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THE *ALLOPERLA LEONARDA* GROUP OF EASTERN NORTH AMERICA, WITH SEM IMAGES OF FOUR OUT-GROUP SPECIES (PLECOPTERA: CHLOROPERLIDAE)

Michele R. Willett[1] and Bill P. Stark[2]
[1] Box 4045, Department of Biology, Mississippi College, Clinton, Mississippi, U.S.A. 39058
E-mail: michele_willett@yahoo.com
[2] Box 4045, Department of Biology, Mississippi College, Clinton, Mississippi, U.S.A. 39058
E-mail: stark@mc.edu

ABSTRACT
The epiproct complex for six members of the *Alloperla leonarda* Ricker species group is examined with scanning electron microscopy for the first time, and monophyly for the group is asserted. Images for each species are presented and structures of the epiproct complex are compared and redescribed. Species included in the group are *A. furcula* Surdick, *A. lenati* Kondratieff & Kirchner, *A. leonarda* Ricker, *A. natchez* Surdick & Stark, *A. ouachita* Stark & Stewart and *A. prognoides* Surdick & Stark. Images of other eastern Nearctic *Alloperla* species were examined to provide outgroup data.

Keywords: Plecoptera, Chloroperlidae, *Alloperla leonarda* group, eastern North America

INTRODUCTION
The genus *Alloperla* is a Nearctic and eastern Palearctic stonefly group whose greatest diversity may occur in eastern North America. Currently, 26 species, are known from this region (Surdick 2004; Kondratieff & Kirchner 2004), and several species groups appear to be represented (Baumann & Kondratieff 2009) although little formal analysis has been presented. Surdick (1985, 2004) did recognize the *Alloperla severa* group and suggested both eastern and western Nearctic species were included, and she also recognized several species pairs and small groups of sibling species in both publications. In 2004, for example, she states, "*Alloperla imbecilla, A. atlantica, A. banksi* and *A. hamata* seem to be related sibling species."

An exception to this general pattern might occur with *A. leonarda* Ricker (Ricker 1952), and a group of similar species which have been suggested by various authors to represent a cluster of closely related species. Surdick & Stark (1980), for example, noted the similarity in the enlarged epiproct cowl for *A. leonarda* and their newly described species, *A. natchez* Surdick & Stark, and Stark et al. (1983) referred to "…the *A. leonarda* complex…" in their description of *A. ouachita* Stark & Stewart. The latter authors indicate the complex also includes *A. furcula* Surdick (Surdick 1981) and *A. natchez*; an additional species, *A. lenati* Kondratieff & Kirchner, was described by Kondratieff & Kirchner (2004), and another, *A. prognoides* Surdick & Stark, was described in Surdick (2004). In addition to an enlarged epiproct cowl whose lateral lobes extend along either side of the epiproct nearly to, or slightly beyond, its tip, the apical area of the epiproct bears ventrolateral rows of prominent setae, and the tip is bifurcate, or bears a pair of prominent horns. The known species occur in the southeastern United States from Arkansas to

North Carolina, except for *A. leonarda*, which ranges from Missouri to the provinces of Atlantic Canada (Surdick 2004). Although adequate illustrations and descriptions exist for these species, no SEM images have been published for them, and the desirability for studies of this type has been demonstrated in other *Alloperla* species groups (Baumann & Kondratieff 2008, 2009; Kondratieff & Kirchner 1993; Lyon & Stark 1997; Stark & Nelson 2000).

MATERIALS AND METHODS

We obtained samples for the known species in the presumptive complex for study with SEM, and images of *A. aracoma* Harper & Kirchner, *A. atlantica* Baumann, *A. biserrata* Nelson & Kondratieff, and *A. imbecilla* (Say) were prepared to provide outgroup data. Additional outgroup data were gleaned from unpublished images prepared by Lyon and from Baumann & Kondratieff (2008, 2009). An attempt was made to study topotype or paratype specimens when possible and this was achieved for several species. *Alloperla leonarda* specimens from two widely separated populations (Nova Scotia *vs* Missouri) are designated as "Type A" and "Type B" respectively.

The wings were clipped for specimens utilized in SEM studies, and the bodies placed in dishes of 80% ethanol and sonicated for 12-15 seconds to remove debris. Cleaned specimens were dehydrated through a dilution series of 90%, 95% and 100% ethanol for 10 minutes each and then placed in Hexamethyldisilizane for 30 minutes. Following this treatment, specimens were attached to aluminum stubs with double stick copper tape, coated with gold-palladium and examined with an Amray 1810 scanning electron microscope. Specimens utilized in this study are from the collections of the C.P. Gillette Museum, Colorado State University, Fort Collins (CSU), the Monte L. Bean Life Science Museum, Brigham Young University, Provo (BYU), the K.W. Stewart collection, University of North Texas, Denton (KWS) and the B.P. Stark collection, Mississippi College, Clinton (BPS), as indicated in the text.

The *Alloperla leonarda* Species Group

Alloperla furcula Surdick
(Figs. 1-6)

Alloperla furcula Surdick, 1981:349. Holotype ♂ (United States National Museum), Upper Three Runs Creek, Aiken Co., South Carolina
Alloperla furcula: Surdick, 2004:15. Redescription

Material examined. SC: Aiken Co., Upper Three Runs Creek, Savannah River Plant, 1 April 1977, Herlong, Prichard, 5 ♂ (BPS). Same location, 4 May 1977, Herlong, Prichard, 10 ♂, 4 ♀ (BPS). Aiken Co., Tinker Creek, Savannah River Plant, 1 June 1977, Herlong, Prichard, 1 ♂, 6 ♀ (BPS).

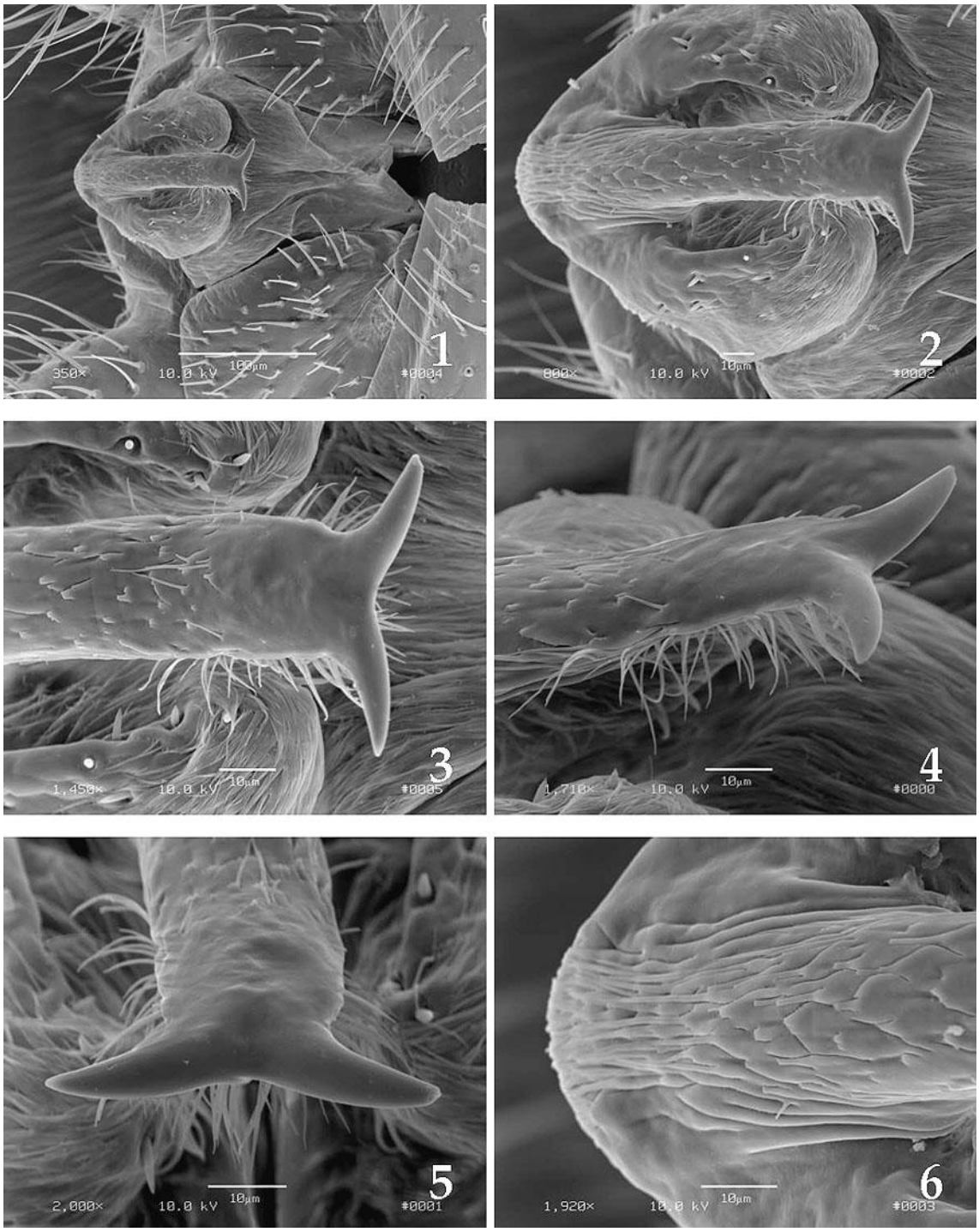
Epiproct. Length from base to fork, ca. 146 µm. Greatest pre-apical width, ca. 27 µm; apical width, ca. 53 µm. Cowl reaching well beyond apical third of epiproct tip (Figs. 1-2). Dorsum of epiproct bare in apical third but basal two thirds bearing a sparse covering of appressed setae and a few long setae with freely curled tips (Figs. 2-3, 6); subapical area of epiproct bearing lateral rows of long, ventrolaterally directed setae (Figs. 3-5). Dorsal aspect of epiproct becoming slightly wider from basal fusion with cowl to abrupt subapical narrowing. Strong laterally directed arms of apical fork present a "fish tail" appearance (Figs. 2-3).

Alloperla lenati Kondratieff & Kirchner
(Figs. 7-12)

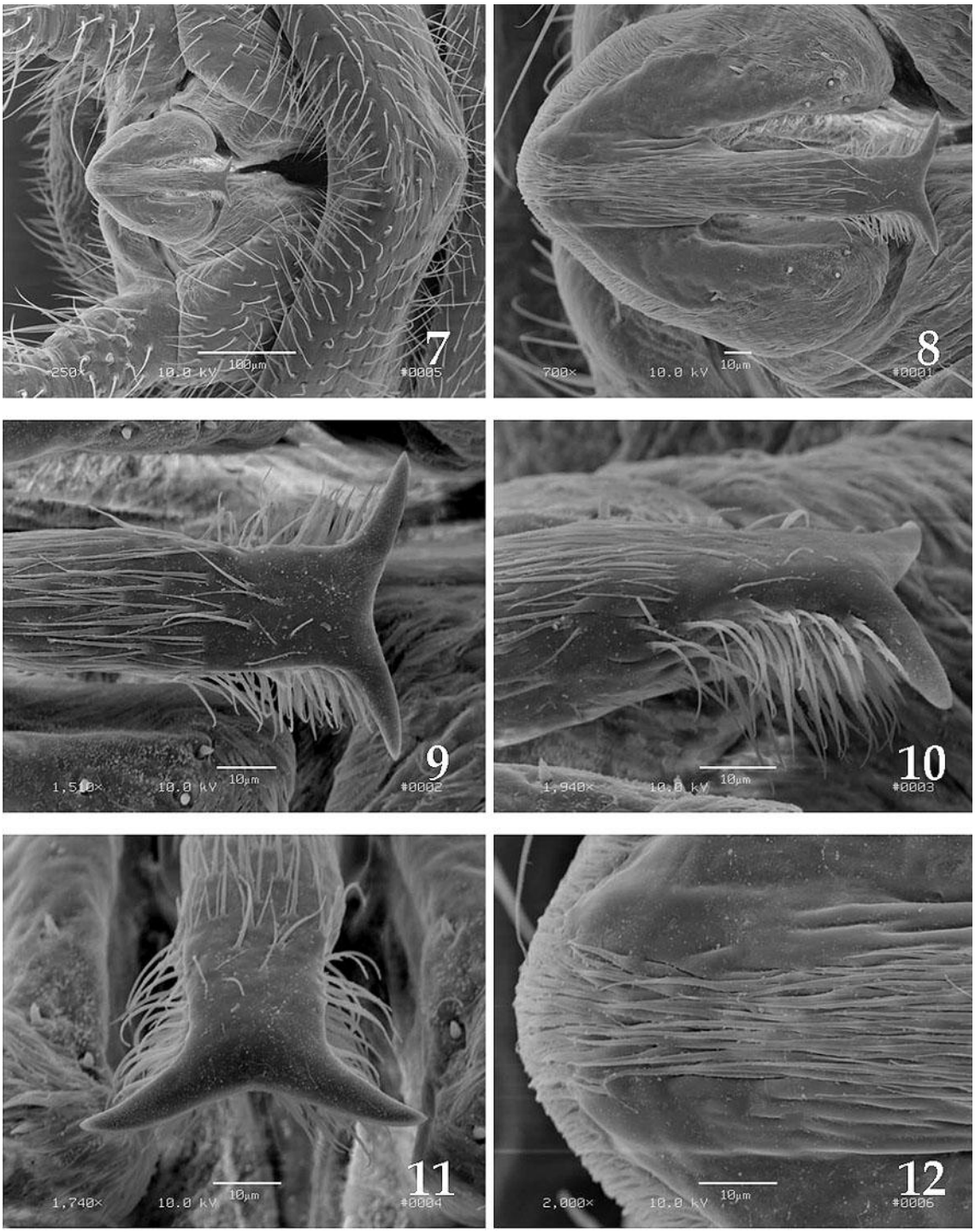
Alloperla lenati Kondratieff & Kirchner, 2004:361. Holotype ♂ (United States National Museum), Lumber River, Hwy 401, Hoke/Scotland Co. line, North Carolina

Material examined. NC: Harnett Co., Little River, Hwy 217, SW of Irwin, 3 May 2005, B.C. Kondratieff, R.F. Kirchner, R.E. Zuellig, D.R. Lenat, 2 ♂, 2 ♀ (CSU).

Epiproct. Length from base to apical fork, ca. 134 µm. Greatest pre-apical width, ca. 28 µm; apical width, ca. 49 µm. Cowl reaching ca. apical tenth of epiproct tip (Figs. 7-8). Dorsum of epiproct bare near apex but sparsely setose over most of length (Figs. 8, 10, 12); subapical area of epiproct bearing lateral rows of long, ventrolaterally directed setae (Figs. 8-9, 10-11). Dorsal aspect of epiproct narrowed beyond basal fusion point with cowl, and more subtly narrowed near base of ventrolateral setal row. Apex forked, arms of fork curved slightly ventrad in lateral and frontal aspects (Figs. 10-11).



Figs. 1-6. *Alloperla furcula* epiproct structures, Upper 3-Runs Creek, Aiken Co., SC. 1. Male terminalia, dorsal aspect. 2. Epiproct and cowl, dorsal aspect. 3. Apical half of epiproct, dorsal aspect. 4. Epiproct apex, dorsolateral aspect. 5. Epiproct apex, frontal aspect. 6. Detail of basal epiproct surface.



Figs. 7-12. *Alloperla lenati* epiproct structures, Little River, Harnett Co., NC. 7. Male terminalia, dorsal aspect. 8. Epiproct and cowl, dorsal aspect. 9. Apical half of epiproct, dorsal aspect. 10. Epiproct apex, dorsolateral aspect. 11. Epiproct apex, frontal aspect 12. Detail of basal epiproct surface.

Alloperla leonarda Ricker
(Figs. 13-24)

Alloperla leonarda Ricker, 1952:177. Holotype ♂ (Illinois Natural History Survey), North Branch Otter River, Houghton Co., Michigan
Alloperla sylvia Harden & Mickel, 1952:60. Holotype ♂ (University of Minnesota), Big Sand Creek, Pine Co., Minnesota. Syn. Ricker in Illies, 1966
Alloperla quadrata Harden & Mickel, 1952:61. Holotype ♀ (University of Minnesota), Kettle River, Pine Co., Minnesota. Syn. Surdick, 1981
Alloperla leonarda: Stark et al., 1983:56. Redescription
Alloperla leonarda: Surdick, 2004:17. Redescription and distribution update

Type A
(13-18)

Material. NS: Hants Co., Nine Mile River, Hwy 14, 23 June 1993, B.C. Kondratieff, R.W. Baumann, 4 ♂ (CSU).
Epiproct. Length from base to midline of apex, ca. 129 µm. Greatest pre-apical width, ca. 29 µm; apical width, ca. 61 µm. Cowl reaching to apex of epiproct (Figs. 13-14). Dorsum of epiproct with an elevated, broadly rounded ridge covered with a densely setose, broad median band over basal 80%; epiproct bare over apex and along low marginal bands (Figs. 14-18); subapical area of epiproct bearing lateral rows of long ventrolaterally directed setae (Figs. 14-15). Width slightly constricted in dorsal aspect around midlength. Apex rounded, but with short, lateral horns curved slightly caudad in lateral aspect (Fig. 16), and projecting straight laterad in frontal aspect (Fig. 17).

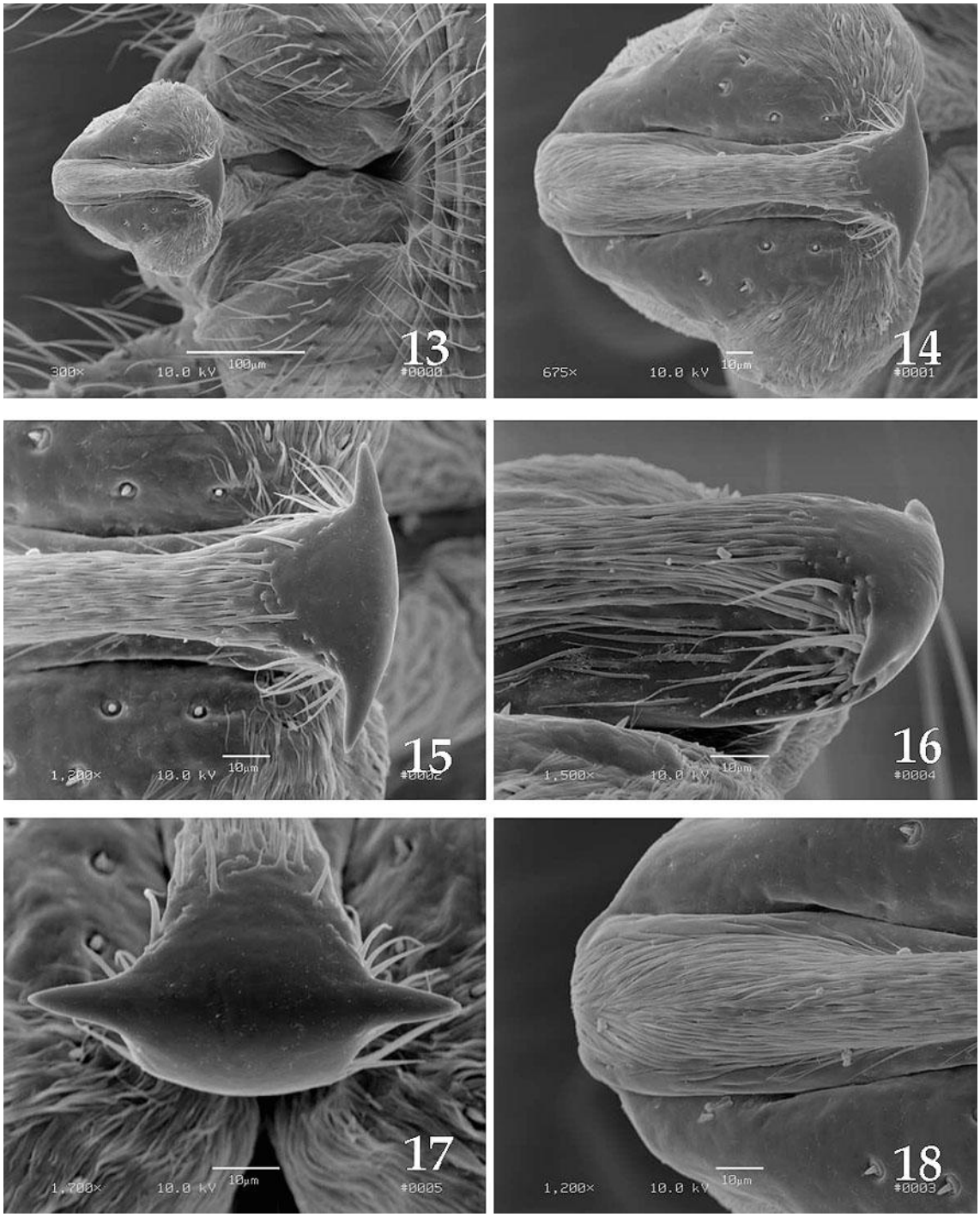
Type B
(19-24)

Material examined. MO: Christian Co., Bull Creek, Hwy W, S Ozark, 10 May 1972, B.K. Newman, 1 ♂ (BYU).
Epiproct. Length from base to midline of apex, ca. 206 µm. Greatest pre-apical width, ca. 40 µm; apical width, ca. 109 µm. Cowl reaching almost to apex of epiproct (Figs. 19-20). Dorsum of epiproct densely setose over entire surface except apex and along lateral margins (Figs. 20-24); subapical area of epiproct bearing rows of long ventrolaterally directed setae (Figs. 21-23). Width constricted in dorsal aspect at fusion point with cowl and slightly narrowed beyond midlength to subapical area (Fig. 20). Apex appearing almost truncate, but rounded, and armed with lateral horns about as long as subapical width (Figs. 21, 23).
Remarks. These two forms might represent distinct species, or individual variation for a species with a large geographic range. Evaluation of either hypothesis is beyond the scope of this study, but should be undertaken by someone with access to the holotype, and to a large series of specimens from throughout the presumptive range.

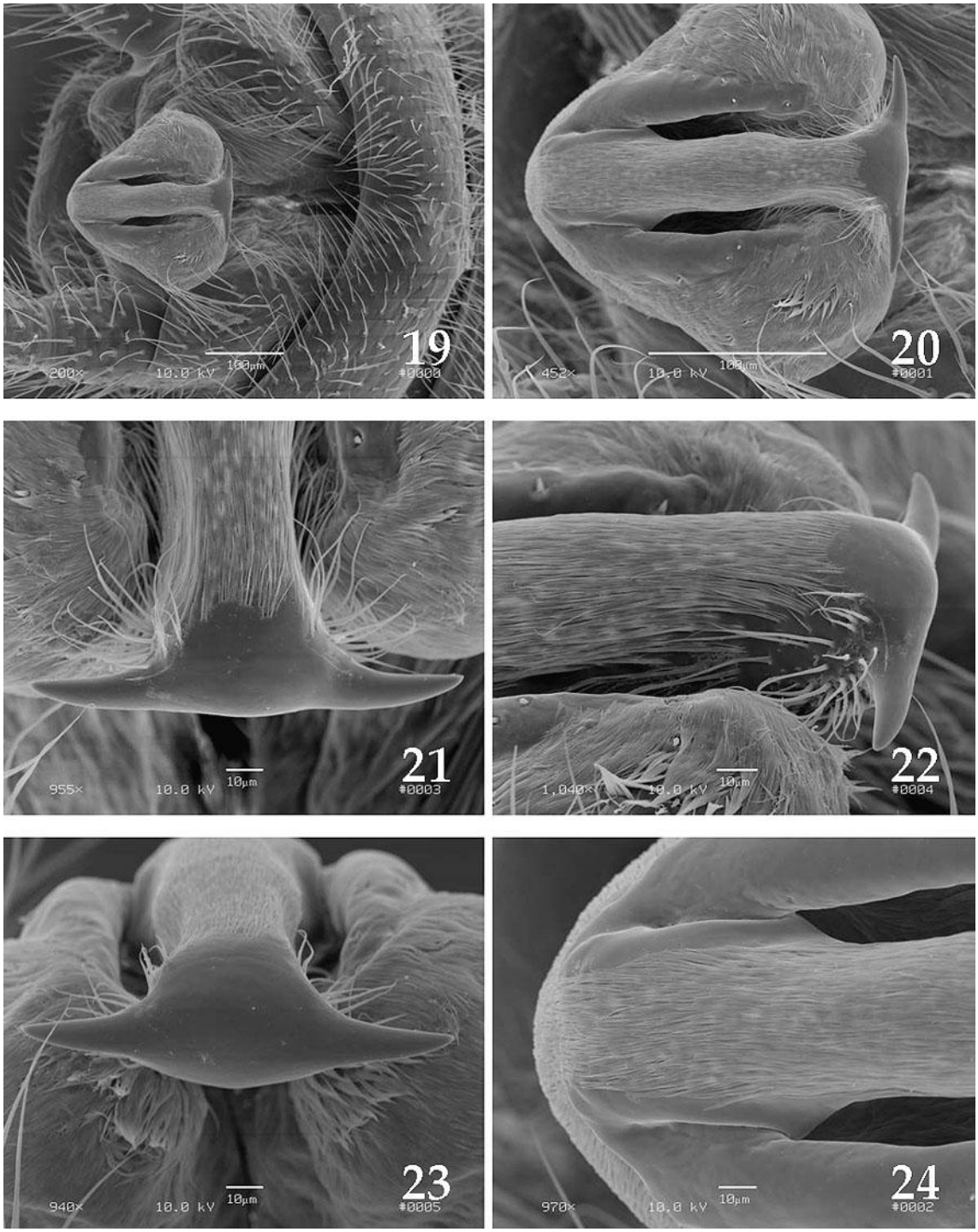
Alloperla natchez Surdick & Stark
(Figs. 25-30)

Alloperla natchez Surdick & Stark, 1980:71. Holotype ♂ (United States National Museum), Little Sand Creek, Natchez Trace Parkway, Claiborne Co., Mississippi
Alloperla natchez: Brown & Stark, 1995:122. Description of nymph and egg
Alloperla natchez: Hardy et al., 1994:368. Distribution
Alloperla natchez: Surdick, 2004:18. Redescription

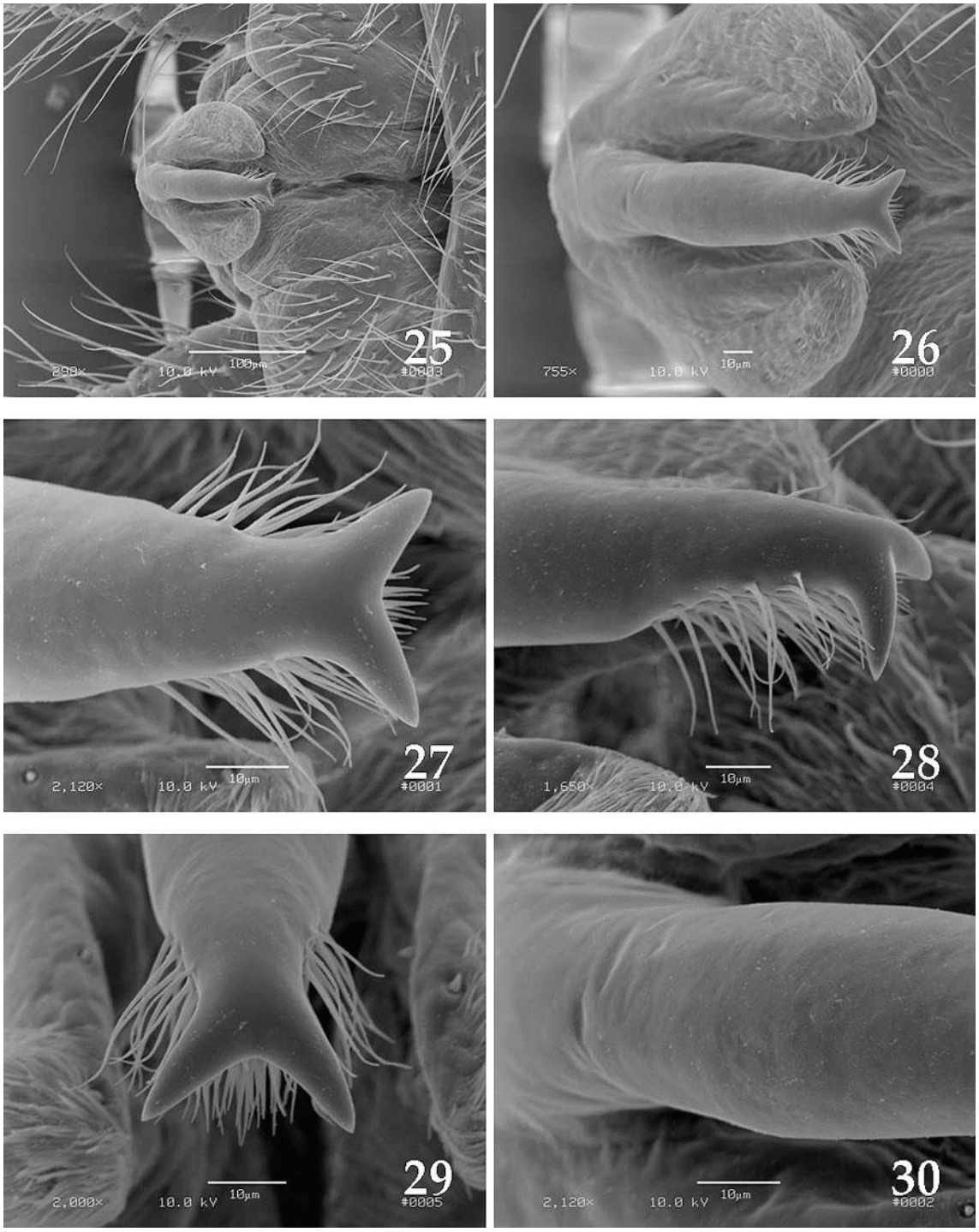
Material examined. MS: Claiborne Co., Ragsdale Creek, Regan Rd, 17 April 1993, B. Stark, 9 ♂, 7 ♀ (BPS). Franklin Co., Mill Branch, Homochitto National Forest, 14 May 1993, N. Phiefer, 2 ♂, 19 ♀ (BPS). Franklin Co., tributary of Porter Creek, 13 April 1993, C. Hardy, C. Boll, 9 ♂, 6 ♀ (BPS). Smith Co., Clear Creek, 3 mi SW Mize, 24 April 1991, B. Stark, D. Tanner, 1 ♂, 5 ♀ (BPS).
Epiproct. Length from base to fork, ca. 101 µm. Greatest pre-apical width, ca. 28 µm; apical width, ca. 27 µm. Cowl reaching almost to base of epiproct fork (Figs. 25-26). Epiproct dorsum completely bare (Figs. 27, 30), but apical third armed with irregular lateral rows of large, ventrolaterally directed setae (Figs. 26-29). Width relatively uniform from base to beyond midlength, but gradually narrowed in apical third to base of fork (Figs. 26-27). Arms of fork project downward in lateral and frontal aspects (Figs. 28-29).



Figs. 13-18. *Alloperla leonarda*, Type A, epiproct structures, Nine Mile River, Hants Co., NS. 13. Male terminalia, dorsal aspect. 14. Epiproct and cowl, dorsal aspect. 15. Apical half of epiproct, dorsal aspect. 16. Apical half of epiproct, dorsolateral aspect. 17. Epiproct apex, frontal aspect. 18. Detail of basal epiproct surface.



Figs. 19-24. *Alloperla leonarda*, Type B, epiproct structures, Bull Creek, Christian Co., MO. 19. Male terminalia, dorsal aspect. 20. Epiproct and cowl, dorsal aspect. 21. Apical half of epiproct, dorsal aspect. 22. Apical half of epiproct, dorsolateral aspect. 23. Epiproct apex, frontal aspect. 24. Detail of basal epiproct surface.



Figs. 25-30. *Alloperla natchez* epiproct structures, Porter Creek, Franklin Co., MS. 25. Male terminalia, dorsal aspect. 26. Epiproct and cowl, dorsal aspect. 27. Apical half of epiproct, dorsal aspect. 28. Epiproct and cowl, dorsolateral aspect. 29. Epiproct apex, frontal aspect. 30. Detail of basal epiproct surface.

Figs. 31-36. *Alloperla ouachita* epiproct structures, Little Missouri River, Montgomery Co., AR. 31. Male terminalia, dorsal aspect. 32. Epiproct and cowl, dorsal aspect. 33. Apical half of epiproct, dorsal aspect. 34. Apical half of epiproct, dorsolateral aspect. 35. Epiproct apex, frontal aspect. 36. Detail of basal epiproct surface.

Alloperla ouachita Stark & Stewart
(Figs. 31-36)

Alloperla ouachita Stark & Stewart in Stark et al., 1983:56. Holotype ♂ (United States National Museum), Little Missouri River, Montgomery Co., Arkansas
Alloperla ouachita: Surdick, 2004:19. Redescription

Material examined. AR: Montgomery Co., Little Missouri River, 20 June 1980, J.W. Feminella, 5 ♂ paratypes (KWS, BPS).
Epiproct. Length from base to apex, ca. 151 µm. Greatest pre-apical width, ca. 86 µm; apical width, ca. 109 µm. Cowl length exceeding apex of epiproct (Figs. 31-32, 34). Epiproct hairy along rounded dorsomedian keel, but bare along flanged lateral margins (Figs. 32-33, 35-36); ventrolaterally directed setae inconspicuous but present near apex. Lateral margins strongly divergent from basal fusion point with cowl, but narrowed abruptly at base of apical spines. Apex capped with smooth sclerite, clearly offset from body of epiproct by a narrow groove (Figs. 33-34); apex bears a pair of large, laterally directed, curved horns (Figs. 32-33, 35) and, in some specimens, a smaller pair of dorsomedian projections.

Alloperla prognoides Surdick & Stark
(Figs. 37-42)

Alloperla furcula: Stark & Harris, 1986:177. Not Surdick, 1981.
Alloperla prognoides Surdick & Stark in Surdick, 2004:20. Holotype ♂ (United States National Museum), Little River, Hwy 59, Baldwin Co., Alabama

Material examined. AL: Autauga Co., Autauga Creek, Hwy 20, 31 May 1985, S.C. Harris, paratype ♂ (BPS). Baldwin Co., Little River, Hwy 59, 27 April 1985, S.C. Harris, paratype ♂ (BPS).
Epiproct. Length from base to fork, ca. 120 µm. Greatest pre-apical width, ca. 46 µm; apical width, ca. 65 µm. Cowl reaching almost to tips of epiproct (Figs. 37-38, 40). Epiproct bare except for small basal patch (Fig. 42), and ventrolaterally directed rows of long lateral setae near apex (Figs. 38-39, 40). Width greatest near base, and gradually narrowed to base of fork; arms of fork long and thin and directed downward (Figs. 39, 40-41).

Out-Group Species

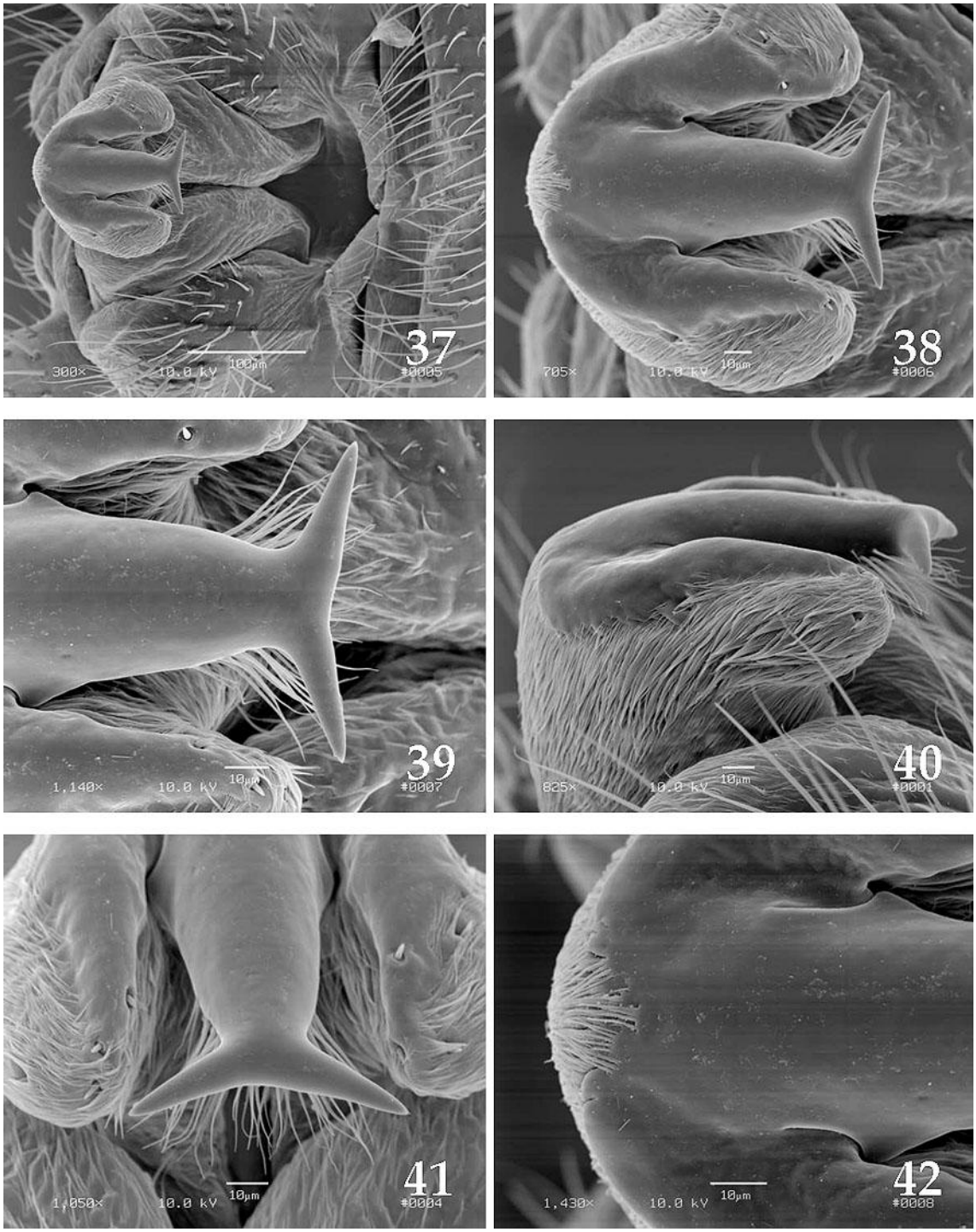
Alloperla aracoma Harper & Kirchner
(Figs. 43-48)

Alloperla aracoma Harper & Kirchner, 1978:403. Holotype ♂ (United States National Museum), Frogtown Hollow of Copperas Mine Fork of Island Creek, Holden, Logan Co., West Virginia
Alloperla aracoma: Surdick, 2004:10. Redescription and distribution update

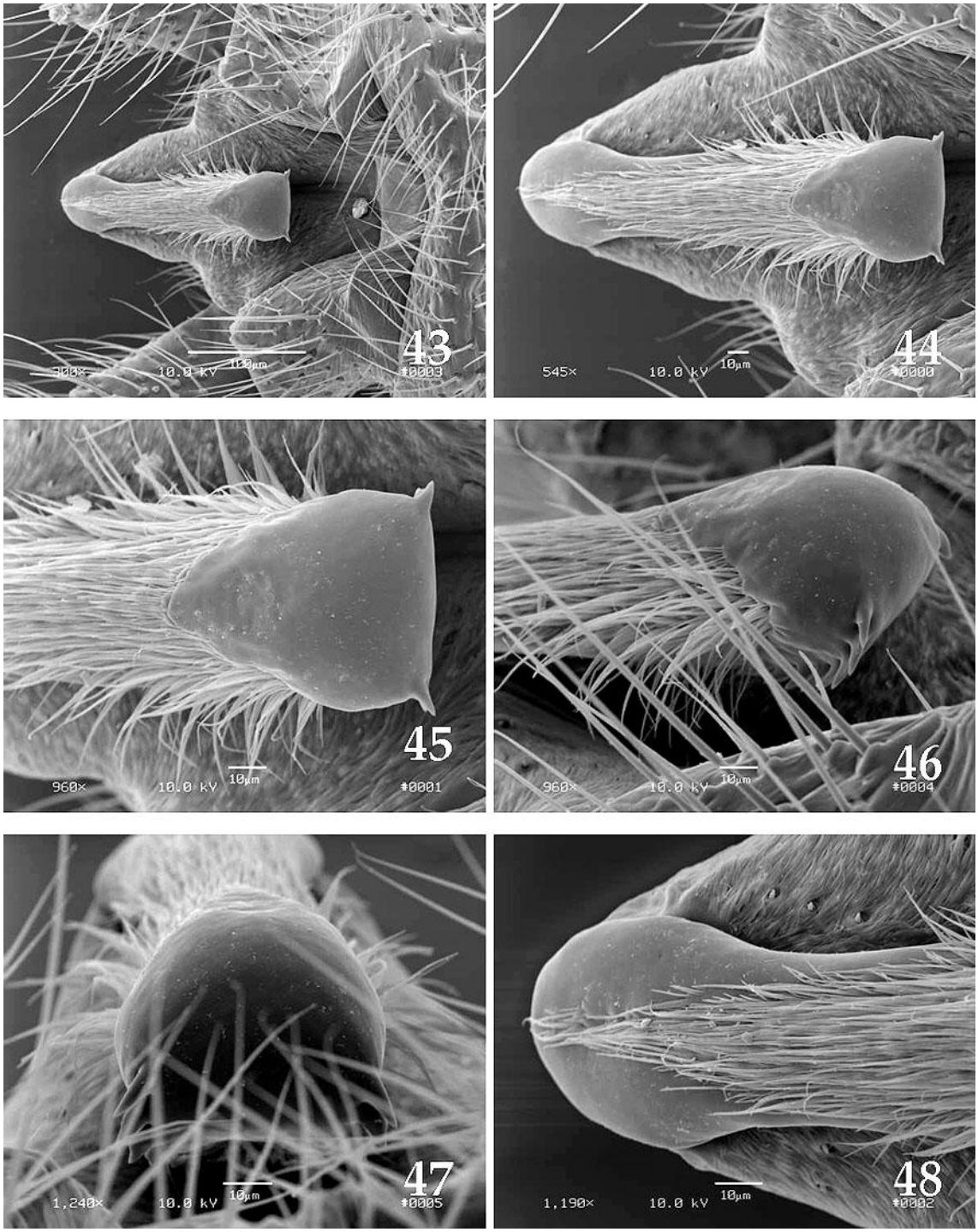
Material examined. WV: Logan Co., Frogtown Hollow of Copperas Mine Fork, Holden, 10 May 1980, R.F. Kirchner, 4 ♂, 4 ♀ (BPS).
Epiproct. Length, ca. 220 µm. Greatest width, ca. 66 µm. Epiproct cowl without enlarged lobes (Figs. 43-44, 48). Epiproct slightly constricted beyond base, then gradually widened to subapical part of bare area and constricted slightly proximal to pair of short, anterolateral projections. Dorsal surface covered with dense, appressed setal mat, except for apical and basal bare areas (Figs. 45-48); lateral margins with many setae projecting posterolaterally giving a shaggy appearence. Apex in lateral and frontal aspect (Figs. 46-47) bearing a series of ca. 8 serrae; dorsal pair of serrae form the anterolateral projections visible in Figs. 43-45.
Remarks. The dorsal aspect of the epiproct of *A. aracoma* is generally similar to that of *A. leonarda* as noted by Harper & Kirchner (1978), however *A. aracoma* lacks the enlarged cowl found in *A. leonarda* and the presence of anterolateral serrae on the epiproct tip clearly separate this species from members of the *A. leonarda* group. A single male specimen collected by the junior author from Devils Fork, Scott Co., Virginia in 1997 may represent an undescribed sister species to *A. aracoma*.

Alloperla atlantica Baumann
(Figs. 49-54)

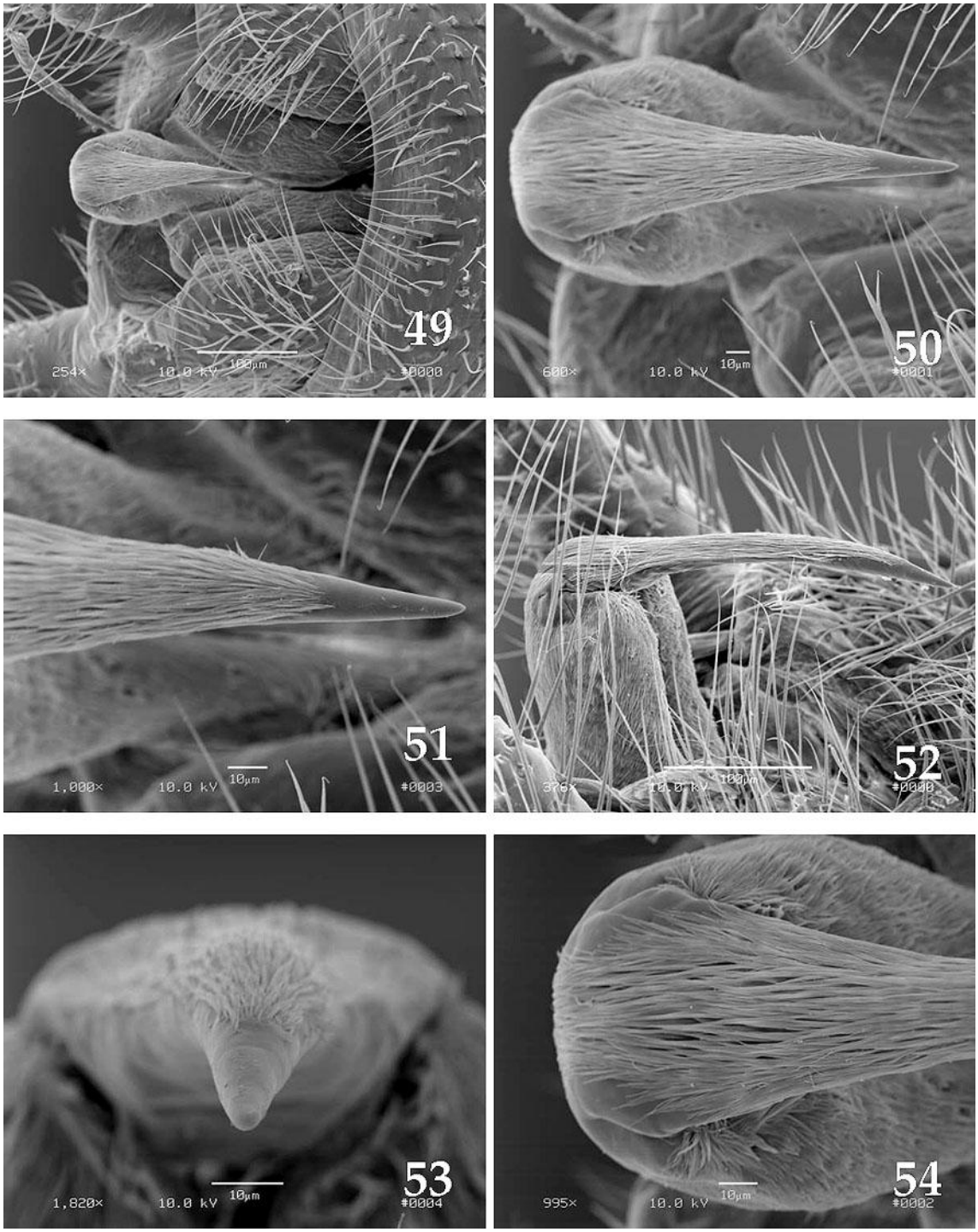
Alloperla atlantica Baumann, 1974:260. Holotype ♂ (United States National Museum), Fishing Creek, Frederick Co., Maryland
Alloperla atlantica: Surdick, 2004:11. Redescription and distribution update



Figs. 37-42. *Alloperla prognoides* epiproct structures, Autauga Creek, Autauga Co., AL. 37. Male terminalia, dorsal aspect. 38. Epiproct and cowl, dorsal aspect. 39. Apical half of epiproct, dorsal aspect. 40. Epiproct and cowl, lateral aspect. 41. Epiproct apex, frontal aspect. 42. Detail of basal epiproct surface.



Figs. 43-48. *Alloperla aracoma* epiproct structures, Frogtown Hollow, Logan Co., WV. 43. Male terminalia, dorsal aspect. 44. Epiproct and cowl, dorsal aspect. 45. Apical half of epiproct, dorsal aspect. 46. Apical half of epiproct, lateral aspect. 47. Epiproct apex, frontal aspect. 48. Detail of basal epiproct surface.



Figs. 49-54. *Alloperla atlantica* epiproct structures, Fishers Creek, Clarke Co., AL. 49. Male terminalia, dorsal aspect. 50. Epiproct and cowl, dorsal aspect. 51. Apical half of epiproct, dorsal aspect. 52. Epiproct and cowl, lateral aspect. 53. Epiproct apex, frontal aspect. 54. Detail of basal epiproct surface.

Material examined. AL: Clarke Co., Fishers Creek, Whatley, 30 April 1986, S.C. Harris, P. O'Neil, 9 ♂, 2 ♀ (BPS). Randolph Co., Cutnose Creek, Hwy 48, 20 May 1984, S.C. Harris, P. Lago, 4 ♂, 3 ♀ (BPS). GA: Fannin Co., Cutcane Creek, Cutcane Road, 19 July 2008, M. Willett, 1 ♂ (BPS). NC: Macon Co., Tellico Creek, Tellico Rd, 27 May 1993, B. Stark, R. Simmons, D. Kelly, 1 ♂, 3 ♀ (BPS). TN: Sevier Co., Little River, Great Smoky Mountains National Park, Sinks area, 25 April 1976, T. Wolff, B. Beavill, 1 ♂, 1 ♀ (BPS).
Epiproct. Length from base to tip, ca. 240 µm. Greatest width, ca. 58 µm. Epiproct cowl without enlarged lobes extending beyond epiproct base (Figs. 49-50, 52). Epiproct gradually narrowed from base to tip (Figs. 49-53), apex pointed and bent ventrad (Figs. 52-53). Dorsum covered with dense, appressed, setal mat but apex and venter bare (Figs. 51-54).

Alloperla biserrata Nelson & Kondratieff
(Figs. 55-60)

Alloperla biserrata Nelson & Kondratieff, 1980:802. Holotype ♂ (United States National Museum), tributary Craigs Creek, CR 621, Montgomery Co., Virginia
Alloperla biserrata: Surdick, 2004:12. Redescription and distribution update

Material examined. VA: Montgomery Co., tributary Craigs Creek, CR 621, 5 June 1983, B.C. Kondratieff, 5 ♂, 1 ♀ (BPS).
Epiproct. Length from base to tip, ca. 178 µm. Width near base, ca. 40 µm; width near midlength, ca. 19 µm. Thickness through basal tooth, ca. 42 µm. Epiproct cowl without enlarged lobes. Epiproct widest near base, abruptly narrowed near midlength and only slightly narrowed to tip (Fig. 56). Dorsum covered with closely appressed setal mat for about half of length, but apical half and basolateral areas bare (Figs. 55-57, 60); apical half bearing prominent setal patches in lateral aspect (Figs. 58-59), venter bare to base. Apex bearing a shallow notch in dorsal and frontal aspects and bearing six prominent teeth laterally (Figs. 58-59).

Alloperla caudata Frison

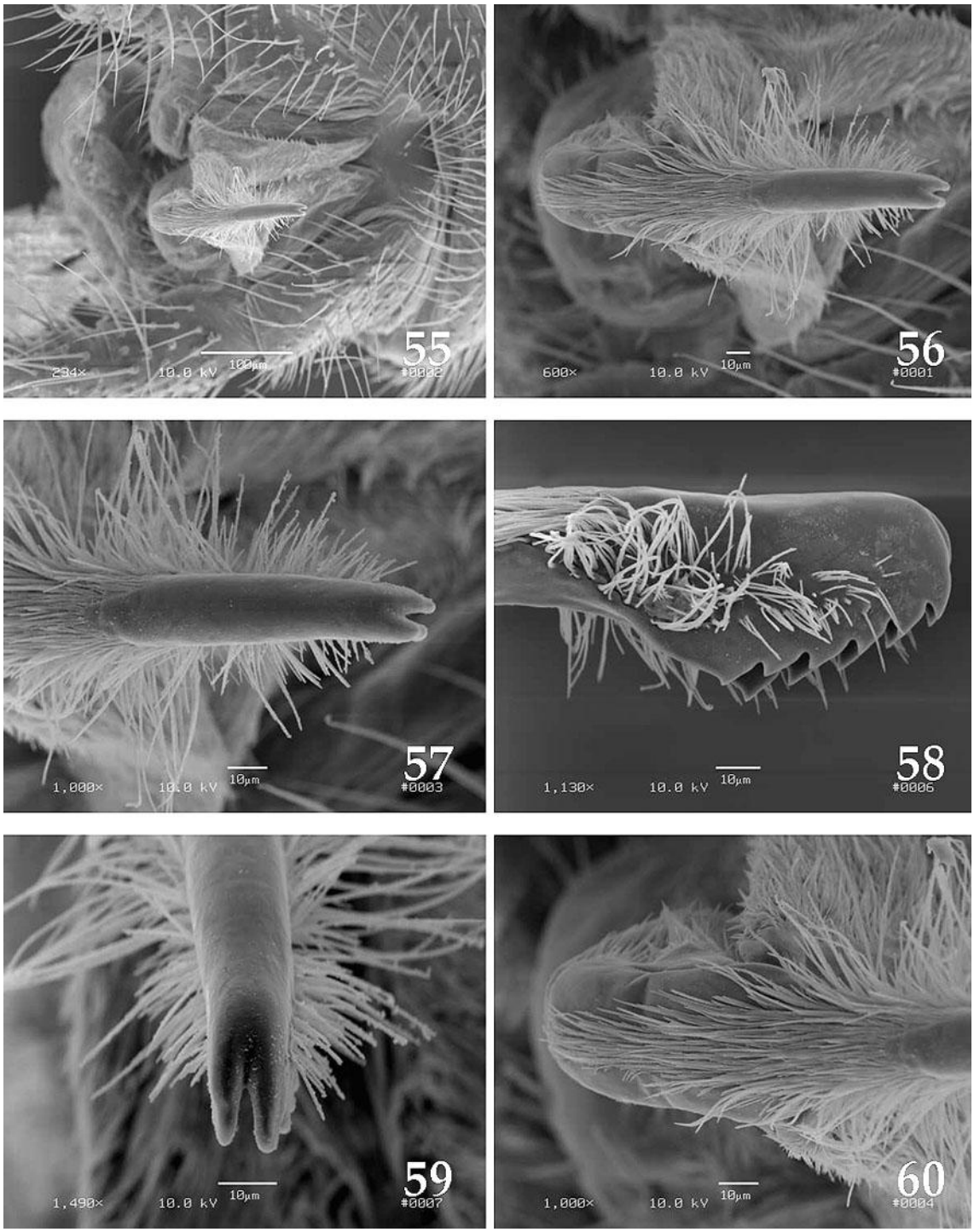
Alloperla caudata Frison, 1934:27. Holotype ♂ (Illinois Natural History Survey), Adair Co., Oklahoma
Alloperla caudata: Surdick, 2004:13. Redescription and distribution update
Alloperla caudata: Baumann & Kondratieff, 2009:100. SEM of epiproct

Images prepared by M.H. Lyon from the following material are in the Stark collection; additional images prepared recently from Mississippi specimens are very similar to those presented by Baumann & Kondratieff (2009).
Material examined. AL: Colbert Co., Henson Creek, Hwy 49, 5 June 1985, S.C. Harris, 2 ♂, 4 ♀ (BPS). MO: La Clede Co., Brush Creek, Hwy PP, date not given, B.C. Poulton, 3 ♂ (BPS). MS: Tishomingo Co., Clear Creek, Hwy 172, 18 May 2009, B. Stark, 19 ♂, 14 ♀ (BPS). OK: Cherokee Co., Barron Fork Creek, 3 June 1984, W.D. Shepard, 1 ♂ (BPS).
Epiproct. Length from base to tip, ca. 235-244 µm. Greatest width, ca. 90-109 µm. Greatest thickness, ca. 100 µm. Apical cap diameter, ca. 50 µm. Epiproct cowl without enlarged lobes but cowl extending almost to midlength; epiproct slightly widened from base to subapex, and slightly narrowed to bare apical cap; apex bearing a prominent, bare, sclerotized cap offset from body of epiproct by a groove, and not expanded on venter. Lateral aspect of epiproct inflated to apical third and narrowed beyond to cap. Entire surface of epiproct covered by a dense, closely appressed, setal mat.
Remarks. The Mississippi specimens represent a new state record for this species.

Alloperla hamata Surdick

Alloperla hamata Surdick, 1981:349. Holotype ♂ (United States National Museum), intermittent stream [tributary Larkin Fork], Jackson Co., Alabama
Alloperla hamata: Surdick, 2004:16. Redescription and distribution update

Images prepared by M.H. Lyon from the following material are in the Stark collection.
Material examined. AL: Lawrence Co., unknown site, 28 May 1985, S.C. Harris, 1 ♂ (BPS).
Epiproct. Length from base to tip, ca. 239 µm. Greatest width, ca. 63 µm. Epiproct cowl without enlarged lobes but base extending almost to midlength; epiproct widest near midlength and



Figs. 55-60. *Alloperla biserrata* epiproct structures, tributary Craigs Creek, Montgomery Co., VA. 55. Male terminalia, dorsal aspect. 56. Epiproct and cowl, dorsal aspect. 57. Apex of epiproct, dorsal aspect. 58. Apex of epiproct, lateral aspect. 59. Apex of epiproct, frontal aspect. 60. Detail of basal epiproct surface.

slightly narrowed in apical third. Most of dorsal surface covered with dense setal mat; apex mostly bare but a narrow median hirsute band extends almost to tip. Margins of apical area serrate, bearing eight teeth on each side; apex also armed with a small, upturned hook. Lateral aspect of epiproct curved downward from base to midlength and curved slightly upward beyond midlength.

Alloperla imbecilla (Say)
(Figs. 61-66)

Sialis imbecilla Say, 1823:165. Type lost, Ohio River, Cincinnati, Ohio
Alloperla imbecilla: Baumann, 1974:258. Neotype ♂ (United States National Museum), Vastine Run, Lower Twin Creek, Adams Co., Ohio
Alloperla imbecilla: Surdick, 2004:17. Redescription and distribution update

Material examined. VA: Scott Co., Devils Fork, FR 619, 17 May 1997, B. Stark, 8 ♂, 8 ♀ (BPS). Same site, 19 May 2009, B. Stark, 10 ♂, 6 ♀ (BPS). Scott Co., Big Stony Creek, FR 657, 19 May 2009, B. Stark, 1 ♂ (BPS).
Epiproct. Length from base to tip, ca. 266-275 µm. Greatest width beyond base, ca. 39-46 µm. Greatest apical thickness, ca. 43 µm. Epiproct cowl without enlarged lobes (Figs. 61-62, 66); densely setose over most of cowl surface but bare near base of epiproct. Epiproct widest at base (ca. 61 µm) and on subapical cap (ca. 39 µm), but similar in width through most of length (Fig. 62). Most of dorsum covered with a closely appressed, densely setose mat (Figs. 62-63, 66), but small basolateral and apical areas, and entire ventral surface bare; apex with a distinctive ventral row of long setae (Figs. 63-65) and a median longitudinal patch of additional setae extends onto spiny process laterally or basolaterally (Fig. 63); apex bearing a slightly thickened, multispined process (Figs. 63-64).
Remarks. The specimens examined in this study represent the southern most population known for this species, and they exhibit subtle variations from the figures presented by Surdick (2004) and Baumann (1974). A comparative SEM study is needed for several populations to evaluate the extent of variation in the shape, setation and number of serrae for the apical spiny portion of the epiproct.

Alloperla nanina Banks

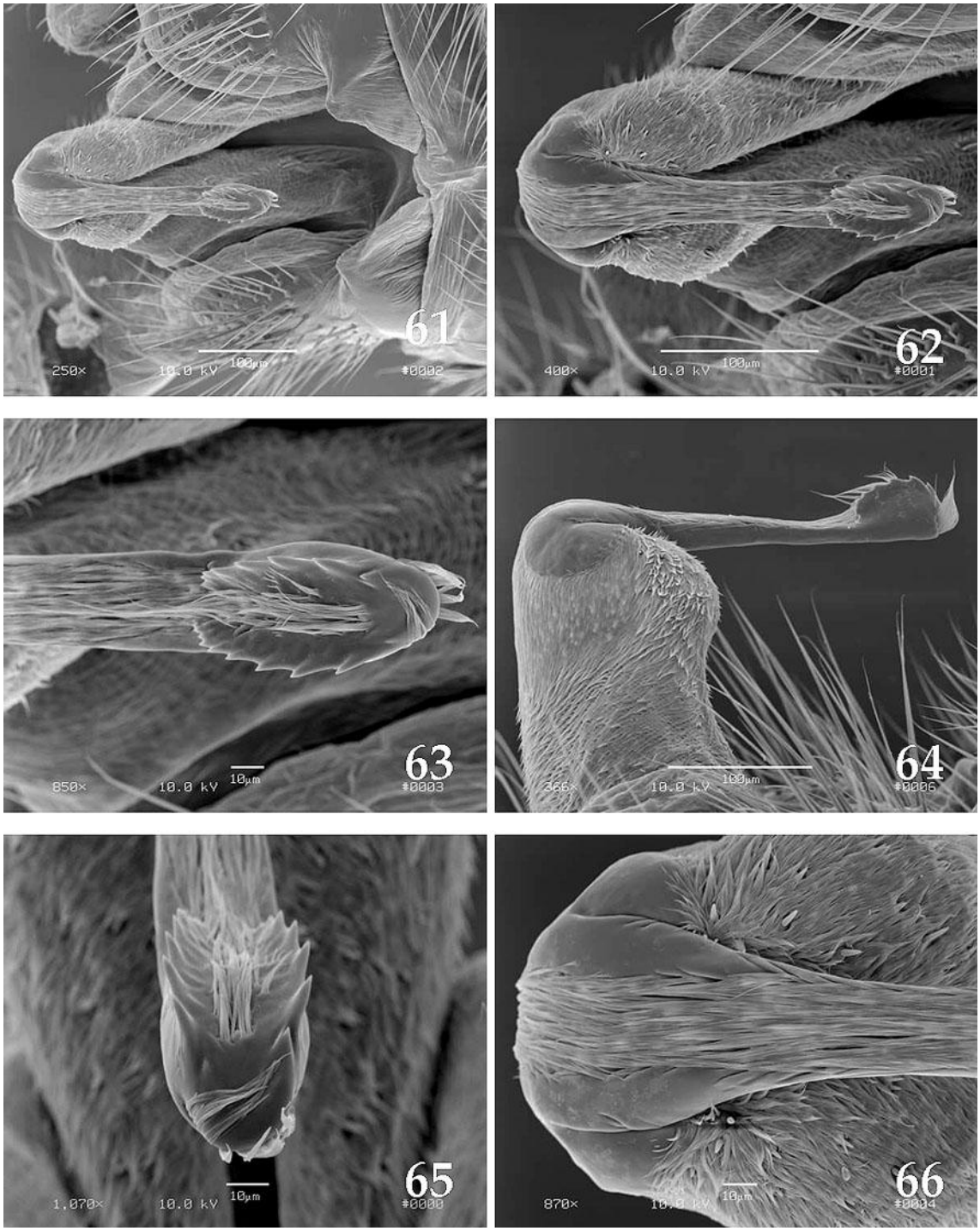
Alloperla nanina Banks, 1911:336. Lectotype ♂ (Museum of Comparative Zoology), North Fork Swannanoa River, Black Mountains, North Carolina
Alloperla lodgei Frison, 1935:340. Holotype ♂ (Illinois Natural History Survey), Fighting Creek, [Sevier Co.], Gatlinburg, Tennessee. Syn. Frison, 1942
Alloperla nanina: Surdick, 2004:18. Redescription and distribution update

Images prepared by M.H. Lyon from the following material are in the Stark collection.
Material examined. NC: Macon Co., Robin Branch, Wayah Bald, 13 June 1996, B. Stark, 1 ♂ (BPS). Watauga/Caldwell Co. line, Hwy 221, 25 May 1994, B. Stark, S.W. Szczytko, J. Sandberg, 1 ♂ (BPS).
Epiproct. Length from base to tip, ca. 89 µm. Cowl without enlarged lobes. Dorsal surface broadly rounded, wide at base and gradually narrowed to a slender, bifurcate apex; entire surface bare. Ventrolateral margins of apical third bearing a strongly serrate section of ca. 7 lateral teeth.

Alloperla neglecta Frison

Alloperla neglecta Frison, 1935:336. Holotype ♂ (Illinois Natural History Survey), Newfound Gap, North Carolina
Alloperla neglecta: Kondratieff & Kirchner, 1993:74. Redescription and SEM of epiproct
Alloperla neglecta: Surdick, 2004:18. Redescription and distribution update

Images prepared by M.H. Lyon from the following material are in the Stark collection.
Material examined. TN: Sevier Co., Greenbrier Cove, 17 May 1983, B. Stark, B.C. Kondratieff, R.F. Kirchner, 1 ♂, 1 ♀ (BPS). Sevier Co., Little Pigeon River, 2 June 1978, B. Stark, K.W. Stewart, 3 ♂, 8 ♀ (BPS).
Epiproct. Length from base to tip, ca. 98 µm. Greatest width, ca. 59 µm. Cowl without enlarged lobes. Dorsal surface entirely bare, broadly rounded and wide throughout length; anterior margin slanted toward midpoint and armed along ventral surface with ca. 12 teeth.



Figs. 61-66. *Alloperla imbecilla* epiproct structures, Devils Fork, Scott Co., VA. 61. Male terminalia, dorsal aspect. 62. Epiproct and cowl, dorsal aspect. 63. Apex of epiproct, dorsal aspect. 64. Apex of epiproct, lateral aspect. 65. Apex of epiproct, frontal aspect. 66. Detail of basal epiproct surface.

DISCUSSION

Alloperla epiproct tips show considerable variation, ranging from the small, almost spherical, densely hairy structures of *A. vostoki* Ricker (Baumann & Kondratieff 2009), to elongate, slender processes of *A. atlantica* (Surdick 2004). Most species examined with SEM have significant areas of setation on the dorsal surface, many have marginal serrations, and most lack enlarged lobes of the cowl (Baumann & Kondratieff 2008, 2009). The following epiproct characters appear to establish the *A. leonarda* group as a monophyletic group within *Alloperla.*

1 Epiproct cowl lobes enlarged *vs* not enlarged: The six members of the *A. leonarda* group share this common, presumptively apomorphic, feature of an enlarged cowl. The outgroup species examined all lack this structure and so do an additional nine *Alloperla* species examined by Baumann & Kondratieff (2008, 2009) and Kondratieff & Kirchner (1993). Only one species, *A. voinae* Ricker, has an appearance approaching the cowl structure seen for in-group species, and this may be as much due to extreme epiproct stem reduction as to cowl elaboration.

2 Epiproct apex armed with prominent horns *vs* apex without large horns: All in-group species share this presumptive apomorphic feature of large apical horns, and nothing approaching these structures is known among other *Alloperla* (Baumann & Kondratieff 2008, 2009). The apex in *A. nanina* Banks and *A. biserrata* does have a short bifurcation (Nelson & Kondratieff 1980; Surdick 2004), and *A. usa* has a prominent terminal notch (Baumann & Kondratieff 2009) but neither of these features appear to be homologous with the apical structure for species of the in-group.

3 Ventrolateral epiproct margin bearing a row of large setae *vs* ventrolateral setal row absent: All in-group species share the presumptive apomorphic feature of ventrolateral setae present, whereas this feature is absent in all outgroup species, except *A. nanina* and *A. biserrata* (Nelson & Kondratieff 1980), and in this pair of species, the setal arrangement in lateral aspect appears to differ from the more linear arrangement observed in the in-group.

Although we do not present a phylogenetic analysis of the *A. leonarda* group at this time, the data do support tentative recognition of three sister groups within the complex.

1 *A. leonarda* and *A. ouachita* share a mesal, longitudinal ridge and bare, lateral wings on the epiproct, and they also share the unusual, caudolaterally directed apical horns (Figs. 14, 17, 20, 23, 32, 35). These features appear to be unique to these two species.

An additional issue that needs resolution is the status of Ozark populations of *A. leonarda*. Comparison of Figs. 14 and 20, or 15 and 21 indicate significant variation in the length of apical epiproct prongs. The total epiproct length and apical width for Nova Scotia specimens is 129 μm and 61 μm respectively, whereas in the Missouri specimen examined these dimensions are 206 μm and 109 μm respectively. A larger Ozark sample, and additional northern samples of *A. leonarda*, particularly from the type locality are needed in order to evaluate the status of these populations.

2 *A. furcula* and *A. lenati* share a sparsely setose epiproct over the basal portion of the tip, and the tip is bare over a larger area than is often seen in the genus (Figs. 2, 8). These species are similar enough that an argument could be posed in support of placing *A. lenati* as a synonym, however a larger sample is needed in order to evaluate the status of these species. In specimens at hand, the dorsal epiproct setation is more strongly reduced in *A. furcula,* and that species has a slight anteapical constriction of the epiproct at the base of the prongs (Figs. 3, 5); in addition the apical prongs are directed ventrally in *A. lenati* (Figs. 10-11) and more laterally in *A. furcula* (Figs. 4-5).

Members of the *A. severa* complex (Baumann & Kondratieff 2008; Lyon & Stark 1997) also share a relatively large bare area on the epiproct stem, but the setation in these species forms a dense mat over the posterior portion of the stem.

3 *A. natchez* and *A. prognoides* share an epiproct tip that is bare over the entire dorsal surface, except on the extreme basal area of *A. prognoides* (Figs. 26, 30, 38, 42). Bare epiprocts also occur in some

of the outgroup species like *A. neglecta* and *A. concolor* (Kondratieff & Kirchner 1993), but this feature is uncommon among species of *Alloperla.*

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