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Unseeing and Unseen: On the Distribution, Morphology, and Larva of One of North America's Rarest Histerid Beetles, *Geocolus caecus* Wenzel (Coleoptera: Histeridae)

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Abstract

We have revealed a surprisingly wide distribution for the blind, subterranean histerid species, *Geocolus caecus* Wenzel, largely through the use of buried "pipe" traps. This species is now known from Georgia, Alabama, South Carolina, and Kentucky, and we also describe its newly discovered larva, associated by DNA sequences. The phylogenetic position of this unusual genus has received little attention, but its continued placement in Dendrophilinae, though not in any specific tribe, appears justified. Morphological similarities to other putative relatives, especially the Mediterranean *Triballodes* Schmidt, less so New Zealand's *Brounister* Leschen and Ôhara, are suggestive, though at least some are likely to be symplesiomorphies.

Keywords: Dendrophilinae, hypogean, aptery, buried pitfall traps

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Introduction

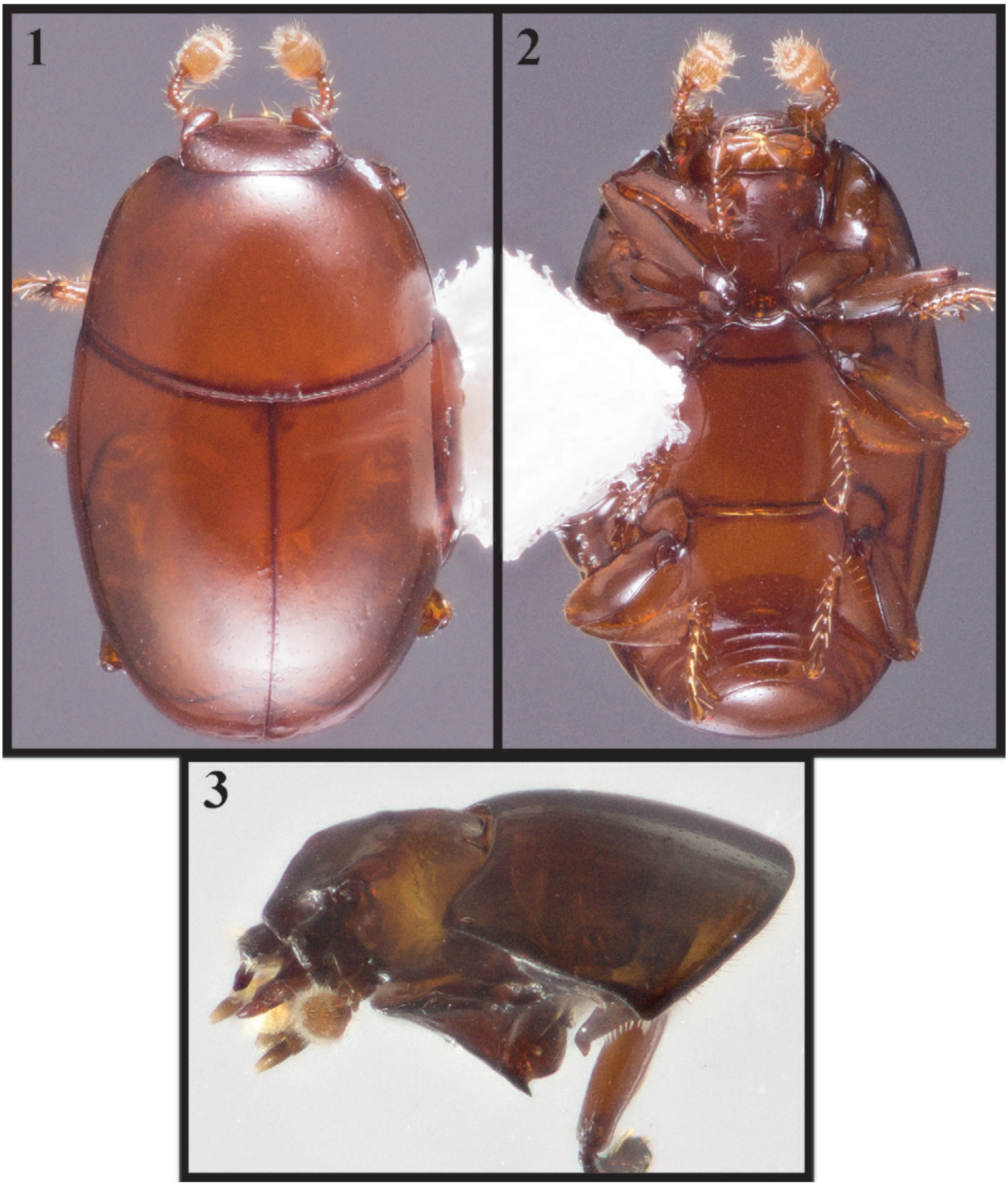
Geocolus caecus Wenzel (Figs. 1–3) is a remarkable blind, flightless, hypogean histerid beetle, one of only a few such species of the family worldwide. It was originally described from two specimens collected from peach orchard soil in central Georgia, USA (Wenzel 1944), and since that time, only one additional location for the species, in north-central Alabama, has been known. The species was originally placed in the subfamily Dendrophilinae, and suggested by Wenzel to be phylogenetically close to the monotypic Mediterranean genus *Triballodes* Schmidt. Both genera have since been consistently placed in the dendrophiline tribe Bacaniini by Mazur (1984, 2011), which was established for a few other genera by Kryzhanovskij and Reichardt (1976). Lackner (2008) revisited the placement of *Triballodes*, questioning the fit within Bacaniini, but ultimately leaving it there despite its lack of some of the tribe's synapomorphies. The specific placement of *Geocolus* Wenzel has never been discussed beyond Wenzel's tentative assignment, and the genus remains an obscure enigma.

Recent collections of *G. caecus* from several new localities reveal the species to be surprisingly widespread for a flightless soil dweller. These collections have also yielded specimens fresh enough for DNA extraction, as well as probable larvae for the species. These discoveries prompted us to provide an up-to-date snapshot of the species' biology and distribution, and to provide additional data on the morphology of the species, particularly of its larva. The number of fully described histerid larvae remains relatively small (Caterino and Tishechkin 2006; Gomy 1965; Kovarik and Passoa 1993; Zaitsev and Zaitsev 2019), but there is significant potential for their morphology to help resolve relationships in the family.

Materials and Methods

Specimens from Cherokee Co., AL and Oconee Co., SC were hand collected by turning embedded rocks and inspecting the soil surface and underside of the rock with a headlamp. Those from Highland Lake, AL were collected by Tim King through Berlese extraction of sifted soil "two to three feet" deep, from the vicinity of old tree stumps. Attempts by the authors to collect *Geocolus* using this method in SC have not been successful. During February 2021, an unsuccessful attempt was made to collect specimens from two sites near the type locality in Peach Co., GA: author CWH and Kyle Schnepp (Florida State Collection of Arthropods) performed soil washing for several hours in Fort Valley and near the Flint River. The flotant was dried and placed in Berlese funnels for extraction.

Most of the adult specimens and all of the larvae studied were collected using buried modified pitfall traps based on an unpublished design of James L. LaBonte (retired, Oregon Department of Agriculture). A detailed summary of the trap design and performance is in preparation by CWH and K. Ivanov. In brief, the traps are sections of 2-inch outer diameter PVC pipe between 8 and 12 inches



Figs. 1–3. Adult of *Geocolus caecus*. **1)** Dorsal view; **2)** Ventral view; **3)** Prothorax and head, lateral view.

in length, with slots cut across at regular intervals. A glass spice jar or similar container is filled with a small amount of pure propylene glycol and attached to one end of the pipe with duct tape. The pipe is installed vertically in a shaft created in the bottom of a shallow hole using a soil auger and the soil is carefully filled in around it while a modified broom handle is inserted into the pipe to prevent soil entering. A plastic lid ~15 cm in diameter is placed on top before the trap is buried and left in place for several months. The traps are either unbaited or contain a small amount of rotten meat or cheese in a plastic tube suspended in the pipe using fishing line. Since 2017, CWH has collected 275 buried trap samples from 27 sites in VA, WV, KY, NC, SC, and GA, targeting anilline carabids. Trapping data for the sites where *Geocolus* was collected are given in the results section below.

We attempted to extract DNA from nine specimens. Two putative larvae were extracted, a first instar from Monroe Co., KY, and a second instar from Pickens Co., SC. Extractions were attempted for seven adults from five localities: the two preceding localities where larvae were collected, plus Blount and Cherokee counties, AL, and Oconee Co., SC. Adults were separated at the prothorax-mesothorax junction prior to extraction, while the larvae were punctured behind the head capsule. ThermoFisher's GeneJet extraction kit (Vilnius, Lithuania) was used for extractions. Our best success with amplification for marginally preserved specimens was for a short portion of the barcoding region of COI using primers BF2-BR2 (GCHCCHGAYATRGCHTTYCC and TCDGGRTGNCCRAARAAYCA, respectively; Elbrecht and Leese 2017), which worked for one larval and five adult specimens. Successful amplifications were Sanger sequenced by Psomagen (Rockville, MD). Fragments were aligned to existing data for Histeroidea (*e.g.*, Caterino and Vogler 2002) using MAFFT online (Katoh *et al.* 2017).

Following DNA extraction, the larval specimens were temporarily slide mounted in glycerin and examined under a compound microscope. Initial pencil drawings were digitized using a drawing pad into Adobe Illustrator and edited as vector graphics. Setal and pore homologies were assessed by comparison to detailed descriptions of *Onthophilus* Leach (Kovarik and Passoa 1993) and Haeteriinae (Caterino and Tishechkin 2006). Our descriptions follow Kovarik and Passoa (1993; "K&P" where referenced in the description below) with respect to presentation, terminology and numbering. This does not necessarily imply agreement with their homology assessments (either serially among segments or among different taxa), but is done to facilitate direct comparison among them. In the text all setae and pores are referred to by two capital letters for each body region (MN = mandible; MX = maxilla; LA = labium; AN = antenna; SE = antennal sensorium; FR = frontale [nasale]; PA = parietal [head]; TE = thoracic and abdominal dorsum; PR = presternum; ST = thoracic and abdominal sternum; UG = urogomphus; PP = pygopod [abdominal segment X]). These codes are followed by a numeral for setae and a lower-case letter for pores. Where thoracic and abdominal (TE, ST only) features share number or letter codes across segments it is indicative of their putative serial homology. A lower-case "g" preceding a code indicates a group of setae, treated collectively. A few autapomorphic features are not presently assigned codes. In all cases where a number of setae or pores is given for a particular region, it refers to the number present on only one side of the body.

Results

Histeridae Gyllenhal, 1808
Dendrophilinae Reitter, 1909
Bacaniini Kryzhanovskij, 1976
Geocolus Wenzel, 1944
Geocolus caecus Wenzel, 1944

Subterranean pitfall trapping has revealed *G. caecus* to be surprisingly widespread. In addition to the type locality in central Georgia, and a locality previously posted to BugGuide (www.bugguide.net) in north-central Alabama (Blount County, ~33.8847°N, 86.4219°W), the species is now also known from northwestern South Carolina (Pickens and Oconee counties) and southeastern Kentucky (Monroe County), a range spanning over 300 km of latitudinal and longitudinal distance (see Fig. 5, and Appendix 1 for details on all specimens; all vouchers are deposited in the Clemson University Arthropod Collection). For a blind, flightless, subterranean beetle, attaining such a broad range indicates a long residence time.

Five adult specimens were collected by hand underneath embedded rocks. One individual was found under a large flat rock on damp sand near the Little River (34.3964°N, 85.6271°W) in Cherokee Co., AL on 11 October 2021. The beetle was on a soil casting produced by either a worm or a millipede and became active as soon as it was exposed. Four specimens were found under rocks near Martin Creek Landing (34.6388°N, 82.8644°W) on Lake Hartwell in Oconee Co., SC on 22 October 2021. The rocks were all deeply embedded in damp, sandy soil in deciduous woods. Two specimens were under the same rock (one on the soil surface, the other on the underside of the rock); the other two individuals were found singly, one on soil and the other on a moist, rotten root. Other invertebrates found under the same rocks were diplurans, linyphiid spiders, anilline carabids, and Diptera larvae (possibly bibionids). No *Geocolus* were collected from the soil washing samples taken near the type locality in Peach Co., GA.

Subterranean pitfall trapping produced 36 adult specimens, all but one of them from a forested plot in a residential neighborhood (34.7252°N, 82.8247°W) in Pickens Co., SC. From 26 April 2020 to 14 August 2021, three traps were operated at this site. They were collected and reset on 12 July and 2 October 2020; and 16 January, 11 April, and 14 August 2021. Total numbers of captured *Geocolus* for each of the three traps were zero, three, and 22. After 14 August 2021, the least productive trap was removed and four new traps were installed. The six traps were collected on 24 October 2021, and produced 10 additional specimens, with all but one trap collecting at least one. Three individuals were collected from traps near Hestand, in Monroe Co., KY: a single adult female was collected between 8 May and 3 July 2021 in one of four traps set in a small patch of deciduous forest behind a residence, with hayfields on either side (36.6579°N, 85.6259°W). A single larva was collected in another trap at the same site from the same period. Traps set from 25 February–8 May and 3 July–4 September 2021 collected no specimens at this site. During the same 8 May–3 July 2021 period, one larval specimen was also collected from a trap set in a mature deciduous forest in a steep gorge nearby (36.6580°N, 85.6218°W). No adults were collected at this last site.

With regard to seasonality, it seems that adults may be active nearly year-round. Alabama collections have been made during January, March, May, and December. For other localities, successful traps were out over longer ranges, from April–July and July–October in South Carolina, and from May–July in Kentucky. Further cool season trapping will continue in order to document clearer patterns in activity times.

We obtained COI sequences from adult specimens from Alabama (three) and South Carolina (two), and a first-instar larva from Kentucky (deposited in GenBank under accession numbers ON072257–ON072262; see Supplemental File 1 for data matrix). Phylogenetic analyses of these sequences along with various available Histeridae barcode sequences, including representatives of five other Dendrophilinae (*Dendrophilus* Leach [two spp.], *Bacanius* LeConte [two spp.], and *Paromalus* Erichson) joined all putative *Geocolus* sequences into one clade with > 90% parsimony bootstrap support (Fig. 4), supporting unambiguously the identity of the first-instar larval specimen from Kentucky with *Geocolus*. Sequences of *Geocolus* from the three localities differed by over 8% (pairwise uncorrected p-distance), ranging from 8.3% KY-AL to 12.7% SC-AL. Under some common assumptions of mitochondrial divergence rates (2.3–3.5%/lineage/million years; Brower 1994; Papadopoulou *et al.* 2010), this suggests somewhere between 1.8 and 2.8 million years of separation for populations across this range. Other prospective relationships were poorly supported, as expected for COI alone at such deep divergences.

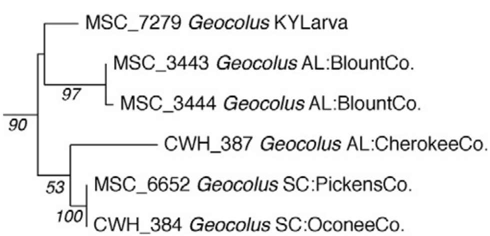


Fig. 4. Parsimony cladogram showing monophyly of adult and larval *Geocolus caecus*, with bootstrap values under branches. Outgroup sequences have been pruned.

Such divergence levels point to the possibility that these populations could represent distinct species. However, close examination of available specimens does not reveal clear morphological differences to support such a hypothesis. The genitalia of males from the South Carolina and Alabama localities do show slight differences in size proportions of the aedeagus (see Figs. 6–9), with that from

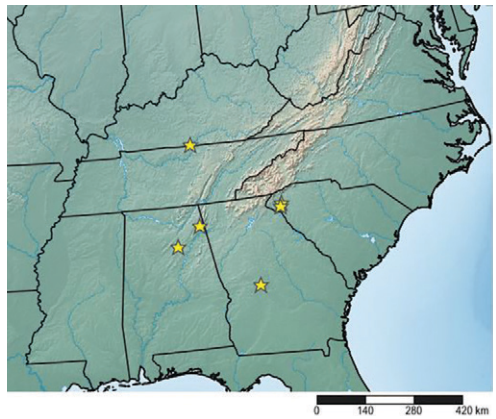
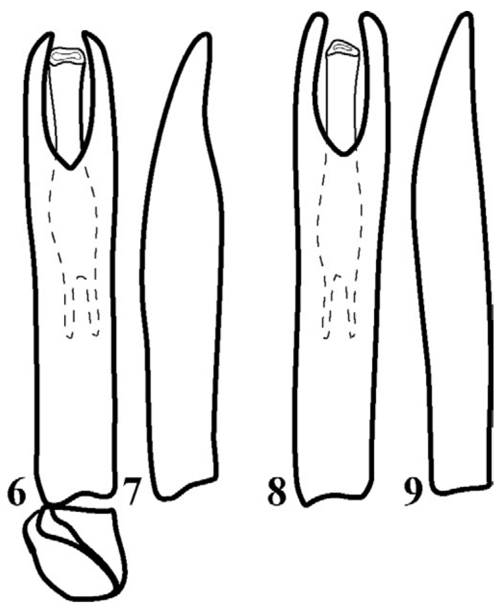


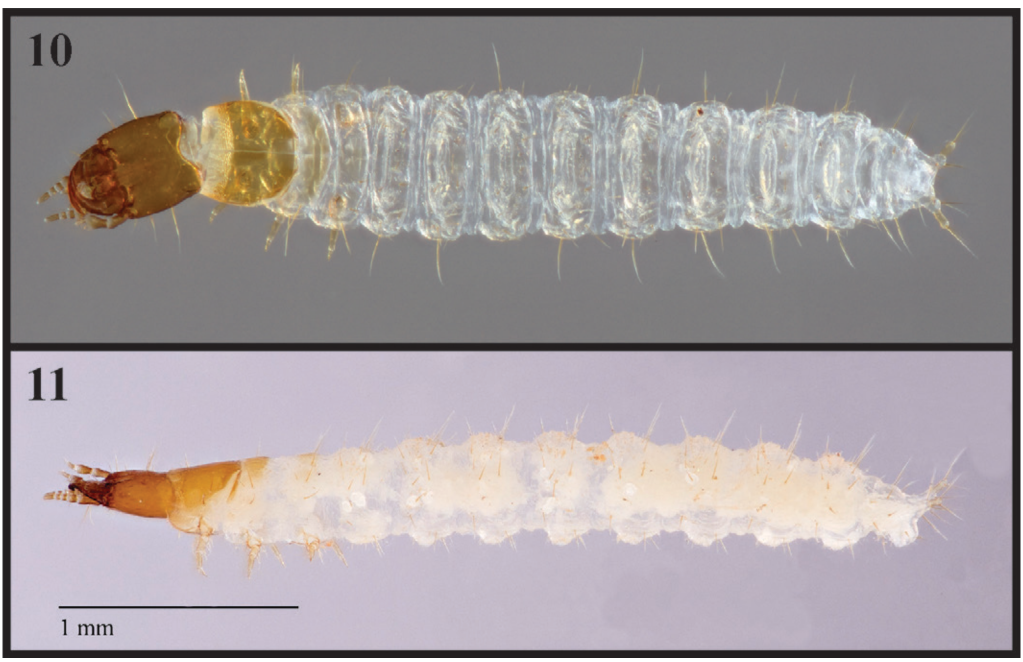
Fig. 5. Map of known localities for *Geocolus caecus*.



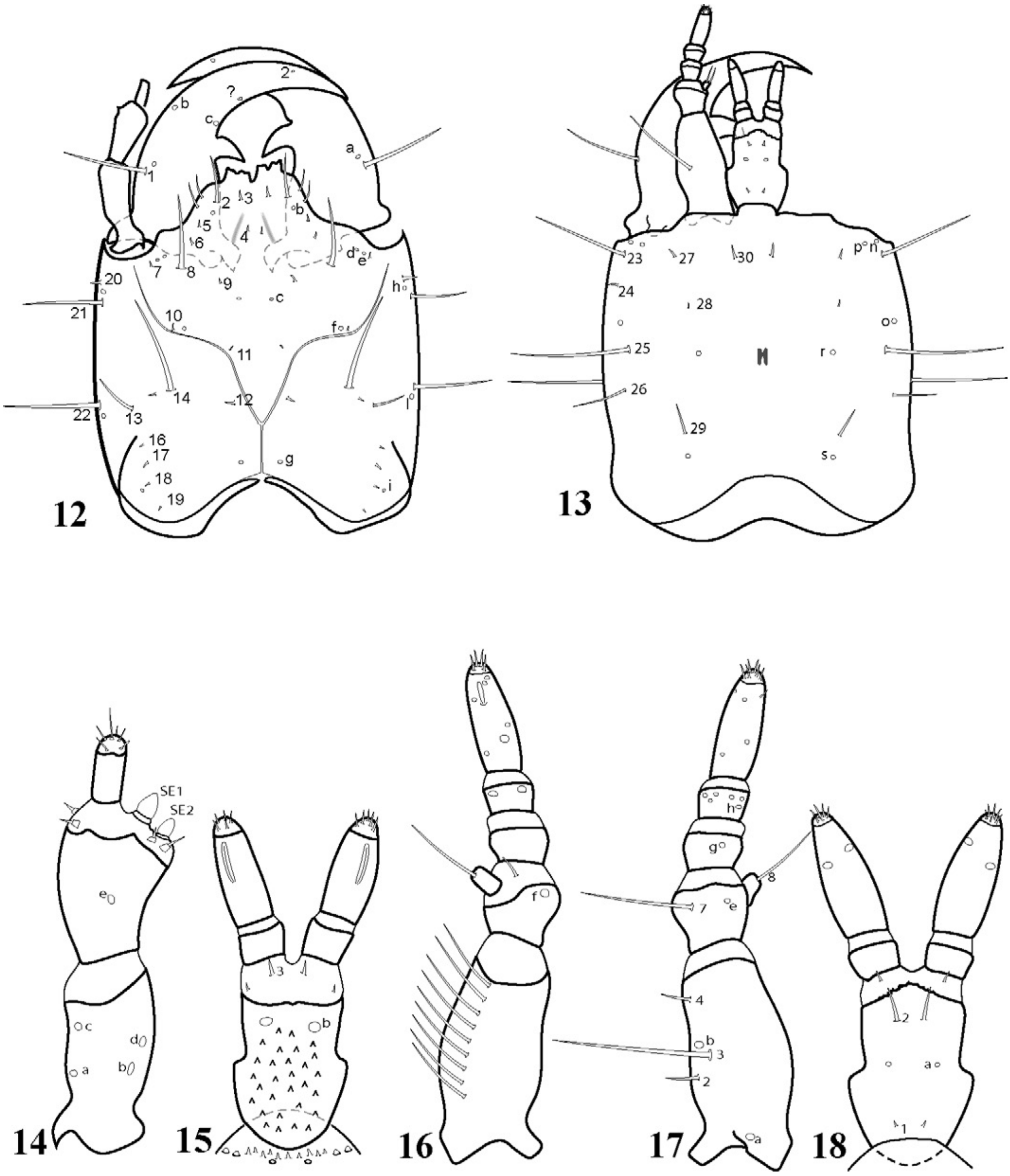
Figs. 6–9. Aedeagus of male *Geocolus caecus*. **6)** From Blount Co., AL, dorsal view; **7)** From Blount Co., AL, lateral view (tegmen only); **8)** From Pickens Co., SC, dorsal view (tegmen and median lobe); **9)** From Pickens Co., SC, lateral view (tegmen only).

Alabama being slightly shorter in length, and thicker in depth. We have not compared these directly to the male type specimen (from Georgia), but Wenzel's figures suggest a thicker aedeagus similar to that of the Alabama male. No males from Kentucky are yet available to compare. Future exploration of detailed differences from additional populations, and sequences of additional genes, may eventually support distinct species status for some of these locations.

Description of the First-Instar Larva. *Length*: 1.8 mm. *Body* elongate, slightly narrowed posteriad, conspicuously setose, creamy white, head and prothorax light brown, with smaller and more weakly pigmented sclerites on other thoracic and abdominal segments, intersegmental membranes thin, weakly secondarily annulate, wrinkled. *Head capsule, dorsal* (Figs. 10, 12): Depressed, nearly parallel-sided, slightly longer than wide, lacking stemmata; epicranial sutures completely dividing base of vertex, united at base, divergent anteriad to near antennal insertions; nasale with 2 obliquely truncate teeth, subacute apicolaterally, each with fine median emargination; nasale anterolaterally with 2 medium-length frontal marginal setae (gFR); setae PA2 and PA8 prominent on nasale, PA3–6 small and interspersed; seta PA22 longest of those on head, extending laterad about one-half head capsule width, inserted about one-third from head base; PA21 slightly shorter, inserted close to antennal insertion; most other dorsal parietal setae and pores identified by K&P present and similar in position, except PA13 in a more medial position, between the large PA14 and PA22; head ventrally (Fig. 13) with conspicuous tentorial fossa, anterior margin of head capsule with narrow, rounded lobe produced below base of labium; setae PA23–26 conspicuous along lateral margin, pores PAn–p, r–s present as in K&P, PAq absent. *Mandible* with single, mesal tooth, inner edges smooth, dense penicillus restricted to small area near mesal base; with MN1 long, one-third from base, MN2 minute, pore MNa present, close to MN1, MNb near lateral margin two-thirds from base, MNc distad mesal tooth near mesal edge. *Maxilla* (Figs. 14–15): Stipes with gMX1 linear, conspicuous, comprising ~10 long setae, weakly plumose; gMX2 absent; MX2–4, a–b present on ventral surface, MX3 longest; inner apical membrane of stipes lacking setae; basal palpomere with MX7 long, MXe (ventral) and MXf (dorsal) present, its apical membrane with 1 fine seta near base of appendage; digitiform appendage of basal palpomere with 1 long seta, MX8; palpomere 2 lacking setae, with pore MXg; palpomere 3 with MXh on ventral surface, and single series of circumferential pores (figured but not individually identified by K&P); apical palpomere with numerous pores, elongate sensorium near apex of dorsal surface, and



Figs. 10–11. Larval habitus of *Geocolus caecus.* **10)** Cleared second-instar larva, dorsal view; **11)** Uncleared second-instar larva, lateral view.



Figs. 12–18. Larva of *Geocolus caecus*, first instar. **12)** Head, dorsal view (in this and the next figure, setae are numbered on the left side of the figure, pores are lettered on the right side); **13)** Head, ventral view; **14)** Antenna, dorsal view; **15)** Labium, dorsal (inside) view; **16)** Maxilla, dorsal (inside) view; **17)** Maxilla, ventral view; **18)** Labium, ventral view.

about 5 small terminal setae. *Labium* (Figs. 15, 18): Prementum about 1.5× as long as wide, lateral margin with blunt expansions just basad middle; ventral surface of prementum with tiny LA1 seta near base, LA2 close to apex of sclerotized portion, LAa near midline; dorsum of prementum with numerous small teeth uniformly distributed to near apex; LAb large, toward apex, MX3 in its apical membrane, with unnumbered seta basolaterally; basal labial palpomere short, without setae or pores; apical palpomere with single conspicuous ventral pore two-thirds from base (not identified among those figured by K&P), inner, dorsal surface with elongate sensorium ("SD" of K&P) near apex, apex with ~6 short setae. *Antenna* (Fig. 14): Basal antennomere with dorsal ANa and ANc near inner edge, ANb and

ANd near outer edge; second antennomere with ANe about one-third from base, apex with large sensoria SE1 and SE2, with 4 smaller sensoria, 2 basad of SE2, 2 along outer edge; terminal antennomere with 6 apical sensilla; all antennal sensilla with distinctly broad bases and narrow apices.

Thorax (Figs. 19–20): Pronotum with broad sclerotized shield, with separate sclerotization along posterolateral edge, desclerotized along midline, with "brick-wall-like" pattern of microsclerites anteriad; anterior margin of shield with (from midline to lateral corner) TEa, small TE1, TEb, medium TE2, TEc, TE13, a small unrecognized pore, then TE12 laterad; lateral TE4 short, TE5 long, nearly half pronotal width; middle of disc with TE8–11, TEd–i; posterior margin with 2 small pores TEa–b with 2 small setae TE1–2 between them; small pleural sclerite bearing 1 seta TE17; large lateral TE19 present at side; ventrally, presternal plates lightly sclerotized, very finely asperate, anterolateral sclerites more lightly sclerotized; median presternal sclerite with PR7, 9; lateral presternal sclerite with PR4–5; PR23–24 short, present on lower edge of hypomeral sclerite, ST40 present on hypomeron laterad procoxa; prosternite with SE44, SE46; ST30 absent; precoxite present, small, bearing setae ST32, ST36. *Mesothorax*: Dorsally with broad median and small lateral sclerites present, median mesotergite desclerotized along median ecdysial line and more weakly at sides, seta TE5 very long, inserted at posterolateral corner, TE4 medium, in anterolateral corner, small TE8 at middle of anterior margin, with TEf–g slightly behind, equally spaced to midline; TE7, TE9 (longest), and TE11 present near posterior margin, TE10 not evident, TEi present anterolaterad TE7; lateral sclerite bearing large TE19, medium TE16 anteriad, and 2 small setae (TE17 posteriorly, other unidentified) along inner edge; TE2 and TEb present in small sclerite between major tergites; mesosternum with large quadrate median sclerite with ST30 anteriad midline and ST44 and ST46 along lateral margin, membrane anteriad and laterad mesosternite with numerous minute denticles; small anterolateral sclerite (precoxite of K&P) with ST31, 32; ST35 and ST36 present in membrane anteriad mesocoxa; triangular laterosternite present behind coxa, lacking setae; small sclerite laterad coxa with ST23, 24, and 40; ST28 free in pleuron. *Metathorax*: Dorsal sclerites similar to those of mesothorax, though shorter and narrower, with medially divided mesotergite and small, elongate lateral sclerites, chaetotaxy same; metasternite shorter, wider than mesosternite, otherwise metaventral sclerites and chaetotaxy similar to mesothorax.

Legs: All legs similar in form and chaetotaxy, homologies with K&P not determined; coxa with approximately 8 medium setae around apical margin; trochanter with 2 medium and 4 small setae; femur with several ventral setae; tibia with 2 small ventrobasal setae, numerous tiny apical setae; 2 setae in membrane near base of claw, and 2 setae on ventral base of claw; tarsungulus not divided into basal ring and apical claw (as K&P show for *Onthophilus*).

Abdomen (Figs. 19–20): Segments separated by strong intersegmental constriction; each segment further subdivided all the way around the body by weaker constriction into major anterior (bearing all sclerites) and minor posterior subsegments; dorsum with transverse band of ampullar asperities, ventrally these become increasingly concentrated into paired bilateral ampullae toward end of abdomen. *Segment I*: Dorsum of abdominal segment I with wide tergites, narrowly divided transversely by a dense band of asperities; AB1 with small egg-bursting teeth (eb) present on posterior edge of anterior tergite; anterior tergite weakly subdivided at sides, with long lateral seta TE3 and closely associated pore TEe; posterior tergite partially subdivided by anterolateral indentations, bearing minute TE10–11 along anterior margin near midline, TE9 large, TE8 minute, and pore TEg closely associated with base of TE9; TE4 in anterior corner, and TE5 posterolaterad separation; triangular anterolateral sclerite bears TE16 medially and TE19 laterally; small lateral sclerite bears small TE26 and long TE27; posterior abdominal sterna with more distinctly defined bilateral ampullae, with setae ST44–45 immediately behind them; else similar through sternum VIII, small ST46 setae becoming obsolete; tergum IX with single wide, short median sclerite, bearing only TE16 at its side; TE21 on small lateral swelling and TE26–27 on small lateral sclerite; sternum IX with narrow, transverse sclerite bearing small ST38 near middle and large ST40 at side, ST27 and ST28 present in lateral membrane; segment X (pygopod) dorsally with weakly subdivided oval median sclerite with PP9 medially, larger PP5 laterally, PP19 on round lateral sclerite; fine PP18 in membrane behind median sclerite; thick, distinctly peglike UG3 present in membrane near base of urogomphus, with fine UG2, UG4 on either side; ventrally with anterolateral PP7, laterally with tiny PP6, posterior surface of pygopod with PP2 and PP4 large, PP5 small and nestled between them; base of urogomphus with strong UG6 ventrally, penultimate segment of urogomphus with 2 setae, UG8–9, along inner apical margin with 2 pores UGc–d interspersed; terminal segment of urogomphus with UGe on dorsum and long UG12–13 at apex.

Differences in Putative Second Instar (from SC, No Sequence Obtained): Marginal teeth of nasale blunter; appendages of head (antennae, labium, maxilla) narrower, more elongate; lateral processes of prementum less prominent, and teeth of dorsal surface of labium restricted to basal third of surface.

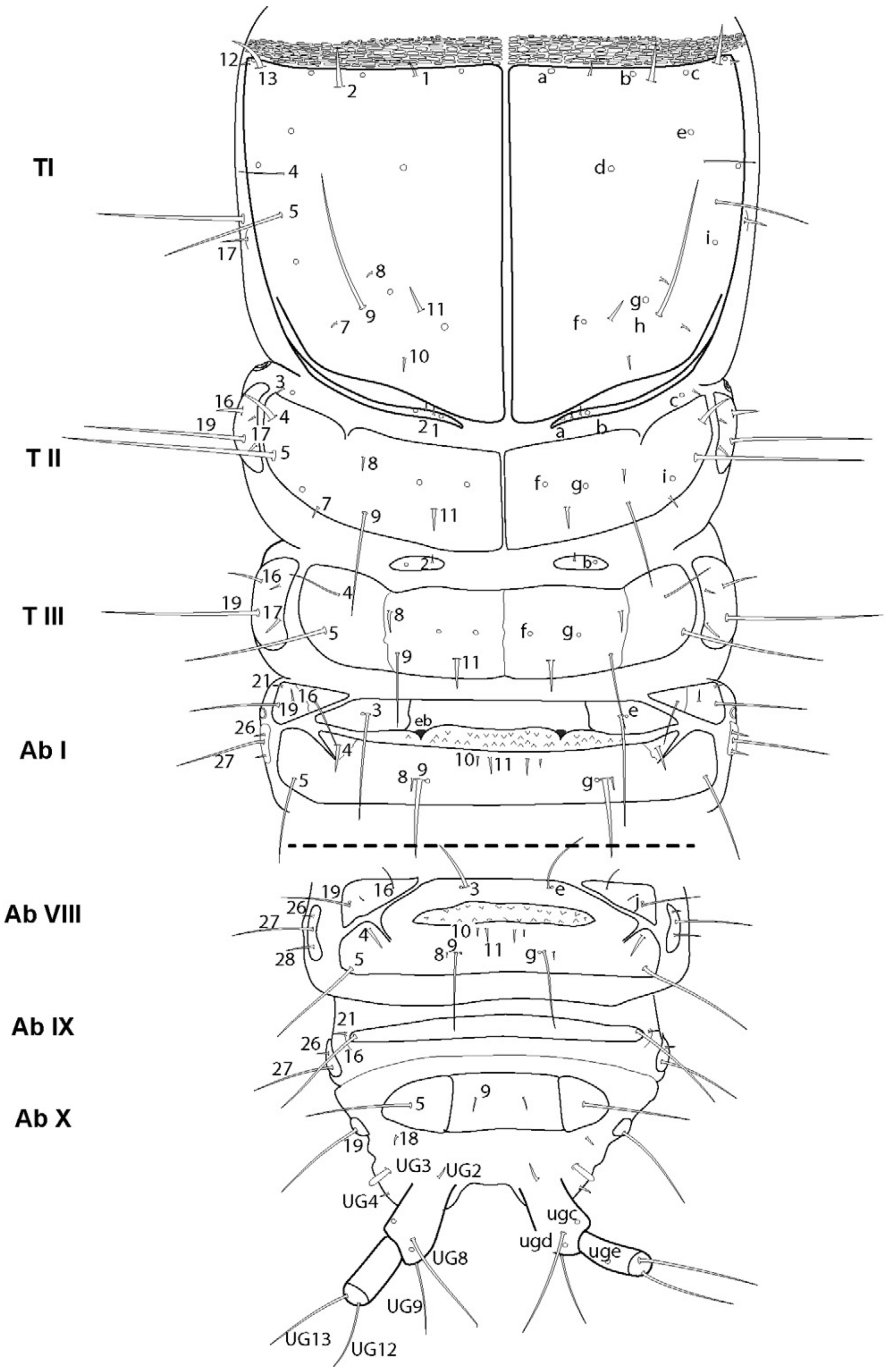


Fig. 19. Larva of *Geocolus caecus*, first instar, dorsal view, thoracic (I–III) and abdominal (VIII–X) terga (setae numbered on the left side, pores lettered on the right side).

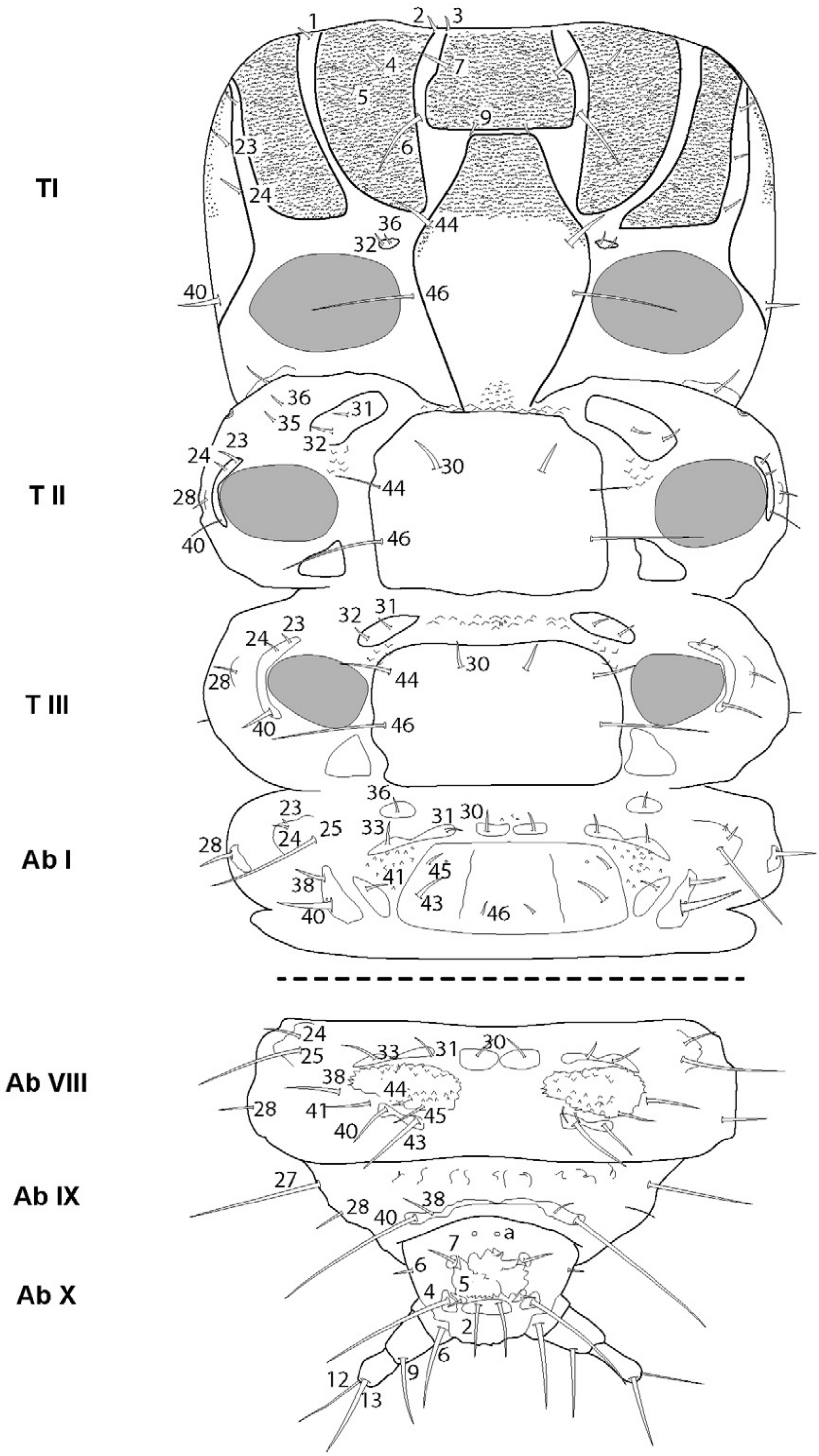


Fig. 20. Larva of *Geocolus caecus*, first instar, ventral view, thoracic (I–III) and abdominal (VIII–X) sterna (setae numbered on the left side, pores lettered on the right side).

Posterolateral margins of the pronotal shield thickened, darker. Cervical PR1–3 setae not evident anteriad median prosternal plate. PR4 and PR5 obscured among asperities of anterolateral prosternal plates. Large posterior TE9 seta missing, possibly broken off (though also not visible in pre-extraction photos); TE1, 2, and 13 absent from anterior pronotal margin (possibly missing due to damage). Meso- and metatergites not weakly subdivided at sides, thoracic chaetotaxy otherwise similar. Egg bursters absent from abdominal tergum I. Median sclerites of abdominal ventrites largely coalesced into wide plate, transversely sulcate, the sulcus weakly connecting lateral ampullar fields.

Discussion

Additional material of *G. caecus* has allowed us to examine a few details of the adult morphology that were not previously available, and to compare the adult morphology with potentially related taxa whose morphology is better documented now than when the species was initially described. These may help shed some light on relationships of the genus. These prospective relatives are mainly other Dendrophilinae, particularly species in the tribes Bacaniini (where *Geocolus* presently resides), Anapleini, and Dendrophilini. Within Bacaniini, the genus *Triballodes* is of special interest, given Wenzel's original suggestion of a relationship. We were not able to examine material of this taxon, but the description and illustrations of *Triballodes acritoides* (Reitter) by Lackner (2008) are useful. Some members of Abraeinae also provide potentially useful context, particularly more generalized members of *Abraeus* Leach, since inclusion of Bacaniini in Abraeinae has been previously proposed (*e.g.*, Ślipiński and Mazur 1999). Finally, the New Zealand endemic *Brounhister vividulus* (Broun), originally described in Tribalinae though subsequently moved to Abraeinae *incertae sedis* (Leschen and Ôhara 2017), shares some features with *Geocolus*.

The head of *Geocolus* exhibits numerous characters considered plesiomorphic in the family (following Caterino and Vogler 2002): plurisetose labrum, simply annulate antennal club, and lack of a frontal stria. The plurisetose labrum is widely shared by *Triballodes*, most *Bacanius*, *Dendrophilus*, and *Anapleus* Horn, as well as some Abraeini and Acritini in the Abraeinae. It is distinct from many others where the labrum is characteristically bisetose (*Brounhister*, and all Paromalini, Tribalinae, and Onthophilinae). The simply annulate antennal club, with transverse series of setae potentially indicating the former boundaries between antennomeres, is similar to that of *Triballodes* and *Brounhister*, while distinct from many other Dendrophilinae—in *Dendrophilus* divisions between the antennomeres are marked by fine grooves that are inwardly directed; in *Anapleus* the divisions between antennomeres appear to be real subdivisions, at least toward the sides of the club. The antennal club of *Bacanius* is somewhat varied, some with simple annuli, others with the annuli seemingly displaced outwardly toward the apex, as seen frequently in Abraeinae. Among the unique features of *Bacanius*, which might be required for membership in the same tribe, is what Caterino and Vogler (2002) termed the "epicranial suture". This inverted v-shaped frontal line is probably not a true suture, but an indication of internal strengthening ridges that appear darker. These can be marked by fine grooves in some species [such as the eastern US *Bacanius punctiformis* (LeConte)], but this is probably secondary. In *Geocolus* similar internal ridges are present at the sides (seen especially well in more teneral specimens), though they do not meet medially as they do in *Bacanius*. This may be a meaningful similarity. No such structures are described for *Triballodes*, and they are not apparent in *Brounhister*. The gular sutures of *Geocolus* are united, like nearly all other histerids, except in *Dendrophilus*, in which they are clearly separate.

The prosternum of *Geocolus* is similar in most informative details to that of *Triballodes* and to that of *Brounhister*. All have a rather well developed prosternal lobe, or "chin-piece", though it is not set off by a presternal suture as it is in various higher Histeridae. The anterior marginal stria of the prosternal lobe is present and then diverges from the margin about two-thirds of the way to the side to terminate in distinct foveae in both *Triballodes* and *Geocolus*. Both also have a lateral stria on the prosternal lobe that reaches from the inner corner of the procoxa to the anterior margin of the prosternal lobe at its lateral corner, where a fairly distinct edge sets it off from the antennal groove. In *Brounhister* no inner striae or foveae are discernable. There is only a weak lateral stria that merges with the margin of the lobe, becoming obsolete over the middle. Similarly, in *Bacanius* these median prosternal foveae are not distinct, and only lateral striae are present, merging with the margin at a more or less distinct "step", an interruption of the anterior margin of the prosternal lobe near the anterior corner. The prosternal lobes of *Dendrophilus* and *Anapleus* are similar to that of *Bacanius*, with only a lateral stria and a step near the corner. *Anapleus*, however, does have pronounced foveae at the bases of those lateral striae. *Dendrophilus* has what appears to be a rudimentary presternal stria separating its lobe from its keel, a significant difference from any of these. Looking briefly at undisputed Abraeinae, *Abraeus* has no prosternal lobe whatsoever, and while this may be secondary (some Acritini, like *Halacritus*, have a more distinct prosternal lobe) there are enough other characters supporting Abraeinae monophyly, principally the fused aedeagal basal piece (separate in *Brounhister*), that they are probably not directly relevant to the placement of *Geocolus.*

Another character worth considering on the sides of the prosternal lobe and keel is the degree of coadaptation with the apex of the protibia. In Dendrophilini and Paromalini, there is a distinctive depression just mediad the antennal groove where the large protibial spur lies in repose. In *Anapleus* and *Bacanius*, the protibial spur is not well developed, but there is a conspicuous depression on the prosternal lobe where the apex of the narrow protibia is received. In *Geocolus*, which does have well developed protibial spurs, there is only the faintest depression for the apex of the tibia, and nothing for the spur. *Triballodes* appears very similar to this. In *Brounhister*, it does not appear that the prosternal keel is at all modified to receive the apex of the protibia.

The last part of the prosternum that must be considered is the antennal cavity, or the form and degree to which the prosternum is modified to receive the antennal club in repose. *Geocolus* has a well-defined antennal cavity, deeply depressed, margined by carinae on posteromedial (except where delimited by the procoxa), lateral, and anterior margins. This depression reaches the anterior corner of the prosternum, and is separated from the head by a prominent inner lamina of the lateral part of the prosternum. That of *Triballodes* is identical in every respect—Lackner's (2008) SEM images clearly show the deep depression, the well-defined edges, and the anteromedial lamina. For the most part, *Brounhister* conforms to the same plan, the only real exception being that the depression is slightly less well defined in the posterior corners. In none of the other taxa considered here is such a well-defined cavity present. In *Bacanius* there is only a broad depression anterior to the procoxa, and sometimes a weak anterior carina where a submarginal pronotal ridge diverges to the prosternal-hypomeral junction. In *Dendrophilus* the club is very small relative to a broadly depressed anterolateral area, with no definition of a discrete cavity. *Anapleus* exhibits distinct anterior and lateral carinae delimiting the antennal cavity, but it is well-removed from the anterior hypomeral corner, lying just anterior to the sides of the procoxae. That of *Abraeus* could be characterized similarly to that of *Anapleus*.

One previously described thoracic feature of *Geocolus* that seems a potentially strong character uniting it with Bacaniini is the hidden metanepisternum. We confirmed that it is indeed hidden beneath the edge of the elytral epipleuron in *Geocolus*. This important character also distinguishes it from nearly everything else under consideration here. Both *Triballodes* and *Brounhister* have exposed metanepisterna, as do *Dendrophilus* and *Anapleus.* The metanepisternum is also at least partially exposed in *Abraeus*, though it does become hidden under the epipleuron in many other Abraeinae. This feature may be generally associated with size reduction, but many of these taxa can be characterized as "small", so it cannot be disregarded too casually as homoplasy.

Another feature often used to define Bacaniini is that the propygidium (abdominal tergite VI) appears largely hidden beneath the apices of prolonged elytra. In *Geocolus* this tergite is about half-covered by the elytra, with a distinct transverse line across the middle of the tergite at this point. This may be a meaningful similarity; however, it is more difficult to interpret in *Bacanius* than initially meets the eye. Firstly, tergite VI in *Bacanius* is distinctly shortened, and in most cases it appears that less than half of it is actually concealed. The level of concealment is variable, however, and many species have not been examined for this character. Lackner (2008) described the *Triballodes* propygidum as almost completely covered by the elytra. This character was not specifically mentioned by Leschen and Ôhara (2017) for *Brounhister*, but the propygidum appears to be largely exposed, as it is in *Dendrophilus*, *Anapleus*, and *Abraeus.*

The last set of characters to consider are those of genitalia. Caterino and Vogler (2002) highlighted the plesiomorphic character of an unfused basal piece of the aedeagus, with a spiral fissure from its base to its apex, in *Dendrophilus*, *Anapleus*, and *Onthophilus*, as an important feature distinguishing them from all other Histeridae, including other members of their respective subfamilies. This plesiomorphic type of basal piece is also found in *Geocolus* and *Brounhister* (and outgroups such as *Sphaerites* Duftschmid). Lackner (2008) did not specifically note this state of the basal piece in *Triballodes*, and his drawings appear to show it as fused into a ring, but this character would be worth reassessing. In this respect, all Abraeinae are also quite divergent in not having an articulated basal piece at all (though it remains unclear if it has become lost or fused with the tegmen). A distinct, completely tubular basal piece appears to be present in all *Bacanius*, and in many species it is nearly as long as the tegmen, distinguishing them sharply from *Geocolus* and others considered here. Characters of female genitalia are much more sparsely documented, and cannot currently shed much light on any of these relationships. However, we do provide an illustration for that of *Geocolus* (Fig. 21), showing valvifers that are more trough-like than paddle-like, also in common with the plesiomorphic trio of *Dendrophilus*, *Anapleus*, and *Onthophilus*. In *Brounhister* this seems also to be the state, though the longitudinal sclerotizations that

Fig. 21. Female genitalia of *Geocolus caecus*.

define the stem of the paddle in many other Histeridae are more strongly developed there. *Geocolus* has a well sclerotized, spherical spermathecal bulb, borne on a long tube, with a short glandular sac opposite. Somewhat similar structures are found in numerous other histerids, and according to Ôhara (1994) represent the plesiomorphic state for the family (or even the superfamily). Some of the finer details may ultimately prove informative, but too few taxa are known in adequate detail to make much use of them now.

What level of resolution might be derived from larval characters? Morphological details are consistent with a dendrophiline association, based on known subfamily characters (Newton 1991). The larva has 4-segmented maxillary and 2-segmented labial palpi, which excludes Abraeinae (which have, respectively, 5- and 3-segmented palpi); it lacks a membranous setose area on the dorsal surface of the prementum, which excludes Saprininae; its prementum does have lateral processes and small dorsal denticles, which excludes Histerinae, and places the larva in either Dendrophilinae or Tribalinae. In an unpublished key, Newton has subdivided these further, based on still-unpublished larval descriptions. The closest candidates to *Geocolus* in that key would be *Dendrophilus* or *Bacanius*, and neither quite fits (lacking setae on the lateral lobe of the prementum characteristic of the former, and having the longest antennal sensillum shorter than the apical antennal segment, unlike the latter). It also does not key to Paromalini, represented by three genera in Newton's key, as it has two long urogomphal setae (as opposed to three short ones). Ultimately the larva fails to key clearly to any higher taxon, not fitting any combination of characters of the Onthophilinae and Tribalinae remaining. Given the locally known fauna, only one other serious possibility for larval assignment seems to exist, the tribaline *Caerosternus* LeConte, which does occur at the same Pickens County, SC locality, but whose larva is not described. We have generated a barcode sequence for a *Caerosternus* specimen from South Carolina, and can rule this taxon out on that basis. The associations of the larvae described here with *Geocolus* should be considered highly likely.

Considering all the characters discussed above, larval and adult, there is no support for assigning *Geocolus* to any recognized tribe of Dendrophilinae, although for the present the subfamily assignment seems appropriate (the subfamily's questionable monophyly notwithstanding). A close relationship of *Geocolus* to *Triballodes*, originally suggested by Wenzel, remains a viable hypothesis, although enough significant differences remain (the exposure of the metanepisternite, hidden propygidium, and apparently completely cylindrical basal piece in *Triballodes*) that creating a taxon for the two seems premature. Both could conceivably lie along a stem lineage leading to Bacaniini, while *Brounhister* could occupy an analogous position with respect to Abraeinae. Most of the interesting states of these taxa seem to be plesiomorphies, however, and so cannot support any particular resolutions. Their similarities may simply represent non-divergence, and they may all reside near the base of early histerid diversification, retaining many of the family's basal characteristics. As such, these taxa should figure prominently in future efforts to resolve the family's basal phylogeny. Better documentation of their adult and larval morphologies, and obtaining specimens sufficiently well preserved for DNA sequencing, should be high priorities.

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APPENDIX 1

Unique identifiers and collection data for all voucher specimens.

Extract #	Locality	Collected	Collector	Life stage	CUAC #	GenBank #
MSC_7279	KY: Monroe Co., Hestand, 36.6579, −85.6259	5/8–7/3/21	Harden	larva	CUAC000016471	ON072260
none	KY: Monroe Co., Hestand, 36.6580, −85.6218	5/8–7/3/21	Harden	larva	CUAC000016441	
CWH_198	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	4/26–7/12/2020	Harden	larva	CUAC000016472	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	8/4/21	Harden	larva	CUAC000016442	
none	KY: Monroe Co., Hestand, 36.6579, −85.6259	5/8–7/3/21	Harden	adult	CUAC000157713	
MSC_3435	AL: Blount Co., Highland Lake, 33.8847, −86.4219	3/18/16	T. King	adult	CUAC000157618	
MSC_3436	AL: Blount Co., Highland Lake, 33.8847, −86.4219	3/18/16	T. King	adult	CUAC000157619	
none	AL: Blount Co., Highland Lake, 33.8847, −86.4219	3/18/16	T. King	adult	CUAC000157620	
none	AL: Blount Co., Highland Lake, 33.8847, −86.4219	3/18/16	T. King	adult	CUAC000157621	
MSC_3443	AL: Blount Co., Highland Lake, 33.8847, −86.4219	12/01/19	T. King	adult	CUAC000157622	ON072257
MSC_3444	AL: Blount Co., Highland Lake, 33.8847, −86.4219	12/01/19	T. King	adult	CUAC000157623	ON072259
none	AL: Blount Co., Highland Lake, 33.8847, −86.4219	12/01/19	T. King	adult	CUAC000157624	
CWH_387	AL: Cherokee Co., Little River, 34.3964, −85.6271	10/11/21	Harden	adult	CUAC000153602	ON072262
CWH_384	SC: Oconee Co., Martin Creek Landing, 34.6388, −82.8640	10/22/21	Harden	adult	CUAC000153589	ON072261
none	SC: Oconee Co., Martin Creek Landing, 34.6388, −82.8640	10/22/21	Harden	adult	CUAC000157655	
none	SC: Oconee Co., Martin Creek Landing, 34.6388, −82.8640	10/22/21	Harden	adult	CUAC000157656	
none	SC: Oconee Co., Martin Creek Landing, 34.6388, −82.8640	10/22/21	Harden	adult	CUAC000157657	
MSC_6652	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	4/26–7/12/2020	Harden	adult	CUAC000157626	ON072258
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	4/26–7/12/2020	Harden	adult	CUAC000157627	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	4/26–7/12/2020	Harden	adult	CUAC000157628	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	4/26–7/12/2020	Harden	adult	CUAC000157629	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	4/26–7/12/2020	Harden	adult	CUAC000157630	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	4/26–7/12/2020	Harden	adult	CUAC000157631	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	4/26–7/12/2020	Harden	adult	CUAC000157632	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	4/26–7/12/2020	Harden	adult	CUAC000157633	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	4/26–7/12/2020	Harden	adult	CUAC000157634	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	4/26–7/12/2020	Harden	adult	CUAC000157635	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	4/26–7/12/2020	Harden	adult	CUAC000157636	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	4/26–7/12/2020	Harden	adult	CUAC000157637	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	4/26–7/12/2020	Harden	adult	CUAC000157638	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	4/26–7/12/2020	Harden	adult	CUAC000016413	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	4/11–8/14/2021	Harden	adult	CUAC000157639	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	4/11–8/14/2021	Harden	adult	CUAC000157640	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	4/11–8/14/2021	Harden	adult	CUAC000157641	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	4/11–8/14/2021	Harden	adult	CUAC000157642	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	4/11–8/14/2021	Harden	adult	CUAC000157643	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	8/14–10/24/2021	Harden	adult	CUAC000157644	

(*Continued*)

Appendix 1. (*Continued*)

Extract #	Locality	Collected	Collector	Life stage	CUAC #	GenBank #
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	8/14–10/24/2021	Harden	adult	CUAC000157645	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	8/14–10/24/2021	Harden	adult	CUAC000157646	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	8/14–10/24/2021	Harden	adult	CUAC000157647	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	8/14–10/24/2021	Harden	adult	CUAC000157648	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	8/14–10/24/2021	Harden	adult	CUAC000157649	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	8/14–10/24/2021	Harden	adult	CUAC000157650	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	8/14–10/24/2021	Harden	adult	CUAC000157651	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	8/14–10/24/2021	Harden	adult	CUAC000157652	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	8/14–10/24/2021	Harden	adult	CUAC000157653	
none	SC: Pickens Co., 3 mi. N. Clemson, 34.7252, −82.8245	8/14–10/24/2021	Harden	adult	CUAC000157654	