Article

Four new species of *Cleidogona* Cook & Collins, 1895 (Diplopoda: Chordeumatida: Cleidogonidae) from the Great Smoky Mountains National Park, USA

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Abstract

We provide an update to our knowledge of the millipede fauna of the Great Smoky Mountains National Park, North Carolina and Tennessee, USA. In addition to one new park record (*Cleidogona jocassee* Hoffman, 1950a), we describe four new species of millipedes: *Cleidogona chilhoweensis* **sp. nov.**, *Cleidogona columbicauda* **sp. nov.**, *Cleidogona hendrixi* **sp. nov.**, and *Cleidogona sparta* **sp. nov.** These bring the number of described *Cleidogona* to 93 and *Cleidogona* known from the park to 10 species.

Key words: biodiversity, eastern North America, southeastern United States, All-Taxa Biodiversity Inventory

Introduction

The family Cleidogonidae Cook, 1896a occurs primarily in North America, from Connecticut in the northeastern United States, to Panama in Central America. The greatest species diversity is to be found in the central and southern Appalachian Mountains, in a region from southern Indiana to the Ozark Mountains in Missouri and Arkansas, and in central and southeastern Mexico. The American genera are keyed in Shear (2024). A single genus, *Tianella* Attems, 1904 is known from Central and South Asia: Kazakhstan, Kyrgyzstan, Nepal, and southwest China (Shear 2024; Shear unpublished data). Two European families, Entomobielziidae Verhoeff, 1899 and Lusitaniosomatidae Schubart, 1953 are obviously closely related to Cleidogonidae and may become synonyms of Cleidogonidae in the future.

Cleidogona Cook & Collins, 1895 is a highly diverse genus of chordeumatidan millipedes found from central and eastern North America south to Costa Rica, with 89 valid species (Shear 1972; Sierwald *et al*. 2025). Of the previously known species, 32 occur in North America east of the Mississippi River. Species found in the southern Appalachians tend to be short-range endemics, but many are known only from their type localities and so their actual distribution is unknown. In the northern part of the generic range, species seem to have larger ranges, and one species (*C. nantahala* Shear, 1972) apparently has been transported from its native range in North Carolina to southern New England, where it has become established (Snyder & Seewagen 2010). *Cleidogona caesioannulata* (Wood, 1865), and *C. major* Cook & Collins, 1895, are widely distributed from southern Pennsylvania and central Ohio south to North Carolina.

Although many undescribed *Cleidogona* are known to exist (both authors, unpublished data), only 16 have been described since the revision of the family over 50 years ago (Shear 1972). Only one of these, *C. medialis* Shelley, 1976, is from eastern North America. Like *C. medialis*, many undescribed *Cleidogona* are found in the southern Appalachian Mountains, a hotspot for millipede diversity and a likely center of evolution for *Cleidogona* (Shear 1972).

The Great Smoky Mountains National Park (GSMNP), the largest and most visited US National Park, is one of the most biodiverse locations in eastern North America. This biodiversity is quite well known, thanks in large part to the All-Taxa Biodiversity Inventory (ATBI), an effort to document all species in the park (Parker & Bernard 2006). ATBI-collected specimens drove the creation of a preliminary millipede checklist (Snyder 2008) and additional species have been added since (e.g., Recuero & Caterino 2023) resulting in ~80 millipede species now known in GSMNP.

Five species of *Cleidogona* were previously recorded from GSMNP (Snyder 2008): *C. inexpectata* Hoffman, 1950a (Cades Cove, Tremont, Chimneys); *C. margarita* Hoffman, 1950a (widespread on both North Carolina and Tennessee sides of the park); *C. medialis* (Goshen Prong, Twin Creeks); *C. nantahala* Shear, 1972 (Chilhowee); and *C. tallapoosa* Shear, 1972 (Cades Cove). In addition, *C. jocassee* Hoffman, 1950a was listed as likely in GSMNP by Snyder (2008). Here, we update our knowledge of the fauna with one new park record and four new species.

Methods

Specimens of undescribed *Cleidogona* were identified during previous work summarizing the fauna of GSMNP (Snyder 2008). Most of the specimens were collected during ATBI structured sampling (Parker & Bernard 2006). ATBI pitfall trap arrays consisted of 10 traps at each site, placed 3 m apart on a transect; each trap was a 6 cm diameter plastic cup, inserted in the ground with the top flush with the soil surface, with propylene glycol as a preservative, and with a plastic cover to prevent flooding by rain (Lessard *et al.* 2007). Collectors for ATBI samples are C. R. Parker, I. C. Stocks, and M. J. Petersen unless otherwise specified. Some specimens were collected during an investigation of millipede and earthworm interactions (Snyder *et al.* 2011), an investigation of invasive earthworm depredation (Straube 2013), and a soil fauna community post-wildfire study (Olliff 2021). All specimens were stored in 70% ethanol. Morphological studies were completed using a Leica M80 stereomicroscope.

Representative specimens of each species were selected for Scanning Electron Microscopy (SEM). Gonopods, male ninth and tenth legs, and, when available, female genitalia were carefully dissected out using fine point forceps and insect pins. These were cleaned in an ultrasonic cleaner (Cody CD-4800) for 180 seconds, air-dried, attached to a 12.2 mm diameter aluminum stub with an adhesive carbon conductive disk, and sputter coated with gold for 200s on a Denton Desk V (DentonVaccum, Moorestown, NJ, USA). Images were captured with a JEOL JSM-IT100 Scanning Electron Microscope at Georgia College, edited in GIMP, and plates were composed in InkScape.

Holotypes will be deposited in the National Museum of Natural History, Washington, District of Columbia (USNM). Paratypes will be deposited in the Invertebrate Zoology collection at the William P. Wall Museum of Natural History at Georgia College & State University (GCIZ) and the Virginia Museum of Natural History, Martinsville, Virginia (VMNH); additional paratypes and any non-type material examined will be deposited in the GSMNP museum collection in Gatlinburg, Tennessee (GRSM). SEM stubs and associated specimens will be retained by the Snyder Lab at Georgia College.

Map (Fig. 29) was created by Lance Andrew using QGIS 3.40.8-Bratislava LTR (QGIS Development Team 2025). Political boundaries were from the USGS National Boundary Dataset and roads were from the USGS National Transportation Dataset (sciencebase.gov). National Park boundaries were from the National Geospatial Data Asset NPS National Parks Dataset (irma.nps.gov).

Abbreviations used in the figures

ab	anterior branch of angiocoxite
ac	angiocoxite
cc	colpocoxite
cg	coxal gland
cp	coxal process
cx	coxa
cx10	coxa of leg 10
dcp	distal colpocoxite process

dl	dorsal lamella
f9	femur of leg 9
h	hook
iv	inner valve
ll	laciniate lobe
lp	lateral process
mp	medial process
ov	outer valve
p	process between angiocoxites
pb	posterior branch of angiocoxite
pgp	postgenital plate
r	receptacle
s	sternum
s10	sternum of legpair 10
t	tooth
vl	ventral lamella

Results

Taxonomy

Family Cleidogonidae Cook, 1896a

Diagnosis. In North America, chordeumatid millipedes with mentum divided, unlike Conotylidae Cook, 1896a and Adritylidae Shear, 1971. Anterior gonopods with prominent angiocoxites, sometimes divided into two branches, but always lacking flagella, unlike families in Striariidea Cook, 1896b and Brannerioidea Cook, 1896b. Colpocoxites fused at their bases, unlike Trichopetalidae Verhoeff, 1914.

    Remarks. The interpretation of cleidogonid gonopods by Shear (1972) seemed correct at the time, but more extensive experience with the family has resulted in changes. The structures previously called colpocoxites (derivatives of the sclerotized coxal glands) are now considered angiocoxites (formed from the rims of coxal glands), and the previous "telopodites" are actually the colpocoxites (Shear 2024). Cleidogonid gonopods have entirely lost telopodites. The ninth legpair, formerly referred to as posterior gonopods, are now best called ninth legs since, though modified, they play no role in spermatophore transfer. Further description of the gonopods, specific to *Cleidogona,* are in the discussion below.

Genus *Cleidogona* Cook & Collins, 1895

Diagnosis. Cleidogonidae with undivided gonopod angiocoxites, unlike *Psuedotremia* Cope, 1869 and *Solaenogona* Hoffman, 1950b. *Cleidogona* lacks sternal projections anterior to the angiocoxites found in *Dybasia* Loomis, 1964. Distinct from *Tianella* in lacking groups of flagelliform strips on the angiocoxites. Male ninth legs are only slightly reduced in size, consist of 4–6 articles, and femora are enlarged and triangular, unlike *Cabraca* Shear, 1982, which has a single article, *Tiganogona* Chamberlin, 1928 which has 2–3 articles, and *Lineagona* Shear, 2024 which lacks enlarged, triangular prefemora.

    Remarks. Males of *Cleidogona,* in addition to the gonopods (as described above for the family), have secondary sexual modifications of some of the legs. Legpairs 3–7 are much enlarged, with mesally curved prefemora and femora. These have been observed to clasp the head and anterior segments of the female during mating (pers. obs., WAS). The seventh legpair usually has prominent posterior knobs. These help perhaps in stabilizing the gonopods when retracted. The ninth legpair is variously reduced, but in North American species retains five or six podomeres; the prefemur and coxa are frequently fused. This has led to misinterpretations in some past studies, where the femora are referred to as prefemora. The ninth leg coxae usually have median knobs or processes which interlock

with the gonopod colpocoxites at rest, holding the gonopods in the retracted position, and may also carry vestigial basal gland pores. The femora are elongate and distally enlarged, giving the impression of a triangular podomere. Coxae of the tenth and eleventh legpair are elongate and apically bear the openings of coxal glands; frequently the margins of these glands show modifications such as knobs or shelves. A prominent process extends anteriorly from the midline of sternum of the twelfth legs (Shear 1972).

The gonopods consist of four elements, a sternum, two coxae and paired angiocoxites and colpocoxites. The sternum is broad anteriorly, with a distinct median depression and lateral lobes; posteriorly the sternum is narrow and in some species may be incomplete. The coxae are pyramidal in shape and well separated. They bear from 3 to 12 or more setae and there may or may not be a triangular process extending posteriorly. The angiocoxites are generally the most complex and distinctive of the elements. They extend dorsally to separate the coxae and in most species appear to be bilaterally fused. Distally there are anterior and posterior elements, the anterior being relatively complex and the posterior with a vertical groove containing many fine cuticular fimbriae. The colpocoxites are almost always smaller and less complex than the angiocoxites, but like them are basally fused. They are evenly curved, with the anterior part of the arc usually visible between the angiocoxites. The posterior part is always longer and distally divided into short, blunt, finger-like processes that at rest clasp the tips of the colpocoxites. The coxal knobs of the ninth legs interlock with the basal, posterior part of the posterior arc. The colpocoxites are freely movable through the agency of muscles internal to the gonopods and concealed by the sternum; their attachment to the gonopod complex is membranous.

Unlike most higher taxa of choredumatidans, the female genitalia of many species of *Cleidogona* have characters that permit species identification. The anterior receptacle is usually reduced to a simple, rounded lobe. The lateral and medial vulval valves may be entirely separate, or anteriorly fused (as is the case with the four species described herein). The valves frequently bear paired processes which may have distinctive shapes. The vulvae are subtended posteriorly by a postgenital plate that also may be distinctive. The postgenital plate appears to be a development of the second sternum.

Cleidogona jocassee Hoffman, 1950a NEW PARK RECORD

Cleidogona jocassee Hoffman, 1950a: 19–21, pl. 7, fig. 15–18—Shear (1972: 229, figs 316–319), Snyder (2008: 29)

Material Examined: NORTH CAROLINA: *Haywood Co*., Purchase Knob ATBI Plot, 35° 35' 31" N 83° 3' 37" W: pitfall trap 35, 22 May–8 Jun 2001, 1 male; pitfall trap 36, 18 Jun–3 Jul 2002, 1 male, 1 female, 1 immature; pitfall trap 40, 23 Apr–15 May 2001, I. C. Stocks, 1 male; pitfall trap 38, 8 May–4 Jun 2002, P. E. Super & J. Lowe, 1 male; pitfall trap 37, 26 Apr–8 May 2002, 1 male; pitfall trap 38, 18 Jun–3 Jul 2002, J. & D. Lowe, 2 males.

Remarks. *Cleidogona jocassee* was recorded as likely to be in GSMNP by Snyder (2008) since it was known from Haywood and Swain Cos., North Carolina, but outside the GSMNP boundary (Shear 1972). It is now documented from Purchase Knob.
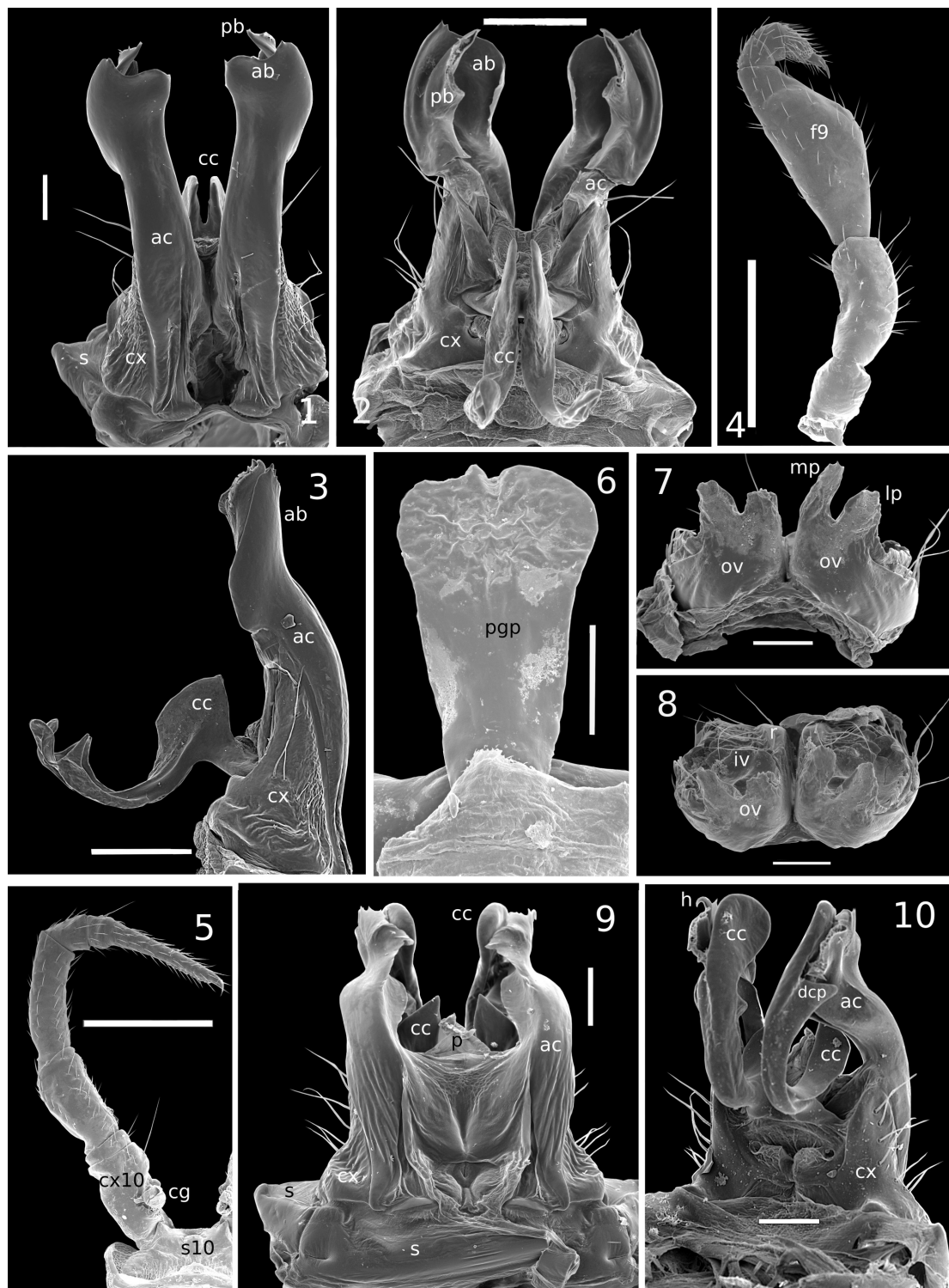
Cleidogona chilhoweensis Snyder & Shear, sp. nov.
urn:lsid:zoobank.org:act:63A63F36-124E-473A-96F9-07926EE1C77A
Figs 1–8

Material Examined. *Types*: Holotype: 1 male, TENNESSEE: Blount Co., along US Highway 129 adjacent to Lake Chilhowee, Plot C+15, 35° 33.0' N 83° 59.5' W, 269–291 m elevation, hand collection, 14 Oct 2006, B. A. Snyder *et al.* (USNMENT02180525). Paratypes: 1 male and 1 female, TENNESSEE: Blount Co., along US Highway 129 adjacent to Lake Chilhowee, site 3, near 35° 33' 20" N 83° 59' 51" W, hand collection, 27 Oct 2004, B. A. Snyder (GCIZ 9000); 1 male, same collection (GRSM 228785).

Non-types: TENNESSEE: Blount Co., along US Highway 129 adjacent to Lake Chilhowee, site 1, 5m from roadside, hand collection, 27 Oct 2004, B. A. Snyder, 1 male. Blount Co., along US Highway 129 adjacent to Lake Chilhowee, hand collection, 13 Apr 2007, B. A. Snyder, 1 female. Both specimens used for SEM.

FIGURES 1–10. *Cleidogona chilhoweensis* **sp. nov.**, and *C. columbicauda* **sp. nov. Figs 1–8.** *C. chilhoweensis* **sp. nov. Fig. 1.** Gonopods, anterior view. **Fig. 2.** Gonopods, posterior view. **Fig. 3.** Gonopods, lateral view. **Fig. 4.** Left leg 9, anterior view. **Fig. 5.** Left leg 10, anterior view. **Fig. 6.** Postgenital plate, posterior view. **Fig. 7.** Female genitalia, posterior view. **Fig. 8.** Female genitalia, ventral view. **Figs 9, 10.** *C. columbicauda* **sp. nov. Fig. 9.** Gonopods, anterior view. **Fig. 10.** Gonopods, posterior view. Abbreviations: **ab**, anterior branch of angiocoxite; **ac**, angiocoxite; **cc**, colpocoxite; **cg**, coxal gland; **cx**, coxa; **cx10**, coxa of leg 10; **dcp**, distal colpocoxite process; **f9**, femur of leg 9; **h**, hook; **iv**, inner valve; **lp**, lateral process; **mp**, medial process; **ov**, outer valve; **p**, process between angiocoxites; **pb**, posterior branch of angiocoxite; **pgp**, postgenital plate; **r**, receptacle; **s**, sternum; **s10**, sternum of legpair 10. Scale bars are 100 μm for Figs 1, 6–10; 200 μm for Figs 2, 3; 500 μm for Figs 4, 5. SEM stubs and associated specimens are retained by the Snyder Lab at Georgia College.

Diagnosis. Distinct from other *Cleidogona* in the details of the gonopods. *Cleidogona chilhoweensis* **sp. nov.** is most similar to and co-occurs with *C. nantahala*; both lack a coxal process. The colpocoxite of *C. nantahala* has a small mid-length flange and lacks a large basal flange and distal thumb-like projections.

Etymology. The species name refers to the type locality, the westernmost area of GSMNP adjacent to Lake Chilhowee, an impoundment of the Little Tennessee River formed in the 1950s. The area was previously the Cherokee settlement of Chilhowee. Adjective.

Description. Length of holotype 14.5 mm, greatest width 1.6 mm at segment 7. Ommatidia 26 (left side) or 27 (right side) in 7 rows. Color faded in preserved specimens, but typical of the genus in life. Segments cylindrical. Somatic characters and secondary sexual modifications typical for the genus (see above; also Shear 1972).

Gonopods (Figs 1–3): In anterior view (Fig. 1), sternum (**s**) narrow and bandlike medially, expanded below coxae. Coxae (**cx**) elongate but mostly obscured by angiocoxites (**ac**) (Figs 1–3). Angiocoxites robust, smooth, expanded distally into shield-like anterior branches (**ab**) with sinuous distal margins. Posterior branches (**pb**) extending above concave sections of these margins. Angiocoxites narrowing basally, extending down to sternum. Laterally flattened flanges of colpocoxites (**cc**) visible between angiocoxites.

In lateral view (Fig. 3), coxa (**cx**) elongate, subtriangular, lacking a coxal process, with a small tooth on the posterior edge towards the base. Angiocoxite (**ac**) upright, with a gentle curve anterior to the coxa but continuing straight distally. Angiocoxite apically divided, the anterior branch (**ab**) shield-like, wrapping laterally to obscure the view of the division. The posterior (inner) branch (**pb**) begins as a flange and is only separated distally (this is best seen in posterior view, Fig. 2). The apex is blade-shaped with a slightly curved tip.

Proximally, the colpocoxite (**cc**) makes a sharp 90° bend dorsad and then curves back ventrad almost 90°. Proximal bend with a large flange extending anteriad and ventrad, and a corner pointed towards the angiocoxite. Distal tip of the colpocoxite bluntly rounded with a thumb-like process on the lateral side which also points towards the angiocoxite.

Ninth legs (Fig. 4) typical for the genus, coxae and prefemora fused, with constriction at one third the length from the base. Femora (**f9**) triangular, subequal in length to the coxae. Tenth legs (Fig. 5) typical for the genus, sternum (**s10**) expanded into a tooth at the base of each leg and a very low medial ridge, coxae (**cx10**) elongate, slightly curved, with prominent gland at base (**cg**).

Females similar to males in all nonsexual aspects. Postgenital plate (**pgp**), (Fig. 6) not divided, upright, distally expanded laterad with a small medial apical notch. Vulvae (Figs 7, 8) with an inner valve (**iv**), outer valve (**ov**) and receptacle (**r**). Outer valves with paired projections on the posterior edge, medial projections (**mp**) longer than lateral projections (**lp**) (right medial projection broken in Figs 7, 8).

Distribution. Only known from the type locality (Fig. 29; full site description in Snyder *et al.* 2011).

Remarks. The type locality, on the western edge of GSMNP, is the warmest and driest location in the park.

Cleidogona columbicauda Snyder & Shear, sp. nov.
urn:lsid:zoobank.org:act:2AA08882-F203-4EB6-8C24-F126CEB2EB26
Figs 9–15

Material Examined. *Types*: Holotype: 1 male, TENNESSEE: Cocke Co., Snakeden Ridge ATBI Plot, 35° 44' 36" N 83° 13' 12" W, pitfall trap 91, 10 Mar–6 Apr 2002 (USNMENT02180526). Paratypes: 1 male, 2 females, TENNESSEE: Cocke Co., Snakeden Ridge ATBI Plot, 35° 44' 36" N 83° 13' 12" W, pitfall trap 95, 1–13 Dec 2000 (GCIZ 9001). 1 male, 1 female, TENNESSEE: Cocke Co., Snakeden Ridge ATBI Plot, 35° 44' 36" N 83° 13' 12" W, pitfall trap 91, 16 Jan–13 Feb 2002, (VMNH112502.1, VMNH112502.2). 1 male, 1 female, TENNESSEE: Cocke Co., Snakeden Ridge ATBI Plot, 35° 44' 36" N 83° 13' 12" W, pitfall trap 93, 6 May–5 Jun 2002 (GRSM 228786).

Non-types: TENNESSEE: *Blount Co.*, Cades Cove ATBI Plot, 35° 35' 29" N 83° 50' 15" W: pitfall trap 18, 2–16 Jul 2001, 1 male, 1 immature. *Sevier Co.*, Goshen Prong ATBI Plot, 35° 36' 38" N 83° 32' 34" W: pitfall trap 101, 19–26 Feb 2001, 1 male, 1 female; pitfall trap 103, 10 Feb–7 Mar 2002, 1 male; pitfall trap 104, 17 Sep–22 Oct 2001, 1 male. Indian Gap ATBI Plot, 35° 36' 39" N 83° 26' 37" W: pitfall trap 23, 10 May–19 Jun 2002, 1 male; pitfall trap 25, 15–28 Mar 2002, 1 male; pitfall trap 25, 4 Apr–10 May 2003, 1 male (used for SEM); pitfall trap 27, 14–27 Apr 2002, 1 male; pitfall trap 27, 16–28 Mar 2002, 1 male (used for SEM); pitfall trap 28, 4 Apr–10 May 2003, 1 male. Twin Creeks ATBI Plot, 35° 41' 6" N 83° 29' 56" W: pitfall trap 10, 27 Mar–11 Apr 2001, 1

male. Under bark of rotten logs, old growth forest nr. Rocky Spur Branch, 963m, 8 Apr 1995, C. R. Parker, 1 male, 2 females. Brushy Mountain ATBI Plot, 35° 40' 36" N 83° 25' 51" W: pitfall trap 61, 6 Apr–23 Jun 2003, 1 male, 1 immature; pitfall trap 61, 27 Feb–12 Mar 2003, 1 male; pitfall trap 63, 5–21 Jul 2001, 1 male, 1 immature; pitfall trap 63, 6 Apr–23 Jun 2003, 1 male; pitfall trap 63, 23 May–5 Jun 2001, 1 male; pitfall trap 64, 7–19 Dec 2001, 1 male; pitfall trap 64, 5–21 Jun 2001, 1 male, 1 female; pitfall trap 64, 30 Apr–12 May 2002, 1 male; pitfall trap 64, 5–21 Jul 2001, 1 male; pitfall trap 64, 13–27 Mar 2002, 1 male; pitfall trap 64, 18–30 Jun 2002, 1 male; pitfall trap 65, 13–27 Mar 2002, 1 male; pitfall trap 66, 12 Dec 2000–16 Jan 2001, 1 male; pitfall trap 66, 6 Apr–23 Jun 2003, 1 male; pitfall trap 68, 11–26 Apr 2001, 1 male; pitfall trap 69, 6 Apr–23 Jun 2003, 1 male; pitfall trap 70, 25 Apr–23 May 2003, M. J. Petersen, S. Higdon & C. R. Parker, 1 male, 1 female (used for SEM); pitfall trap 70, 15 Jan–15 Feb 2002, 1 male. *Cocke Co.*, Albright Grove ATBI Plot, 35° 43' 60" N 83° 16' 50" W: pitfall trap 81, 9 Mar–4 May 2003, 1 male; pitfall trap 82, 9 Mar–4 May 2003, 1 male, 1 female; pitfall trap 83, 8 Feb–9 Mar 2003, 1 male; pitfall trap 84, 8 Feb–9 Mar 2003, 2 males; pitfall trap 84, 9 Mar–5 Apr 2003, 1 male; pitfall trap 86, 14–29 Mar 2002, 1 male; pitfall trap 87, 21 Jul–1 Aug 2001, 1 male; pitfall trap 87, 9 Mar–5 Apr 2003, 1 male; pitfall trap 89, 12 May–15 Jun 2002, 1 male, 1 immature. Snakeden Ridge ATBI Plot, 35° 44' 36" N 83° 13' 12" W: pitfall trap 91, 5–16 Jan 2002, 1 male; pitfall trap 91, 3 Mar–30 Apr 2003, 1 male, 1 female; pitfall trap 91, 6 Apr–6 May 2002, 1 male; pitfall trap 91, 19 Nov–4 Dec 2001, 2 males; pitfall trap 91, 6–19 Nov 2001, 1 male; pitfall trap 92, 30 Jan–15 Feb 2001, 1 male (used for SEM); pitfall trap 94, 25 Apr–9 May 2001, 1 male, 1 immature; pitfall trap 94, 3–25 Apr 2001, I. C. Stocks & J. Breeden, 1 male; pitfall trap 94, 6 Apr–6 May 2002, 1 male; pitfall trap 95, 4–21 Dec 2001, 1 male; pitfall trap 95, 22 May–4 Jun 2001, 1 male; pitfall trap 95, 17–30 Jan 2001, 1 male; pitfall trap 97, 10 Mar–6 Apr 2002, 2 males; pitfall trap 97, 16 Feb–5 Mar 2001, 2 males; pitfall trap 98, 15 Mar–3 Apr 2001, I. C. Stocks & J. Breeden, 1 male, 2 females; pitfall trap 98, 3–25 Apr 2001, 1 male, 1 immature; pitfall trap 98, 16 Jan–13 Feb 2002, 1 male; pitfall trap 98, 13 Dec 2000–7 Jan 2001, 1 male; pitfall trap 99, 15 Mar–3 Apr 2001, I. C. Stocks & J. Breeden, 2 males; pitfall trap 99, 4–21 Dec 2001, 1 male; pitfall trap 99, 18 Feb–3 Mar 2003, 1 male; pitfall trap 100, 10 Mar–6 Apr 2002, 1 male; pitfall trap 100, 3 Mar–30 Apr 2003, 1 male; Malaise trap 20, 16 Feb–5 Mar 2001, 1 male.

NORTH CAROLINA: *Swain Co.*, Kuwohi (Clingmans Dome) ATBI Plot, 35° 33' 37" N 83° 29' 43" W: pitfall trap 56, 18 Oct–13 Nov 2000, 1 male; pitfall trap 71, 8–24 Nov 2001, 2 males; pitfall trap 76, 24 Oct–8 Nov 2001, 1 male, 1 female; pitfall trap 77, 6–25 Jun 2001, 1 male; pitfall trap 79, 27 Apr–10 May 2002, 1 male; pitfall trap 79, 25 Jun–3 Jul 2001, 1 male. Andrews Bald ATBI Plot, 35° 32' 20" N 83° 29' 39" W: pitfall trap 54, 28 Mar–14 Apr 2002, 1 male, 1 female; pitfall trap 54, 24 27 Apr–10 May 2002, 1 male (used for SEM); pitfall trap 54, 24 Oct–8 Nov 2001, 1 male; pitfall trap 55, 18 Jul–1 Aug 2002, 1 male; pitfall trap 56, 13–29 Nov 2000, 1 male; pitfall trap 56, 16 Mar–24 Apr 2001, 1 male; pitfall trap 57, 1 Feb–16 Mar 2001, 2 males; pitfall trap 57, 16 Mar–24 Apr 2001, 1 male; pitfall trap 58, 20 Oct–13 Nov 2000, 1 male, 1 female; pitfall trap 58, 28 Mar–14 Apr 2002, 1 male; pitfall trap 60, 24 Mar–16 Apr 2001, 1 male; pitfall trap 60, 24 Oct–8 Nov 2001, 1 male; 9721, App Tr 350m E Road Prong Trailhead, hog exclosure, 5400' elevation, beech gap forest, 1m² litter #2, 10 Jun 1997, Coyle, Stocks, Aiken, Davis, 1 male.

Diagnosis. *Cleidogona columbicauda* **sp. nov.** is most similar to *C. medialis* in the overall shape of the gonopods, but they differ in the shape of the angiocoxite processes. *Cleidogona medialis* has medially directed processes which are separated from the angiocoxite apices, whereas *C. columbicauda* **sp. nov.** has lamellae that point mediad proximally and continue distad on the angiocoxite apices. Additional differences include the coxae of the male tenth legs (lateral process in *C. columbicauda* **sp. nov.**, medial process in *C. medialis*) and the female postgenital plate (low, undivided in *C. columbicauda* **sp. nov.**, divided in *C. medialis*).

Etymology. The species name refers to the interleaving of the distal ends of the angiocoxites and colpocoxites, which is reminiscent of the close fit of a dovetail joint in woodworking. The name is a combination of the Latin for dove (*columba*) and the Latin for tail (*cauda*). Noun in apposition.

Description. Length of holotype 11.9 mm, greatest width 1.3 mm at segment 7. Ommatidia 26 in 7 rows. Color faded in holotype and most preserved specimens, but typical of the genus in some specimens. Segments cylindrical, with low shoulders. Somatic characters and secondary sexual modifications are typical for the genus (see above; also Shear 1972).
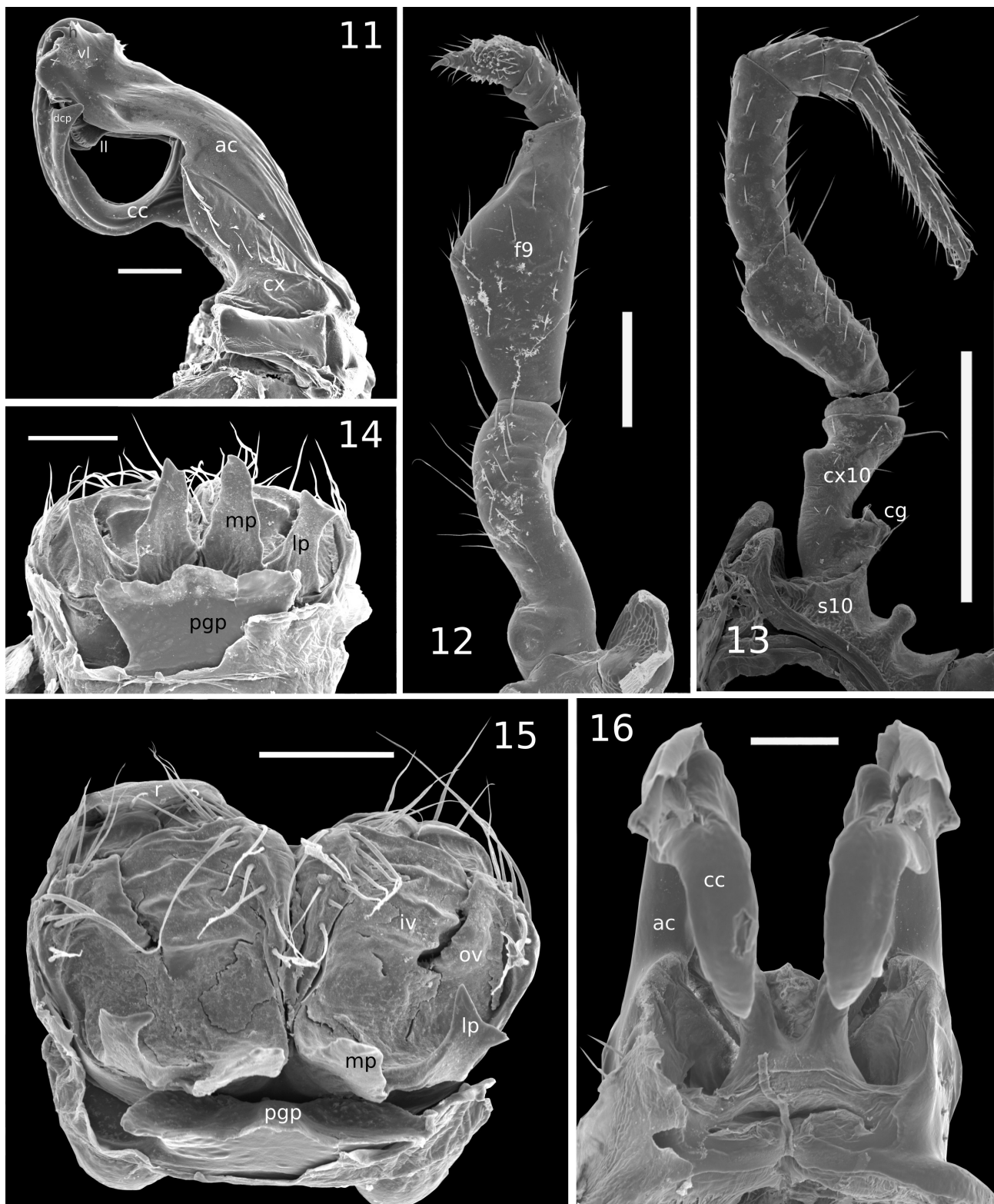
FIGURES 11–16. *Cleidogona columbicauda* **sp. nov.**, and *C. hendrixi* **sp. nov.** Figs 11–15. *C. columbicauda* **sp. nov. Fig. 11.** Gonopods, lateral view. **Fig. 12.** Right leg 9, anterior view. **Fig. 13.** Left leg 10, anterior view. **Fig. 14.** Female genitalia, posterior view. **Fig. 15.** Female genitalia, ventral view. **Fig. 16.** Gonopods of *C. hendrixi* **sp. nov.**, posterior view. Abbreviations: **ac**, angiocoxite; **cc**, colpocoxite; **cg**, coxal gland; **cx**, coxa; **cx10**, coxa of leg 10; **dcp**, distal colpocoxite process; **f9**, femur of leg 9; **h**, hook; **iv**, inner valve; **ll**, laciniate lobe; **lp**, lateral process; **mp**, medial process; **ov**, outer valve; **pgp**, post genital plate; **s10**, sternum of legpair 10; **vl**, ventral lamella. Scale bars are 100 µm for Figs 11, 14–16; 200 µm for Fig. 12, 3; 500 µm for Fig. 13. SEM stubs and associated specimens are retained by the Snyder Lab at Georgia College.

Gonopods (Figs 9–11): In anterior view (Fig. 9), sternum (**s**) a narrow band, expanded laterally. Coxae (**cx**) subtriangular. Angiocoxites (**ac**) linear, stout proximally, with sinuous edges. Middle of proximal region wrinkled. Distally, angiocoxites curve posteriad, narrow, and bear a flange on their medial surfaces. Each angiocoxite ends in a broad, rugose, medially curving lamella that wraps around the distal end of the colpocoxite; the distal colpocoxite process (**dcp**) is lateral to the lamellae. The edges of the lamellae are toothed and a small hook (**h**) is present distally. A process (**p**) arises between the angiocoxites, variable in length (see remarks). The proximal ends of the colpocoxites (**cc**) are visible on either side of this process.

In lateral view (Fig. 11), coxae (**cx**) elongate, lacking a coxal process, base somewhat expanded laterad. Angiocoxite (**ac**) gently curving posteriad, wrinkled proximally, small dorsal notch just distal to coxa, expanding distally into a large, posteriodorsally directed laciniate lobe (**ll**) and a thin, ventrally located lamella (**vl**). The lamella curves medially, with a toothed edge and a distal hook (**h**). The distal end of the angiocoxite almost completely covers the distal end of the colpocoxite (**cc**), except for the distal colpocoxite process (**dcp**) that is lateral to the angiocoxite. The colpocoxite is curved with two large ridges. The inner ridge continues between the middle of the angiocoxites and becomes a laterally flattened, bluntly pointed proximal process. The outer ridge ends in a large triangular tooth (**dcp**). The main stem of the colpocoxite is greatly expanded distally and nests medial to the angiocoxite lobe and flange.

Ninth legs (Fig. 12) typical for the genus, sternum with a small medial bump, fused prefemora and coxae sinuous, vestigial glands produced on knobs. Femora (**f9**) triangular, slightly longer than the fused prefemora and coxae. Tenth legs (Fig. 13) typical for the genus, sternum (**s10**) expanded into a tooth medially at the base of each leg and a pronounced medial ridge. Coxal glands (**cg**) produced on knobs giving the appearance of a short branch. Coxae (**cx10**) with distal lateral knobs and an abrupt widening at the distal ends.

Females similar to males in all nonsexual aspects. Postgenital plate (**pgp**) not divided, low, expanded ventrally into three weakly divided lobes (Figs 14, 15). Vulvae with an inner valve (**iv**), outer valve (**ov**), and paired projections on the posterior edge (Figs 14, 15). Medial projections (**mp**) pointed, longer; lateral projections (**lp**) narrow distally before widening into two teeth.

Distribution. *Cleidogona columbicauda* **sp. nov.** is widely distributed in GSMNP, having been collected at 9 of 19 ATBI plots and a few additional sites (Fig. 29). Its range stretches from Cades Cove east to Snakeden Ridge, and south to Andrews Bald, with elevations from 522 m at Cades Cove to 1954 m at Kuwohi (formerly Clingmans Dome). It appears to be more common at higher elevation sites; 94% of specimens collected were from sites above 950 m, and 45% over 1450 m. Habitats include open and forested sites: old field, heath bald, grassy bald; cove forests (second-growth and old-growth), hemlock forest, high-elevation beech forest, and spruce-fir forest.

Remarks. The process between the angiocoxites is variable in length. In most specimens it is prominent, extending about halfway to the lamellae, but it some it is short, and in others it is lacking. Specimens with the process exist at all sites where *C. columbicauda* **sp. nov.** has been collected, but specimens lacking the process co-occur at all high-elevation sites (above 1450 m). Specimens with and without the process have even been found in the same pitfall trap.

Cleidogona hendrixi Snyder & Shear, sp. nov.
urn:lsid:zoobank.org:act:DEAB45DD-F2D4-4409-B327-85FE8FC0A135
Figs 16–20

Material Examined. *Types*: Holotype: 1 male, NORTH CAROLINA: Haywood Co., Purchase Knob ATBI Plot, 35° 35' 31" N 83° 3' 37" W, pitfall trap 35, 7–21 Dec 2001 (USNMENT02180527). Paratypes: 1 male, same location, pitfall trap 35, 9–23 Nov 2002 (GCIZ 9002); 1 male, same location, pitfall trap 37, 27 Apr–15 May 2001 (GRSM 228787).

Non-types: In addition to the types, 1 male was collected from pitfall trap 35 on each of the following dates: 2 Oct–9 Nov 2002 (used for SEM), 9–23 Nov 2002, and 15 Mar–10 May 2003 (used for SEM).

Diagnosis. *Cleidogona hendrixi* **sp. nov.** is unique in that no other *Cleidogona* has both dorsal and ventral lamellae on the angiocoxites of the gonopods. Several Mexican *Cleidogona* species (e.g., *C. tequila* Shear 1972 and *C. totonaca* Shear 1972) have generally similar curved, rod-like angiocoxites with dorsal lamellae, but these all lack ventral lamellae and the colpocoxites are not reflexed.

FIGURES 17–22. *Cleidogona hendrixi* **sp. nov.**, and *C. sparta* **sp. nov.** Figs 17–20. *C. hendrixi* **sp. nov. Fig. 17.** Gonopods, anterior view. **Fig. 18.** Gonopods, lateral view. **Fig. 19.** Right leg 9, anterior view. **Fig. 20.** Left leg 10, anterior view. **Figs 21, 22.** *C. sparta* **sp. nov. Fig. 21.** Gonopods, anterior view. **Fig. 22.** Gonopods, posterior view. Abbreviations: **ab**, anterior branch of angiocoxite; **ac**, angiocoxite; **cc**, colpocoxite; **cg**, coxal gland; **cx**, coxa; **cx10**, coxa of leg 10; **dl**, dorsal lamella; **f9**, femur of leg 9; **pb**, posterior branch of angiocoxite; **s**, sternum; **s10**, sternum of legpair 10; **vl**, ventral lamella. Scale bars are 100 µm for Figs 17, 18; 500 µm for Figs 19, 20; 200 µm for Figs 21, 22. SEM stubs and associated specimens are retained by the Snyder Lab at Georgia College.

Etymology. This species is named for Dr. Paul F. Hendrix, the first author's PhD advisor, who initially sent him to the Smokies, setting him on a path to describe these species. Noun in the genitive case.

Description. Length of holotype 15.1 mm, greatest width 1.8 mm at segment 7. Ommatidia 28 in 7 rows. Color faded in preserved specimens except for head, antennae, and tarsi, which are brown. Segments cylindrical. Somatic characters and secondary sexual modifications are typical for the genus (see above; also Shear 1972).

Gonopods (Figs 16–18): In anterior view (Fig. 17), sternum broad and flat. Coxae (**cx**) almost entirely obscured by angiocoxites. Angiocoxites (**ac**) curve strongly posteriorly (Figs 16, 17). They are widely spaced and parallel (or slightly converging) proximally and then gently curve apart (laterad) distally, while gradually narrowing. A thin mohawk-like ventral lamella is present for the distal 1/2 to 2/3 of the length. The entirety of the colpocoxites (**cc**) are visible between angiocoxites, extending posteriad and reflexing towards the base of the angiocoxites.

In lateral view (Fig. 18), coxa (**cx**) elongate, straight-sided where it meets the angiocoxite (**ac**), squared on the posterior corner, and rounded dorsally. Proximally, the angiocoxite broadens into an elongate shape that has a small bump adjacent to the rod-like distal portion but otherwise mirrors the shape of the coxa. The coxa and angiocoxite proximal area together form an almost symmetrical shield-like shape. The angiocoxite is rod-like distally, curving at midlength and tapering to a blunt point. Lamellae are present on both the ventral (**vl**) and dorsal (**dl**) sides; the ventral lamella is visible from the curve of the angiocoxite to just before the tip, where it is tallest (subequal to the width of the narrowing angiocoxite). The ventral lamella originates somewhat more proximally and on the ventromedial face of the angiocoxite. The dorsal lamella originates at the proximal end of the rod-like portion of the angiocoxite and is continuous to the distal end. The lamella is somewhat shorter at the bend of the angiocoxite and also very short in a distal region, which aligns with where the colpocoxite (**cc**) would contact the angiocoxite if flexed. The lamella is so small here that it appears to be absent in some specimens. Proximally, the colpocoxite (**cc**) curves posteriad and reflexes 180° to point anteriad, ending parallel and just dorsal of the angiocoxite. The distal tip of the colpocoxite is broadly expanded with a lateral thumb-like process, also directed anteriad.

Ninth legs (Fig. 19) typical for the genus, coxae with pores on large knobs, slightly constricted above, and bean-shaped distally. Femora (**f9**) subequal in length to the coxae, triangular, with a small knob on the ventral corner. Tenth legs (Fig. 20) typical for the genus, sternum (**s10**) expanded into a tooth at the base of each leg and a pronounced medial ridge. Coxal glands (**cg**) produced on knobs. Coxae (**cx10**) sublinear, widening distally.

Females unknown.

Distribution. Only known from the type locality, the Purchase Knob ATBI plot (Fig. 29), a second-growth southern Appalachian cove forest at 1346 m elevation (Parker & Bernard 2006).

Remarks. Three *Cleidogona* are found at Purchase Knob: *C. hendrixi* **sp. nov.,** *C. jocassee*, and *C. margarita*. The latter two species are described and illustrated in Shear (1972).

Cleidogona sparta **Snyder & Shear, sp. nov.**
urn:lsid:zoobank.org:act:91FA18B2-69A1-4CBD-92AC-C2E6C5C19773
Figs 21–28

Material Examined. *Types*: Holotype: 1 male, TENNESSEE: Sevier Co., Twin Creeks ATBI Plot, 35° 41' 6" N 83° 29' 56" W, pitfall trap 10, 16–31 Jul 2002 (USNMENT02180528). Paratypes: 1 male, 3 females, TENNESSEE: Sevier Co., Twin Creeks ATBI Plot, 35° 41' 6" N 83° 29' 56" W, pitfall trap 06, 6–21 June 2001 (GCIZ 9003). 1 male, TENNESSEE: Sevier Co., Twin Creeks ATBI Plot, 35° 41' 6" N 83° 29' 56" W, pitfall trap 07, 30 Jul–13 Aug 2001 (VMNH112503). 1 male, 1 female, TENNESSEE: Sevier Co., Twin Creeks ATBI Plot, 35° 41' 6" N 83° 29' 56" W, pitfall trap 03, 15 Aug–10 Sep 2002 (GRSM 228788).

Non-types: TENNESSEE: *Sevier Co.*, Goshen Prong ATBI Plot, 35° 36' 38" N 83° 32' 34" W: pitfall trap 101, 17–30 July 2001, 1 male, 2 females; pitfall trap 103, 17 July–5 Aug 2002, 2 males (1 used for SEM); pitfall trap 104, 18 Jun–2 Jul 2001, 1 male, 1 immature; pitfall trap 104, 17 July–5 Aug 2002, 1 male, 1 immature; pitfall trap 106, 13–27 Aug 2001, I. C. Stocks & M. Williams, 1 male; pitfall trap 106, 17 July–5 Aug 2002, 1 male, 1 immature; pitfall trap 108, 2–17 July 2001, 1 male. Twin Creeks ATBI Plot, 35° 41' 6" N 83° 29' 56" W: pitfall trap 02, 16–31 July 2002, 2 males; pitfall trap 03, 6–16 July 2001, 1 male; pitfall trap 03, 16–31 Jul 2002, 1 male; pitfall trap 03, 26 Aug–10 Sep 2002, 1 male (used for SEM); pitfall trap 05, 15 Aug–10 Sep 2002, 1 male; pitfall trap 06, 6–21 June 2001, 1 female (used for SEM); pitfall trap 07, 5–21 June 2001, 1 male, 1 immature. Porter's Flat, 9731 #1, hardwood cove forest, 737.6 m, 31 July 1997, Aiken/Coyle/Davis/Stocks, 1 male, 4 females. Off Cherokee Orchard Road, near Twin Creeks Science Center, Baer 4 pitfall, 35° 41' 14" N 83° 30' 13" W, 22 Jul 2010, D. Straube *et al.*, 1 male. Off Cherokee Orchard Road, near Old Sugarlands Trailhead, Old trail 1 pitfall, 35° 40' 28" N 83° 29' 29" W, 20 Aug 2010, D. Straube *et al.*, 1 male (used for SEM). Near riverview quiet walkway east of Huskey Gap Trailhead, 35° 39' 49.2" N, 83° 31'17.4" W, post-fire study plot UB2 litter, hand collected, 12 July 2018, C. M. Hawley, G.

Chapman, M. A. Callaham Jr., M. K. Taylor, 1 male. Near riverview quiet walkway east of Huskey Gap Trailhead, 35° 39' 49.2" N, 83° 31'17.4" W, post-fire study plot BP4 litter, hand collected, 12 July 2018, C. M. Hawley, G. Chapman, M. A. Callaham Jr., M. K. Taylor, 1 male. *Cocke Co.*, Albright Grove ATBI Plot, 35° 43' 60" N 83° 16' 50" W, pitfall trap 89, 6–12 May 2002, 1 male (used for SEM).

FIGURES 23–28. *Cleidogona sparta* **sp. nov. Fig. 23.** Gonopods, lateral view. **Fig. 24.** Right leg 9, anterior view. **Fig. 25.** Left leg 10, anterior view. **Fig. 26.** Female genitalia, posterior view. **Fig. 27.** Sculpture of postgenital plate. **Fig. 28.** Female genitalia, ventral view. Abbreviations: **ab**, anterior branch of angiocoxite; **ac**, angiocoxite; **cc**, colpocoxite; **cg**, coxal gland; **cp**, coxal process; **cx**, coxa; **cx10**, coxa of leg 10; **f9**, femur of leg 9; **iv**, inner valve; **ov**, outer valve; **pb**, posterior branch of angiocoxite; **pgp**, post genital plate; **r**, receptacle; **s**, sternum; **t**, tooth. Scale bars are 200 µm for Fig. 23; 500 µm for Figs 24, 25; 100 µm for Figs 26, 28; 10 µm for Fig. 27. SEM stubs and associated specimens are retained by the Snyder Lab at Georgia College.

Diagnosis. The gonopods of *Cleidogona sparta* **sp. nov.** are similar in overall shape to those of *C. major* Cook & Collins 1895, but have several distinctive differences. The colpocoxites differ, with *C. sparta* **sp. nov.** having a large, distinct tooth. The anterior angiocoxite branch is shieldlike in *C. sparta* **sp. nov.** but not in *C. major*. In *C. sparta* **sp. nov.**, the coxal process is smaller and rounded, and the transition from coxal process to the posterior edge of angiocoxite is a smooth curve; in *C. major* the coxal process is longer and squared off, and is demarcated from the angiocoxite by a sharp angle. The shapes of the posterior angiocoxite branch differ greatly in lateral view, with *C.*

sparta **sp. nov.** being much broader than *C. major*. The female postgential plate differs between *C. sparta* **sp. nov.** and *C. major* as well. The shape of the *C. sparta* **sp. nov.** posterior angiocoxite branch in lateral view is similar to that of *C. atropos* Shear 1972, however the *C. atropos* angiocoxite branches are greatly different lengths, rather than equal in *C. sparta* **sp. nov.** *Cleidogona jocassee* and *C. margarita* are also similar and geographically proximate, but *C. jocassee* lacks a coxal process and *C. margarita* has a large, quadrate coxal process.

Etymology. The species name refers to the lateral view of the colpocoxite apices, which are reminiscent of the profile of a Spartan/Trojan helmet with forward pointing plume. Noun in apposition.

Description. Length of holotype 24.9 mm, greatest width 2.2 mm at segment 7. Ommatidia 28 in 7 rows. Color faded in preserved specimens, except on the epicranium and frons. Segments cylindrical, with low shoulders. Somatic characters and secondary sexual modifications are typical for the genus (see above; also Shear 1972).

Gonopods (Figs 21–23): In anterior view (Fig. 21), sternum (**s**) broad, widest laterally. Coxae (**cx**) elongate, triangular. Angiocoxites (**ac**) close together, broad, robust, narrowing distally before dividing into two apical branches of equal length. Branches are about 1/4 the length of the angiocoxite. The anterior branch (**ab**) arises from the medial half of angiocoxite and has blunt apices, variably squared off or slightly rounded. The posterior branch (**pb**) arises laterally and the apices are almost squared off with a medial subapical notch. In anterior view, the anterior branch is wider than, medial to, and does not conceal the posterior branch. In some specimens, the anterior branch slightly covers part of the posterior branch. In posterior view (Fig. 22), colpocoxites (**cc**) appear lobe-like, somewhat flattened. They diverge laterally, forming a V shape.

In lateral view (Fig. 23), coxa (**cx**) elongate with a coxal process (**cp**) at the apex, ending in a blunt point. The space between the coxal process and the angiocoxite (**ac**) is a rounded notch. Anterior edge of angiocoxite (**ac**) gently curving posteriad until division. Anterior angiocoxite branch (**ab**) is shieldlike, anteriomedial to the posterior branch. Posterior edge of angiocoxite has a small tooth (**t**) just distal to notch above the coxal process. Posterior angiocoxite branch (**pb**) expands posteriad and narrows into an acuminate point; posterior edge is fringed in this region. Colpocoxite (**cc**) linear, rod-like proximally and expanded apically. The posterior edge continues in a semicircle through the distal edge, terminating in an anteriorly directed tooth as distal as the division between angiocoxite branches. The anterior side of the colpocoxite has a flange-like expansion on the distal half, ending at the base of the tooth. .

Ninth legs (Fig. 24) typical for the genus, coxae with pores on wide knob-like projections, sublinear distally. Femora (**f9**) longer than coxae, expanded distally. Tenth legs (Fig. 25) typical for the genus, sternum with a low medial ridge. Coxae (**cx10**) wide proximally at gland (**cg**) locations, and abruptly widening at the distal ends.

Females similar to males in all nonsexual aspects. Postgenital plate (**pgp**) fused basally but otherwise divided into two projections, each with two branches that curve slightly towards each other, resembling a thumb and forefinger (Fig. 26). Lateral branches, shorter, wider, and textured with small bumps (Fig. 27). Vulvae do not have any projections on the posterior edge (Figs. 26, 28).

Distribution. Known from the eastern half of the Tennessee (northern) side of GSMNP, from Goshen Prong to Albright Grove (Fig. 29). Habitats include Southern Appalachian cove forests: second-growth, rich montane type (Goshen Prong); second-growth, typic montane type (Twin Creeks); and old-growth, Silverbell type (Albright Grove); elevations range from 617–1051 m (Parker & Bernard 2006).

Remarks. Although having affinity with *C. major*, these species are geographically separated by what appears to be a long distance as most *Cleidogona* species are known to be short-range endemics. The closest published record of *C. major* is approximately 120 km to the northeast (Shear 1972).

Discussion

With the addition of *C. jocassee* and the four new species, the total number of *Cleidogona* documented in GSMNP has doubled to 10. It is interesting from evolutionary and ecological perspectives that at almost all sites we find 2–4 *Cleidogona* spp. per site (Table 1, Fig. 29). This pattern is not seen broadly with *Cleidogona*. However, the fauna is still quite poorly known, and many *Cleidogona* remain to be described. One challenge to our understanding of *Cleidogona* is that the vast majority of adults are collected during the cooler part of the year, particularly October-March (data herein; Snyder 2008). The winter months are an atypical time of activity for most field biologists and an especially difficult time to travel in mountainous regions. The ATBI sampling scheme of continuous pitfall trapping throughout the year was instrumental in alleviating the collecting portion of this challenge.

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TABLE 1. Distribution of *Cleidogona* species across sites in the Great Smoky Mountains National Park. Sites ordered roughly from northwest to southeast (see Fig. 29). All sites listed here except for Chilhowee and Chimneys were ATBI sampling sites.

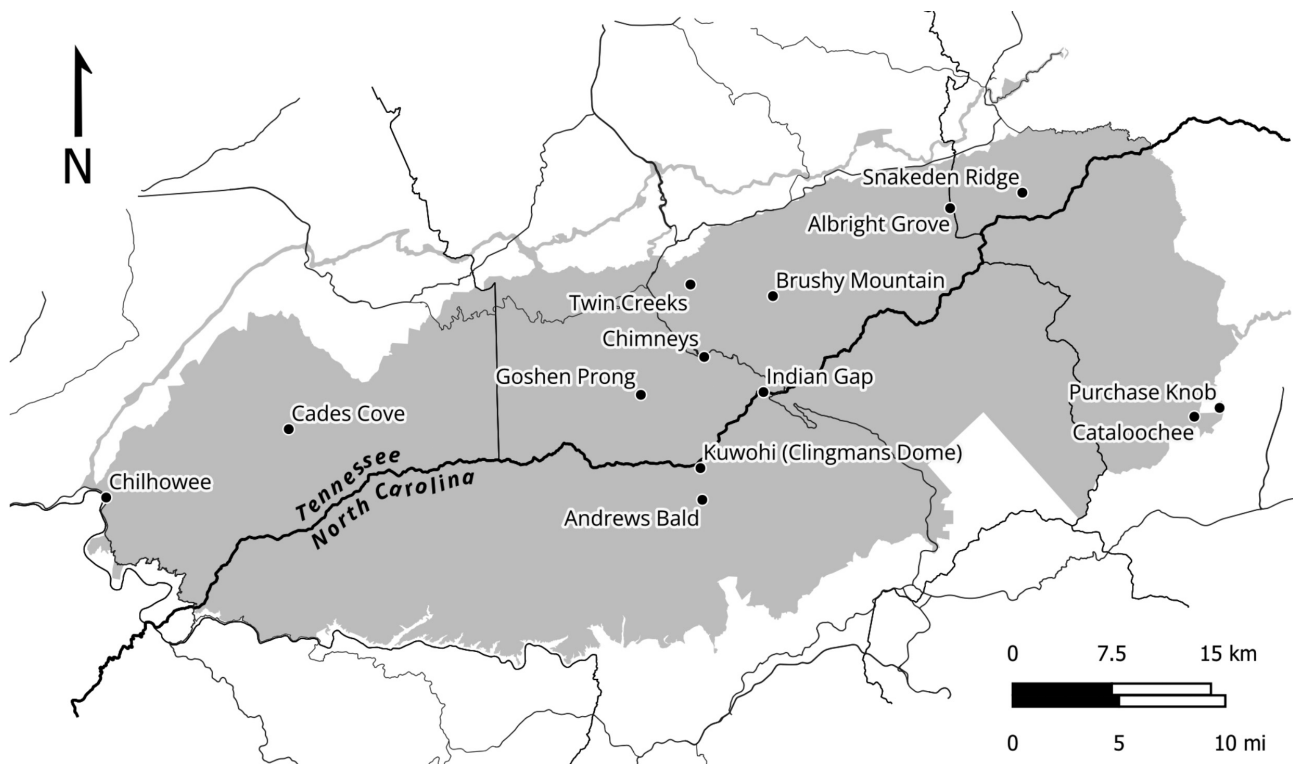| State	Tennessee									North Carolina			
County	Blount		Sevier				Cocke			Swain		Haywood	
Site	Chilhowee	Cades Cove	Goshen Prong	Twin Creeks	Chimneys	Indian Gap	Brushy Mountain	Albright Grove	Snakeden Ridge	Kuwohi (Clingmans Dome)	Andrews Bald	Cataloochee	Purchase Knob
chilhoweensis	x												
columbicauda		x	x	x		x	x	x	x	x	x		
hendrixi													x
inexpectata		x			x								
jocassee													x
margarita			x	x	x	x	x	x	x	x	x	x	x
medialis			x	x									
nantahala	x												
sparta			x	x				x					
tallapoosa		x											
Species per site	2	3	4	4	2	2	2	3	2	2	2	1	3

FIGURE 29. Site locations of *Cleidogona* collections in the Great Smoky Mountains National Park. For species, see Table 1. Park property is shaded grey. Black lines denote state (thick) and county (thin) boundaries; grey lines are major roads.

While the GSMNP fauna is relatively well known, there remains work to be done, including one undescribed *Cleidogona* which is only represented by a single male. It would also not be surprising to find additional species on the North Carolina side of GSMNP where fewer ATBI plots were located. Very little sampling has occurred in the southwest, between Chilhowee and Andrews Bald, south of Cades Cove; there is also a large gap in the remote area between Cataloochee/Purchase Knob and the North Carolina/Tennessee border.

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