



## Three new species of *Pogonognathellus* (Collembola: Tomoceridae) from North America

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### Abstract

Three species of *Pogonognathellus* Paclt are described from eastern North America: *P. belmontorum* n. sp. from the southern Appalachians, Alabama and Florida, *P. brevifulvus* n. sp. from Massachusetts and Michigan, and *P. magnibrunneus* n. sp. from the southern Appalachians and New York. The first two species are members of the pale/grey clade and the third is a member of the *longicornis* clade. The setal complexes at the apices of the third and fourth antennal segments are described.

**Key words:** antennal chaetotaxy, Appalachian Mountains, Blue Ridge Parkway, Great Smoky Mountains National Park, Hudson River valley, taxonomy

### Introduction

The family Tomoceridae currently has 158 species in 16 genera worldwide, most of which occur in the northern hemisphere (Fjellberg 2007; Bellinger *et al.* 2011). In North America *Pogonognathellus* Paclt is an abundant and diverse tomocerid genus consisting of large springtails, with body lengths of 3–7 mm and antennae frequently equal to or longer than the body length. The family and genus generally were considered well-known in North America (Folsom 1913; Mills 1934; Maynard 1951; Christiansen 1964; Christiansen & Bellinger 1980, 1998) until a combined morphological-molecular analysis demonstrated that several recognised *Pogonognathellus* spp. appeared to be complex species groups (Felderhoff 2007, Felderhoff *et al.* 2010). However, *P. flavescens* (Tullberg), considered previously to occur over most of temperate North America, was not found and probably does not exist naturally in the New World (Felderhoff *et al.* 2010). Currently, seven described *Pogonognathellus* spp. are definitely known in North America: *P. bidentatus* (Folsom), *P. celsus* Christiansen, *P. danieli* Felderhoff, Bernard and Moulton, *P. dubius* Christiansen, *P. elongatus* (Maynard), *P. mystax* Felderhoff, Bernard and Moulton, and *P. nigritus* (Maynard) (Christiansen & Bellinger 1998; Felderhoff *et al.* 2010).

The molecular analysis by Felderhoff *et al.* (2010) suggested three clades within the genus, with one undescribed species in the *longicornis* clade and many in the “pale/grey” clade. The purpose of this paper is to describe the *longicornis*-clade species and two of the pale/grey-clade species.

### Material and methods

**Collection and imaging.** Specimens were collected in Great Smoky Mountains National Park, Tennessee and North Carolina, USA, and the surrounding southern Appalachian region and southern Coastal Plain. Others were collected in northeastern states. They were collected live by aspiration, with Tullgren funnels from leaf litter and moss samples, or were beaten from tree foliage or branches. Live specimens were maintained singly in small plas-

tic jars with a plaster of Paris-activated charcoal substrate. Each specimen was provided food in the form of small pieces of lichen or partially decayed leaf, and was examined once every two days to determine if it had molted. Molting was detected by the presence of pieces of exuvia or a specimen with a pristine coat of scales. Newly molted specimens were photographed live with a 3.34-megapixel CoolPix 990 or 12.5-megapixel Coolpix 5100 digital camera (Nikon, Melville, NY) mounted on a stereo microscope, then preserved in 95% ethanol and photographed again to show the colour of the cuticle.

**Morphology.** For microscopic study of entire individuals, specimens were cleared in Marc André I fluid (Christiansen & Bellinger 1998), then dissected to separate the head, legs, and furcula from the rest of the body. Mandibles, maxillae and labium were pulled from the head capsule before mounting. Legs were mounted as separate pairs, each pair under a separate cover slip. The furcula was mounted dorsal side up, and one dens was severed at midpoint to insure that at least one mucro could be viewed in profile. The body cuticle was carefully cut along the ventral side and cleaned of internal organs, then mounted dorsal side up under a separate cover slip. Five intact antennae from five separate individuals of each species were removed and mounted for study of the distal parts of the third and fourth segments. All parts were mounted in Hoyer's medium. Slides were dried and hardened in a 60° C oven for 2–4 days, then ringed with sealant. Specimens were examined with bright-field, differential interference-contrast, and phase-contrast microscopes.

Dorsal head macrochaetotaxy was determined for the area running the length of the head and to a width defined by the exterior edges of the eyespots. The anterior cluster of macrochaetae on the anterior margin was not illustrated and its macrochaetae were not counted. Figures of the chaetotaxy were standardised after Christiansen (1964) to facilitate comparisons of species. Dental spine composition was expressed according to the formula used by Folsom (1913) and Christiansen and Bellinger (1998): the number preceding the slash indicates spines anterior to the basal subsegment of the dens, and conspicuously larger spines are italicised. Eight distinct kinds of antennal setae were designated as plump sensillum (PLS), rod-like sensillum (RLS), truncate sensillum (TRS), typical seta (SE), hooked seta (SH), spike-like seta (SP), slender sensilliform seta with rounded tip (RSS), and pointed sensilliform seta with weakly defined socket (PSS) (Table 1). We refer to the antennal segments as Ant. I, II, III, IV and to the abdominal segments as Abd. I, II, III, IV, V, VI.

**Molecular analysis.** Specimens of two of the three species were included in the analysis by Felderhoff *et al.* (2010) of a ca. 800-base pair portion of the gene encoding 5'-3' exoribonuclease II (ExoII) or in analysis of additional specimens (J. K. Moulton & E. C. Bernard, unpublished). Details of preparation, amplification, and analysis are in Felderhoff *et al.* (2010).

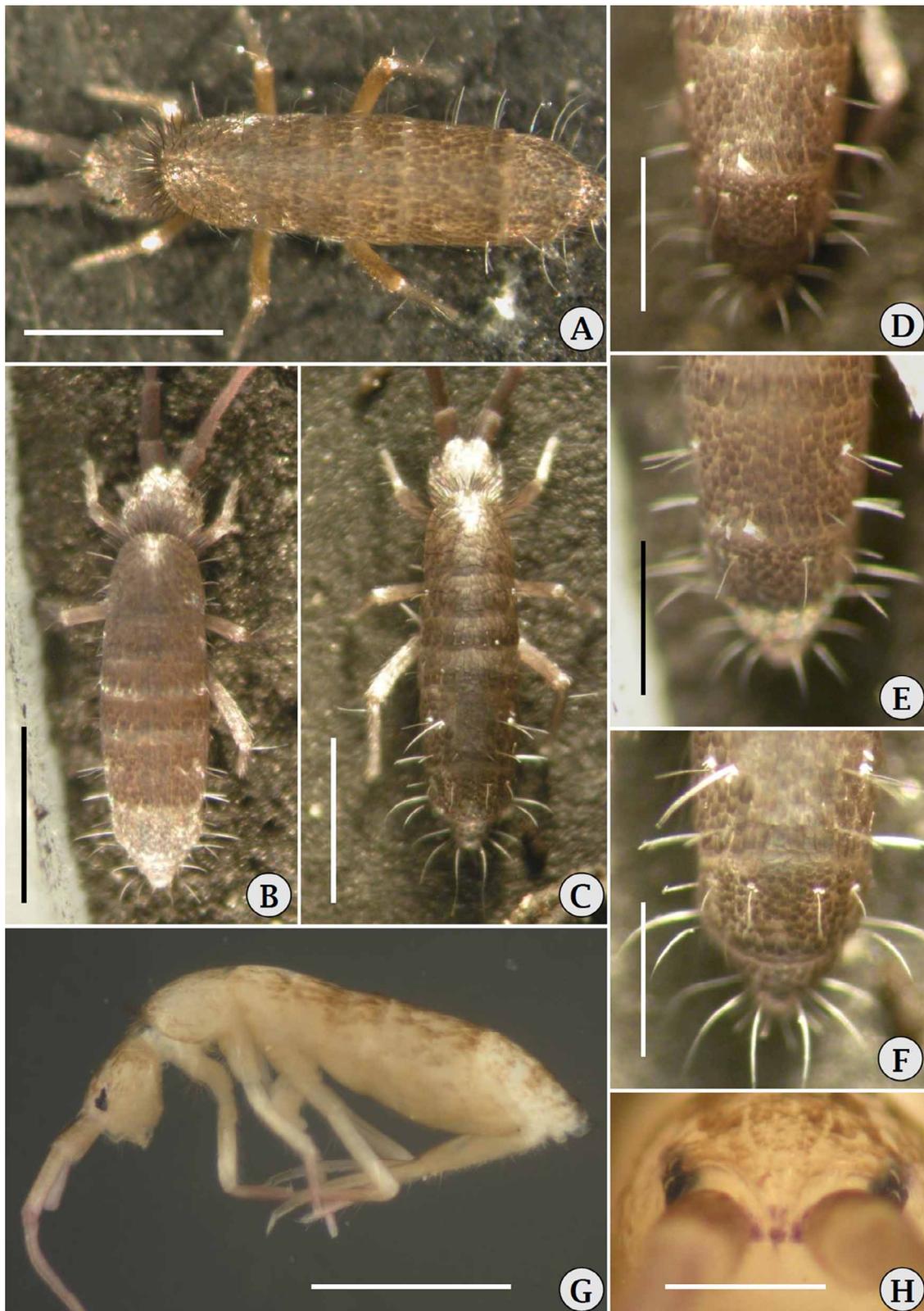
**Deposition of specimens.** Holotypes are deposited in the Illinois Natural History Survey Collembola collection, University of Illinois, Champaign, IL (INHS). Paratypes are deposited in INHS; the National Institute of Biological Resources, Incheon, Republic of Korea (NIBR); the University of Tennessee Insect Collection, Knoxville, TN (UTIC), Great Smoky Mountains National Park Museum, Gatlinburg, TN (GRSM) and other depositories as designated. Listed additional specimens are deposited in UTIC.

## Descriptions

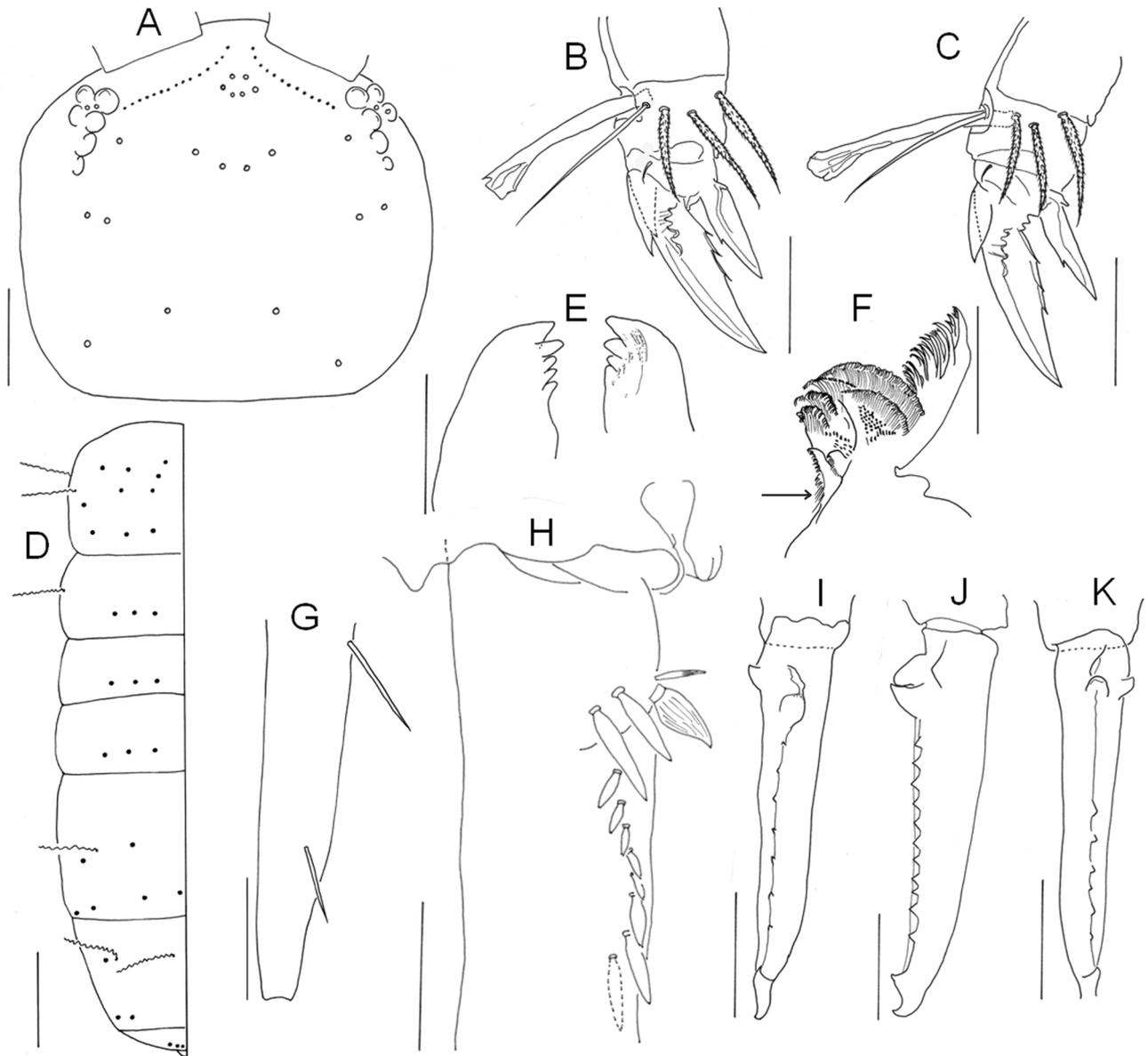
### *Pogonognathellus belmontorum* n. sp.

(Figs. 1, 2, 7A, E–G)

Maximum length 5 mm. Scaled individuals largely brown to greyish brown, weakly iridescent anteriorly (Figs. 1A–C); scales on posterior of terga with silver-grey and brown rows of scales of variable intensity; light and dark scales on terga IV–VI alternating to form a checkerboard-like pattern (Figs. 1D–F). Bothriotrichal sockets surrounded by a few white scales forming small but distinct white spots (Figs. 1D–F). Cuticle ivory to pale yellow, becoming paler in preserved specimens (Fig. 1G). Clypeus ivory to light yellow-orange; interantennal region pigmented, pattern varying from several symmetrical dots (Fig. 1H) to complete M-shaped figure. Eye patches dark blue to black, roughly triangular. Small pigmented spot directly posterior to eyespot. Antennal bases purple. Antennal segments I–II pale to light violet, III–IV grey-violet. Coxae, trochanters, and femora pale or speckled with orange pigment; tibiotarsi light purple. Furcula and ventral tube ivory to pale yellow. Posterior half of Abd. IV tergite and tergites of Abd. V–VI often light orange-brown.



**FIGURE 1.** *Pogonognathellus belmontorum* n. sp. (A–F) Live specimens. (A) Dorsal view, specimen from Swain County, NC (GenBank Accession 169367) (K. F. Oten). (B) Dorsal view, specimen from Nassau County, FL, anterior and posterior illumination. (C) Dorsal view, second specimen from Nassau County, FL, anterior illumination. (D, E) Posterior abdomen of specimen in Fig. 1B, anterior and posterior illumination, respectively. (F) Posterior abdomen of specimen in Fig. 1C, anterior illumination. (G) Lateral view of ethanol-preserved specimen, Swain County, NC. (H) Spot pattern between antennae. Scale bars: A–C, G, 2 mm; D–F, 1 mm; H, 500  $\mu$ m.



**FIGURE 2.** (A–J) *Pogonognathellus belmontorum* n. sp. (A) Dorsal head chaetotaxy. (B) Forefoot complex. (C) Middle foot complex. (D) Dorsal body chaetotaxy, left side: filled circles indicate macrochaetae, wavy lines indicate bothriotricha. (E) Mandible. (F) Maxilla. (G) Spines of hind tibiotarsus. (H) Dental spines, left side. (I) Mucro, dorsal view. (J) Mucro, lateral view. (K) *P. flavescens*, mucro, specimen from Sweden. Scale bars: A, G, 200  $\mu$ m; B, C, E, F, I–K, 50  $\mu$ m; D, 400  $\mu$ m; H, 100  $\mu$ m.

Eyes 6+6. Antennae slightly shorter than body, up to 0.9 times body length. Fourth segment fusiform, without strongly projecting apex, with 9–11 subsegments; with rod-like sensilla scattered sparsely along its length (Fig. 7E); pin seta stout, finely rounded at tip, with proximal spur (Fig. 7F); stout spike-like seta anterior to pin seta; one truncate sensillum near apex with associated hooked setae and rod-like sensillum slightly behind hooked setae (Fig. 7F). More proximally, several rod-like sensilla of various lengths; longer setae composed of thin sensilliform setae with rounded tips and pointed sensilliform setae in weakly defined sockets. Apex of Ant. III with truncate sensillum and associated hooked seta, one pair of plump sensilla, an additional plump sensillum, and several rod-like sensilla; longer setae consisting of typical setae and slender, round-tipped sensilliform setae (Fig. 7G).

Left mandible with 5 distal teeth, right mandible with 4 distal teeth (Fig. 2E). Maxilla (Fig. 2F) with broad lamella 1 bearing many rows of strong, curved, rake-like denticles behind apical border of fine cilia; lamella 2 with two regular rows of curved coarse rakes followed by a proximal field of finer denticles; lamella 5 without prominent proximal beard-like projection but with elongated basal teeth.

Unguis with 3 inner teeth in basal half, close to one another, distal tooth proximal to unguiculus tip (Figs. 2B, C); wavy internal ridging prominent. Unguiculus lanceolate, gradually becoming acuminate distally, with one inner tooth midway from inner base (Figs. 2B, C). Tenent hair stout, clavate, longer than inner margin of unguis. Spine-like setae absent on inner side of fore and mesotibiotarsi (Fig. 7A), 2 spine-like setae on metatibiotarsus (Fig. 2G). Pretarsal setae finely ciliate.

Manubrium dorsally with hyaline, acuminate macrochaetae. Dens with broad, striated, scale-like spine at inner base. Dental spines brown, smooth to finely striate, terminal spines considerably longer than others, formula 0–1, 2/6–9, 2, usually 2/6–8, 2 (Fig. 2H), number of spines sometimes different on each side. Mucro (Figs. 2I, J) elongate with basal lamella and 7–13 intermediate denticles. Dorsal basal tooth less than one-fourth the length of mucro from base, in line with lamella; outer basal tooth level with basal lamella. Terminal teeth subequal.

Head with 2+4 antero-medial macrochaetae, 3+3 interocular macrochaetae, 2+2 postocular macrochaetae and 2+2 posterior cephalic macrochaetae (Fig. 2A). Tergal macrochaetal formula on each side 10,3/3,3,6,3,3; Abd. III with 2+2 anterior and 4+4 posterior macrochaetae; Abd. IV with 1 pair of anterior and 2 pairs of posterior macrochaetae (Fig. 2D). Caudal macrochaetae of Abd. VI short and straight, about same length as segment; macrochaetae of Abd. V long and curved, more than half the length of Abd. IV–VI, directed caudally. Tenaculum with 1 seta.

**Etymology.** This species is named with pleasure for Michael, Nicholas and Sophia Belmont, benefactors of Discover Life in America ([www.dlia.org](http://www.dlia.org)), the governing body of the All-Taxa Biodiversity Inventory in Great Smoky Mountains National Park.

**Type specimens.** Holotype female and 5 paratypes, North Carolina, Swain County, Great Smoky Mountains National Park, Enloe Cemetery, 290707E 3932327N, moist leaf litter, 18 March 2008, K.-H. Park, coll.; 1 paratype (designated 189 in Felderhoff [2007], partial DNA sequence GenBank GU169367), same location, leaf litter from riparian zone, 3 April 2006, K. L. Felderhoff & M. MacCarroll, coll.; 35 paratypes, Tennessee, Sevier County, Great Smoky Mountains National Park, Rainbow Falls trailhead, 5 November 2008, K.-H. Park & E. C. Bernard, coll.

**Type deposition.** Holotype and 8 paratypes in INHS, 5 paratypes in GRSM Park Museum, remaining paratypes in UTIC.

**Additional material.** One specimen, North Carolina, Haywood County, Great Smoky Mountains National Park, Cataloochee, 17S 0305500 3926814, elev. 1018 m, in plant detritus on rocky seep, 20 October 2008, K.-H. Park, coll. Specimens from North Carolina, Jackson County, Blue Ridge Parkway: 7 specimens, Cranberry Ridge Overlook, 17S 0305497 3926812, elev. 1,660 m, among grasses, moss, dead leaves below rocky vertical seep, 20 October 2008, K.H. Park, coll.; 5 specimens, about 800 m west of Soco Gap, moist but not saturated litter below seeps, 35,52541 -83.233967, 21 May 2008, E. C. Bernard, coll.; 1 specimen, Roy Taylor Forest overlook, 35°22.716N 83°00.830W, elev. 1,737 m, open hillside east of parking lot, *Vaccinium* sp. and bright green moss, 21 May 2008, E. C. Bernard, coll. Specimens from other states: 8 specimens, Tennessee, Sullivan County, Cherokee National Forest, Jacobs Creek Recreation Area, 36.5788N 81.9861W, elev. 487 m, 11 June 2008, leaf litter, K.H. Park, coll.; 3 specimens, Alabama, Winston County, seep near crossing of Route 95 and County Road 8, 8 May 2005, J. K. Moulton, coll.; 5 specimens, Florida, Nassau County, Amelia Island Plantation, 12 December 2008, E. Bernard, coll.

**Diagnosis.** *Pogonognathellus belmontorum* n. sp. lacks spine-like setae on the fore and mesotibiotarsi and long spines in the middle of the dental spine row, but possesses anterior macrochaetae on Abd. IV; therefore, it is a member of the pale/grey clade as defined by Felderhoff *et al.* (2010). It is distinct from all other described members of its clade by the proximal position of the unguis teeth and the presence of 1 tenaculum seta. *Pogonognathellus beckeri* Börner, a Japanese species, also has 3 proximal unguis teeth but possesses 6–9 tenaculum setae and has a bearded maxilla (Yosii 1967). This arrangement is similar to that of *P. magnibrunneus* n. sp., described below, but that species is a member of the *longicornis* clade.

**Remarks.** The cephalic chaetotaxy in this species is typical of the *longicornis* clade rather than the pale/grey clade. The postocular macrochaetae are paired rather than widely separated, and 2+2 posterior macrochaetae are present. Previously examined species of the pale/grey clade have the postocular chaetae well separated and lack the more posterior pair of posterior macrochaetae (Felderhoff *et al.* 2010).

In the phylogenetic tree illustrated in Felderhoff *et al.* (2010), this species is represented by the specimen labeled 189, which appears to be basal to the rest of the pale/grey clade. The collecting locality for this specimen given in Table 1 (as flav189) of that paper is incorrect. The locality for flav189 is Enloe Cemetery, Great Smoky Mountains National Park, Swain County, North Carolina. The GenBank accession number for this specimen is GU169367.

**TABLE 1.** Nomenclature used in this paper for setal types, with equivalents from Lukic *et al.* (2010).

Name	Abbreviations used in Figs. 7F–N	Description	Location	Equivalent in Lukić <i>et al.</i> (2010)
Typical seta	SE	Dark, pointed, with well-defined socket	Entire antenna except apex of fourth segment	Ordinary mesochaetae
Spike-like seta	SP	Dark, strong, straight, with narrowly rounded tip	Near pin seta of fourth segment	
Hooked seta	SH	Dark, distal portion recurved	Apex of third and fourth segments	
Sensillum-like seta with rounded tip	RSS	Hyaline, long, thin, tip rounded, socket well-defined	All of third and fourth segments	S-like mesochaetae
Sensillum-like seta with pointed tip	PSS	Hyaline, wide at base, tapering to point, socket weakly defined	Fourth antennal segment	
Plump sensillum	PLS	Hyaline, broadly oval, short	Scattered along third and fourth segments	
Rod-like sensillum	RLS	Hyaline, parallel-sided	Scattered along third and fourth segments, more abundant at apices	S-chaetae
Truncate sensillum	TRS	Blunt, rod-like, minutely lobed or brush-like at tip	Apices of third and fourth segments	

The general appearance of ethanol-preserved specimens resembles that of *P. flavescens*, including specimens provided by Arne Fjellberg (Sweden) and Mikhail Potapov (Russia). This new species, which may be widespread in the southeastern states, could account for many of the previous records of *P. flavescens* from North America. Besides the characters mentioned in Felderhoff *et al.* (2010) that separate *P. flavescens* from all North American *Pogonognathellus* spp, *P. flavescens* has only few mucronal denticles and the beginning of the denticle row is in the middle third of the mucro (Fig. 2K; Fjellberg 2007). The denticles of *P. belmontorum* **n. sp.** are more numerous (7–13) and occupy the entire length of the mucro between basal and subapical teeth. In addition, the outer mucronal basal tooth of *P. belmontorum* **n. sp.** is level with the mucronal basal lamella; in *P. flavescens*, the outer tooth is level with the basal tooth.

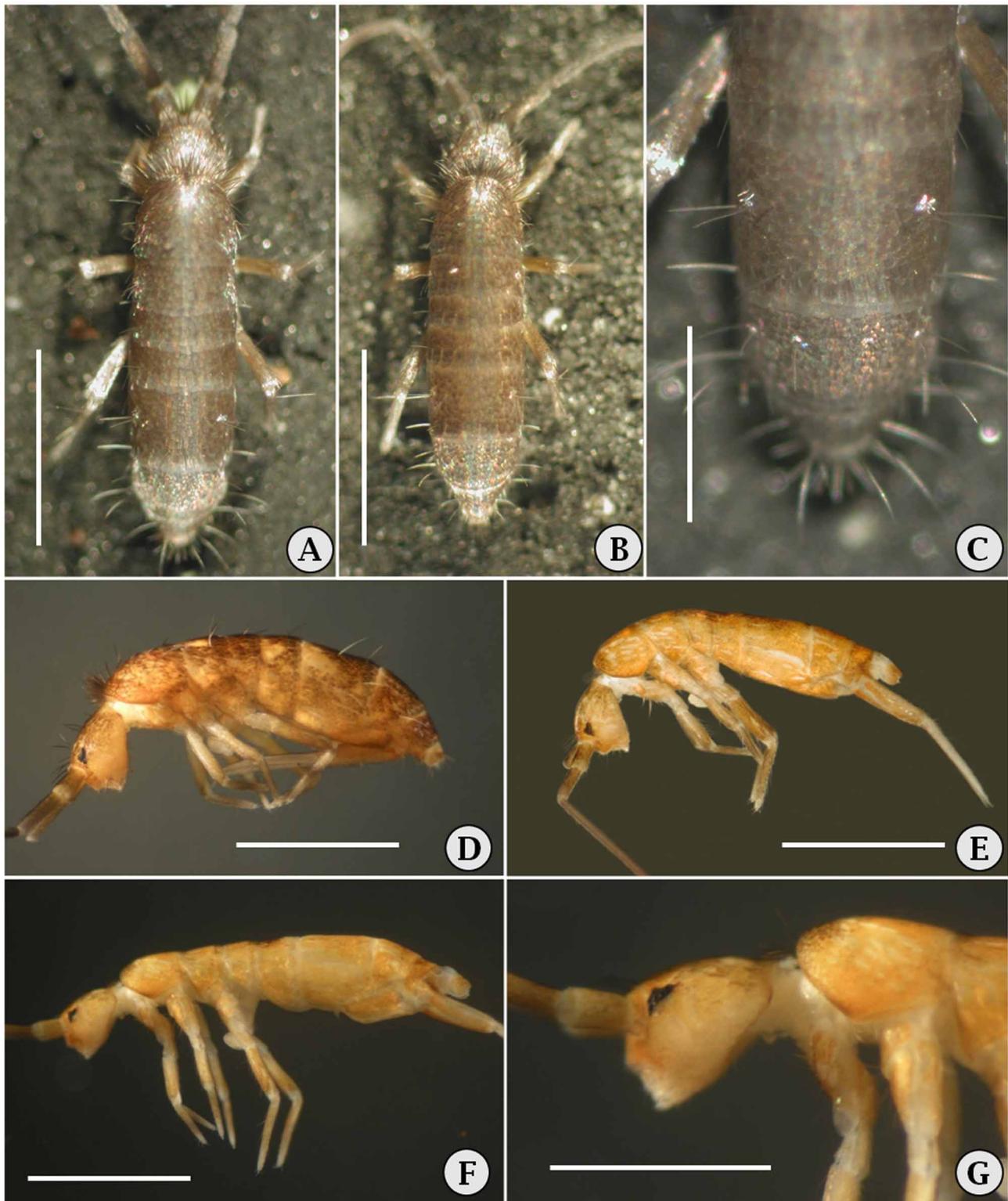
### *Pogonognathellus brevifulvus* **n. sp.**

(Figs. 3, 4, 7B, H, I)

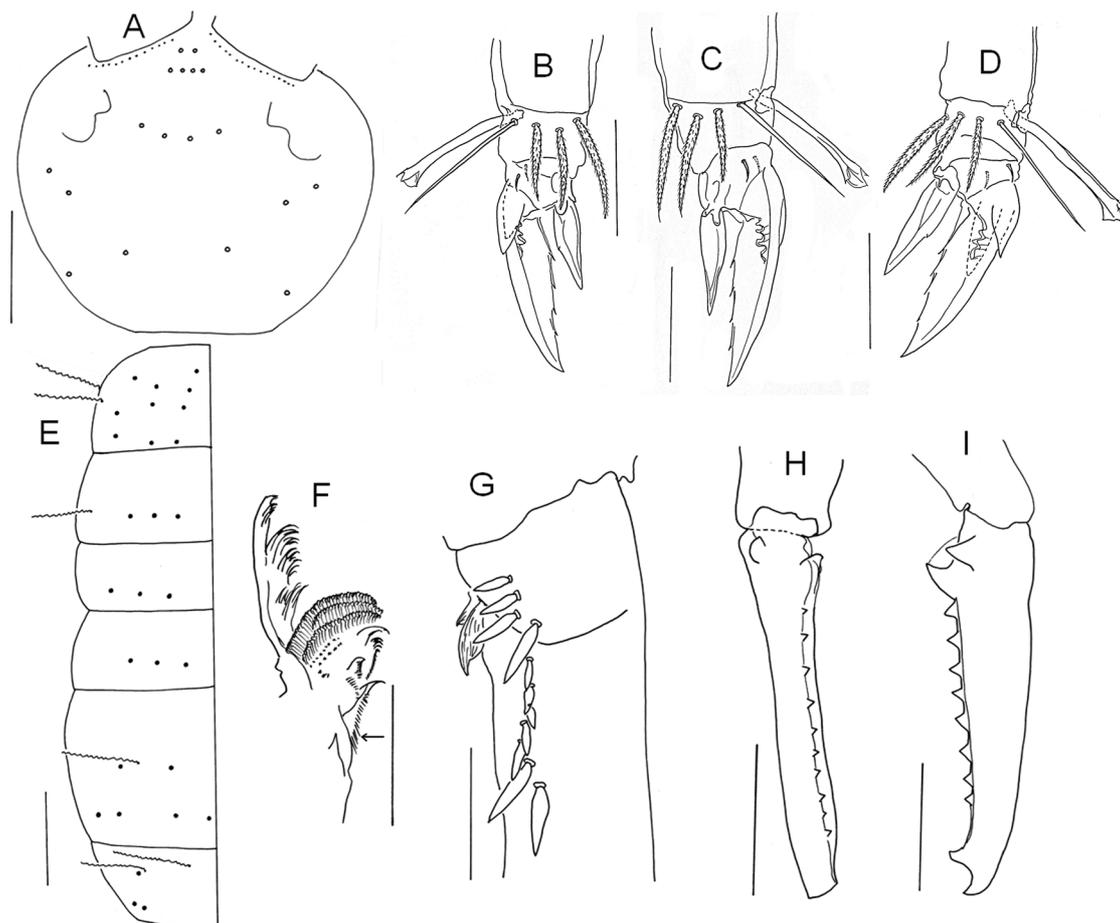
Maximum length up to 5 mm. Scale covering yellowish brown to grey-brown, posterior edges of segments appearing banded with transverse rows of large brown and grey scales (Figs. 3A, B); bothriotracha surrounded by a few white scales, those on Abd. IV with only 1 or 2 white scales; scales of Abd. IV weakly iridescent (Fig. 3C). Cuticle yellow-orange to orange (Figs. 3D–G). Eye patches dark blue to black, roughly triangular. Small pigmented spot directly posterior to eyespot. Antennal base purple, prominent ring-shaped. Small pigmented triangular patch between bases of antennae. Antennal segments with dark brown pigment, interantennal segments pale. Legs with dark orange to dark brown pigment, gradually becoming dark brown distally; coxae of all legs orange. Ventral tube and manubrium orange; dens and mucro pale.

Eyes 6+6. Antennae shorter than body, up to 0.9 times body length. Fourth segment fusiform, with rounded apex, with 9–11 subsegments; rod-like sensilla scattered sparsely along its length; pin seta slender, finely rounded at tip, with proximal spur (Fig. 7H); stout spike-like seta near base of pin seta; one truncate sensillum near apex with associated hooked setae and rod-like sensillum slightly behind hooked setae (Fig. 7H). More proximally, longer setae composed of thin sensilliform setae with rounded tips and pointed sensilliform setae in weakly defined sockets. Apex of Ant. III with truncate sensillum and associated hooked seta, 1 pair of rod-like sensilla, and several

scattered rod-like sensilla; longer setae consisting of typical setae and slender, round-tipped sensilliform setae (Fig. 7I).



**FIGURE 3.** *Pogonognathellus brevifulvus* n. sp. (A–C) Live specimens. (A) Dorsal view, specimen from Worcester County, Massachusetts, anterior and posterior illumination. (B) Dorsal view, specimen from St. Clair County, Michigan, anterior and posterior illumination. (C) Posterior abdomen of second specimen from Worcester County, MA, high-angle anterior illumination. (D–G) Lateral views of specimens in ethanol. (D) Specimen from Sevier County, TN. (E–F) Specimens from Worcester County, MA. (G) Enlargement of specimen in Fig. 2F. Scale bars: A, B, D–F, 2 mm; C, G, 1 mm.



**FIGURE 4.** *Pogonognathellus brevifulvus* n. sp. (A) Dorsal head chaetotaxy. (B–D) Fore, middle and hind foot complex, respectively. (E) Dorsal body chaetotaxy, left side: filled circles indicate macrochaetae, wavy lines indicate bothriotricha. (F) Maxilla. (G) Dental spines, right side. (H) Mucro, dorso-lateral view. (I) Mucro, lateral view. Scale bars: A, 200  $\mu$ m; B–D, F, H, I, 50  $\mu$ m; E, 400  $\mu$ m; G, 100  $\mu$ m.

Maxilla with broad lamella 1 bearing many rows of strong curved rake-like denticles behind the apical border of fine cilia. Lamella 2 with two regular rows of curved coarse rakes followed by a proximal field of finer denticles. Lamella 5 without prominent proximal beard-like projection but with long basal teeth (Fig. 4F).

Ungual inner teeth usually 4, rarely a specimen with 3 teeth on one unguis, evenly spaced on inner margin; number of teeth sometimes different on unguis of the same pair of legs. Third inner tooth from base of fore and middle unguis usually above the tip of the unguiculus. Wavy internal ridging of unguis prominent. Unguiculus lanceolate, usually with one small inner tooth, sometimes tooth absent. Tenent hair clavate, moderately stout, as long as the inner margin of unguis (Figs. 4B–D). Two strong spines on metatibiotarsus, one proximal and longer, the other distal and shorter (Fig. 7B); fore and mesotibiotarsi without differentiated spine-like setae. Pretarsal setae finely ciliate.

Manubrium dorsally with acuminate macrochaetae. Dens with spine-like scale at inner base. Dental spines brown, smooth to finely striate, terminal spines considerably longer than others, furcula 0–2, 2/5–6, 2, usually 2/5–6, 2 (Fig. 4G), number of spines sometimes different on each side. Mucro elongate with numerous ciliate setae, basal lamella, and 8–13 intermediate teeth; basal tooth less than one-fourth length of mucro away from base, lateral mucronal tooth even with basal lamella, slightly proximal to basal tooth; apical teeth subequal (Figs. 4H, I).

Head with 2+4 antero-medial macrochaetae, 2+2 interocular macrochaetae, 2+2 postocular macrochaetae, and 2+2 posterior cephalic macrochaetae (Fig. 4A). Tergal macrochaetae on each side 10,3/3,3,6,3,3; Abd. III with 2+2 anterior and 4+4 posterior macrochaetae. On Abd. IV one pair of anterior and two pairs of posterior macrochaetae (Fig. 4E). Caudal setae of Abd. VI short and straight, length about equal to segment; setae of Abd. V longer, curved, length about equal to Abd. V+VI, directed caudally. Tenaculum corpus with 1 seta.

**Etymology.** The name of this species is formed from two Latin words, *brevis* (small) and *fulvus* (reddish yellow), and refers to the relative size of this species compared to the largest members of the genus, in addition to its distinctive, orange pigmentation.

**Type specimens.** Holotype female and 5 paratypes, Massachusetts, Worcester County, Hwy 62 west of Sterling, 42.44775N 71.85141W, elev. 204 m, mixed maple-hemlock-pine forest, on sticks on ground, 8 October 2008, E. C. Bernard, coll.

**Type deposition.** Holotype and 2 paratypes deposited in INHS, 3 paratypes in UTIC.

**Additional material.** Four specimens, Michigan, St. Clair County, Algonac State Park, 42.65317N 82.51841W, elev. 172 m, 25 July 2008, oak forest next to archery range, leaf litter, 25 July 2008, E. C. Bernard, coll.

**Diagnosis.** *Pogonognathellus brevifulvus* n. sp. is distinguished from other species of the genus by its orange cuticular colour, presence of 4 small, evenly spaced unguual teeth, absence of spines on the fore and mid-tibiotarsi, and basal position of the lateral mucronal tooth. It resembles *P. mystax* in the shape of the unguis and the distribution of the dental teeth, but the species differ in head chaetotaxy (*P. brevifulvus* n. sp. possesses posterior cephalic macrochaetae, *P. mystax* lacks them), and in clypeal colour (that of *P. brevifulvus* n. sp. is orange to orange-brown, that of *P. mystax* is violet and resembles a moustache). The orange cuticular colour also occasionally occurs in strongly pigmented specimens of the following species (*P. magnibrunneus* n. sp.), but the lack of spines on the fore and middle tibiotarsi immediately distinguishes *P. brevifulvus* n. sp. This species has not been characterized molecularly.

### ***Pogonognathellus magnibrunneus* n. sp.**

(Figs. 5, 6, 7C, D, J–N)

Maximum length up to 7 mm. Scale cover medium to dark brown, scales on posterior margins of segments slightly darker; white scales around bothriotricha dispersed, forming indistinct white patches (Fig. 5A–C). Cuticle colour pale yellow to pale brown or orange with anterior reddish lateral band extending to posterior corner of mesonotum. Abd. VI orange to pale brown, especially in large specimens (Fig. 5D–G). Eye patches black, trapezoidal. Small purple pigmented triangle between bases of antennae, antennal bases orange. Antennal segment I yellow, Ant. II–IV purple, darker distally; intersegments of antennae pale. Clypeus orange to pale brown or dull violet-grey. Coxae orange to purple, femur dark brown to pale brown or purple, tibiotarsus purple. Manubrium light yellow to light brown, dens and mucro pale.

Eyes 6+6. Antennae equal to or up to 1.1 times body length. Fourth segment cylindrical, apex with prominent conoid terminus, with 16–18 subsegments; rod-like sensilla on most subsegments, occasionally paired, two or three plump sensilla on distal subsegments (Fig. 7J); pin seta finely rounded at tip, with proximal spur (Fig. 7H); stout spike-like seta near base of pin seta; 1–3 truncate sensilla near apex with associated hooked setae and plump sensillum slightly behind hooked setae (Figs. 7K, L). More proximally, longer setae composed of thin sensilliform setae with rounded tips and pointed sensilliform setae in weakly defined sockets. Apex of Ant. III with truncate sensillum and associated hooked seta, one pair of rod-like sensilla, two single plump sensilla, and several rod-like sensilla of various lengths; longer setae consisting of typical setae and slender, round-tipped sensilliform setae (Fig. 7M). Subsegments of third segment with single whorls of typical setae and round-tipped sensilliform setae (Fig. 7D). Tip of regenerating antenna (fourth segment absent) with spike-like setae, pin seta lacking side spur, two truncate sensilla, and numerous rod-like sensilla of various lengths (Fig. 7N).

Maxillary lamella 5 without prominent proximal beard-like projection but with long basal teeth (Fig. 6F). Unguis with 3 large inner teeth, the distal tooth at about the middle of the unguual inner margin. Wavy internal ridging of unguis prominent. Unguiculus lanceolate, usually with one inner tooth distal to the middle of the unguiculus. Tenent hair stout, clavate, slightly longer than inner margin of unguis (Figs. 6B–D). Differentiated macrochaetae on inner side of all tibiotarsi: 4–6, 5–7, 5–7 on fore, meso, and metatibiotarsi, respectively (Figs. 6G, 7C). Pretarsal setae finely ciliate.

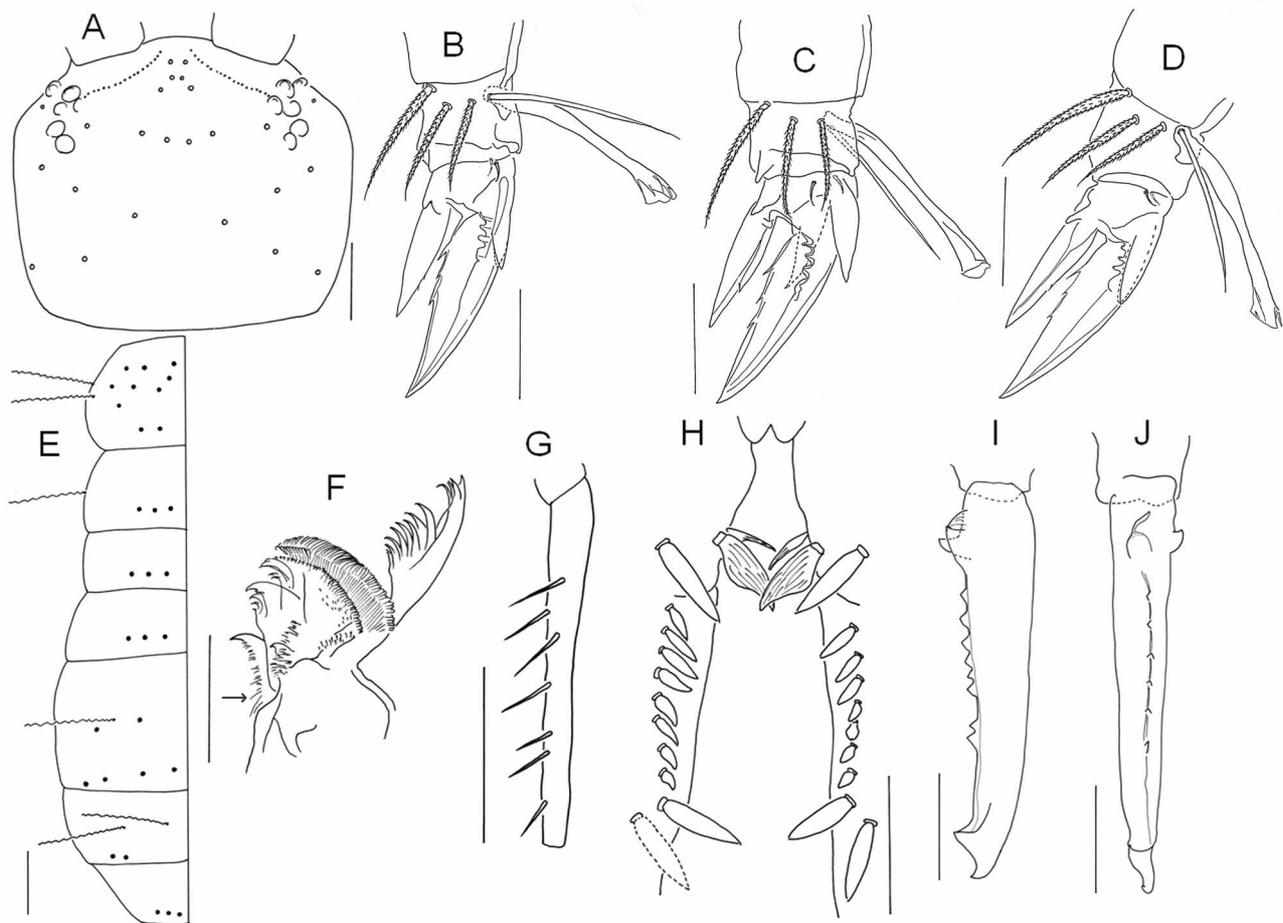
Manubrium and dens without blunt-tipped, spine-like macrochaetae. Dental spines brown, smooth to finely striate, terminal spines longer than middle spines, formula 1/5–8, 2 (Fig. 6H). Mucro elongate with numerous ciliate setae, basal lamella and 4–10 intermediate teeth; lateral basal tooth level with and nearly the same size as dorsal tooth (Figs. 6I, J).

Head with 2+4 antero-medial macrochaetae, 3+3 interocular macrochaetae, 2+2 postocular macrochaetae, and 3+3 posterior cephalic macrochaetae (Fig. 6A). Tergal macrochaetae on each side 10,3/3,3,6,2,3; Abd. III with 2+2 anterior and 4+4 posterior macrochaetae. Anterior macrochaetae absent on Abd. IV (Fig. 6E). Caudal setae of Abd. VI short and straight, length about equal to segment; setae of Abd. V longer, curved, length about equal to Abd. V+VI, directed caudally. Tenaculum corpus with one seta.

**Etymology.** The name of this species is formed from two Latin words, *magnus* (big) and *brunneus* (brown), referring to the substantial size of this species and the basic colour of the scale covering.



**FIGURE 5.** *Pogonognathellus magnibrunneus* n. sp. (A–C) Live images, specimens from Rockland County, NY. (D–G) Specimens in ethanol. (D) Specimen from Rockland County, NY. (E) Specimen from Haywood County, NC. (F) Specimen from Sevier County, TN. (G) Enlargement of specimen in Fig. 5F. Scale bars: A, B, D–F, 2 mm; C, G, 1 mm.



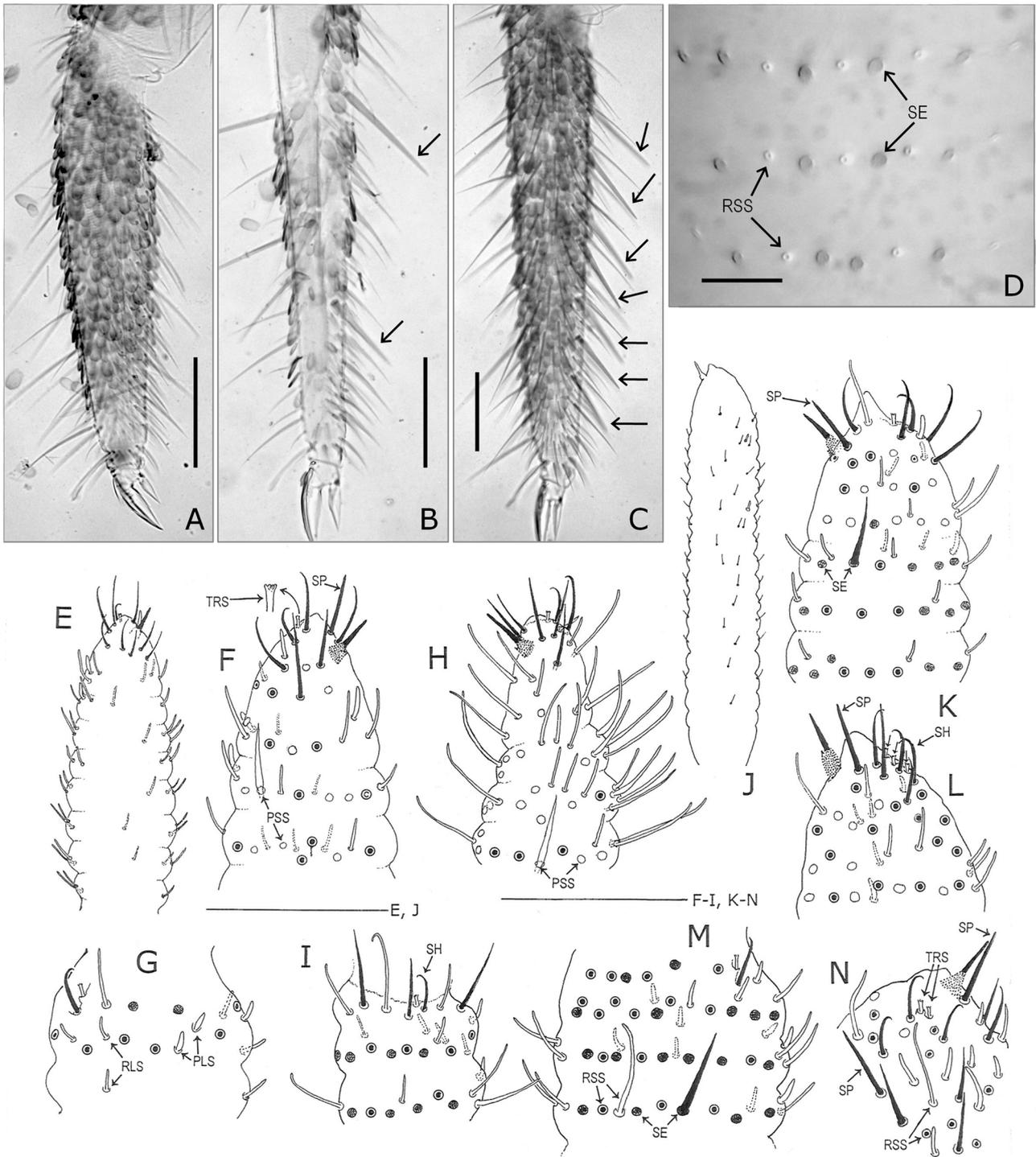
**FIGURE 6.** *Pogonognathellus magnibrunneus* n. sp. (A) Dorsal head chaetotaxy. (B–D) Fore, middle and hind foot complex, respectively. (E) Dorsal body chaetotaxy, left side, filled circles indicate macrochaetae, wavy lines indicate bothriotricha. (F) Maxillae. (G) Spines of hind tibiotarsus. (H) Dental spines. (I) Mucro, dorsal side. (J) Mucro, lateral side. Scale bars: A, 200  $\mu$ m; B–D, F, I, J, 50  $\mu$ m; E, 400  $\mu$ m; G, 500  $\mu$ m; H, 100  $\mu$ m.

**Type specimens.** Holotype female and 7 paratypes, North Carolina, Haywood County, Blue Ridge Parkway, Cranberry Ridge, 35.46580N 83.14356W, elev. 1659 m, grasses and dead leaves on rocky face with seep, 20 October 2008, K.-H. Park & E. C. Bernard, colls.; 4 paratypes, New York, Rockland County, Bear Mountain State Park E of picnic area, 41.31081N 74.00139W, elev. 362m, mixed deciduous forest, beaten from sticks and bark, 10 October 2008, E.C. Bernard, coll.; 2 paratypes dissected on slides (GenBank accession nos. GU169358, GU169359), North Carolina, Swain County, Great Smoky Mountains National Park, K. L. Felderhoff, coll., no other data; 1 paratype dissected on slides (GU169360), North Carolina, Swain County, Great Smoky Mountains National Park, Noland Ridge at Noland Creek headwaters monitor site, 23 June 2006, K. L. Felderhoff, coll.; 2 paratypes dissected on slides (GU169356, GU169357), Tennessee, Knox County, John Sevier Hunter education center, Rifle Range Road, 36.05078N 83.95336W, 25 October 2006, K. L. Felderhoff & E. C. Bernard, colls.

**Type deposition.** Holotype and 2 paratypes deposited in INHS, 2 paratypes in GRSM, 2 paratypes in NIBR, remaining paratypes in UTIC.

**Additional material.** Eighteen specimens, Tennessee, Sullivan County, Jacobs Creek Recreation Area, Jacobs Creek riparian zone, 36.5788N 81.9861W, elev. 487 m, 11 June 2008, K.-H. Park & E. C. Bernard, colls.; numerous specimens, Tennessee, Sevier County, Great Smoky Mountains National Park, Twin Creeks, 35.68613N 83.49929W, 5 November 2008, leaf litter, K.-H. Parks & E. C. Bernard, coll.; numerous specimens, Tennessee, Sevier County, Great Smoky Mountains National Park, Rainbow Falls trailhead, 35.67552N 83.486652W, 5 November 2008, K.-H. Park, coll.

**Diagnosis.** *Pogonognathellus magnibrunneus* n. sp. is a member of the *longicornis* clade, which contains those species with multiple spine-like setae on all tibiotarsi. In North America it shares this character with *P. elongatus* and *P. nigrinus*, but is easily separated by scale pattern, cuticle colour, and appearance of the furcal spine-like



**FIGURE 7.** *Pogonognathellus* spp. characters. (A–C) Tibiotarsal spine distribution. (A) Foretibiotarsus of *P. belmontorum* n. sp., no spines. (B) Hind tibiotarsus of *P. brevifolius* n. sp., two ventral spines (arrows). (C) Hind tibiotarsus of *P. magnibrunneus* n. sp., seven ventral spines (arrows). (D–N) Antennal characters. (D) *P. magnibrunneus* n. sp., distribution of setae on annules of third antennal segment, optical cross-section near setal bases. (E–G) *P. belmontorum* n. sp. (E) Fourth antennal segment, sensilla and apical setae shown. (F) Apex of fourth antennal segment, arrow points to enlargement of truncate sensillum. (G) Apex of third antennal segment. (H, I) *P. brevifolius* n. sp. (H) Apex of fourth antennal segment, most setae illustrated. (I) Apex of third antennal segment. (J–N) *P. magnibrunneus* n. sp. (J) Fourth antennal segment, only sensilla shown. (K) Apex of fourth antennal segment, one truncate sensillum. (L) Apex of fourth antennal segment, 3 truncate sensilla (small arrows). (M) Apex of third antennal segment. (N) Apex of regenerating antenna. Abbreviations: PLS, plump sensillum; PSS or circle, pointed sensilliform seta; RSS or circle with central dot, slender sensilliform seta with rounded apex; SE or darkened circle, typical dark, pointed seta; RLS, rod-like sensillum; SP, spike-like seta; SH, hooked seta; TRS, truncate sensillum. Dotted sensilla are on other side of segment. Scale bars, A–C, 100  $\mu$ m; D, 20  $\mu$ m; E, J, 100  $\mu$ m; F–I, K–N, 50  $\mu$ m.

macrochaetae. In *P. magnibrunneus* the scale covering is predominantly brown and the cuticle is light yellow to yellow-orange. *Pogonognathellus elongatus* has a bold pattern of white, brown, and black scales, and the cuticle is pale with a prominent lateral purple stripe extending from the eyepatch to the posterior of the mesonotum. *Pogonognathellus nigrinus* has a deep glossy violet-black scale covering and the cuticle is largely or completely violet or purple. Both *P. elongatus* and *P. nigrinus* have 6 stout, pigmented, blunt, spine-like macrochaetae on the furcula (2+2 manubrial, 1+1 dental) (Felderhoff *et al.* 2010, Maynard 1951). In the new species these long macrochaetae are pale, slender, and acuminate.

**Remarks.** This species was collected in abundance in the southern Appalachian region of Tennessee and North Carolina, but also was found in the Adirondacks of New York near the Hudson River. It is likely that this species occurs all along the Appalachian range between New England and northern Georgia. In the molecular analysis of Felderhoff *et al.* (2010), this species is represented by GenBank accession numbers GU169356-GU169360.

## Discussion

**Antennae.** The antennae of tomocerids are difficult to study for a variety of reasons. Their long length probably provides enhanced perception of the environment well ahead of the body, but this length is likely to lead to more damage due to premature predator attacks. Often they are broken in life or damaged during capture of the specimen; thrashing of specimens in ethanol frequently results in the antennae breaking between the second and third segments. In preservatives, any jostling of specimens will cause additional breakage. This problem also occurs with the mucrones, dentes, dental spines, and tibiotarsal spines and claws, which often fall off specimens stored for years.

By use of differential interference-contrast microscopy, we differentiated 8 forms of setae and sensillum-like setae on Ant. III and IV (Table 1). Among these, the truncate sensilla (TRS) at the apices of the segments are distinctive. They appear to have lobes or a brush-like tip (Fig. 7F), but our microscopic resolution was not fine enough to determine the exact structure of this sensillum. The TRS always was associated with a hooked seta (SH) and a small sensillum. Most antennae possessed one TRS at the tip of the fourth segment, but *P. magnibrunneus* **n. sp.** also exhibited two or three TRS (Fig. 7L). Increased TRS number may be a reflection of antennal regeneration. Examination of several 3-segmented regenerating antennae of *P. magnibrunneus* **n. sp.** revealed at least two TRS at the apex, along with a pin seta and multiple spike-like setae (SP) (Fig. 7N).

Homologies of *Pogonognathellus* structures with organites and the third segment sensory complex could not be determined with certainty, although the TRS of the fourth segment may be the organite of that segment. Likewise, homologies with the antennal seta designations of Andre (1988) also are uncertain, but based on definitions in Andre (1988), SE, HS, and SP are normal setae, RSS and PSS are eupathidia, and PLS, RLS, and TRS are solenidia.

Prior to the current paper, there appears to have been little study of tomocerid antennae as has occurred with other families. Lukić *et al.* (2010) published SEM images and a photomicrograph of the antennae of *Tritomurus veles* Lukić, Houssin and Deharveng, 2010, a Croatian cave species, that provide important information on the antennal setae and shape of the antennal apex. They differentiated three types of setae on the third antennal segment (Table 1), which we also observed (Figs. 7G, I, M). The arrangement of setae on the third segment also appear similar with alternating dark setae (SE or ordinary mesochaetae) and sensilliform setae (RSS or S-like mesochaetae) in a single whorl about each subsegment (Fig. 7D). *Tritomurus veles* has two well-defined apical lobes on Ant. IV, unlike *Pogonognathellus* spp., which possess one apical projection or none at all.

The basic arrangement of setae and sensilla on *Pogonognathellus* antennae probably are not useful diagnostic characters at the species level, given the similarity of the 3 species described in this paper as well as the difficulty of their observation. Antennae of *P. elongatus* also were examined and were found to be similar. Furthermore, these characters are not exclusive to *Pogonognathellus*. Setae and sensilla of the antennal apices of *Tomocerus vulgaris* Tullberg were nearly identical to those described in this paper, including the presence of TRS at the apices of the third and fourth segments.

**Imaging.** The appearance of scale patterns on live specimens can vary significantly with the direction and angle of lighting. At certain lighting angles the scales can be highly reflective and provide false patterns. For instance, with lighting from behind a specimen, scales may appear to form a striped pattern, especially on the pos-

terior segments (see Fig. 3B). These apparent stripes will move transversely if the light is shifted to one side or another, indicating that the stripes are a product of scale reflectivity, not a true colour. Also, posterior lighting obscures the white scales around the bothriotricha, which appears to be a generic character (Felderhoff *et al.* 2010). Imaging of the posterior segments to illuminate the white spots is best achieved with light from in front of a specimen, at a medium to low angle.

**Projected diversity.** We have taken a conservative approach to the recognition of undescribed *Pogonognathellus* spp. by including only those specimens that were collected in the type locality or that were verified by molecular means as conspecific. We have collected many specimens that at first glance closely resemble the species described previously and herein, but close attention to colour patterns, unequal tooth arrangement, and molecular correlation often has excluded them from the species being described. According to the analysis in Felderhoff *et al.* (2010), North American *Pogonognathellus* spp. are much more diverse than previously recognised, but most morphological characters are similar among the species. More recent collecting in other parts of the continent (upper Plains states, Rocky Mountain states, Pacific Northwest) has resulted in many additional undescribed species that are morphologically and molecularly distinct from those described previously and in this paper. Although the total number of North American *Pogonognathellus* spp. cannot be estimated at this time, the number is certain to be far larger than the sum of currently valid species.

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