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Review of *Agrenia* Börner, 1906 with descriptions of four new species from North America (Collembola, Isotomidae)

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Abstract

The eight known species of *Agrenia* are reviewed and new distributional data are added. Two species groups are suggested for the genus: a *bidenticulata*-group with a mucronal seta and an *agilis*-group without a mucronal seta. Four new species of the second group are described from North America: *A. falcula*, *A. parkeri*, and *A. tarashchukae* from forest streams of the Appalachian Mountains in Tennessee, North Carolina, and New York, and *A. extrema* from glaciers in Washington and Alaska. The head of the maxilla is introduced as a useful character for separation of some species. A key to all species is given.

Key words: allometry, cyclomorphosis, Holarctic, key to species, sexual dimorphism

Introduction

From the time of its description in 1906 until 1986 the genus *Agrenia* Börner, 1906 was considered monotypic with the type species, *Isotoma bidenticulata* Tullberg, 1876, described from Novaja Zemlja, Russia. Fjellberg (1986) described six new species from various parts of the Holarctic region. A seventh species was later described from Pennsylvania (Fjellberg 1988). *Agrenia* spp. are restricted to colder, wetter regions of the Holarctic and usually found along small mountain streams. In eastern North America, the genus extends south into the higher elevations of the southern Appalachian Mountains. The diversity of the genus appears to reach a maximum in the mountainous parts of the eastern and western states of the US and Canada, where currently five species are found. A further two Holarctic species are found in Alaska and northern Canada, and one possibly endemic species is found in Japan. In the present paper three more species are described from edges of forest streams in the Appalachian mountains of Tennessee, North Carolina and New York, and a fourth species is described from glacier ice in Washington and Alaska. In the descriptions below, 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. The claw index is the length of the claw divided by the length of the tunica (Fjellberg 1986).

Agrenia Borner, 1906

Diagnosis

Characters that differentiate *Agrenia* from other genera of Isotomidae are the presence of dorsal tubercles and a prolonged subapical seta on the dens, fused dorsal basal teeth of the claws forming a prominent tunica, trifurcate maxillary palp lacking sublobal setae, and a large number of setae in the proximal and basomedial

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fields of the labial palp. The number of sensilla on the tergites is greater than in related isotomid genera but within species is variable, and thus is of little value for diagnosis of the genus and the species. These sensilla occur in the p-rows on the tergites of Abd. II-V and also in the mid-regions of these segments. The second and third thoracic segments and the first three abdominal segments each have a pair of spine-like microsensilla.

Cyclomorphosis, allometry, and sexual polymorphism

The presence of distinctly different morphological forms that occur during the life cycle of *Agrenia* specimens causes problems for identification of species. The different "morphs" could easily be mistaken for being different species. Three phenomena affect the morphology of *Agrenia* during the lifespan of the individual:

a) Cyclomorphosis is the appearance of distinct summer and winter forms. This phenomenon is common in northern species of the Isotomidae, and was first described in the genus *Desoria* (Fjellberg 1976, 1978, Zettel & Zettel 1986). In *Agrenia* the shape of the claws and mucro are affected. In winter forms, the claws generally become more robust with a relatively larger tunica, the mucro is shortened, and the apical mucronal tooth is reduced (subapical tooth becomes more prominent). This change is observed in *A. riparia* Fjellberg, *A. cyanura* Fjellberg, and *A. parkeri* **n. sp.** Cyclomorphosis may well occur throughout the genus, but for most species sufficient winter samples have not been collected to determine if it is a general phenomenon. Species living permanently in cold environments, such as the glacial species *A. atroviridis* Fjellberg and *A. extrema* **n. sp.**, are “in winter mode" even in summer.

b) Allometry refers to changes in body proportions during growth of the individual. All Collembola change their body proportions during growth from juvenile to adult, but in *Agrenia* these changes also continue into the post-mature instars. In *A. polymorpha* Fjellberg the length of the antennae in relation to head size continues to increase after maturity (Fjellberg 1986). Both females and males are affected, but males generally have longer antennae than females. The same phenomenon is observed in *A. parkeri* **n. sp.** (Fig. 4).

c) Sexual polymorphism refers to the presence of discrete morphs in successive reproductive and non-reproductive instars. In many groups of Collembola, the reproductive male instars have modifications of the setae, extremities, and other characters. This phenomenon is generally called epitoky (Fjellberg 1977). Most common is the transformation of normal setae on the antennae, head, or abdominal tip to short, spiniform setae. Goloshchapova *et al.* (2005) showed that the modified setae of the antennae in reproductive males of *Vertagopus pseudocinereus* probably have a function during male/female courtship. These morphological changes are usually of one type only. In *Agrenia*, however, reproductive males are sometimes polymorphic, displaying several changes. Fjellberg (1986) showed that *A. polymorpha* had three forms. The smallest reproductive males came in two types: neutral, which were similar to females and unreproductive males in having short antennae and without modified setae, and males with short setae, which had prolonged antennae and shortened setae on Abd. V-VI as well as modified (granulate) cuticle on the abdomen and differentiated circumanal setae. The third form consisted of large males, probably representing the next reproductive instar in the growth cycle, having very long antennae with swollen basal segments, shortened setae on Abd. V–VI, and with the terminal abdominal segment enlarged and upturned. These "supermales" display characters that are of an allometric nature, becoming more strongly expressed in successive instars.

Although similar epitokous phenomena have not been studied in detail in other species, they have been observed in *A. lamellosa*, *A. cyanura*, *A. riparia*, and *A. parkeri* **n. sp.**. For instance, males of *A. cyanura* have short, stiff setae on the head, thorax, and abdominal segments I and II, as well as a distinctly rugose cuticle, while the tip of abdomen is unaffected. In certain species the reproductive males are unmodified (*A. bidenticulata*, *A. falcula*).

Systematics and survey of species

No attempt has been made to make a phylogenetic arrangement of the known species of *Agrenia*. The two provisional groups, with and without a lateral seta on the mucro, may reflect a single phyletic cleavage with retention of the seta in the plesiomorphic branch, but the loss of the mucronal seta also may have occurred several times during evolution of the species complex. The well differentiated characters of the maxilla, claws, and mucro are probably adaptive and related to particular feeding habits and a life in close proximity to running water.

a) *A. bidenticulata* group, four species with lateral mucronal seta present

Agrenia bidenticulata (Tullberg, 1876)

This taxon is the type species of the genus. Fjellberg (1986) redescribed the species and designated a lectotype and paralectotypes from the original sample from Novaja Semlja, collected in 1875 and kept in Naturhistoriska Riksmuseet, Stockholm.

Among the species with a mucronal seta, *A. bidenticulata* may be recognised by few (fewer than 13) anterior setae on the ventral tube, a short, curved mucro, and pigmentation of the body usually not uniform (some segments darker than rest). Reproductive specimens lack modified setae.

The species is common in damp Arctic tundra of the Holarctic region (Babenko & Fjellberg 2006) and is also frequent along streams and lakes in the Scandinavian mountains, in the highlands of Great Britain, and in continental Europe south to the Mediterranean area. In Asia the distribution of *A. bidenticulata* follows the Arctic coast, while the southern limit is unknown (Potapov 2001). In North American it is reliably recorded from Alaska and arctic Canada, but more southern populations probably represent other species.

Agrenia pilosa Fjellberg, 1986

This species was described from Japan and no further records are known. It differs from other members of the *A. bidenticulata* group in the increased number of anterior setae on the ventral tube (more than 30 on each side in large specimens) and a dense field of setae ("moustache") along the anterior frontoclypeal edge. The original sample came from snow on Mt. Syari-dake, elevation 600 m, Hokkaido.

Agrenia polymorpha Fjellberg, 1986

This species occurs in the Canadian and U.S. Rocky Mountains where it lives in wet moss along streams, springs and waterfalls. Fjellberg (1986) described a complex sexual polymorphism and allometric growth pattern affecting the shape and relative length of the antennae, and changes in setae and structure of the cuticle. Diagnostic characters of the species are presence of a mucronal seta in combination with few anterior setae on the ventral tube (fewer than 13), uniform body colour, and sexual polymorphism.

Agrenia lamellosa Fjellberg, 1988

This eastern North American species is so far known only from Pennsylvania (Centre, Delaware, Luzerne counties), living in damp moss and litter along forest streams. It has only a few anterior setae on the ventral tube (fewer than 6 on each side), a lateral seta is present on the mucro, and the elongated mucro has a prominent set of broad lamellae. Reproductive males have slightly shortened body setae on Abd. V–VI.

b) *A. agilis* group, eight species with lateral mucronal seta absent

***Agrenia agilis* Fjellberg, 1986**
Figs. 1M; 3A; 6B, E

So far this species is known only from the Pacific Northwest region bordering the Juan de Fuca and Georgia Straits (Olympic National Park, Washington, and Garibaldi Provincial Park, British Columbia, respectively). It was collected from moss along mountain streams and waterfalls. The species is recognised by its markedly prognathous head (Fig. 3A), abundant anterior setae on the ventral tube (more than 10 on each side), apical tooth of mucro much larger than subapical tooth (Fig. 6B), slender claws, and normal, thin, setae on the body.

***Agrenia cyanura* Fjellberg, 1986**
Figs. 3C, D

This species probably is widely distributed in the Rockies, with records from British Columbia, Idaho, Oregon, and Utah, living in wet moss along mountain streams. It is similar to *A. agilis*, but separated by head shape, which is normal and not prognathous, the stouter claws, and dense *Isotomurus*-like setal vestiture on the abdomen. Reproductive males may have short setae and a rugose cuticle on the thorax and anterior abdominal segments.

***Agrenia riparia* Fjellberg, 1986**

Agrenia riparia is a widely distributed northern species, with records from Norway, Sweden, central Alaska (Fairbanks), northwestern Siberia (S Taimyr: Putorana) (Babenko, 2002), and northeastern Siberia (Magadan). In Scandinavia it tends to replace *A. bidenticulata* as a stream bank species in the forested regions, whereas *A. bidenticulata* is more common in arctic and alpine tundra. In the zone of overlap the two species can be separated by the mucronal seta (present in *A. bidenticulata*, absent in *A. riparia*). In winter animals the mucro and claws are shortened. Reproductive males have shorter and finer setae on Abd. IV–VI than non-reproductive males.

***Agrenia atroviridis* Fjellberg, 1986**
Fig. 3B

This species was originally described from glacial ice in Garibaldi Park, British Columbia. We have examined recent material from Alaska (Matanuska Glacier) and British Columbia (Overlord and Wedgemount Glaciers) (all collected by P. Hartzell). The species appears to be restricted to the glacial fauna, having adaptations such as extremely dark greenish black colour all over the body (Fig. 3B) and short extremities. Also, the compact mucro with a small apical tooth is a trait generally present in winter *Agrenia* spp. and other Collembola associated with snow and ice.

***Agrenia parkeri* n. sp.**
Figs. 1C, D, J; 4A, B.

Type material. Holotype (in ethanol, not sexed) and 25 paratypes (ethanol) from USA, Tennessee, Sevier County, Great Smoky Mountains National Park, Rainbow Falls Trail, N35º39.862', W 83º27.599', 06.VI.2007,

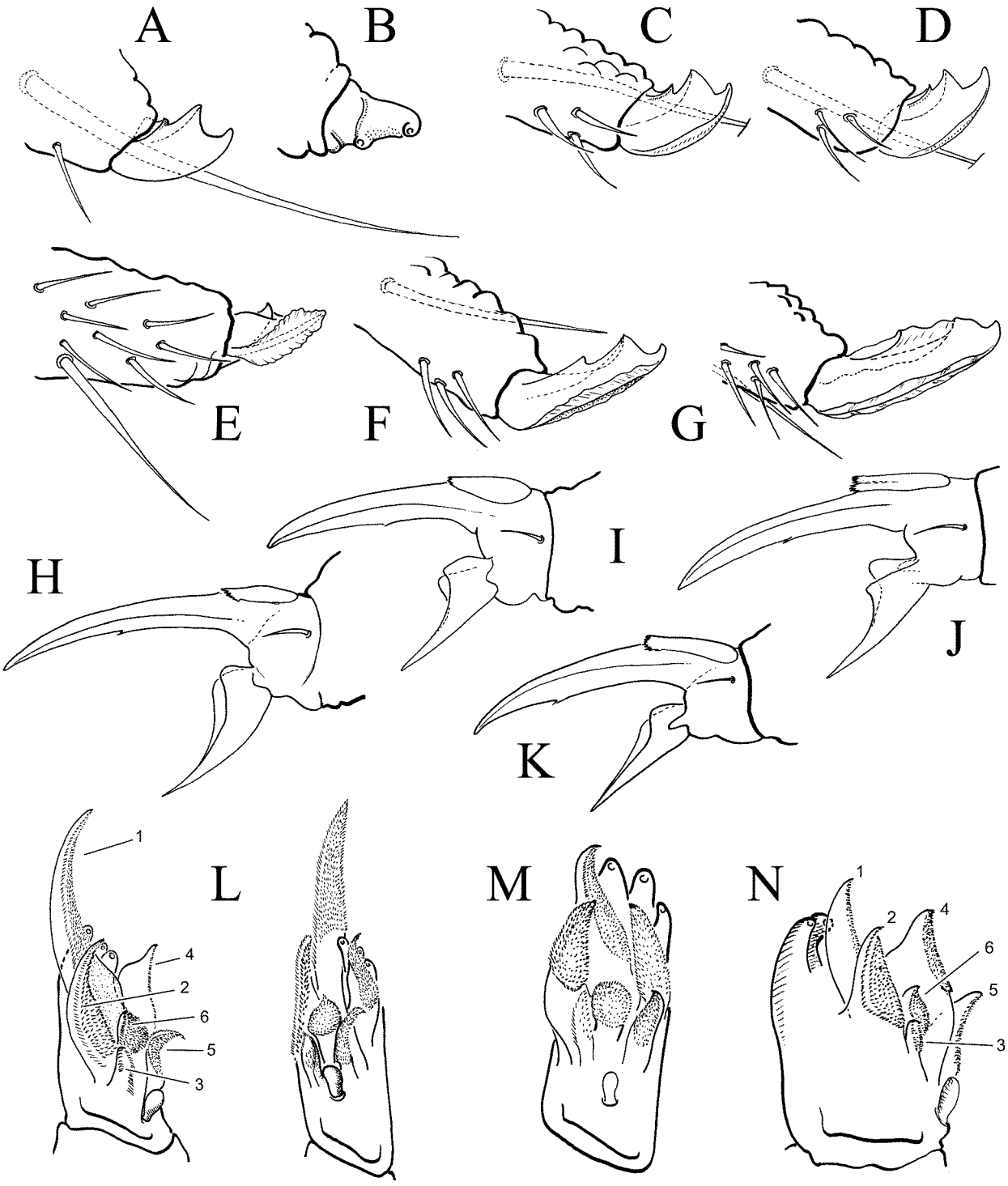

FIGURE 1. A-G, mucro shapes of *Agrenia* spp. A. *A. extrema* **n. sp.**, lateral view; B. *A. extrema* **n. sp.**, dorsal view; C. *A. parkeri* **n. sp.**, winter form; D. *A. parkeri* **n. sp.**, summer form; E. *A. falcula* **n. sp.**, ventral view showing the broad ventral lamella; F. *A. falcula* **n. sp.**, lateral view; G. *A. tarashchukae* **n. sp.** H-K, claws of hind legs. H. *A. falcula* **n. sp.**; I. *A. tarashchukae* **n. sp.**; J. *A.parkeri* **n. sp.**, winter form; K. *A. extrema* **n. sp.** L-N, maxillae. L. *A. extrema* **n. sp.**, ventral side (left) and inner side (right); M. *A. agilis*, inner side; N. *A. falcula* **n. sp.**, ventral side.

moss along stream, elevation 1,372 m, A. Fjellberg, sample number 07.188. Holotype and 15 paratypes deposited in the National Museum of Natural History, Washington, D.C.; remaining paratypes deposited in the University of Tennessee Entomology Collection. Additional material collected in late winter to early summer from Swain County, Great Smoky Mountains National Park, Noland Creek headwaters drift net samples,

20.I.1993 to 11.V.1993 (see Bernard & Felderhoff 2007), and from the banks of many other coldwater streams on the North Carolina side of Great Smoky Mountains National Park (Haywood County: Purchase Knob, Cataloochee River; Swain County: Clingman's Dome; Buncombe County: Elk Pasture Gap), as well as other North Carolina specimens from Graham County (several locations along Cherohala Skyway) and Yancey County (Mt. Mitchell State Park).

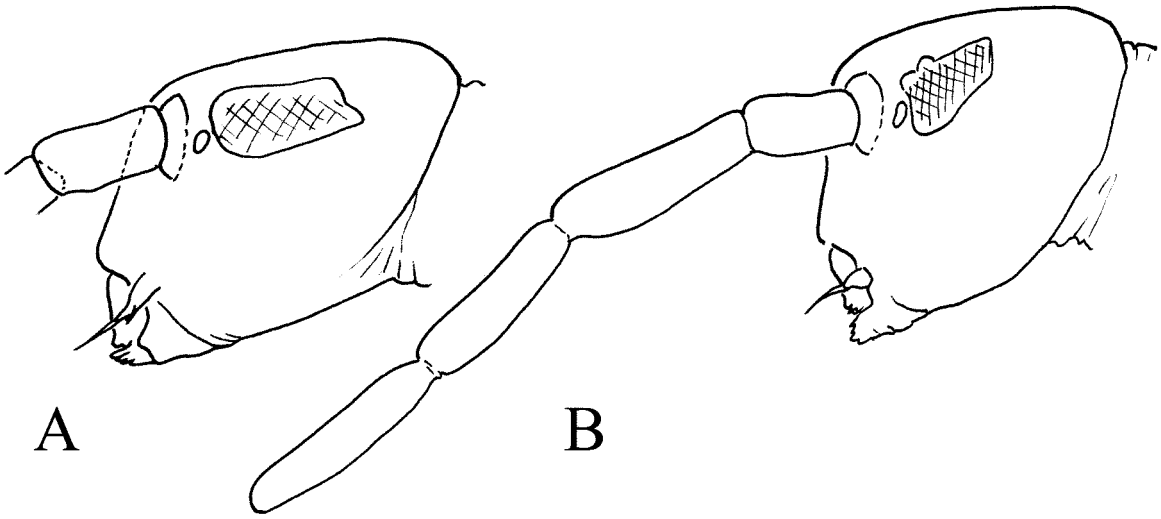

FIGURE 2. Head shape in *Agrenia* spp. A. *A. parkeri* **n. sp.**; B. *A. falcula* **n. sp.**, reproductive male.

FIGURE 3. Habitus of *Agrenia* spp. A. *A. agilis*; B. *A. atroviridis*; C. *A. cyanura*, lateral; (D) *A. cyanura*, dorsal. Scale bars = 1 mm.

FIGURE 4. General habitus of *Agrenia parkeri* **n. sp.**: female (upper left), male (lower left) and from dorsal side. Scale bars = 1 mm.

Description. Size up to 2.1 mm. Colour olive, uniform, darkest on dorsal side. Legs, furca and sides of head paler. Antennae bluish red, paler towards base. No sharp mid-dorsal line on tergites. Specimens with pale ground colour usually with posterior edges of tergites narrowly darkened. Maxillae with short, unmodified lamellae densely packed with fine denticles; lamella 1 just passing tip of maxillary head. Large males with relatively longer antennae than females, up to 2.7 times length of head diagonal; in smaller individuals (juveniles) antennae about 1.5 times length of head diagonal. Sensilla of antennae normal, without particularly dense sensilla on the fourth segment. PAO oval, length about 1.3 times the diameter of nearest ocellus. Head shape in adults slightly prognathous (Fig. 2A). Head and thorax with mixed short and long setae, remainder of body with short, fine setae. In reproductive males setae of Abd. V–VI distinctly shortened. Setae along frontoclypeal edge slightly longer and denser than the rest of the frontoclypeal area. Ventral tube with 0–6 anterior setae on each side (usually 4 or 5), lateral lobes with 10–20 setae on each side, caudal side with more than 35 setae in large individuals. Retinaculum with more than 25 setae in large specimens. Claws long and slender, particularly in animals collected in summer. Winter animals with relatively longer tunica at base of claws (Fig. 1J): claw index 2.0–2.7 (winter), 2.8–4.5 (summer). Inner edge of unguis with small middle tooth. Mucro without lateral seta, in summer animals less curved and with larger apical tooth than in winter animals (Figs. 1C,D). Subapical seta on dens strong, reaching well beyond tip of mucro. Ventral lamella of mucro moderately widened in the middle.

Etymology. Named for Dr. Charles Parker, U.S. Geological Survey, whose collection of hundreds of this species in Noland Creek headwater drift nets stimulated large-scale surveys for Collembola in Great Smoky Mountains National Park.

Discussion. Among species without a mucronal seta, *A. parkeri* **n. sp.** is recognized by the moderate number of anterior setae on the ventral tube (the two northern species *A. atroviridis* and *A. riparia* usually have no anterior setae, at most 1–2 in *A. riparia*), apical mucro tooth subequal to or smaller than subapical

tooth (in *A. agilis* the apical tooth is much larger than the subapical tooth and body colour is not olive), and PAO longer than the diameter of the nearest ocellus (in *A. cyanura* the PAO is smaller, the ventral tube has more anterior setae, and colour is different).

The cyclomorphic (winter/summer) change in shape of claws and mucro is similar to that described for *A. riparia* (Fjellberg 1986). The allometric growth in antennae and modified setae in reproductive males also are seen in *A. polymorpha*.

Distribution and ecology. Apparently widely distributed at higher elevations of the southern Appalachian Mountains (750–1,980 m) where it may be collected in great numbers in moss and debris along cold water streams. Highest numbers near the Noland Creek headwaters (~1,700 m elevation) were collected in drift-net samples in late winter and early spring when snow still covered the ground (Bernard & Felderhoff 2007, recorded as *Agrenia* sp.).

***Agrenia extrema* n. sp.**
Figs. 1A, B, K, L; 6D

Type material. Holotype: Unreproductive male (slide), USA, Washington, Whatcom County, Easton Glacier, N 48º 44' 38", W 121º 50' 01, on snow, 4.VIII.2002, P. Hartzell, coll. Paratypes: One male and one female (on two slides) from the type locality, same data. All types deposited in the National Museum of Natural History, Washington, D.C. Additional material from USA collected by P. Hartzell: Two specimens from Lower Curtis Glacier, Whatcom Co., Washington, on snow, 1,600 m., 6.VIII.2002; six specimens from Columbia Glacier, Snohomish Co., Washington, 1,600 m, 4.VIII.2002; four specimens from Shoup Glacier, Alaska, and two specimens from Ptarmigan Glacier, Alaska, summer 2003.

Description. Size up to 3.5 mm. Colour uniform, dark brownish green. Antennae, legs and furca paler. Antennae long and slender, up to twice the length of head diagonal. Ventroapical and inner side of Ant. IV with dense short, erect sensilla (Fig. 6D). Head distinctly prognathous, frontoclypeal setae not differentiated. PAO oval, slightly longer than diameter of nearest ocellus. Maxilla (Fig. 1L) with lamella 1 reaching far beyond tip of capitulum, with a dense fringe of short cilia along the edges, otherwise covered with fine denticles; lamella 2 reaching tip of capitulum, with short cilia along ventral edge, otherwise with short denticles that are stronger than on other lamellae; lamella 3 small, situated at base of lamella 2, with only a few denticles; lamellae 4–6 densely covered with fine denticles. Body setal vestiture short and fine, macrochaetae only developed on inner side of femora and on tip of abdomen. Ventral tube in adults with 3–10 anterior setae on each side and more than 30 lateral and 40 caudal setae in large specimens. Retinaculum with more than 25 setae. Claws slender, unguis with distinct inner tooth in the middle (Fig. 1J). Claw index 1.8–2.0. Mucro short and compact, apical and subapical teeth subequal, small basolateral tooth present (Figs. 1A,B). Mucronal seta absent. Males present, sexual dimorphism not observed (no reproductive males seen).

Etymology. The name reflects the extreme habitat and the unusual maxilla.

Discussion. This exceptionally large *Agrenia* is immediately recognised by the modified maxilla, in which lamella 1 is much longer than the capitulum. In other species lamella 1 either does not reach the capitulum tip, or only slightly bypasses it. Also, the presence of numerous short, erect sensilla on Ant. IV is unmatched by other species. All *Agrenia* spp. have these sensilla, but never as densely packed as in *A. extrema*.

Distribution and ecology. Alaska and Washington (see above). The remarkable habitat of this species (snow and icefields) and the long, delicate maxillary lamellae probably indicate a feeding habit based on sweeping organic particles from melt water on the glacial ice.

***Agrenia falcula* n. sp.**
Figs. 1E, F, H, N; 2B; 5A, B; 6C

Type material. Holotype (ethanol) and 43 paratypes, USA, North Carolina, Roan Mountain, Powers Branch, Southern Appalachian Highlands Conservancy, seep, elevation 1,423 m, 14.VI.2000, P. Jennings and A. Trently coll. Additional material examined: Two samples from USA, North Carolina, Haywood County, Great Smoky Mountains National Park, Purchase Knob, A. Fjellberg, coll., June 2007. Holotype and 25 paratypes deposited in the National Museum of Natural History, Washington, D.C.; remaining paratypes deposited in the University of Tennessee Entomology Collection.

Description. Size up to 1.4 mm, reproductive male 1.1 mm. Dorsal side of thorax and abdomen bluish or violet brown, usually pale (Fig. 5A). Broad midsections of Th. II-III and Abd. V-VI generally darkest. Posterior edges of tergites narrowly darkened. Tergites without sharp middorsal line. Head very pale, almost white, dark pigment present only as a middrosal occipital spot behind the dark eye fields (Fig. 5B). Area between eyes and antennal base diffusely darkened in large specimens. Mouth region and sides of head completely unpigmented. Head shape weakly prognathous (Fig. 2B). Antennae violet blue, 1.7–2.0 times length of head diagonal. Legs light blue, furca unpigmented. Maxillae with short, unmodified lamellae, lamella 1 slightly bypassing tip of capitulum (Fig. 1N). PAO oval, length about 1.4 times diameter of nearest ocellus. Setae on head and body short, thin, delicate, and sparse, of uniform length. Setae along frontoclypeal edge not differentiated. Ventral tube with 1–5 anterior setae on each side, 6–13 lateral setae, and more than 20 caudal setae. Retinaculum with 15–20 setae. Claws very slender, with small indistinct tooth at middle of inner edge; tunica short, claw index 3.0–3.9 (Fig. 1H). Mucro slender, with apical and subapical teeth of similar size; basal tooth strong (Fig. 6C); ventral edge straight, with broad lamella; mucronal seta absent; differentiated subapical seta on dens not reaching beyond tip of mucro (Figs. 1E-F). Reproductive males with unmodified setae on tip of abdomen.

Etymology. The name reflects the thin, slender claws (*falcula* [L]: little sickle).

Discussion. The small body size, elongate mucro without lateral seta, short subapical seta on dens, and very slender claws with small tunica differentiate this species from other *Agrenia*. The mucro is similar to that of *A. lamellosa*, but in that species the lateral seta is present (Fjellberg 1988). For separation from *A. tarashchukae* **n. sp.**, see below. Only summer animals were seen. Winter samples may have specimens differing in characters of claws, mucro and antennae.

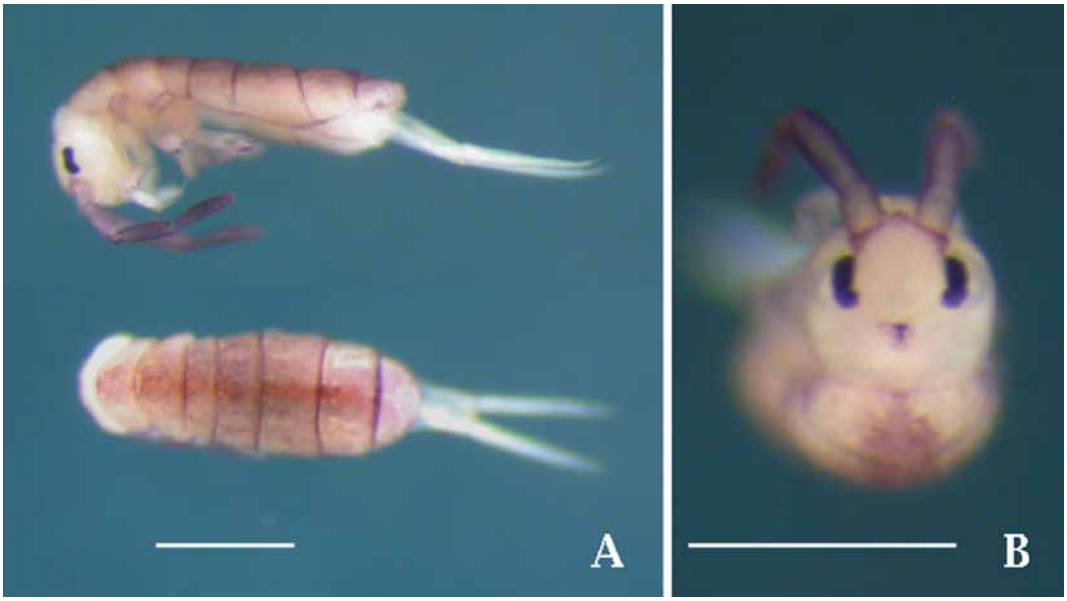

FIGURE 5. *Agrenia falcula* **n. sp.**, holotype. A. Habitus; B. Dorsum of head. Scale bars = 500 μm.

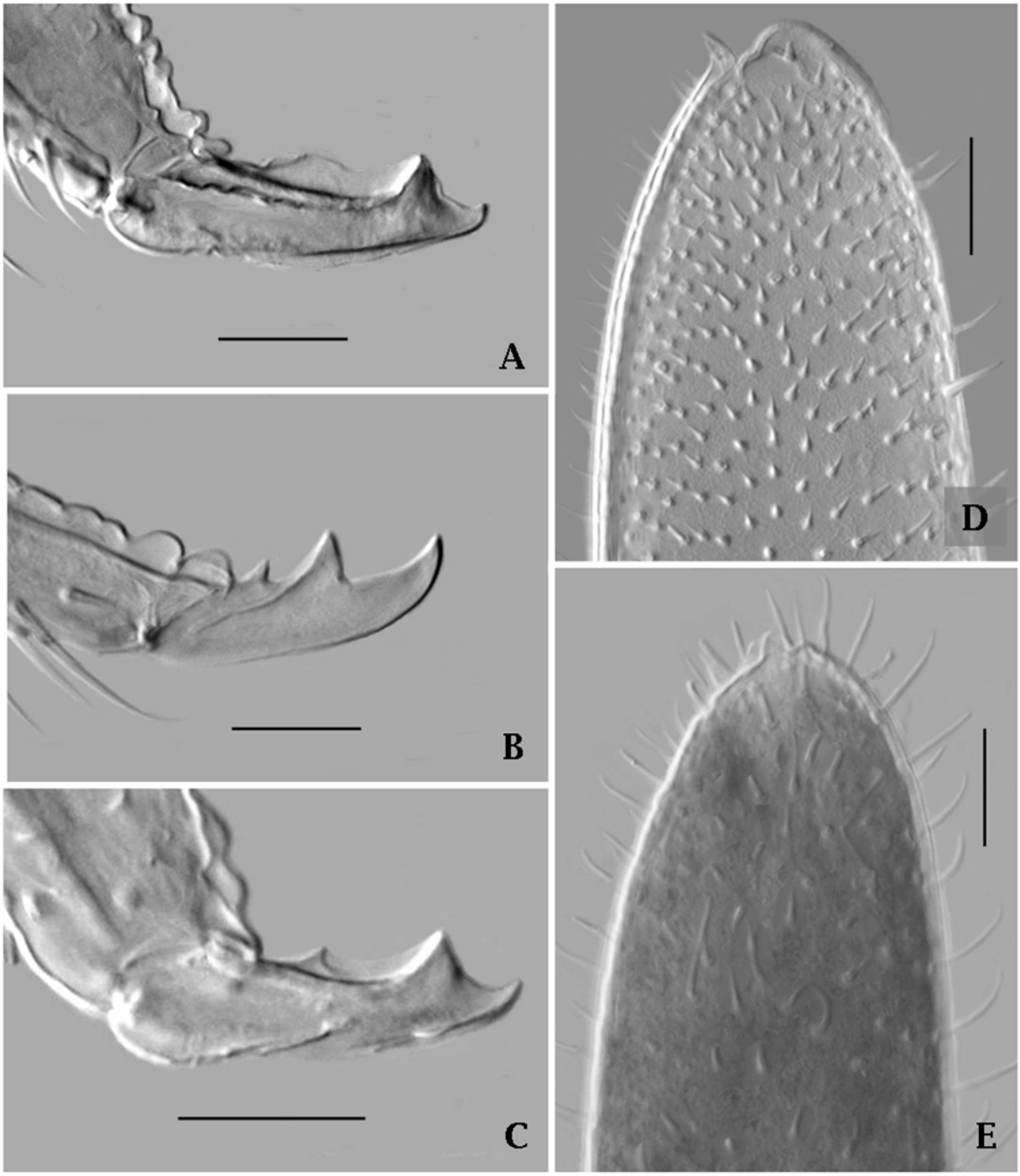

FIGURE 6. *Agrenia* spp. A-C, mucrones. A. *A. tarashchukae* **n. sp.**; B. *A. agilis*; C. *A. falcula* **n. sp.**; D-E. Tips of Ant. IV. D. *A.extrema* **n. sp.**; E. *A. agilis*. Scale bars = 20 μm.

If the samples are representative, this species is the smallest *Agrenia* known. In particular, a reproductive male of only 1.1 mm is unusual. These small adults have "juvenile" traits, e.g., relatively short antennae, few setae on ventral tube, pale colour, and short subapical seta on the dens. We have considered the possibility that *A. falcula* **n. sp.** may be small *A. parkeri* that will develop typical characters of the latter (e.g., long subapical seta on dens) after continued growth. The existence of different reproductive "morphs" appearing during continued growth was described in *A. polymorpha* (Fjellberg 1986). Although we have no clear evidence that *A. falcula* and *A. parkeri* are conspecific, the case should be examined with molecular methods or with long-term studies of field/laboratory populations.

Distribution and ecology. This species is known so far only from high elevations of the southern Appalachian Mountains, in damp moss along cold streams, seeps, and springs.

***Agrenia tarashchukae* n. sp.**
Figs. 1G, I; 6A

Type material. Holotype: Female (slide) and 10 paratypes on 6 slides from USA, New York, Minnewaska State Park Preserve, Awosting Falls, moss in the spray zone, 27.V.1996, M. Tarashchuk, coll. Holotype and 6 paratypes deposited in the National Museum of Natural History, Washington, D.C.; remaining paratypes deposited in the University of Tennessee Entomology Collection.

Description. Largest specimen seen 1.7 mm. Precise colour not observed as only slide specimens were available, but appearing to have been of uniform colour without marked pattern. Head shape normal, not prognathous. Antennae 1.8–1.9 times the length of head diagonal. Maxilla unmodified, lamellae short. PAO oval, about as long as diameter of nearest ocellus. Setae on body dense, moderately stout, and short; those on head and thorax clearly differentiated into short and long setae. Frontoclypeal setae unmodified. Ventral tube with 2–4 anterior setae on each side, 12–24 lateral setae, and more than 35 caudal setae in large specimens. Retinaculum with more than 30 setae in large specimens. Differentiated subapical seta on dens short, not passing tip of mucro. Mucro elongate, with strong, undulating ventral and lateral lamellae (Fig. 1G); apical and subapical teeth of mucro subequal; outer dorsal lamella high and prominent (Fig. 6A). Mucronal seta absent. Claws normal, not elongated (Fig. 1I). Claw index 1.9–2.3. Only non-reproductive females and juveniles seen.

Etymology. Named after the collector, our colleague Dr. Marina Taraschchuk, Kiev.

Discussion. The short subapical seta on the dens, which does not bypass the tip of the mucro, is a character shared only with *A. falcula* **n. sp.** From this species *A. tarashchukae* **n. sp.** differs by having more robust claws (claw index less than 2.5), stronger dorsal lamella on mucro, and coarser body setae. In some *Agrenia* spp. these characters may depend on season or reproductive stage of the individual, but the samples of *A. falcula* and *A. tarashchukae* were made in summer and reproductive males of the former species do not differ from unreproductive individuals.

Distribution and ecology. The single collection of this species was made from wet moss in the spray zone. The type locality is in the Shawanagunk Mountains, in the northeastern part of the Appalachian Range.

Key to the species of *Agrenia*

1. Mucro withlateral seta absent 2
- Mucro with lateral seta present 9
2. Ventral tube in adults with six or fewer anterior setae on each side 3
- Ventral tube in adults with ten or more anterior setae on each side 7
3. Subapical seta on dens reaching well beyond tip of mucro (Fig. 1A) 5
- Subapical seta on dens short, not reaching beyond tip of mucro (Figs. 1E–G) 4
4. Claws very long and slender, claw index 3.0 or more; body setae thin, sparse, uniform; outer dorsal lamella of mucro not prominent (Fig. 1F) ..... *falcula* **n. sp.** (Appalachians)
- Claws shorter, claw index less than 3.0; body setae strong, on head and thorax with mixed short and long setae; outer dorsal lamella of mucro high and distinct (Fig. 1G) ..... *tarashchukae* **n. sp.** (Appalachians)
5. Colour deep greenish black; ventral tube without anterior setae ..... *atroviridis* (Rockies)
- Colour olive; ventral tube with or without anterior setae 6
6. Antennae no more than 1.8 times the length of head diagonal; anterior setae on ventral tube usually absent, occasionally 1–2 on each side; claw index in summer specimens 2.1–2.5, in winter specimens 1.2–1.3 ..... *riparia* (Holarctic)
- Antennae in adults more than 1.8 times the length of head diagonal, in large males up to 2.7 times as long; ventral tube usually with 4–5 anterior setae on each side, rarely absent; claw index 2.8–4.5 (summer) and 2.0–2.7 (winter)..

..... *parkeri* **n. sp.** (Appalachians)

7. Mucro elongate, apical tooth larger than subapical tooth (Fig. 6B); maxilla with short, unmodified lamellae (Fig. 1M) 8
- Mucro short and compact, apical tooth not larger than subapical tooth (Fig. 1A); maxilla with long, modified lamellae (Fig. 1L) ..... *extrema* **n. sp.** (Rockies)
8. Claws long and slender, claw index 2.8 or more; head markedly prognathous; abdominal setae of normal density ... . *agilis* (Pacific Coast Range)
- Claws shorter, shape normal; claw index 2.3 or less; head shape normal, not markedly prognathous; abdominal setae dense, *Isotomurus*-like ..... *cyanura* (Rockies)
9. Ventral tube with fewer than 20 anterior setae on each side; setae along anterior edge of frontoclypeus normal, not differentiated into a "moustache" 10
- Ventral tube in adults with more than 30 anterior setae on each side; frontoclypeal field with a distinct "moustache" ..... *pilosa* (Japan)
10. Mucro short and compact, with narrow ventral lamella 11
- Mucro elongate, with broad ventral lamella (as in Fig. 1E–F) ..... *lamellosa* (Appalachians)
11. Body usually with some segments, or parts of segments, darker than rest; reproductive specimens unmodified .... *bidenticulata* (Holarctic)
- Body colour uniform, without distinctly darker sections; large reproductive specimens with modified setae on tip of abdomen ..... *polymorpha* (Rockies)

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