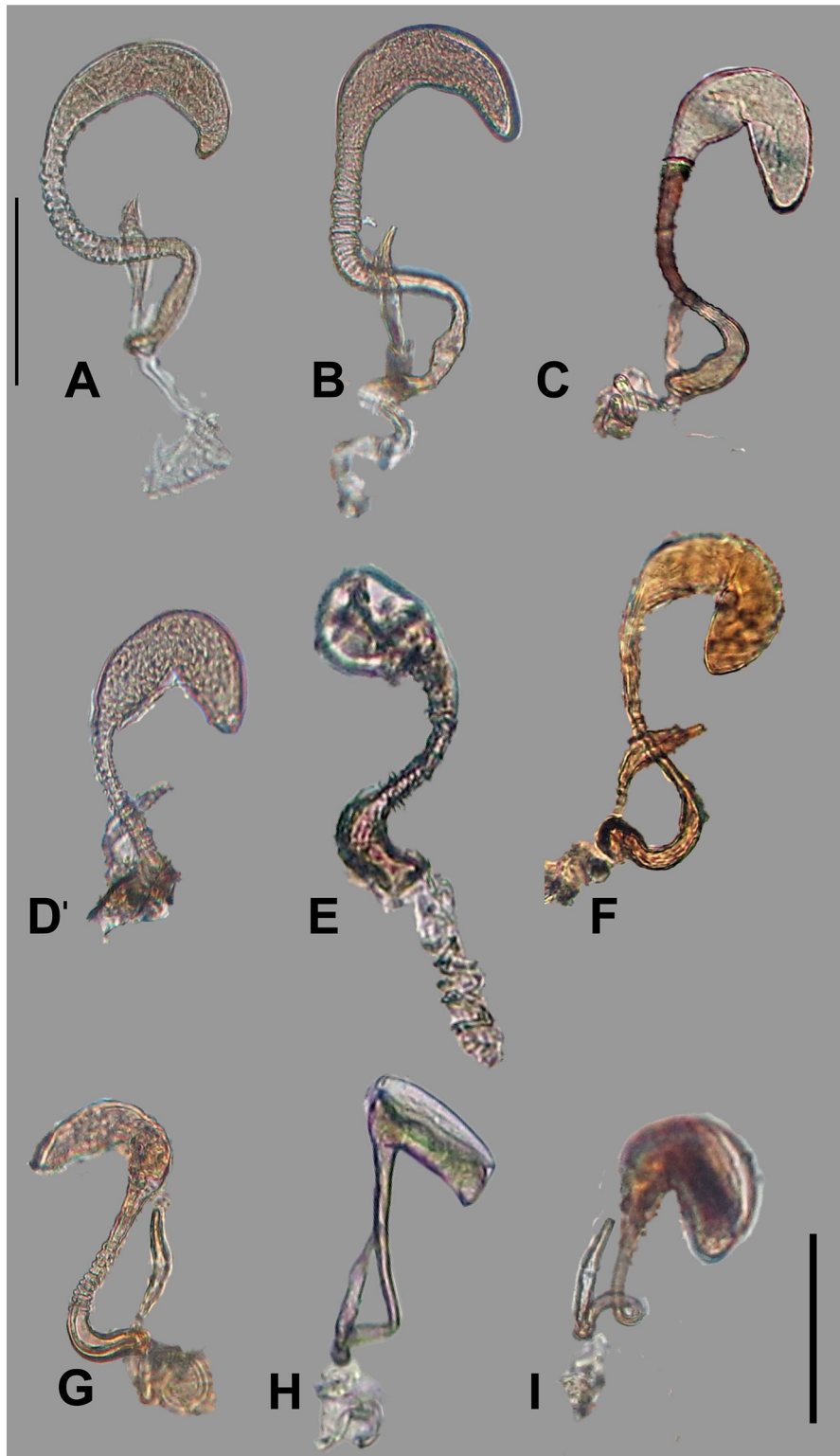


Figure 8. Spermathecae of *Anillinus* species. A) *A. docwatsoni*. B) *A. pecki*. C) *A. arenicollis*. D) *A. elongatus*. E) *A. pittsylvanicus*. F) *A.* sp. “North Carolina, Mint Hill.” G) *A. uwharrie*. H–I) *A. montrex*.

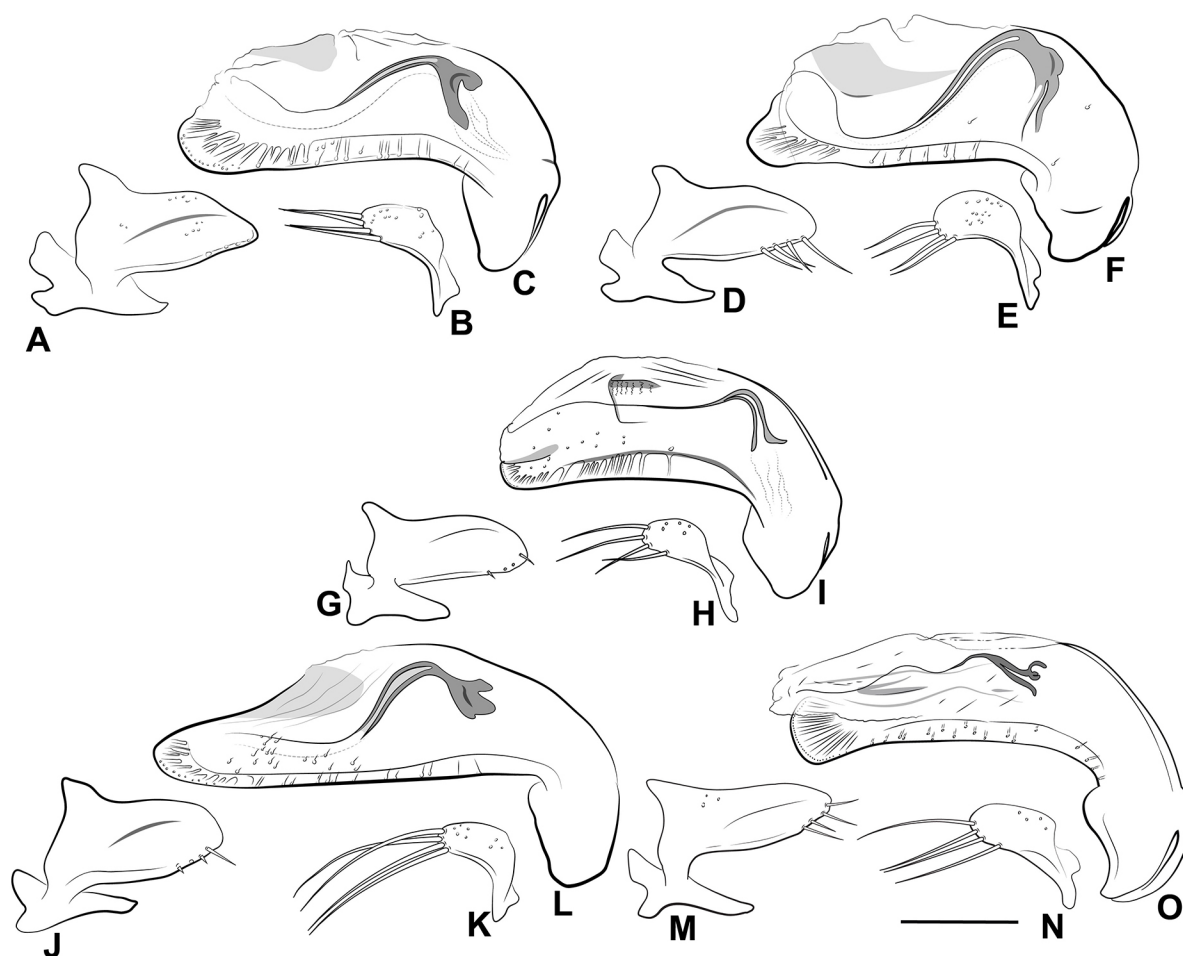


Figure 9. Male genitalia of *elongatus* group *Anillinus* species: left paramere, left lateral aspect (A,D,G,J,M), right paramere, right lateral aspect (B,E,H,K,N), median lobe, right dorsolateral aspect (C,F,I,L,O). **A–C)** *A. elongatus*. **D–F)** *A. pittsylvanicus*. **G–I)** *A. montrex*. **J–L)** *A. uwharrie*. **M–O)** *A. arenicollis*. Scale bar = 0.1 mm.

Rock State Park, top of ridge, 35.4373, –82.2490, 11 Apr. 2023, C.W. Harden leg., under deeply embedded rock (1♂, 1♀); Chimney Rock State Park, slope behind park office, 35.4377, –82.2504, 11 Apr. 2023, C.W. Harden leg., Berlese, sifted soil (3♂); Chimney Rock State Park, slope behind park office, 35.4377, –82.2504, under rocks, C.W. Harden, M.S. Caterino, E. Recuero leg., CUAC000066891, CUAC000066922 and CUAC000066792, CWH-485, CWH-487, CWH-488 (1♂, 2♀); Same data as previous (9♂, 10♀).

Diagnosis. *Anillinus docwatsoni* is externally similar to *A. pecki* and *Anillinus fortis* (Horn), both of which occur nearby, although neither has been found syntopically with *A. docwatsoni*; all three species possess variable microsculpture on the forebody, but usually with microsculpture effaced on each side of vertex and at least weakly impressed on the disc of the pronotum. Males of all three species have adhesive vestiture under protarsomeres 1 and 2, and members of both sexes possess a similar slightly convex and ovoid habitus. Recognition of *A. docwatsoni* is best accomplished through examination of the male genitalia, which are distinctive for the short, weakly sclerotized flagellum, field of small spines on the left side of the internal sac, and absence of stout setae on the ventral margin of the median lobe.

Redescription. *Habitus* (Fig. 6B): Variable in size (ABL 1.67–1.91 mm). Body robust, moderately convex, elytra with rounded sides. Lateral margins of pronotum not sinuate posteriorly. *Integument*: Isodiametric microsculpture on head distinct only as a subtriangular patch on vertex, irregular and patchy on disc of pronotum, largely



Figure 10. Habitats of *elongatus* group species. **A)** Habitat of *A. elongatus* and *A. sp.* “North Carolina, Orange Co. sp. 2”, Duke Forest, Orange Co., NC, 35.9777, -79.1106. **B)** Detail of rock visible in A, where two *A. elongatus* were found on the exposed soil surface. **C)** Habitat of *A. uwharrie*, Uwharrie National Forest, Montgomery Co., NC, 35.3166, -80.0468. **D)** Habitat of *A. arenicollis*, Carolina Sandhills NWR, Chesterfield Co., SC, 34.5672, -80.2113.

absent. *Head*: Moderately sized (avg. HW/PW = 0.71[♂], 0.73[♀]). Frontoclypeal horn present, large. *Legs*: Pro-femora of males unmodified. Male protarsomere 1 expanded and dentate on inner margin, protarsomere 2 not expanded and minutely dentate on inner margin; both male protarsomeres 1 and 2 with adhesive ventral setae (Fig. 3B). Male mesotrochanters unmodified. Male metafemur (Fig. 2B) not swollen, without tooth on posterior face, metatrochanter and metafemur with papillate microsculpture. *Abdominal ventrites*: Unmodified in either sex. *Male genitalia*: Ring sclerite small, less than one fourth body length (RL/ABL = 0.23), shape elongate, asymmetrically tapered posteriorly. Median lobe (Fig. 7B,L) asymmetrical, slightly twisted dorsally from plane of basal lobes; basal bend short; ventral margin slightly expanded, without ventral setae. Internal sac (Fig. 6D, 7L) with weakly sclerotized flagellum sinuate apically; left side of internal sac with dense field of small, weakly sclerotized spines. Left paramere large, conchoidal, ventral margin with four subapical pores bearing short setae except the apical-most which bears a prominent seta. Right paramere short, rounded apically, with four apical setae, similar to that of *A. pecki* (as in Fig. 5A). *Female genitalia*: Spermatheca long, smooth and straight in basal fourth, abruptly curved and ribbed medially, apex slightly expanded (Fig. 8A). Spermathecal duct short and evenly curved, not coiled.

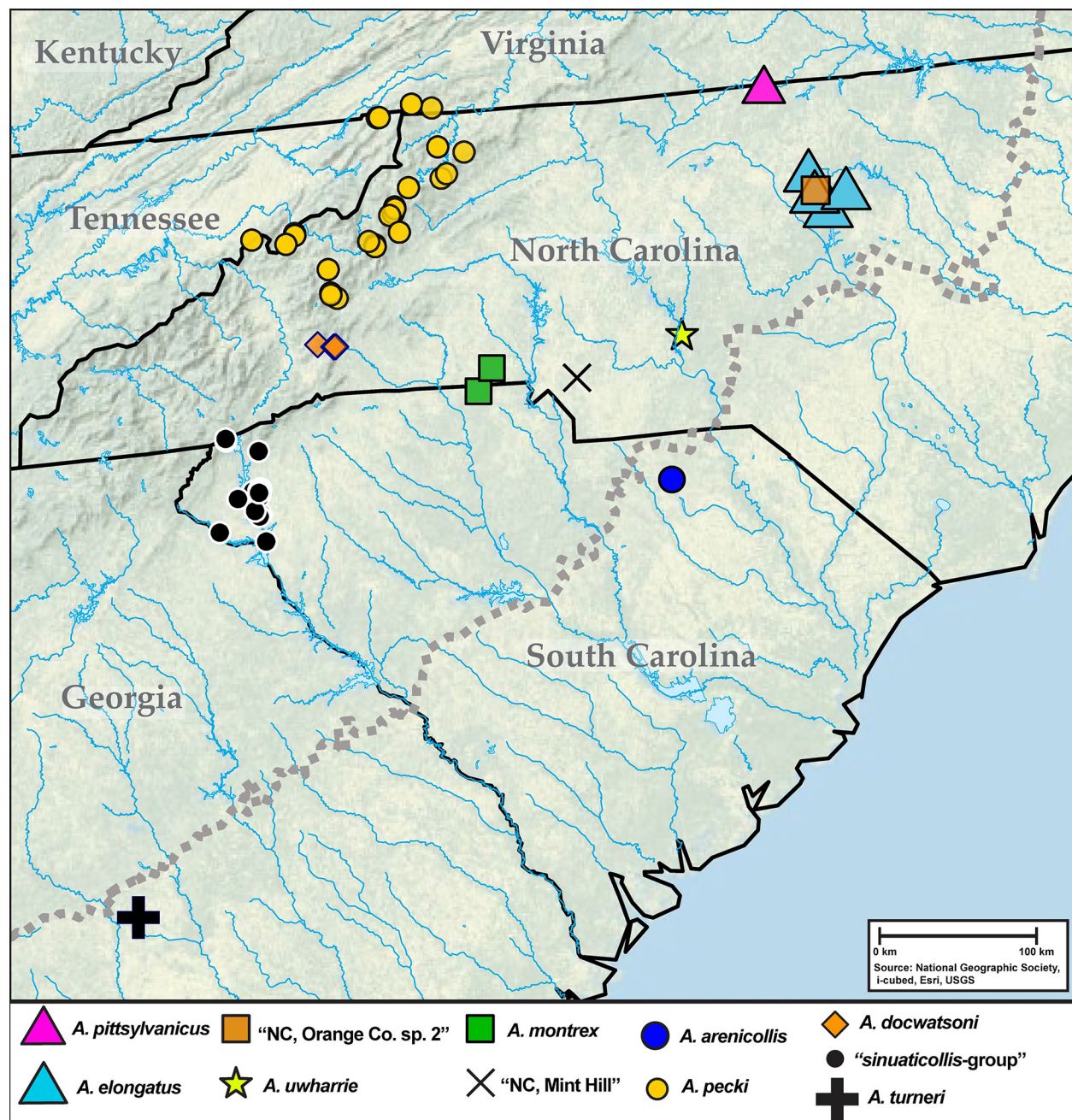


Figure 11. Distribution map of *elongatus* group species and other *Anillinus*. Dotted gray line denotes the Fall Line.

Distribution. The species is known from two localities in western North Carolina (Fig. 11): Chimney Rock State Park (Rutherford Co.) and Bearwallow Mountain (Henderson Co.). The two sites are approximately 10km apart, and are both located on the south side of the Hickory Nut Gorge.

Natural history. At Chimney Rock, specimens were found beneath embedded rocks. Two individuals were under rocks on a dry ridge top, but the remaining specimens were all in a mesic hollow near a small stream. Berlese extraction of soil sifted from beneath the rocks produced three specimens; several large samples of sifted litter did not produce specimens. Despite the lack of morphological modifications associated with an endogean existence, members of this species are apparently endogean in nature, at least in early spring. On nearby Bearwallow

Mountain, a series was collected in August by Berlese extraction of sifted flood debris in a north-facing gully; the male holotype was also extracted from flood debris.

Sympatry. This species is not known to occur with other species of anillines. *Anillinus murrayae*, *A. fortis*, and *Serranillus dunavani* (Jeannel) have been collected elsewhere in the Hickory Nut Gorge and might possibly co-occur. Of these, *A. fortis* is most likely to be confused with *A. docwatsoni* and is best separated by examining male genitalia.

Notes. The holotype (Fig. 6A) is slide mounted ventral-side up. The body and dissected aedeagus are damaged, crushed by the coverslip. The genitalia are in the aspect illustrated by Sokolov et al. (2004), which is a straight right lateral aspect. The median lobe is distorted, forced into a flat plane by the coverslip (Fig. 6C); the median lobe is asymmetrical, so this distortion has forced the apex to be folded upon itself.

Anillinus pecki Giachino, 2011

Anillinus pecki Giachino 2011: 114

Fig. 2A, 3C,I, 4A, 5A, 7A,K, 8B, 11

Material examined. Holotype male (CNC): Studied from photographs available online through the CNC Taxonomy and Specimen Database (Laplante 2024). Specimen is mounted in adhesive on a card and is separated at the pro-mesothoracic junction; the left protibia and protarsus are removed and mounted in the adhesive. The aedeagus appears to be permanently mounted. Original labels: “N. CAR: Avery Co. LinvilleFalls, 3500’ BlueRidge-Pkwy, mi 317 16.VIII.1981 S. Peck rhodo. litter at log” “HOLOTYPUS ♂ *Anillinus pecki* n. sp. P.M. Giachino det 2011 [red cardstock]” “HOLOTYPUS *Anillinus pecki* Giachino 2011 CNC No. 23999 [red cardstock]” “CNC 957913[blue-bordered cardstock]”

Other material (n = 307, CMNH, CUAC, CWHC, NCSU, TLC): USA: NORTH CAROLINA: No County Given: Black Mountains, South Toe Basin, 3500ft, 26 Aug. 1976, T.C. Barr leg. (3♂, 3♀). **Ashe Co.:** Mount Jefferson State Park, southeast of reservoir, 4 Jul. 1960, H.R. Steeves leg., litter extraction (9♂, 4♀, 2 unsexed). **Avery Co.:** Blue Ridge Parkway. Boulder Fields; 36.0981, -81.7874; 17 May 2021; M. Caterino leg.; under rock (1♂, 1♀); Same data as previous but 36.0984, -81.7868, C. W. Harden leg., under rock (6♂, 2♀); Near Grandfather Mountain, 4055 feet, 36.0883, -81.8160, 12 Jul. 2016, T. Lawton leg., sifting litter (9♀). **Burke Co.:** Linville Gorge, Pine Gap, 35.9403, -81.9297, 19 Aug. 2017, M. Caterino and P. Caterino leg., litter extraction (1♂); Linville Gorge, Bynum Bluff, 35.9331, -81.9282, 19 Aug. 2017, M. Caterino and P. Caterino leg., litter extraction (2♂). **Caldwell Co.:** Pisgah National Forest, near Mortimer Campground, 35.9923, -81.7605, 30 Apr. 2006, A.K. Tishechkin leg. (1♂, 1♀). **Madison Co.:** Pisgah National Forest, Camp Creek Bald, 36.0311, -82.7051, 31 May 2023, C. W. Harden and J. R. LaBonte leg., under rocks (12♂, 12♀). **McDowell Co.:** Snooks Nose trail, 35.6862, -82.2019, 25 Jul. 2015, S. Myers and S. Langton leg., litter extraction (1♀). **Watauga Co.:** Boone, 13 Oct. 1968, J.F. Cornell leg. (1♂, 1♀); Pisgah National Forest, ca. 6 miles west of Blowing Rock, 36.1290, -81.7710, 19 Sep. 2016, C.W. Harden leg., sifting litter (4♂, 1♀). **Wilkes Co.:** Blue Ridge Parkway, Sheets Gap, 1020m, 30 Apr. 2006, A.K. Tishechkin leg., sifting litter (1♂); Near Idlewild, 36.2638, -81.4259, 2 Jun. 2017, T. Lawton leg., sifting litter (1♂). **Yancey Co.:** Devils Gap trail, 36.0370, -82.4310, 24 Jul. 2015, S. Myers and S. Langton leg., litter extraction (1♂); Same data as previous but 36.0392, -82.4257 (1♂); Same data as previous, but 36.0442, -82.4279 (1♂); South Toe River Road, 10 Jun. 2016, T. Lawton leg., sifting litter (1♂); Pisgah National Forest, Woody Ridge trail, 35.8447, -82.2369, 15 Jun. 2020, M. Caterino and F. Etzler leg., litter extraction (12♂, 12♀); Pisgah National Forest, Big Bald, 35.9893, -82.4903, 5 Aug. 2020, M. Caterino leg., litter extraction (1♂, 1♀). **VIRGINIA (new state record): Grayson Co.:** Grayson Highlands State Park, 36.6126, -81.4810, 2 Jun. 2021, K. Ivanov leg., litter extraction (5♂, 1♀). **Washington Co.:** Whitetop Mountain, 36.6358, -81.6042, 15 Jun. 2019, T. Lawton leg., sifting litter (2♂, 1♀). **TENNESSEE (new state record): Johnson Co.:** Backbone Rock, 36.5931, -81.8161, 18 Jun. 2016, C.W. Harden leg., sifting litter (3♂, 5♀). **Unicoi Co.:** Cherokee National Forest, Big Bald, 35.9900, -82.4921, 5 Aug. 2020, M. Caterino, A. Haberski, P. Wooden leg., litter extraction (2♂, 9♀); Same data as previous but 35.9938, -82.4873 (10♂, 19♀); Same data as previous but 35.9947, -82.4896 (2♂, 7♀); Cherokee National Forest, Big Bald, 35.9904, -82.4927, 25 May 2021, C.W. Harden, A. Haberski, P. Wooden leg., litter extraction (3♂); Same data as previous but 35.9936, -82.4874 (11♂, 21♀); Same data as previous but 35.9950, -82.4897 (2♂, 1♀); Cherokee National

Forest, Big Bald, 35.9908, -82.4925, 25 May 2021, C.W. Harden leg., under rocks (28♂, 14♀); Same data as previous but 35.9933, -82.4873 (41♂, 12♀).

Diagnosis. From other *Anillinus* species occurring in the same area, *A. pecki* can be recognized by the presence of two dilated protarsomeres of males each with ventral adhesive setae, relatively broad and convex body, and the distinctive male aedeagus, which has several stout setae on the ventral surface of the median lobe. The apparent sister species, *A. docwatsoni* is nearly identical to *A. pecki* in external characters but differs in the shape of the median lobe and the absence of setae on the ventral margin.

Redescription. *Habitus:* (Fig. 4A) Variable in size (ABL = 1.74–1.92 mm), both sexes similarly variable in size. *Integument:* In most specimens seen, microsculpture is mostly lacking from the dorsal surfaces of the forebody, and is irregular and patchy on the head and pronotal disc. However, specimens from two populations in the Black Mountains (Snooks Nose and Woody Ridge) have strong microsculpture on the entire pronotum; the Woody Ridge specimens also have strong microsculpture over the entire head. *Head:* Moderately sized, larger in females (average HW/PW = 0.72[♂], 0.75[♀]). Frontoclypeal horn present, large. *Legs:* Male profemora unmodified. Male protarsus with protarsomeres 1 and 2 bearing adhesive setae ventrally; first protarsomere greatly expanded and dentate on inner margin, second protarsomere weakly expanded and slightly dentate on inner margin (Fig. 3C,I). Mesotrochanters of males unmodified. Metafemur not swollen, posterior face with small patch of weak papillate microsculpture medially (Fig. 2A). *Abdominal ventrites:* Unmodified in either sex. *Male genitalia:* Ring sclerite less than one fourth body length (RL/ABL = 0.24). Median lobe asymmetrical, slightly rotated dorsally from margin of basal lobes; in lateral aspect with ventral margin nearly straight beyond basal curve, bearing four or more stout setae medially (Fig. 7A); flagellum in lateral aspect appearing “m” shaped. In dorsolateral aspect, flagellum appearing broadly curved and slightly sinuate medially (Fig. 7K); dorsal margin of median lobe membranous in apical half, with large weakly sclerotized region near ostium on left side; apex in dorsolateral view appearing evenly rounded, ventral margin expanded and with numerous poriferous canals. Internal sac without sclerotized spines. Right paramere (Fig. 5A) short, bearing four long apical setae. Left paramere conchoidal, with four preapical pores on ventral margin, one or two of which bear short setae. *Female genitalia:* Spermatheca (Fig. 8B) long, relatively strongly sclerotized; shape asymmetrical: rotated 90° beyond proximal curve. Stem smooth proximally until abrupt second curve, beyond which it is strongly ribbed until the enlarged distal region. Spermathecal duct short, not tightly coiled.

Distribution. The range of *A. pecki* is likely continuous at mid to high elevations from the Black Mountains in western North Carolina north to Whitetop Mountain in southwest Virginia, including Grandfather Mountain and the Bald Mountains on the North Carolina–Tennessee border (Fig. 11). The species has not been found in the Craggy Mountains or on Roan Mountain.

Sympatry. Where ranges overlap, this species co-occurs with *Anillinus erwini* Sokolov and Carlton (Black Mountains, Grandfather Mountain, Mt. Rogers area), *Anillinus fortis* (Black Mountains, Great Craggy Mountains, Bald Mountains), and four undescribed endogean species with densely setose right parameres (Grandfather Mountain, Bald Mountains, Mt. Rogers area). An undescribed species of *Serranillus* Barr also commonly co-occurs with *A. pecki* in the Black and Bald Mountains.

Natural history. Most specimens seen ($n = 168$) were collected from leaf litter. However, many ($n = 129$) were collected underneath embedded rocks. On May 25 2021, 95 individuals were collected by C. Harden under rocks at two localities on either side of the summit of Big Bald, Unicoi County, Tennessee. Large samples of sifted litter collected on the same date from the same two localities produced only 35 specimens. Members of *A. pecki* have been collected from approximately 476m to 1687m in elevation.

Notes. Where it occurs, this is the most common species of *Anillinus*. It has been misidentified in collections as *A. erwini*, *A. fortis* and “*Anillinus* new sp. langdoni group”.

elongatus group *sensu novo*

“group V endogean species” (Sokolov et al. 2004), in part.

“sinuaticollis group” (Sokolov 2012), in part

Diagnosis. Recognized among other species occurring in the Piedmont region by the presence of adhesive vestiture ventrally on male protarsomeres 1 and 2 (Fig. 3D–F), metafemur of males bearing one or two teeth on posterior margin (Fig. 2D–I), presence of an elongate, weakly sclerotized flagellum in the internal sac of the aedeagus, quadrisetose right paramere of the aedeagus, and a long, coiled spermatheca duct. Most individuals also have a distinctive habitus, being dorsoventrally flattened, elongate and parallel-sided. The extent of dorsal microsculpture on the forebody varies. We recognize two subgroups within the species group: the elongatus subgroup and *montrex* subgroup; these subgroups were revealed by DNA sequence data (Harden and Caterino, in prep).

Notes. *Anillinus cavicola* Sokolov was described and illustrated as having a quadrisetose right paramere, and was hypothesized to belong to a species group with *A. elongatus* and *A. sinuaticollis* due to its similar habitus (Fig. 4H) and microsculpture pattern (Sokolov 2012). However, our examination of the male holotype (and only known specimen) of *A. cavicola* revealed that the right paramere in fact bears a dense brush of more than eight apical setae (Fig. 5C). The second protarsomere is also unmodified, lacking ventral adhesive setae; this is likely a derived condition within *Anillinus*, and it is not found in any members of the elongatus group. The flagellum of the internal sac in *A. cavicola* is short and strongly sclerotized. Thus, all diagnostic characters of the elongatus group are lacking. In an unpublished molecular phylogeny of *Anillinus* (Harden and Caterino, in prep.), the species of *Anillinus* with only four apical setae on the right paramere (including the elongatus group) form a well-supported “quadrisetose clade.” In addition to the lack of ventral adhesive setae on the second male protarsomere, the presence of a dense brush of setae on the right paramere of *A. cavicola* provides phylogenetic evidence that the species does not belong in the “quadrisetose clade” and thus is not closely related to the elongatus group.

There are published accounts of the occurrence of the anilline genus *Stylulus* Schaufuss in the South Mountains in Burke County, North Carolina (Cornell 1972, 1977a); these accounts probably in fact refer to *Anillinus* belonging to the elongatus group. Members of *Stylulus* can be externally separated from *Anillinus* by their tetramerous tarsi and the presence of a fringe of setae on the posterior margin of the pronotum, but their flattened and parallel-sided habitus is superficially similar to some members of the elongatus group. Cornell’s specimens of putative *Stylulus* have not been found in the NCSU collection, but considering the otherwise strictly Neotropical distribution of *Stylulus* (Jeannel 1963a, Giachino and Sciaky 2002), the specimens are most likely *Anillinus*.

elongatus subgroup

Diagnosis. With the characters of the elongatus group and the base of the spermatheca enlarged and relatively strongly sclerotized, and stem of spermatheca strongly ribbed medially (Fig. 8C–E,G).

Diversity and distribution. This subgroup includes *Anillinus elongatus* Jeannel and three species described below: *Anillinus arenicollis* **new species**, *Anillinus pittsylvanicus* **new species**, and *Anillinus uwharrie* **new species**. With the exception of *A. elongatus*, all species are known from single localities. The collective range of the subgroup extends from southern Virginia to eastern South Carolina. The mislabeled neotype of *A. elongatus* (NCSU) from Mecklenburg County represents a fifth species, discussed below as *Anillinus* sp. “North Carolina, Mint Hill.”

***Anillinus arenicollis* Harden and Caterino, new species**

Fig. 2I, 3H, 4F, 7G,Q, 8C, 9M–O, 10D, 11

Type material. Holotype male (deposited in USNM): point mounted with abdominal ventrites glued to point and genitalia in Euparal on microslide pinned beneath specimen. Original label: “USA: SOUTH CAROLINA, Chesterfield Co. Carolina Sandhills NWR. 34.56758, –80.21175. 30-vi-15.xii.2021. CW Harden & LM Thompson. Buried pipe trap, coarse sand. SAND-02-1215.” “CLEMSON-ENT CUAC000169319” “Harden DNA Voucher CWH-397 A “sandhills” M Ex. 17-December-2021 [green-bordered cardstock]” “HOLOTYPE *Anillinus arenicollis* Harden and Caterino [orange cardstock]”

Paratypes ($n = 39$; CUAC, CMNH, ADC, NCSU, LSAM, VMNH): USA: SOUTH CAROLINA: *Chesterfield Co.*: Carolina Sandhills NWR: Same data as holotype, CUAC000169318, CWH-396, CUAC (1♂); Same data as holotype, CUAC000169320, CWH-398, CUAC (1♀); Same data as holotype, CUAC000169321, CWH-399, CUAC (1♀); Same data as holotype, CUAC000169322 to CUAC000169327, CUAC000167135, CUAC (7♂); Same data as holotype, CUAC000167126 to CUAC000167134, CUAC000167136, CUAC167137, CUAC (12♀); 34.5672, -80.2118, 22 Feb. 2017, M. Caterino & M. Ferro leg., wet riparian litter, CUAC000041490, MSC-2481, CUAC (1♀); 34.56758, -80.21175, 13 Apr. to 30 Jun. 2021, C.W. Harden leg., buried pipe trap, coarse sand, SAND-02, CUAC000169328 to CUAC000169331, CMNH, VMNH (4♂); 34.56722, -80.21139, 13 Apr. to 30 Jun. 2021, C.W. Harden leg., buried pipe trap, dry clay soil, SAND-08, CUAC000169332, VMNH (1♀); 34.56697, -80.21105, 13 Apr. to 30 Jun. 2021, C.W. Harden leg., buried pipe trap, sandy clay soil, CUAC000167138 and CUAC000167139, CMNH (2♀); 34.56762, -80.21190, 30 Jun. to 15 Dec. 2021, C.W. Harden & L.M. Thompson leg., buried pipe trap, coarse sand, SAND-03-1215, CUAC000167140 and CUAC000167141, CUAC (2♂); 34.56762, -80.21195, 30 Jun. to 15 Dec. 2021, C.W. Harden & L.M. Thompson leg., buried pipe trap, coarse sand, SAND-04-1215, CUAC000169333, NCSU (1♂); 34.56728, -80.21135, 30 Jun. to 15 Dec. 2021, C.W. Harden & L.M. Thompson leg., buried pipe trap, dry clay soil, SAND-07-1215, CUAC000167142 to CUAC000167145, LSAM, NCSU (3♂, 1♀); 34.56722, -80.21139, 30 Jun. to 15 Dec. 2021, C.W. Harden & L.M. Thompson leg., buried pipe trap, dry clay soil, SAND-08-1215, CUAC000167146, VMNH (1♂); 34.56697, -80.21105, 30 Jun. to 15 Dec. 2021, C.W. Harden & L.M. Thompson leg., buried pipe trap, sandy clay soil, SAND-09-1215, ADC (1♂, 1♀).

Other material ($n = 8$; CWHC): USA: SOUTH CAROLINA: *Chesterfield Co.*: Carolina Sandhills NWR: 34.56762, -80.21190, 13 Apr. to 30 Jun. 2021, C.W. Harden leg., buried pipe trap, coarse sand, SAND-03 (1♂, 1♀); 34.56762, -80.21195, 13 Apr. to 30 Jun. 2021, C.W. Harden leg., buried pipe trap, coarse sand, SAND-04 (1♂, 1♀); 34.56722, -80.21139, 13 Apr. to 30 Jun. 2021, C.W. Harden leg., buried pipe trap, dry clay soil, SAND-08 (1♀); 34.56758, -80.21175, 30 Jun. to 15 Dec. 2021, C.W. Harden & L.M. Thompson leg., buried pipe trap, sandy clay soil, SAND-02-1215 (1♂); 34.56697, -80.21105, 30 Jun. to 15 Dec. 2021, C.W. Harden & L.M. Thompson leg., buried pipe trap, sandy clay soil, SAND-09-1215 (2♂).

Diagnosis. With the characters of the *elongatus* group and the following: dorsal microsculpture present on entire forebody; second protarsomere of males moderately expanded and dentate on inner margin (Fig. 3H); metafemur of males swollen, with prominent tooth on posterior margin (Fig. 2I); median lobe narrow and long, twisted from plane of basal lobes, apex blocky and deflected ventrally (Fig. 9O).

Description. *Habitus:* (Fig. 4F) ABL 1.65–1.92 mm (avg. 1.79 ± 0.07), forebody large relative to elytra, body dorsoventrally depressed and parallel-sided, narrow (EW/ABL 0.31–0.33). Males (ABL 1.69–1.92 mm) similar in size to females (ABL 1.65–1.89 mm). *Integument:* Isodiametric microsculpture impressed over entire forebody, weaker on disc of pronotum. *Head:* Relatively large (HW/PW = 0.75–0.82), wider in females (0.80–0.82) than males (0.75–0.79). Frontoclypeal horn present, small. Three pairs of supraorbital setae present. *Pronotum:* Relatively broad (PW/EW = 0.87–0.92), basal constriction strong to moderate (PbW/PW = 0.71–0.77). *Elytra:* Parallel sided, dorsoventrally flattened. *Legs:* Profemora of males unmodified. Protarsomeres 1 and 2 of males expanded and dentate on inner margin (Fig. 3H), both bearing adhesive setae ventrally. Male mesotrochanters unmodified. Male metafemur swollen, posterior margin with a triangular tooth (Fig. 2I). *Abdominal ventrites:* Unmodified in either sex. *Male genitalia:* Ring sclerite one fourth body length (RL/ABL=0.25), anterior margin thickened and asymmetrically constricted. Median lobe of aedeagus (Fig. 9O) long and relatively straight, slightly twisted dorsally from plane of basal lobes (Fig. 7G,Q), apex broad, blunt and abruptly deflected ventrally at an obtuse angle. Flagellum rotated dorsally, thicker at base and becoming filamentous in distal half, in lateral view appearing sinuous. Ostium with weakly sclerotized plate on left side. Right paramere (Fig. 9N) relatively short, with four long setae on apical margin. Left paramere (Fig. 9M) conchoidal and narrowed apically, with four relatively long setae.

Female genitalia: Spermatheca (Fig. 8C) long and sinuate, gradually enlarged distally; stem ribbed, not crossed proximally. Spermathecal duct long and tightly coiled.

Distribution. (Fig. 11) Known from a small area within the boundaries of the Carolina Sandhills National Wildlife Refuge in Chesterfield Co., SC (Fig. 10D).

Sympatry. Members of this species have not been collected with other species of anillines.

Natural history. All but one of the specimens were collected using modified buried pitfall traps set in coarse sand or clay soils. The exception was a single female collected in a sample of sifted litter and topsoil in February. One of the specimens collected in a buried trap set from June to December was teneral. Imported red fire ants (*Solenopsis invicta* Buren) were abundant both on the surface and in the traps at the site. The only other carabid species collected in association was *Elaphropus ferrugineus* (Dejean), which has also been reported from subterranean habitats such as caves and ant nests (Larochelle and Larivière 2003). Surface habitat at the locality is longleaf pine (*Pinus palustris* Mill.) savannah, with an understory dominated by shrubby oaks (*Quercus* spp.). The soil from which specimens were collected was coarse sand, mixed with black organic material near the surface and hard clay and gravel at greater depths. The locality is regularly subjected to controlled burning.

Species status justification. The male genitalia are unique within the genus, especially the shape of the median lobe, with its angular, blocky apex.

Derivation of name. The species name is a noun in apposition created by combining the Latin nouns for sand (*arena*) and hill (*collis*), in reference to the habitat.

***Anillinus elongatus* Jeannel, 1963**

Anillinus elongatus Jeannel 1963b: 151

Fig. 2H, 3E, 4D, 7J,T, 8D, 9A–C, 10A,B, 11

Material examined. Holotype female (USNM): point mounted, missing head, prothorax, elytra and most of hind legs. A card pinned below the specimen with a handwritten “♀” symbol in the upper right corner has the hindbody of a male *Anillinus* nr. *barberi* Jeannel glued to it, ventral-side up. Labels below these specimens read “Chapel Hill N.C. April 18 1932 J.M. Valentine” “elongatus Bar ♀ Allotype HSB. 1932” “TYPE [printed on red paper]” “TypeNo 69544 USNM [partially handwritten on red paper]” “specimens destroyed? or on box bottom reglued 28Sept71 T.L. Erwin” “*Anillinus elongatus* type R. Jeannel det., [partially handwritten]”.

Other material (n = 20, CUAC, CWHC, INHS, USNM): USA: NORTH CAROLINA: Orange Co.: Duke Forest, near Eno River, ca. 1.7 miles east of Efland, 36.0816, –79.1406, 10 Dec. 2022, under rock, C.W. Harden leg. (2♂); Same data as previous, but collected by Berlese extraction of sifted soil from beneath rocks (1♀); Duke Forest, ca. 6 miles northwest of Chapel Hill, 35.9777, –79.1109, 10 Dec. 2022, under rock, C.W. Harden leg. (2♂); Duke Forest, ca. 6 miles northwest of Chapel Hill, 35.9778, –79.1105, 27 Jul. to 10 Dec. 2022, buried pipe trap, C.W. Harden leg. (3♂, 8♀); Chapel Hill, 30 Mar. 1935, J.M. Valentine and J.C. Beakley leg. (2♂, 1 unsexed); Durham, 2 to 5 inches deep in clay under oak, 28 Apr. 1945, A.S. Pearse leg., INHS 1060321 (1♂).

Redescription. Habitus: (Fig. 4D) Body size variable (ABL = 1.54–1.82 mm). Body narrow (average EW/ABL = 0.34), parallel sided and moderately flattened dorsoventrally (Fig. 4D). **Integument:** Dorsal surface of head covered with irregular isodiametric sculpticels. Pronotum with irregular microsculpture, variable in extent: largely absent in some specimens, present only along extreme edges, more extensive in others but always with at least some portion of disc lacking distinct sculpticels. **Head:** Relatively large (average HW/PW = 0.76), frontoclypeal horn present and prominent. Three pairs of supraorbital setae present. **Pronotum:** Relatively short (average PL/ABL = 0.23), variably narrowed posteriorly (PbW/PW = 0.73–0.77), lateral margins usually not sinuate, slightly sinuate in some individuals. **Legs:** Profemora of males unmodified. Male protarsi with protarsomere 1 greatly expanded and dentate on inner margin, protarsomere 2 weakly expanded and minutely dentate on inner margin (Fig. 3E); both protarsomeres 1 and 2 with adhesive ventral setae, but difficult to see on second protarsomere except with strong magnification or SEM photography. Mesotrochanters unmodified in either sex. Metafemur of males slightly swollen and bearing a prominent, narrow tooth on posterior margin (Fig. 2H); posterior margin with coarse papillate microsculpture. **Abdominal ventrites:** Unmodified in either sex. **Male genitalia:** Ring sclerite about one fourth body length (average RL/ABL = 0.26). Median lobe (Fig. 9C) asymmetrical, twisted dorsally from margin of basal lobes; in lateral aspect with ventral margin sinuate, and broadly rounded apex (Fig. 7J); in dorsolateral aspect with flagellum long, bisinuate, with relatively long proximal curve (Fig. 7T); ostium on left side with weakly sclerotized region; ventral margin greatly enlarged and bearing numerous poriferous canals.

Right paramere (Fig. 9B) short and bearing four long apical setae. Left paramere (Fig. 9A) conchoidal, with four subapical pores on ventral margin, lacking preapical setae. *Female genitalia*: Spermatheca (Fig. 8D) with base enlarged and relatively strongly sclerotized, stem strongly ribbed from base to where enlarged distal portion begins; spermathecal duct elongate, coiled.

Distribution. We have seen members of this species from four nearby localities in Orange County, North Carolina (Fig. 11). This is a region of rapid human population growth and habitat destruction; all known exact localities are currently managed as natural areas by the Duke Forest and North Carolina Botanical Garden.

Sympatry. Two other species of *Anillinus* have been collected at the same localities as *A. elongatus*, both undescribed. One is related to *Anillinus barberi* Jeannel and the other is a member of the montrex subgroup of the elongatus group, based on DNA sequence data (Harden and Caterino, in prep.). The male *Anillinus* glued to the card beneath the holotype of *A. elongatus* might be conspecific with the barberi group species collected in Duke Forest, which would explain how the two specimens came to be associated. Both undescribed species are much larger than members of *A. elongatus*, and differ in the modifications on male legs: the barberi group species lacks a tooth on the metafemur, and the montrex subgroup species has a tooth on each profemur and two teeth on each metafemur. The montrex subgroup species is discussed in more detail below as *Anillinus* sp. “North Carolina, Orange Co. sp. 2”.

Natural history. Specimens recently collected by C. Harden were found in oak-hickory forest, either hand collected beneath embedded rocks (10A,B) or captured using buried pipe traps. Specimens were hand collected in December and caught in traps operated from August to December but not December to July. Old specimens collected by Valentine were collected in March and April, but the method used is unknown. A specimen in the INHS collection was taken from clay soil “2 to 5 inches deep” using unknown methods. Localities for the species range from approximately 90m to 191m in elevation.

Notes. Sokolov et al. (2004) described a male neotype for *A. elongatus*, collected at the type locality by J.M. Cornell, with label data given as “NC, Orange Co, Chapel Hill, Morgan Cr. 17.IV.94, J.F.Cornell, ex soil 994 IV 17-1-5.” However, the male specimen in the NCSU collection bearing the neotype label is not this specimen. It is neither from the type locality nor conspecific with specimens of *A. elongatus*. The locality label reads, “NC Mecklenburg Co, nr Mint Hill on McAlpine Cr 12Apr94, JF Cornell Ex Soil under Stream Debr.” This locality is over 100km from the type locality of *A. elongatus*, and this male specimen differs from Chapel Hill specimens in several characters, described in the treatment below. It is most likely that the neotype label was accidentally placed on the wrong specimen. However, a specimen with the label data provided by Sokolov et al. (2004) could not be found in the NCSU collection or in the LSAM collection (V. Bayless pers. comm). In fact, none of the specimens of *A. elongatus* listed by Sokolov et al. (2004) other than the two Mecklenburg County specimens could be located. The existence of the holotype was known to Sokolov et al. (2004), who studied it. The Code (ICZN 1999, Article 75.1) specifies that a neotype is to be designated only when no name-bearing type is believed to be extant. Therefore, the neotype designation for *A. elongatus* is invalid under the Code and does not affect the nomenclature of the species.

Cornell (1977a) stated that three specimens of his “*Anillinus n. sp. C*” were collected near Chapel Hill. These specimens were not found in the NCSU collection, so it is not known if they belong to *A. elongatus* or one of the two undescribed species known from the vicinity of Chapel Hill.

***Anillinus* sp. “North Carolina, Mint Hill”**

Fig. 8F

Material examined ($n = 2$, NCSU): USA: NORTH CAROLINA: **Mecklenburg Co.**: Near Mint Hill on McAlpine Creek, 12 Apr. 1994, ex soil under stream debris, J.F. Cornell leg. (1♂); McAlpine Creek, 25 Mar. 1995, washed soil, J.F. Cornell leg. (1♀).

Diagnosis. The male specimen is large for the elongatus group (ABL = 2.06 mm), with the second protarsomere markedly expanded, nearly as much so as in *A. montrex* sp. n. (as in Fig. 3G). The metafemora are tucked against the specimen, but they appear to match the illustration of *A. elongatus* in Sokolov et al. (2004): swollen, with the posterior margin triangularly produced but lacking a distinct tooth. The median lobe is damaged, completely

crushed laterally into a thin plane so that the walls are folded over each other; the apical third is detached and distorted; the ventral margin of the median lobe is greatly expanded, more so than in *A. elongatus*, and the apex appears to have been broadly rounded. The flagellum is much shorter than in *A. elongatus*, but this could be an artifact due to the damaged condition. The right paramere is missing. The left paramere is conchoidal and bears four preapical pores on the ventral margin, the inner two of which bear short setae. The spermatheca (Fig. 8F) is long and S-shaped, slightly enlarged basally; the stem is mostly smooth except for a short medial region that is slightly ribbed. The spermathecal duct is coiled and elongate.

Distribution. The precise collection locality of these specimens is unknown. However, a likely locality is McAlpine Creek Park (35.149, -80.741) (Fig. 11), a publicly accessible property in Mecklenburg County near Mint Hill. This property is within the greater Charlotte metropolitan area.

Notes. In their redescription of *A. elongatus*, Sokolov et al. (2004) consider these two specimens identical to *A. elongatus* from Chapel Hill, aside from the larger body size. We have not seen the Chapel Hill specimens that those authors studied, but all of the male *A. elongatus* we have seen from the Chapel Hill area (including historic specimens collected by Valentine) differ from the “Mint Hill” specimens by possessing a prominent tooth on the posterior margin of the metafemur, having a much less expanded second protarsomere, and a left paramere without preapical setae. Females from the two localities differ markedly in spermathecal structure, with those from the Chapel Hill area being shorter and strongly ribbed medially (Fig. 8D). Two specimens were also reported by Sokolov et al. (2004) from Cabarrus County, five miles west of Davidson. We have not seen these specimens either, and they could represent an additional undescribed species as this locality is not near any other occurrences of the *elongatus* group. Cornell (1977b) mentions three specimens of “*Anillinus n. sp. A*” collected 4.8 km west of Monroe in Union Co., North Carolina in 1973. These specimens were not found in the NCSU collection, where Cornell’s collection was deposited after his death. The locality is approximately 22 km southeast of the Mint Hill site, and *Anillinus* sp. “North Carolina, Mint Hill” and Cornell’s “*Anillinus n. sp. A*” could be the same species.

***Anillinus pittsylvanicus* Harden and Caterino, new species**

Fig. 2G, 4E, 7I,S, 8E, 9D–F

Type material. Holotype male (deposited in USNM): point mounted with genitalia in Euparal on microslide pinned beneath specimen. Original label: “VIRGINIA, City of Danville. Anglers Park. N36.56519, W79.35644. 13April – 5August – 2018. C.W. Harden. Buried baited pipe trap. Dry oak-hickory woods. DAN-BUR-01.” “*Anillinus* not *elongatus* ♂ det C.W. Harden 2018” “HOLOTYPE *Anillinus pittsylvanicus* Harden & Caterino [orange cardstock]”

Paratypes (n = 27, CUAC, VMNH): USA: VIRGINIA: Pittsylvania Co.: City of Danville, Anglers Park: Same data as holotype, CUAC, VMNH (3♂, 5♀); 36.5640, -79.3506, 24 Dec. 2018, under small embedded rock in middle of logging road, clay soil, between clearcut and young forest, C.W. Harden leg., CUAC000185541, CWH-059, CUAC (1♀); 36.5640, -79.3506, 24 Dec. 2017, under small embedded quartz, in middle of logging road, clay soil, between clearcut and young forest, VMNH (1♂); 36.56519, -79.35644, 13 Apr. to 5 Aug. 2018, buried baited pipe trap, DAN-BUR-02, VMNH (1♂, 4♀); 36.56519, -79.35644, 13 Apr. to 5 Aug. 2018, buried baited pipe trap, DAN-BUR-03, VMNH (1♀); 36.56438, -79.35689, 5 Aug. to 23 Nov. 2018, buried pipe trap, DAN-01-1123, C.W. Harden and K. Ivanov leg., VMNH (4♂, 7♀).

Other material (n = 2): USA: VIRGINIA: Pittsylvania Co.: City of Danville, Anglers Park: 36.56519, -79.35644, 13 Apr. to 5 Aug. 2018, buried baited pipe trap, DAN-BUR-01, CWHC (1♂); Same data as previous, but DAN-BUR-02, CWHC (1♀); 36.5628, -79.3589, 10 Nov. 2023, C.W. Harden leg., under rock, CWHC (1♂).

Diagnosis. This species is most similar to *A. elongatus*, but differs by: presence of several setae on left paramere (Fig. 9D), median lobe with longer curve proximally (Fig. 7I) and with ventral margin not as expanded (Fig. 9F), apex smaller and slightly deflected ventrally, flagellum longer and more deeply sinuate, hind femora with smaller tooth (Fig. 2G).

Description. Habitus: (Fig. 4E) Body size variable (ABL= 1.50–1.84 mm, average = 1.62), average size of males (1.72 mm) greater than females (1.58 mm); body narrow (average EW/ABL=0.33). **Integument:** Irregular

isodiametric microsculpture distinct dorsally on entire head except for center of frons, where it is somewhat effaced; absent from disc of pronotum, present along margins. *Head*: Relatively large (average HW/PW = 0.78), frontoclypeal horn present, conspicuous. *Pronotum*: Relatively short (average PL/ABL = 0.22); constricted posteriorly (average PbW/PW = 0.72); sides slightly sinuate posteriorly. *Elytra*: Parallel sided and flattened, narrow (average EW/EL=0.62). *Legs*: Profemora of males unmodified. Protarsi of males with first protarsomere greatly expanded and dentate on inner margin, second protarsomere slightly expanded and minutely dentate on inner margin; ventral adhesive setae present under both protarsomeres 1 and 2, but difficult to see on protarsomere 2 in most specimens without strong magnification. Male metafemur not swollen, with a triangular tooth on posterior margin that is relatively low, not prominent (Fig. 2G). *Abdominal ventrites*: Unmodified in either sex. *Male genitalia*: Ring sclerite one-fourth body length (RL/ABL = 0.25). Median lobe (Fig. 9F) slightly asymmetrical, rotated dorsally from plane of basal lobes; in lateral aspect, ventral margin nearly straight until apex, which is deflected ventrally (Fig. 7I); in dorsolateral aspect with flagellum broadly sinuate (Fig. 7S); ventral margin narrowly expanded except at apex, which bears several large poriferous canals. Right paramere (Fig. 9E) short, with four long apical setae. Left paramere (Fig. 9D) conchoidal, ventral margin with four long preapical setae. *Female genitalia*: Spermatheca (Fig. 8E) with base enlarged and relatively strongly sclerotized; stem strongly ribbed medially, smooth near base and enlarged distal portion; spermatheca duct elongate and tightly coiled.

Distribution. This species is known only from a small area within Anglers Park in Danville, Virginia (Fig. 11). The locality is just north of the Dan River, a major tributary of the Roanoke River. This is the northernmost known occurrence of a member of the elongatus group. The property where the species occurs is owned by the City of Danville and managed primarily for outdoor recreation. Anglers Park is also the type locality of the recently described short range endemic milliped *Nannaria hardeni* Means, Hennen and Marek (Means et al. 2021).

Sympatry. Other anilline species are not known to occur with *A. pittsylvanicus*. A single aberrant female collected with the type series of *A. pittsylvanicus* might belong to a different species and is discussed in the Notes section below.

Natural history. Specimens of *A. pittsylvanicus* have been collected by C. Harden from the underside of small rocks and by using buried pipe traps set in clay soil in a young oak-pine forest. The site is approximately 146m in elevation. Hand-collected specimens were found in November and December.

Species status justification. The morphological and molecular data (Harden and Caterino, in prep.) indicate that the closest relative of *A. pittsylvanicus* is *A. elongatus*. Males of the two species differ in the form of the hind femora (tooth smaller in *A. pittsylvanicus*) and the aedeagus (median lobe of *A. pittsylvanicus* more arcuate, less expanded ventrally, with smaller apex that is slightly deflected ventrally, and flagellum differently shaped). Populations of *A. elongatus* are distributed in the Neuse and Cape Fear River basins, while *A. pittsylvanicus* occurs in the Roanoke River basin, which could serve to isolate the two species if hydrochory is an important method of dispersal of these beetles.

Derivation of name. The species name, a masculine adjective, comes from Pittsylvania County, where the type locality is located, and is also a phonetic homage to the common specific epithet “pennsylvanicus”.

Notes. A single female specimen (CWHC) collected in a buried pipe trap with several typical *A. pittsylvanicus* differs in being much narrower and more elongate and having strong microsculpture distinct across the entire dorsal surface of the pronotum. This specimen could represent a different species.

***Anillinus uwharrie* Harden and Caterino, new species**

Fig. 1A,B, 2F, 3F, 4C, 7H,R, 8G, 9J–L, 10C, 11

Type material. Holotype male (deposited in USNM): point mounted with genitalia in Euparal on plastic microslide pinned beneath specimen. Original label: “USA: NC, Montgomery Co. Uwharrie NF, ~12km E of Albemarle. 35.3166, -80.0468. 16.February.2023. CW Harden. Under rock.” “[QR code] CLEMSON-ENT CUAC000178983” “Harden DNA Voucher CWH-473 *Anillinus* M Uwharrie Ext. 27/February/2023 [green-bordered cardstock]” “HOLOTYPE *Anillinus uwharrie* Harden & Caterino [orange cardstock]”

Paratypes ($n = 21$, ADC, CMNH, CUAC, LSAM, NCSU, VMNH): USA: NORTH CAROLINA: *Montgomery Co.*: Uwharrie National Forest, ca. 12km east of Albemarle: Same data as holotype, CUAC000178984 to CUAC000178986, CWH-474 to CWH-476, CUAC (1♂, 2♀); Same data as holotype, LSAM, VMNH (6♂, 4♀); 35.3166, -80.0468, 16 Feb. 2023, soil Berlese, C.W. Harden leg., ADC, CMNH, CUAC, NCSU (6♂, 2♀).

Other material ($n = 2$, CWHC): USA: NORTH CAROLINA: *Montgomery Co.*: Uwharrie National Forest, ca. 12km east of Albemarle, 35.3166, -80.0468, 16 Feb. 2023, soil Berlese, C.W. Harden leg. (1♂, 1♀).

Diagnosis. The shape of the median lobe is unique within the genus: abruptly bent 90 degrees from basal lobes, ventral margin nearly perfectly straight, and dorsal margin declivitous apically, giving the median lobe an awl shape in lateral aspect (Fig. 7H). In male specimens viewed in alcohol, the large and distinctive aedeagus is easily visible through the abdomen without dissecting.

Description. *Habitus*: (Fig. 1A,B, 4C) Body relatively narrow (average EW/ABL = 0.35), dorsoventrally depressed, elytra parallel sided, sides of pronotum not sinuate posteriorly. ABL = 1.53–1.83 mm, males (1.61–1.82, average = 1.70 mm) usually larger than females (1.53–1.83, average ABL=1.68). *Integument*: Dorsal surface of head entirely covered with irregular isodiametric microsculpture, sculpticels weaker on center of vertex; microsculpture absent from disc of pronotum, visible along margins; disc of pronotum rugose in some specimens. *Head*: Variable in size, larger in females (average HW/PW = 0.76) than in males (average HW/PW = 0.73). Frontoclypeal horn well developed, conspicuous. Head with three pairs of supraorbital setae. *Pronotum*: Variable in form, narrow or broad (PW/EW = 0.82–0.90), appearing robust or cordate; relatively long (PL/ABL = 0.23–0.25), moderately narrowed posteriorly (PbW/PW = 0.76–0.83). *Elytra*: Relatively broad (average EW/EL = 0.64), parallel sided and flattened dorsoventrally. *Legs*: Profemora of males unmodified. Protarsi of males with first protarsomere greatly expanded and dentate on inner margin, second protarsomere slightly expanded and minutely dentate on inner margin. Both protarsomeres 1 and 2 with adhesive setae ventrally (Fig. 3F), setae usually easily visible on second protarsomere at 45X magnification. Male mesotrochanters unmodified. Male metafemur slightly swollen, posterior margin granulate due to coarse microsculpture with posterior region of sculpticels raised, bearing a prominent peg-like tooth covered in coarse microsculpture (Fig. 2F). *Abdominal ventrites*: Unmodified in either sex. *Male genitalia*: Ring sclerite more than one-fourth length of body (RL/ABL = 0.27). Median lobe of aedeagus (Fig. 9L) asymmetrical, slightly rotated dorsally from plane of basal lobes; in lateral view appearing elongate and tapered apically, with short basal bend before ventral margin which is nearly straight to apex (Fig. 7H); in dorso-lateral view appearing similar, with apex bluntly rounded (Fig. 7R); ventral margin not enlarged; internal sac with flagellum sinuate and elongate, apical curve much less pronounced than basal curve. Right paramere (Fig. 9K) short, bearing four long setae. Left paramere (Fig. 9J) conchoidal, with four ventral pores, apical one bearing a short seta, one or two others bearing minute setae. *Female genitalia*: Spermatheca (Fig. 8G) elongate, sinuate, base enlarged and relatively strongly sclerotized; stem strongly ribbed medially, smooth near base and enlarged apical portion. Spermathecal duct elongate and coiled.

Distribution. (Fig. 11) This species is known from a single hillside in Uwharrie National Forest (Fig. 10C).

Sympatry. *Serranillus dunavani* has been collected in the Uwharrie National Forest not far from the type locality of *A. uwharrie*, and could occur with the species. An aberrant female collected with the type series of *A. uwharrie* might represent a second species and is discussed in the Notes section below.

Natural history. All specimens were collected from endogean habitats, either under embedded rocks or extracted from sifted soil dug from beneath the same rocks. The habitat at the site was a mixed deciduous forest with an overstory of *Quercus* L. and *Carya* Nutt. and scattered *Pinus* L. and *Ilex* L. The site is at approximately 155m in elevation, on the southern side of a small drainage above a small stream where numerous small to medium sized rocks were present (Fig. 10C). Four individuals, one male and three females, that were collected from the soil sample were picked out by hand and kept alive in a small petri dish lined with moist clay that was sterilized by freezing at -80°C (Fig. 1A,B). Springtails were offered as live food. The beetles ignored all of them except for small (likely first instar) globular springtails (Symphypleona), which were readily eaten. Dead springtails were ignored by the beetles. Several adult sciarid flies were inadvertently introduced to the dish as well, and were similarly ignored; they were also observed to flee the beetles when encountered. On 25 March, two female beetles were observed to have greatly distended abdomens, indicating either that feeding had occurred or that they were

gravid. The male was removed on this date. The three females were last observed alive on 12 June, over 4 months after collection. On 8 July it was observed that all were dead.

Species status justification. The male genitalia of the species are unique within the genus, especially the overall shape of the median lobe, which is abruptly bent from base and ventrally straight in lateral aspect.

Derivation of name. The species name is a noun in apposition from the type locality, Uwharrie National Forest, itself named for the Uwharrie Mountains, a geologically isolated ridge in the Piedmont of North Carolina.

Notes. Cornell (1977a) states that his “*Anillinus n. sp. B*” was “known from six specimens collected along the Uwharrie River near Ophir, Montgomery County.” These specimens were not found in the NCSU collection. The location is approximately 20 km north of the locality of *A. uwharrie*, and Cornell’s “*Anillinus n. sp. B*” might be conspecific with *A. uwharrie*. However, as in the series of *A. pittsylvanicus*, there is a single female specimen (CWHC) collected with the type series of *A. uwharrie* which differs in being narrower and more elongate, and having strong microsculpture distinct across the entire dorsal surface of the pronotum. More than one species might be present in the Uwharrie National Forest in Montgomery County.

montrex subgroup

Diagnosis. As in the *elongatus* subgroup, but possessing elytra that are narrower and more parallel-sided, and a more flattened habitus (Fig. 4G). The spermatheca is known only for *Anillinus montrex* **new species**, and it differs from the *elongatus* subgroup by lacking a thickened base and having a smooth stem (Fig. 8H,I).

Diversity and distribution. Two species are known, *A. montrex* **new species** from Kings Mountain State Park in York County, SC and a species collected in Duke Forest in Orange County, NC. The latter species is known only from one damaged male (lacking a head), and its formal description awaits more material. It is diagnosed below as *Anillinus* sp. “North Carolina, Orange Co. sp. 2.” The two species differ in male secondary leg modifications and male genitalic morphology, but their sister relationship is strongly supported by DNA sequence data (Harden and Caterino, in prep.).

Anillinus montrex Harden and Caterino, new species

Fig. 2E, 3D,G, 4G, 7F,P, 8H,I, 9G–I, 11

Type material. Holotype male (deposited in USNM): point mounted with abdominal ventrites glued to point and genitalia in Euparal on microslide pinned beneath labels. Original labels: “USA: SOUTH CAROLINA, York Co. King’s Mountain State Park. 35.13062, –81.36439. 26-September-2020. C.W. Harden. Under rocks near stream, mesic hardwoods” “CLEMSON-ENT CUAC000170080” “Harden DNA Voucher CWH-242 Anill. ‘kingsmntsp2’ M Ext. 30/September/2020 [green-bordered cardstock]” “HOLOTYPE *Anillinus montrex* Harden & Caterino [orange cardstock]”

Paratypes (n = 5, CUAC): USA: SOUTH CAROLINA: York Co.: Kings Mountain State Park: Same data as holotype, CUAC000170080 to CUAC000170082, CWH-242 to CWH-244 (2♂, 1♀); 35.13018, –81.36205, 23 Dec. 2021, C.W. Harden leg., under embedded rock, hill above small stream, CUAC000170083 and CUAC00017084, CWH-430 and CWH-431 (1♂, 1♀).

Other material (n = 1, CUAC): USA: NORTH CAROLINA: Gaston Co.: Crowders Mountain State Park, Linwood Access, 35.2417, –81.2717, 29 Apr. 2023, C.W. Harden leg., under embedded rock, CUAC000182316, CWH-514 (1♀).

Diagnosis. Males of this species have the second protarsomere more expanded than any other known species of eastern *Anillinus* (Fig. 3D,G). Members of both sexes are strongly flattened dorsoventrally, narrow and parallel sided (Fig. 4G). The median lobe of the aedeagus (Fig. 7P, 9I) has a distinctive apex that is small and abruptly bisected by the membranous dorsal margin.

Description. Habitus: Small (ABL = 1.54–1.71 mm, average = 1.64 ± 0.07 mm), dorsoventrally flattened and elongate (Fig. 4G), narrow (EW/ABL 0.32–0.34). Average ABL of males greater (1.68 mm, n = 3) than females (1.57 mm, n = 2). **Integument:** Microsculpture strongly impressed on dorsal surface of head except for small area in center of vertex, where the mesh is open and lightly impressed, appearing absent in certain lighting; effaced from disc

of pronotum, present along edges and at base. *Head*: Relatively large ($HW/PW = 0.75-0.78$); frontoclypeal horn present. Mentum with median pair of setae posterior to the bead of the subtriangular mentum tooth. *Pronotum*: Relatively broad ($PW/EW = 0.83-0.89$) and long ($PL/PW = 0.82-0.85$), basal constriction strong to moderate ($PbW/PW = 0.72-0.75$). *Elytra*: Parallel sided and narrow ($EW/ABL = 0.32-0.34$); humeri well developed; disc strongly flattened dorsoventrally, lateral declivity abrupt and steep. *Legs*: Profemora of males swollen, ventral surface somewhat tuberculate in basal third. Protarsi with segments 1 and 2 both expanded with inner margin spinose, both with adhesive setae ventrally (Fig. 3D,G). Metafemur of males swollen distally and with prominent peg-like tooth on posterior margin in distal third (Fig. 2E). *Abdominal ventrites*: Unmodified in either sex. *Male genitalia*: Relatively small ($RL/ABL = 0.22$), ring sclerite thickened and egg shaped in ventral aspect. Median lobe of aedeagus (Fig. 9I) narrow, slightly twisted dorsally (Fig. 7F,P), ventral margin broadly expanded medially. Flagellum elongate, basal curve shorter than in other members of the group, becoming filamentous and nearly straight past proximal third. Right side of ostium with weakly sclerotized strip. Right paramere (Fig. 9H) short, with four long setae on apical margin. Left paramere (Fig. 9G) conchoidal, slightly narrowed apically, with four setiferous pores on apical margin; outer two apical setae longer than middle two, which are minute. *Female genitalia*: Spermatheca (Fig. 8H,I) not swollen basally, abruptly enlarged in distal half, and stem of spermatheca smooth, with short, abrupt perpendicular curve proximally, appearing differently depending on orientation (Fig. 8H,I). Spermathecal duct long and tightly coiled.

Distribution. (Fig. 11) This species is known from a small area in Kings Mountain State Park in York Co., SC. A single female that is similar to this species was collected in Crowders Mountain State Park in Gaston Co., NC. The specimen is not included in the type series, and assignment of this population to species will require male specimens.

Sympatry. Members of this species have been collected with an undescribed member of the *valentinei* group under embedded rocks. *Anillinus cornelli* Sokolov and Carlton and a large, undescribed species of *Serranillus* also occur within Kings Mountain State Park.

Natural history. All of the specimens were collected from the undersides of rocks embedded in soil on the same hillside above a small ephemeral stream. Specimens were collected in September and December, but these were also the only times of year when collecting attempts were made. No specimens were collected in three samples of sifted litter and soil taken from the same hillside. The species is presumably endogean in habit.

Species status justification. The strongly flattened and parallel-sided body, greatly expanded second male protarsomeres, peg-like spine of the male metafemora, and male genitalia are unique within the genus.

Derivation of name. The species name is a noun in apposition, created by combining the Latin for mountain (*montanus*) and king (*rex*), in reference to the type locality, Kings Mountain, a monadnock spanning the South Carolina — North Carolina border.

***Anillinus* sp. “North Carolina, Orange Co. sp. 2”**

Fig. 2D, 7E,O, 10A,B, 11

Material examined. USA: NORTH CAROLINA: *Orange Co.*: Duke Forest, ca. 6 miles northwest of Chapel Hill, 35.9778, -79.1105, 10 Dec. 2022 to 4 Jul. 2023, C.W. Harden leg., buried pipe trap, CUAC000185902, CWH-520, CUAC (1♂).

Diagnosis. This undescribed species is known from a single male collected in a buried pipe trap set in December 2022 and collected in July 2023. The specimen was found missing its head. The specimen is by far the largest individual of the *elongatus* group known (ABL without head = 2.14 mm). The secondary leg modifications are unique within the genus: the profemora are swollen and each possess a prominent tooth on the ventral face, and the metafemora are swollen and bear two proximate teeth on the posterior margin: the proximal tooth blunt, placed more dorsad and directed posteriorly, the distal tooth sharp, placed more ventrad and directed laterally (Fig. 2D). The second abdominal ventrite bears two weak parallel carinae. The male genitalia are distinctive also, especially the median lobe (Fig. 7E,O), which is strongly curved and bladeliike.

Notes. Profemoral modifications are rare within *Anillinus*. They have not been previously documented in any

species, but we have observed that the male profemora of one previously described species, *Anillinus lescheni* Sokolov and Carlton, each possess a prominent triangular tooth. Two undescribed *Anillinus* species also possess teeth on the profemora, one from South Carolina that is most closely related to *Anillinus albrittonorum* Sokolov and Schnepf (Harden and Caterino in prep.) and one from Alabama that is probably related to *Anillinus hirsutus* Sokolov.

Species group *incertae sedis*

Anillinus turneri Jeannel, 1963

Anillinus turneri Jeannel, 1963a: 77

Fig. 2C, 3A, 4B, 5B, 7C,M

Material examined. Holotype female (USNM): glued to card, labeled: "Peach Co., Ga. Nov. 15. 1941. In soil peach orch. 18954 W.F. Turner." "TYPE" "TypeNo 69543 USNM".

Other material (CMNH): 2♂, same data as holotype.

Diagnosis. First protarsomere of males with adhesive vestiture ventrally, second protarsomere unmodified (Fig. 3A). Right paramere of aedeagus quadrisetose, greatly elongate and narrow (Fig. 5B). Median lobe of aedeagus strongly sclerotized dorsally, strongly asymmetrical and twisted dorsally from plane of basal lobes, apex deflected ventrally (Fig. 7C,M). Flagellum short, "open" laterally, several large, triangular teeth present on left side of internal sac behind flagellum. Metafemora modified, with a peg-like tooth on the posterior margin (Fig. 2C).

Redescription. Habitus: (Fig. 4B) ABL = 1.68 mm. Body robust, parallel sided, slightly depressed dorsoventrally. *Integument:* Isodiametric microsculpture impressed over entire head; absent from disc of pronotum, present along margins. *Head:* HW/PW = 0.76; frontoclypeal horn present, conspicuous; three supraorbital setae present on each side; submedial setae of mentum placed posterior to tooth. *Pronotum:* Broad (PW/EW = 0.84), cordate, with sides slightly sinuate before posterior angles which are right and slightly constricted (PbW/PW = 0.76). *Legs:* Profemora of males unmodified. Male protarsomere 1 expanded and dentate on inner margin, with ventral adhesive setae; male protarsomere 2 unmodified (Fig. 3A). Mesotrochanters unmodified. Male metafemur with prominent peg-like spine on posterior margin in apical third (Fig. 2C). *Abdominal ventrites:* Unmodified in either sex. *Male genitalia:* Ring sclerite greater than one fourth body length (RL/ABL = 0.31). Median lobe (Fig. 7C,M) strongly asymmetrical, twisted dorsally from plane of basal lobes. Dorsal margin thickened, strongly sclerotized. Ventral margin expanded, deflected ventrally apically. Internal sac with flagellum weakly sclerotized and evenly curved, relatively short; left side of sac armed with field of large, weakly sclerotized triangular spines. Right paramere narrow and elongate, with four short apical setae (Fig. 5). Left paramere large, conchoidal, ventral margin with four preapical setae. *Female genitalia:* Not examined. Sokolov and Schnepf (2021) reported that the spermatheca has a "question mark shape."

Distribution. This species is known only from Peach County, Georgia. The records from South Carolina (Ciegler 2000) and Atlanta (Sokolov and Schnepf 2021) are erroneous.

Sympatry. The species is not known to be sympatric with other species of anillines.

Notes. Attempts in recent years by C. Harden, K. Schnepf, T. Cottrell, and R. Hartley to collect fresh material of this species in Peach County have been unsuccessful. Several large samples of deep soil, washed and unwashed, were extracted in Berlese funnels. Five deep soil traps were operated by C. Harden in mature wooded habitats at the USDA Byron Research Station for one year. These traps were flooded by water repeatedly, and captured numerous amphipod crustaceans; the site was probably too wet for *Anillinus*, and future trapping attempts in Peach County should take place in more well drained locations. The type material was collected by Berlese extraction of soil dug from a peach orchard, so perhaps mature forests are not an ideal place to search for *A. turneri*.

The lack of ventral adhesive setae on protarsomere 2 of males of *A. turneri* is a presumably derived character state that is shared with members of the sinuaticollis group. However, this character has evolved several times (Harden and Caterino, in prep.) and the form of the median lobe of *A. turneri* (Fig. 7C,M) is different from species of the sinuaticollis group; that of *Anillinus cf. felicianus* Sokolov is shown in Fig. 7D,N.

Discussion

The members of the *elongatus* group are the flattest and narrowest species of *Anillinus* in the eastern Piedmont, a body form associated with their use of deep soil habitats. As the single February collection of *A. arenicollis* in a litter sample demonstrates, the beetles in this group are capable of moving up vertically to shallower strata during certain conditions, but all other collections have been from endogean habitats, indicating that they usually inhabit deep mineral soil layers. Sampling throughout the range of the *elongatus* group has not been dense enough to test biogeographic hypotheses, but the known distributions of the species suggest that large rivers serve as important dispersal barriers. In other endogean anillines, occasional long-distance dispersal by hydrochory has been proposed as an important biogeographic process (Ortuño and Gilgado 2011, Andújar et al. 2017), and there is some evidence that it might have been important in the *elongatus* group. The likely sister species *A. elongatus* and *A. pittsylvanicus* are closely similar in many characters and are geographically separated largely by drainage basins; the populations of *A. elongatus* are at the head of the Neuse and Cape Fear basins, just south of the divide between those and the large Roanoke River basin, which *A. pittsylvanicus* inhabits. Only a single locality of *A. pittsylvanicus* is known, and it is north of the Dan River, which itself could be a barrier to dispersal. *Anillinus uwharrie* is separated from other *elongatus* group populations by the Pee Dee and Cape Fear Rivers. The Pee Dee also separates *A. arenicollis*, which occurs just south of it. The locality of *A. arenicollis* is also unusual in being east of the Fall Line, the transition point between the Piedmont and the Coastal Plain. The only other *Anillinus* species known east of the Fall Line on the eastern seaboard is *A. turneri*.

The two species of the *montrex* subgroup are geographically disjunct and both occupy isolated, rocky hills. Although named Bald Mountain, the term “mountain” is generous for the locality of *A. sp.* “North Carolina, Orange Co. sp. 2.” The condition of the weathered rock at the site probably makes the endogean microhabitats distinct from the lower surrounding area, however; when C. Harden was digging holes for installation of the buried traps that eventually discovered the species, the soil matrix was full of sharp, gravel-sized rock fragments. These fragmented deposits were created, at least in part, as waste piles produced by prehistoric quarrying by humans (Moore and Irwin 2006). Perhaps *A. sp.* “North Carolina, Orange Co. sp. 2” and *A. montrex* are more adapted to the soil–rock interface, whereas the species in the *elongatus* subgroup live mostly within soil crevices.

Anillinus docwatsoni is known only from the south side of the Hickory Nut Gorge, whereas *Anillinus pecki* occupies a relatively large area in the mountains northeast of the French Broad River (FBR). Both species are known from a wide range of elevations, with the two known localities of *A. docwatsoni* being 350 m at Chimney Rock State Park and 1240 m at Bearwallow Mountain and *A. pecki* ranging from 480 to 1660 m. The wide range of *A. pecki* suggests a history of active dispersal, and the range of the common ancestor of both species was probably continuous across the modern range of *A. pecki* south to that of *A. docwatsoni*. Subsequent warming may have created a lowland barrier to dispersal between the two populations that gave rise to *A. docwatsoni* and *A. pecki*, but no such barrier is apparent in current topography. An increase in precipitation during the Pleistocene and resulting water volume and erosion of the Broad River in the Hickory Nut Gorge could have also divided the populations. The east–west orientation of the Hickory Nut Gorge and the wide variety of microhabitats available along the steep sides of the gorge would have made it a suitable refuge for dispersal-limited animals during unstable climatic periods, and the ancestral population of *A. docwatsoni* could have become isolated in the gorge while the ancestral populations of *A. pecki* occupied a more continuous patchwork of refugia to the north. The Hickory Nut Gorge harbors other unique taxa, including endemic species of salamanders (Patton et al. 2019) and lampshade spiders (Keith and Hedin 2012). The unusual snail *Paravitrea nunnehi* Slapcinsky et al. is known only from rock outcrops along the Broad River (Slapcinsky et al. 2023)

Molecular phylogenetics suggests that the sister group to the *pecki* group is the *sinuaticollis* group (Harden and Caterino, in prep). In the southern Appalachians, the *sinuaticollis* group occurs in the northwest corner of South Carolina (Fig. 11) and in northern Alabama (CUAC and CMNH data). Other disjunct occurrences of the group are known in southern Kentucky, central Tennessee, and eastern Louisiana, making the group one of the most widespread in the genus. If the sister relationship between *A. pecki* and the *sinuaticollis* group is corroborated, then it reflects a rare example in anillines of vicariance across the FBR basin. The other examples of anilline lineages that span the FBR are either widespread species that occur on both sides (such as *Anillinus murrayae*

Sokolov and Carlton) or lineages whose distributions are broader and disjunct (such as the langdoni group), and not clearly separated by the FBR. The FBR is a classic example of a lowland barrier to dispersal in flightless Appalachian animals, but in most cases the taxa on opposite sides are not sister to each other (Hedin and Thomas 2010, Hedin and McCormack 2017, Garrick et al. 2018) and thus not the result of vicariance caused by climatic warming and subsequent uninhabitability of the FBR.

The systematic position of *A. turneri* remains uncertain. Based on the spermatheca shape, it is unlikely to be related to the Florida endemic *A. albrittonorum*, which it superficially resembles in habitus (Sokolov and Schnepf 2021). *Anillinus turneri* also shares with *A. albrittonorum* the absence of ventral adhesive setae on the second male protarsomere (C. Harden personal observation). The latter character is likely a derived condition within the genus, but it has also likely evolved multiple times. The pattern of dorsal microsculpture on the forebody of *A. turneri* agrees with the *sinuaticollis* group, as does the size and shape of the flagellum, but the polarity of these characters is unknown. The female holotype of *Anillinus sinuaticollis* Jeannel appears similar in overall habitus to the type of *A. turneri*; the male genitalia of *A. sinuaticollis* are unknown, as is the exact type locality. Previous authors have hypothesized that *A. turneri* is related to *A. elongatus* Jeannel, based on the habitus and pattern of dorsal microsculpture on the forebody (Sokolov et al. 2004, Sokolov 2012). However, our study of male characters of *A. turneri* does not support such a relationship. The second male protarsomeres in *A. turneri* lack ventral adhesive setae, and the median lobe of the aedeagus has a thick, strongly sclerotized dorsal margin and a short, evenly curved flagellum, both of which depart from all known *elongatus* group species.

Conclusion

Much basic inventory work and taxonomy remain to be done with anillines in the eastern United States. Despite an active modern taxonomic period, eastern Nearctic anillines continue to suffer from “Overlooked Syndrome” (Park et al. 2010). The most widespread and abundant species treated in this study, *Anillinus pecki*, had previously been reported only from nine specimens from three localities (Giachino 2011). *Anillinus docwatsoni* was until now one of many examples of species described from a single specimen and never seen in the decades since. As we have shown, the species is in fact extant and abundant at the type locality and can be collected in relatively large series with the proper collecting techniques. Lastly, the discovery of numerous short-range endemic species of the *elongatus* group in the densely populated Piedmont region not only highlights the extent of our ignorance of soil biodiversity, but also offers a promising opportunity for fine-scale biogeographic studies in an ancient and geologically complex landscape where natural habitats are rapidly being lost.

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Literature Cited

- Andújar C, Pérez-González S, Arribas P, Zaballos JP, Vogler AP, Ribera I. 2017.** Speciation below ground: Tempo and mode of diversification in a radiation of endogean ground beetles. *Molecular Ecology* 26: 6053–6070. <https://doi.org/10.1111/mec.14358>
- Barr TC Jr. 1995.** Notes on some anillines (Coleoptera, Carabidae, Bembidiinae) from Southeastern United States, with descriptions of a new genus and two new species. *Special Bulletin of the Japanese Society of Coleopterology* 4: 239–248.
- 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 TL. 1918.** *Memoirs on the Coleoptera*. VIII. The New Era Printing Company; Lancaster, Pennsylvania. 427 p.
- Cieglar JC. 2000.** Ground beetles and wrinkled bark beetles of South Carolina (Coleoptera: Geadephaga: Carabidae and Rhysodidae). Clemson University; Clemson, South Carolina. 149 p.
- Cornell JF. 1972.** The eyeless beetles of North Carolina with notes on their ecology and evolution (Insecta: Coleoptera). *Journal of the Elisha Mitchell Scientific Society* 88: 260–264.
- Cornell JF. 1977a.** Freshwater and terrestrial arthropods: Species of special concern: Insecta; Coleoptera; Carabidae (Ground Beetles). p. 221–222. In: Cooper JE, Robinson SS, Funderburg JB (eds.). *Endangered and threatened plants and animals of North Carolina: Proceedings of the symposium on endangered and threatened biota of North Carolina*. 1. Biological concerns. Meredith College, Raleigh, November 7–8, 1975. North Carolina State Museum of Natural History. 444 p.
- Cornell JF. 1977b.** Freshwater and terrestrial arthropods: Threatened species: Insecta; Coleoptera; Carabidae (Ground Beetles). p. 207–208. In: Cooper JE, Robinson SS, Funderburg JB (eds.). *Endangered and threatened plants and animals of North Carolina: proceedings of the Symposium on Endangered and Threatened Biota of North Carolina*. 1. Biological Concerns. Meredith College, Raleigh, November 7–8, 1975. North Carolina State Museum of Natural History. 444 p.
- Dury C. 1902.** A revised list of the Coleoptera observed near Cincinnati, Ohio, with notes on localities, bibliographical references and description of six new species. *The Journal of the Cincinnati Society of Natural History* 20: 107–196.
- Garrick RC, Newton KE, Worthington RJ. 2018.** Cryptic diversity in the southern Appalachian Mountains: genetic data reveal that the red centipede, *Scolopocryptops sexspinosus*, is a species complex. *Journal of Insect Conservation* 22: 799–805. <https://doi.org/10.1007/s10841-018-0107-3>
- Giachino PM. 2011.** A description of two new species of Anillina from North Carolina with notes about the geographical distribution of the genus *Anillinus* Casey, 1918 (Coleoptera: Carabidae: Bembidiini). *Studies and Reports, Taxonomical Series* 7: 109–116.
- Giachino PM, Sciaky R. 2002.** A new genus and two new species of Anillini from the Lesser Antilles (Coleoptera: Carabidae: Bembidiini). *Elytron* 16: 31–40.
- Hedin M, McCormack M. 2017.** Biogeographical evidence for common vicariance and rare dispersal in a southern Appalachian harvestman (Sabaconidae, *Sabacon cavicolens*). *Journal of Biogeography* 44: 1665–1678. <https://doi.org/10.1111/jbi.12973>
- Hedin M, Thomas SM. 2010.** Molecular systematics of eastern North American Phalangodidae (Arachnida: Opiliones: Laniatores), demonstrating convergent morphological evolution in caves. *Molecular Phylogenetics and Evolution* 54: 107–121. <https://doi.org/10.1016/j.ympev.2009.08.020>
- ICZN [International Commission on Zoological Nomenclature]. 1999.** *International code of zoological nomenclature*. Fourth edition. International Trust for Zoological Nomenclature; London. 306 p.
- 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.
- Keith R, Hedin M. 2012.** Extreme mitochondrial population subdivision in southern Appalachian paleoendemic spiders (Araneae: Hypochilidae: *Hypochilus*), with implications for species delimitation. *Journal of Arachnology* 40: 167–181. <https://doi.org/10.1636/A11-49.1>
- Laplante, S. 2024.** Canadian National Collection Taxonomy and Specimen Database. Specimen details for CNC95913, holotype of *Anillinus pecki*. Available at <https://www.cnc.agr.gc.ca/taxonomy/Specimen.php?id=3435> (Last accessed May 2024.)

- Larochelle A, Larivière M-C. 2003.** A natural history of the ground-beetles (Coleoptera: Carabidae) of America north of Mexico. Pensoft Publishers; Sofia, Bulgaria. 583 p.
- Means JC, Hennen DA, Marek PE. 2021.** A revision of the *minor* species group in the millipede genus *Nannaria* Chamberlin, 1918 (Diplopoda, Polydesmida, Xystodesmidae). *ZooKeys* 1030: 1–180. <https://doi.org/10.3897/zookeys.1030.62544>
- Moore CR, Irwin JD. 2006.** Chapter 3. Quarries and artifacts. p. 16–41. In: Steponaitis VP, Irwin JD, McReynolds TE, Moore CR (eds.). Stone quarries and sourcing in the Carolina Slate Belt. Research report No. 25. Research Laboratories of Archaeology; University of North Carolina at Chapel Hill. 195 p.
- Ortuño VM, Gilgado JD. 2011.** Historical perspective, new contributions and an enlightening dispersal mechanism for the endogean genus *Typhlocharis* Dieck 1869 (Coleoptera: Carabidae: Trechinae). *Journal of Natural History* 45: 1233–1256. <https://doi.org/10.1080/00222933.2011.566944>
- Park J-S, Carlton CE, Ferro ML. 2010.** Diversity and taxonomic review of *Leptusa* Kraatz (Coleoptera: Staphylinidae: Aleocharinae) from Great Smoky Mountains National Park, U.S.A., with descriptions of four new species. *Zootaxa* 2662: 1–27.
- Patton A, Apodaca JJ, Corser JD, Wilson CR, Williams LA, Cameron AD, Wake DB. 2019.** A new green salamander in the Southern Appalachians: Evolutionary history of *Aneides aeneus* and implications for management and conservation with the description of a cryptic microendemic species. *Copeia* 107: 748. <https://doi.org/10.1643/CH-18-052>
- Slapcinsky J, Furr D, Devender AV, Devender RWV. 2023.** A river runs through it: The unusual distribution of a new *Paravitrea* (Gastropoda: Stylommatophora: Oxychilidae) from the Piedmont of North Carolina, with the description of a new species. *The Nautilus* 137: 91–97.
- Slipinski A, Lawrence JF. 2013.** 1. Introduction. p. 1–94. In: Slipinski A, Lawrence JF. Australian beetles volume 1: Morphology, classification and keys. CSIRO publishing; Collingwood, Victoria, Australia. 576 p.
- Sokolov IM. 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 IM. 2021.** Two new species of the genus *Anillinus* Casey (Coleoptera, Carabidae, Anillini) from the southern United States. *ZooKeys* 1016: 63–76. <https://doi.org/10.3897/zookeys.1016.61397>
- Sokolov IM. 2022.** Two new cavernicolous species of *Anillinus* Casey (Carabidae, Trechinae, Anillini) from Texas with a revised key to Texas species. *Subterranean Biology* 44: 153–166. <https://doi.org/10.3897/subtbiol.44.91002>
- Sokolov IM, Carlton CE. 2010.** New species of *Anillinus* Casey (Carabidae: Trechinae: Bembidiini) from the Southern Appalachians and phylogeography of the *A. loweae* species group. *Zootaxa* 2502: 1–23. <https://doi.org/10.11646/zootaxa.2502.1.1>
- Sokolov IM, Carlton C, Cornell JF. 2004.** Review of *Anillinus*, with descriptions of 17 new species and a key to soil and litter species (Coleoptera: Carabidae: Trechinae: Bembidiini). *The Coleopterists Bulletin* 58: 185–233. <https://doi.org/10.1649/611>
- Sokolov IM, Carlton CE, Watrous LE, Robison HW. 2017.** *Anillinus alleni* Sokolov and Carlton (Coleoptera: Carabidae: Trechinae: Bembidiini), a new species from the Ozark Interior Highlands of Arkansas, USA. *The Coleopterists Bulletin* 71: 289–297. <https://doi.org/10.1649/0010-065X-71.2.289>
- Sokolov IM, Reddell J, Kavanaugh D. 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>
- Sokolov IM, Schnepf KE. 2021.** A new subterranean species of *Anillinus* Casey (Carabidae, Trechinae, Anillini) from Florida. *Subterranean Biology* 39: 33–44. <https://doi.org/10.3897/subtbiol.39.65769>
- Sokolov IM, Sokolova YY, Carlton CE. 2007.** New species of *Anillinus* Casey (Carabidae: Trechinae: Bembidiini) from Great Smoky Mountains National Park, U.S.A. and phylogeography of the *A. langdoni* species group. *Zootaxa* 1542: 1–20. <https://doi.org/10.11646/zootaxa.1542.1.1>
- Sokolov IM, Watrous LE. 2008.** A new species and the first record of the genus *Anillinus* (Carabidae: Trechinae: Bembidiini) from the Ozark region. *The Coleopterists Bulletin* 62: 537–543. <https://doi.org/10.1649/1114.1>

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