A REVISION OF THE NEARCTIC AMELETUS MAYFLIES BASED ON ADULT MALES, WITH DESCRIPTIONS OF SEVEN NEW SPECIES (EPHEMEROPTERA: AMELETIDAE)

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Abstract

The Canadian Entomologist 128: 293-346 (1996)

A systematic revision of North American species of the genus Ameletus, excluding parthenogenetic species, is presented. Seven new species are described (A. andersoni, A. bellulus, A. doddsianus, A. edmundsi, A. majusculus, A. pritchardi, and A. tolae), separate keys are given to western and eastern species, annotated accounts of all 30 presently recognized bisexual species are provided, taxonomic characters are illustrated, and distribution data are presented for all species. The following nomenclatural changes are proposed: Ameletus aequivocus is considered a junior synonym of A. sparsatus; A. alticolus and A. celeroides junior synonyms of A. celer; A. connectina and A. connectus junior synonyms of A. velox; A. facilis a junior synonym of A. vancouverensis; A. monta a junior synonym of A. similior; A. querulus a junior synonym of A. shepherdi. The specific status of A. tuberculatus is questioned and it is provisionally considered to be the same as A. celer.

Zloty, J. 1996. Révision du genre néarctique Ameletus (Ephemeroptera: Ameletidae) basée sur les mâles adultes et description de sept nouvelles espèces. The Canadian Entomologist 128: 293-346.

Résumé

On trouvera ici une révision systématique des espèces nord-américaines du genre Ameletus, à l'exception des espèces parthénogénétiques. Sept nouvelles espèces sont décrites (A. andersoni, A. bellulus, A. doddsianus, A. edmundsi, A. majusculus, A. pritchardi et A. tolae) et des clés distinctes permettront de reconnaître les espèces de l'est; on trouvera aussi des descriptions commentées des 30 espèces bisexuées actuellement reconnues, des illustrations de leurs caractéristiques diagnostiques et des données sur leur répartition. Les changements taxonomiques suivants sont proposés: Ameletus aequivocus devient synonyme d'A. sparsatus; A. alticolus et A. celeroides deviennent synonymes d'A. celer, A. connectina et A. connectus deviennent synonymes d'A. velox; A. facilis devient synonyme d'A. vancouverensis; A. monta devient synonyme d'A. similior; A. querulus devient synonyme d'A. shepherdi. Le statut taxonomique d'A. tuberculatus est mis en doute et l'espèce est considérée provisoirement comme synonyme d'A. celer.

[Traduit par la Rédaction]

INTRODUCTION

Mayflies of the genus *Ameletus* are common inhabitants of running waters, generally in mountainous areas. The genus is represented by only one species (*Ameletus inopinatus*) in Europe, but 23 species have been described from Asia (12 from male imagoes, three from female imagoes, and eight from larvae). However, no comprehensive study exists for the Asian species and the literature consists mainly of isolated descriptions of one or more species (Navás 1915; Ulmer 1927; Brodsky 1930; Imanishi 1932; Matsumura 1931; Traver 1939; Baykova 1976; Sinitshenkova 1977, 1981; Soldán 1978; Kluge 1979; Sinitshenkova and Varykhanova 1990; Kang and Yang 1994). Undoubtedly, some of the 23 Asian species are synonymous, but also some species certainly await description (Kluge, pers. comm.). In North America, the genus is speciose and reaches its greatest diversity in the western part of the continent where as many as 10 (Harper et al. 1995) to 12 (Zloty et al. 1993) species can occur at a single site. The genus occurs from the extreme southwestern United States to the

most northern parts of Alaska, Yukon, and the Northwest Territories in the west, and from South Carolina to Quebec in the east, but is absent from a broad band from the Gulf of Mexico, through the Great Plains, to Hudson Bay. Many species have widespread distributions and large population sizes (Edmunds et al. 1976).

Despite the common occurrence of *Ameletus* in North America, their taxonomy has been little studied and the necessity to revise the genus was already apparent 4 decades ago (Edmunds 1952). Unfortunately, the identification of species is very difficult. As Edmunds et al. (1976) pointed out, this is principally because adults have seldom been collected in numbers sufficient to determine the full range of morphological variation. Also, descriptions of new species have rarely furnished adequate details of the genitalia, and specialists often neglected to examine type material of existing species.

McDunnough (1923, 1924, 1928, 1929, 1931, 1933a, 1933b, 1934, 1936, 1938, 1939) described 19 species of North American Ameletus, but never provided a key. The only comprehensive study of the genus in North America is in Needham et al. (1935). However, this work included only 19 species and had many imperfections (McDunnough 1936; Spieth 1941), and the key is now of little use. The few other papers treating Ameletus have been isolated descriptions of single species: Needham (1905), Dodds (1923), Traver (1932, 1934), Mayo (1939, 1952), Day (1952), Harper (1970), Carle (1978), and Burrows (1987).

Attempts to introduce regional identification keys were made by Burks (1953) and Day (1956). Burks (1953) had only two species to consider in Illinois, and Day (1956) dealt with seven species in California. Regional accounts also occur in the theses of Edmunds (1952) for Utah, Jensen (1966) for Idaho, and Gustafson (1991) for the Gallatin River drainage, Montana, but none of these data were ever published as identification keys. An annotated list of mayflies of Maine was recently published by Burian and Gibbs (1991), including information on ecology, habitat, seasonal occurrence, and distribution of four species of *Ameletus*, but no identification keys. This lack of keys for species identification has strongly limited the number and usefulness of non-taxonomic publications on *Ameletus* (Zloty et al. 1993).

Of the 30 published names proposed for bisexual species for this genus in North America, I recognize 23 as valid, and I propose another seven in this paper; of these, 24 are western species (Table 1), five are eastern species (Table 2), and one, *Ameletus subnotatus*, occurs in both east and west. The total number is probably greater than this, as field work, especially in the southwestern United States and northern Canada and Alaska, has been very limited (Argyle and Edmunds 1962; Allen and Chao 1981; Harper and Harper 1981; McCafferty 1985). Furthermore, D.H. Funk (SWRC) is currently studying the eastern species and plans to include descriptions of new species and make some changes to the status of currently recognized parthenogenetic species (D.H. Funk, pers. comm.). However, it is not expected that changes will be made to the bisexual species that I include in the present paper.

In this paper, I provide an updated account of all North American bisexual species that I consider valid (the eastern parthenogenetic forms, A. lineatus and A. ludens, are not included), giving synonymies, diagnoses, comments on new synonymies, and full descriptions of new species. I have seen most of the type material and examined many hundreds of specimens from the collections listed below. I illustrate the genitalia and other important morphological characters for all known adult males of Nearctic Ameletus. All illustrations were produced with the aid of a camera lucida. I follow Kluge's (1994) nomenclatural interpretation of the pterothorax. I briefly outline species distributions, indicating records from the literature that I accept as valid with an asterisk. I also provide distributional maps for the western species. Because I have examined most of the available material from North America and have seen many misidentified specimens in collections, these distribution maps are based primarily on specimens examined by me. A single distribution mark on the map

TABLE 1. Summary of all names used or associated with western North American Ameletus and the current disposition of each

| Name | Reference | Current status |
|----------------|----------------------|-------------------|
| aequivocus | McDunnough, 1934 | A. sparsatus |
| alticolus | McDunnough, 1934 | A. celer |
| amador | Mayo, 1939 | A. amador |
| andersoni | Zloty, this paper | A. andersoni |
| bellulus | Zloty, this paper | A. bellulus |
| celer | McDunnough, 1934 | A. celer |
| celeroides | McDunnough, 1934 | A. celer |
| chlorops | Edmunds, 1952 | A. doddsianus |
| connectina | McDunnough, 1939 | A. velox |
| connectus | McDunnough, 1936 | A. velox |
| cooki | McDunnough, 1929 | A. cooki |
| dissitus | Eaton, 1885 | A. dissitus |
| doddsianus | Zloty, this paper | A. doddsianus |
| edmundsi | Zloty, this paper | A. edmundsi |
| exquisitus | Eaton, 1885 | A. exquisitus |
| facilis | Day, 1952 | A. vancouverensis |
| falsus | McDunnough, 1938 | A. falsus |
| imbellis | Day, 1952 | A. imbellis |
| inopinatus | Eaton, 1887 | A. inopinatus |
| majusculus | Zloty, this paper | A. majusculus |
| monta | Mayo, 1952 | A. similior |
| needhami | Edmunds, 1952 | A. oregonensis |
| oregonensis | McDunnough, 1933 | A. oregonensis |
| pritchardi | Zloty, this paper | A. pritchardi |
| querulus | McDunnough, 1938 | A. shepherdi |
| shepherdi | Traver, 1934 | A. shepherdi |
| similior | McDunnough, 1928 | A. similior |
| sparsatus | McDunnough, 1931 | A. sparsatus |
| subnotatus* | Eaton, 1885 | A. subnotatus |
| suffusus | McDunnough, 1936 | A. suffusus |
| tolae | Zloty, this paper | A. tolae |
| tuberculatus | McDunnough, 1939 | A. celer (?) |
| validus | McDunnough, 1923 | A. validus |
| vancouverensis | McDunnough, 1933 | A. vancouverensis |
| velox | Dodds, 1923 | A. velox |
| vernalis | McDunnough, 1924 | A. vernalis |
| Ameletus sp. A | Allen and Chao, 1981 | A. doddsianus |
| Ameletus sp. B | Allen and Chao, 1981 | A. falsus (?) |
| Ameletus sp. C | Allen and Chao, 1981 | A. falsus |

^{*}This species occurs in both eastern and western North America.

Table 2. Summary of all names used or associated with eastern North American Ameletus and the current disposition of each

| Name | Reference | Current status |
|----------------|------------------|-------------------|
| browni | McDunnough, 1933 | A. browni |
| cryptostimulus | Carle, 1978 | A. cryptostimulus |
| subnotatus* | Eaton, 1885 | A. subnotatus |
| tarteri | Burrows, 1987 | A. tarteri |
| tertius | McDunnough, 1938 | A. tertius |
| walleyi | Harper, 1970 | A. walleyi |

^{*} This species occurs in both eastern and western North America.

can indicate more than one collecting site if the sites are in proximity. The specific distribution list for each species can be obtained on request. Emergence periods of adults are based on months when adult specimens or last-instar larvae were collected and are indicated by roman numerals following the geographic distribution. I provide separate keys to males of the western and eastern species. Females are not treated here, because they have not been described for all species and because they are generally difficult to identify without associated males.

MATERIALS AND METHODS

Material was examined from the following museum and private collections:

ANSP Academy of Natural Sciences of Philadelphia, Pennsylvania.

BMNH The Natural History Museum, London [formerly British Museum (Natural History)].

CAS California Academy of Sciences, San Francisco, California.

CNC Canadian National Collection, Ottawa, Ontario.
CSU Colorado State University, Fort Collins, Colorado.

CU Cornell University, Ithaca, New York.

GFE George F. Edmunds, Jr. collection, Salt Lake City, Utah. JF John F. Flannagan collection, Winnipeg, Manitoba. MSU Montana State University, Bozeman, Montana.

MW Michael J. Wigle collection, Bella Coola, British Columbia.

OSU Oregon State University, Corvallis, Oregon.
PU Purdue University, West Lafayette, Indiana.

RA Richard K. Allen collection, San Marcos, California (currently at CAS).

SWRC Stroud Water Research Center, Avondale, Pennsylvania.

TF Thomas J. Fink collection, DeKalb, Illinois (currently at UC).

UC University of Calgary, Alberta.

UF University of Fribourg, Fribourg, Switzerland.

UM University of Montreal, Ouebec.

US University of Saskatoon, Saskatchewan.
USNM U.S. National Museum of Natural History.

I have used the following characters in evaluating species status:

Head. Male eyes are various shades of brown or green. In laboratory-reared specimens the green condition varies according to ambient light intensity. Also, the green colour is not retained in preserved specimens, so this characteristic is of limited value for identification purposes. Nevertheless, I provide the state of this feature for fresh specimens that I have reared.

Thorax. The thorax in *Ameletus* varies from dark brown to yellow and can have lighter and darker markings. In a few species the colour of the thorax can be used in identification, but it is variable within populations of other species.

Wings. Wings have a transparent or suffused condition and have light or dark venation that in some species can be bordered with brown giving them a speckled appearance. These features are diagnostic for most species, but in others are too variable to be of value. However, the brown bordering around the cross-veins is more easily determined in subimagoes. Thus, species with transparent wings in adults usually have uniformly suffused wings in subimagoes (e.g. A. celer, A. cooki, A. inopinatus, A. pritchardi, A. similior, A. tolae, A. velox); species with suffused wings in adults have uniformly but strongly suffused wings in subimagoes (e.g. A. suffusus, A. validus, A. vancouverensis); species with brown bordering around the cross-veins in adults (intensity of bordering may vary) have suffused wings with dark brown bordering around the cross-veins in subimagoes (e.g. A. amador, A. andersoni,

A. bellulus, A. doddsianus, A. edmundsi, A. falsus, A. oregonensis, A. sparsatus, A. subnotatus, A. walleyi).

Abdomen. The most useful characters found on the abdomen are the presence or absence of dark markings at the centre of each sternite and the pigmentation of the ganglia which can be seen through the cuticle. Ganglionic markings are fixed for most species, but *A. velox* is polymorphic for this feature.

Genitalia. The most important diagnostic characters used to differentiate males of *Ameletus* species are found on the lateral lobes and on the ventral plates of the penis. I illustrate these features with three views for most species: a dorsal view showing only the lateral lobes, a ventral view along with the accompanying ventral plates, and a lateral view which was often neglected in the past but can show important details.

Lateral lobe. The shape of the lateral lobe, best seen in lateral view, varies. It may have a foot-shaped end (A. bellulus, A. vernalis) or an acute and curved apex (A. andersoni); it can have an inwardly or outwardly twisted apex (A. inopinatus and A. validus, respectively); it may possess accessory spicules or spines (A. doddsianus, A. majusculus). The shape of the lateral lobe can be distorted if specimens are not relaxed before being preserved in 70% alcohol. I achieve this by killing specimens with ether.

Ventral plate. The presence or absence of this structure, its size and shape, and the presence and the number of spines, spinules, or teeth, are the most reliable identification features. The ventral plates may vary, and for some species I illustrate variations. In smaller species ventral plates should be viewed under high magnification.

The term "titillator" is used for a single, elongated, pointed spine that is formed from the apical end of each ventral plate; when a titillator is present there are no other accessory spines on the ventral plate. However, it is sometimes difficult to determine, without preparing for microscopical observation, whether a species (e.g. A. cooki, A. majusculus, or A. validus) has elongated titillators or only stout spines. Thus, in the keys, these species are included with both groups, with and without titillators.

The keys, accompanied by illustrations, should successfully identify most imaginal male *Ameletus*. Because most of eastern and western species are so well separated geographically (Fig. 49) and morphologically, I provide separate keys. I have also included variations of various species and have tried to avoid conditional statements, so some species key more than once. Identification should be confirmed by a detailed examination of the genitalia as described in the species accounts. High magnification and rotation of the specimen is necessary to view the small accessory spines of the ventral plates and the apical end of the lateral lobes. Microscope slides of the genitalia should be prepared for smaller species. Body length is measured from the anterior margin of the frons to the tip of segment 10, exclusive of antennae and caudal filaments.

SYSTEMATIC ACCOUNTS AND KEYS

GENUS AMELETUS EATON

Ameletus Eaton 1885: 210; Ulmer 1920: 134, 1929: 27; Dodds 1923: 105; Schoenemund 1930: 38; McDunnough 1934: 161, 1935: 100, 1936: 207; Needham et al. 1935: 446; Burks 1953: 100; Edmunds and Traver 1954: 237; Day 1956: 90; Edmunds and Allen 1957: 318; Berner 1959: 4, 1977: 10; Edmunds 1960: 24; 1962: 1; Edmunds et al. 1963: 10; Edmunds et al. 1976: 131; Soldán 1978: 379; Studemann et al. 1988: 310.

Chimura Navás 1915: 149; Edmunds 1960: 24.

Les Parámeletus Lestage 1940: 124; Edmunds and Traver 1954: 237. Type species: Ameletus subnotatus Eaton by original designation.

Eaton (1885) erected the genus Ameletus for A. subnotatus from Colorado. Navás (1915) described Chimura, based on C. aetherea from Kyoto, Japan, and Lestage (1940) created Paleoameletus for Ameletus primitivus Traver (1939), from the Himalayan Mountains. Edmunds and Traver (1954) synonymized Paleoameletus with Ameletus, and Edmunds (1960) synonymized Chimura, also with Ameletus. The European genus Metreletus, established by Demoulin (1951) for Metretopus goethgebueri (Lestage 1938), was later synonymized with Ameletus by Jacob (1984). However, Studemann et al. (1988), Studemann and Tomka (1991), and Studemann et al. (1994) used morphological and electrophoretic data to show clearly that Metreletus should be treated as a valid genus. Finally, McCafferty (1991) transferred both genera to the newly created family Ameletidae. This new arrangement is recognized by Studemann et al. (1994) and by Kluge et al. (1995).

The genus Ameletus comprises a homogeneous assemblage of species, both as larvae and adults. Ameletus can be distinguished from Metreletus in the adult stage by the following morphological characters: (1) cubito-anal vein (CuA) of fore wings attached to hind margin with numerous intercalary veins in Ameletus, but with numerous transversal veins in Metreletus; (2) costal projection of hind wings acute in Ameletus but rounded in Metreletus; (3) posterior margin of pronotum without indentation in Ameletus, but with a deep indentation in Metreletus; (4) posterior arms of prealar bridge (=prescutum) well developed in Ameletus, but reduced in Metreletus; (5) caudal filaments about equal to body length in Ameletus, but about twice the body length in Metreletus; (6) ventral plates of the penis relatively small in Ameletus, but enlarged in Metreletus.

The larvae of *Ameletus* can be distinguished from *Metreletus* by the following morphological characters: (1) gills on segment 1 much smaller (about 50%) than gills on segments 3–5 in *Ameletus*, but about equal in size in *Metreletus*; (2) caudal filaments much shorter than abdomen (<60%) in *Ameletus*, but about equal in length to abdomen in *Metreletus*; (3) intersegmental setae throughout length of caudal filaments in *Ameletus*, but only in the basal half in *Metreletus*; (4) caudal filaments with contrasting dark and pale pattern in *Ameletus*, but uniformly coloured with brown in *Metreletus*; (5) tarsal claws without denticles in *Ameletus*, but with denticles in *Metreletus*.

KEY TO ADULT MALES OF AMELETUS

Western North American Species

| 1. | Individuals with small dichoptic eyes; forceps absent—females (key not provided) Individuals with large holoptic eyes; forceps present —males |
|---------|---|
| 2. | Penis with long, narrow lateral lobes extending beyond the base of the forceps (Figs. 1-5) 4 Penis with short, broad lateral lobes not reaching to the base of the forceps, and with two or three broad, spine-like projections at their apical ends (Fig. 6) |
| 3. | Lateral lobes of penis with three spine-like projections (Fig. 33A, B); basal area of fore and hind wings suffused with dark brown; cross-veins of fore wings not bordered with smoky brown (Fig. 44A) |
| 4. | Ventral plate of penis formed into a single, rod-like titillator (Fig. 25B) |
| 5. — | Penis with ventral plates reduced or absent (Fig. 10B, C) 6 Penis with well-developed ventral plates (Fig. 14B,C) 7 |

299

defined on sternites 2-8; wings tinted with gray exquisitus (in part)

| - | Smaller species (<11 mm); titillators bent outward at apices (Fig. 30B); ganglionic markings visible only on sternite 8; wings tinted with amber (Fig. 47C)vancouverensis (in part) |
|----------------------|---|
| 19. — | Apical half of lateral lobes with a number of strong spicules (Fig. 23A) |
| 20. | Wings speckled with smoky brown (Fig. 46A); abdominal sternites 2–8 with dark brown ganglionic markings; genitalia as in Figure 23 |
| 21. — | Apical ends of titillators formed into sharp inwardly twisted hooks (Fig. 24B) dissitus Apical ends of titillators straight (Fig. 28B, C) or bent (Fig. 25B, C), but never inwardly twisted |
| 22. | Many cross-veins in fore wings bordered with brown giving them a speckled appearance (Figs. 45B, C, 46B) |
| 23. | Titillators relatively long and curved at the apices (Fig. 25C); body size variable |
| 24. | Large species (>14 mm); titillators bent inward at the tips (Fig. 25B); ganglionic markings well defined with dark brown |
| 25. — | Apical margin of titillators straight (Figs. 20B, 28B) or only slightly curved (Figs. 22B, 26B) 26 Apical margin of titillators distinctly curved (Fig. 21B) |
| 26. — 27. — | Tips of lateral lobes bent dorsally (Fig. 22C); ganglionic markings on sternites 7–8 bellulus Tips of lateral lobes straight or only slightly curved (Fig. 27C); ganglionic markings on sternites 2–8 or only on sternite 8 |
| 28. | Second segment of the forceps bent strongly inward near the base (Fig. 8E); west-central California (Map 6) |
| 29. | Large species (>13 mm body length); cross-veins of fore wings bordered with smoky brown and forming four dark patches (Fig. 46B); Sierra Nevada and Cascade Range (Map 1); genitalia as in Figure 20 |
| 30. | Apices of lateral lobes pointed and strongly curved mediodorsally (Fig. 21C) andersoni Apices of lateral lobes rounded and bent dorsally (Fig. 31C) vernalis |
| | Eastern North American Species |
| 1. | Individuals with small dichoptic eyes; forceps absent—females of bisexual species and parthenogenetic species (key not provided) Individuals with large holoptic eyes; forceps present—males |
| 2. | Penis with long, narrow lateral lobes, extending beyond the base of the forceps (Fig. 2) 4 Penis with short, broad lateral lobes, not reaching to the base of the forceps (Fig. 6) 3 |
| | |

- Cross-veins of fore wings not bordered with smoky brown (Fig. 44A); ventral terminal spine acute at the apex and directed dorsally (Fig. 36B) walleyi

- Ventral plates formed into a prominent spine that bears small teeth (Fig. 17B-D)..... tarteri
 Ventral plates not formed into a prominent spine, but armed with small accessory spinules (Fig. 18B-D).... tertius

SPECIES ACCOUNTS

Ameletus amador Mayo

(Figs. 8A, 20)

Ameletus amador Mayo 1939: 149; Day 1956: 90.

Type Material. Male holotype and female allotype: Dry Creek near Drytown, Amador Co., California, 23 May 1938; in CAS (examined).

Diagnosis. Body length: 12–13 mm. Eyes with green pigmentation in living specimens. Mesonotum yellowish with brown laterally; scutellum bright yellow with dark brown laterally. Fore wings transparent, with some cross-veins surrounded with smoky brown giving them a speckled appearance and forming three or four larger dark patches (Fig. 46B). No ganglionic markings on abdominal sternites 2–7.

This species is similar to the common A. sparsatus, which appears to be allopatric. Wings of these two species are distinctly speckled (Fig. 46B, C) and ganglionic markings occur only on sternite 8. The male genitalia resemble those of A. bellulus (Fig. 22), A. falsus (Fig. 26), A. imbellis (Fig. 27), and A. sparsatus (Fig. 28), but can be distinguished by characters in the key.

Distribution (Map 1). Oregon: Lane Co. (US); California: Amador Co. (CAS). V-VII. **Remarks.** The larva was described by Mayo (1939).

Ameletus andersoni sp.nov.

(Figs. 8D, 21, 45B)

Description. Male imago (in alcohol): body length 7–15 mm, fore wings 6–13 mm. Head generally brown with light brown vertex and dark brown ocellar tubercles; upper portion of compound eyes grey, lower portion brown. Prothoracic tergum dark brown with some opaque white at lateral margins; mesotergum yellow with some brown shading in anterior lateral areas; scutellum yellow, infrascutellum dark brown; anterior half of metatergum opaque white, posterior half dark brown; thoracic pleuron brown to dark brown with extensive opaque white between plates, at the centre of the katepimeron, and at the base of the legs and wings. Fore legs dark brown; middle and hind legs amber-brown. Wings transparent, lightly tinged with amber; fore wings with milky suffusion anteriorly, amber in stigmatic area; venation dark brown; cross-veins margined with smoky brown giving them a speckled appearance (Fig. 45B). First abdominal tergite brown to dark brown; tergites 2–9 opaque white without contrasting pattern, with brown along lateral margins and with some

brown shading near posterior margin; tergites 8 and 9 darker; tergite 10 opaque white with a pair of brown triangular patches posteriorly. Abdominal sternite 1 brown to dark brown; sternites 2–10 opaque white, pair of C-shaped markings near subanterior margin of sternites 2–6 (Fig. 40C). Genitalia (Fig. 21): lateral processes large with apices pointing laterally and with a relatively deep cleft between them (Fig. 8D); penis with elongated lateral lobes, strongly curved dorsally (Fig. 21C), tips pointed and bent mesally (Fig. 21A); each ventral plate with a single titillator formed into an elongated rod-like structure, with acute apex bent laterally (Fig. 21B). Caudal filaments uniformly golden brown.

Type Material. Male holotype and female allotype: Oak Burn, 60th St. Corvallis, Benton Co., Oregon, 8 May 1993, N.H. Anderson. Paratypes: same year, locality, and collector as holotype but collected on the following days, 24 April $(1 \circ)$, 25–27 April $(2 \circ \circ)$, 1 May $(1 \circ)$, 8 May $(1 \circ, 1 \circ)$, 10–13 May $(3 \circ \circ)$, 17 May $(2 \circ \circ)$, 29 April $(1 \circ, 3 \circ \circ)$ subimagoes), 25–29 April $(1 \circ, 1 \circ)$ subimago, 1 larva); Quartz Creek 5 km NE of Blue River, Lane Co., Oregon, 10 May 1986 $(1 \circ)$; temporary stream, Oak Creek watershed, McDonald Forest, Benton Co., Oregon, 25 April 1990, M. Dieterich $(3 \circ \circ, 1 \circ, 2 \circ \circ)$ subimagoes), also the same year, locality, and collector but collected on the following days, 25 April $(1 \circ)$, 8 May $(2 \circ \circ, 2 \circ \circ)$, 26 June $(2 \circ \circ, 2 \circ \circ)$ subimagoes, $(1 \circ, 2 \circ \circ)$ subimagoes), 26 June $(2 \circ \circ, 1 \circ)$ subimago, $(1 \circ, 2 \circ)$ subimagoes); Kalama Springs, 5 mi. W of Merrill Lake, Cowlitz Co., Washington, June, 1968, N.H. Anderson $(1 \circ, 2 \circ)$ subimagoes). The holotype and the allotype will be deposited in CNC; paratypes will be housed in CAS, OSU, and UC.

Etymology. I name this new species after Norman Anderson, Department of Entomology, Oregon State University, Corvallis, who has contributed greatly to our knowledge of the aquatic entomofauna of Oregon.

Diagnosis. Male genitalia are similar to those of A. dissitus, A. exquisitus, A. suffusus, A. vancouverensis, and A. vernalis, but differ in possessing strongly curved and pointed lateral lobes (Fig. 21C). Other diagnostic features are given in the key.

Distribution (Map 1). Washington: Cowlitz Co. (US); Oregon: Benton Co. and Lane Co. (OSU, UC, US), IV-VII.

Remarks. Adults of this species have a very long emergence period that lasts from the beginning of April to late July. Body size decreases over the emergence period. All of the type material from Benton Co. was collected from emergence traps set in summer-dry headwater streams. Information on larval habitat was provided by Dieterich (1992).

Ameletus bellulus sp.nov.

(Figs. 22, 46B)

Description. Male imago (description based on specimens freshly preserved in alcohol): body length 14–16 mm, fore wings 12–13 mm. Head brown with opaque white patches on face and between antennae; compound eyes green dorsally and brown ventrally in living individuals. Prothoracic tergum brown with white lateral and posterior margins; mesotergum yellowish with brown streaks along anterolateral margin, scutellum yellow changing to dark brown and black at the posterior lateral areas; metatergum amber to brown; thoracic pleuron golden brown to brown with extensive pale white at the base of legs and wings. Fore legs golden brown to brown; middle and hind legs golden brown with dark brown tarsal segments. Wings transparent with brown longitudinal veins and cross-veins; fore wings with brown shadings around some cross-veins giving them a speckled appearance and forming four larger patches (Fig. 46B); amber shading in stigmatic area of fore wings. Abdominal tergites with conspicuous tracheae; tergite 1 brown to deep brown; tergites 2–9 largely pale white with narrow golden brown shading on posterior margin that extends and forms triangular

posterior lateral patches and a pair of median longitudinal markings; tergite 10 light brown with some dark brown shading posteriorly. Abdominal sternites with ganglionic markings on sternites 7 and 8; sternite 1 golden brown to brown; sternites 2–8 largely pale white with some golden brown shading medially; sternite 9 pale with narrow brown shading at anterior and lateral margins. Genitalia (Fig. 22A–C) generally brown to dark brown; lateral processes well developed with apices directed laterally; lateral lobes of the penis relatively short and with dorsally bent apices (Fig. 22C); ventral titillator elongated with acute tip (Fig. 22B). Caudal filaments golden yellow with a dark brown narrow ring at the base of each segment.

Type Material. Male holotype and female allotype: Ford Creek, Alberta (50°48′N 114°51′W, elevation 1707 m), 2.7 km upstream from its confluence with the Elbow River, 11 August 1990 (reared from larva) and 23 July 1991 (reared from larva), respectively, J.S. Zloty. Paratypes: same locality and collector as holotype but collected on the following days, 3 August 1988 (8 \circ \circ , 2 \circ \circ , 2 larvae), 16 August 1988 (3 \circ \circ , 3 \circ \circ , 1 \circ subimago, 2 larvae), 24 August 1988 (1 \circ), 28 August 1990 (1 \circ , 1 \circ subimago); Gold Creek, Blairmont, Alberta, 3 August 1990, J.S. Zloty (1 \circ , 2 larvae); Gold Creek, Blairmont, Alberta, 10 August 1990, J.S. Zloty (1 \circ); Cache Creek, Gallatin Co., Montana, 20 June 1985, D.L. Gustafson (2 larvae) and the same place, year, and collector on 30 June (1 \circ , 1 \circ); Rock Creek, 2 mi. N of Wyoming, 2 August 1991, D.L. Gustafson (11 larvae). The holotype and the allotype will be deposited in CNC; paratypes will be housed in CAS, and UC.

Etymology. *bellulus* = beautiful (Latin).

Diagnosis. Although this species shares many characteristics with A. doddsianus, the distributions of the two species are quite separate, and structure of the genitalia and pigmentation of the wings separate these species. Ameletus bellulus and A. doddsianus are differentiated in the diagnosis for A. doddsianus below. The male genitalia of A. bellulus resemble those of A. amador (Fig. 20), A. falsus (Fig. 26), and A. imbellis (Fig. 27), but can be distinguished by characters in the key.

Distribution (Map 1). Southwestern Alberta (UC); Montana: Carbon Co. (MSU, UC), Gallatin Co. (MSU, UC). VII–VIII.

Remarks. Life history data are provided by Zloty et al. (1993). The larval stage will be described in a future publication on Alberta *Ameletus* larvae.

Ameletus browni McDunnough

(Fig. 37)

Ameletus browni McDunnough 1933b: 278; Needham et al. 1935: 450.

Type Material. Male holotype and female allotype: Mt. Lyall, Gaspé Co., Québec, 11 August 1933; No. 3652 in CNC (examined).

Diagnosis. Body length: 8–9 mm. Mesonotum broadly yellow along the median longitudinal suture. Wings transparent with faint amber tinge and with amber veins and crossveins. Ganglionic markings on abdominal sternites 2–8.

The unique shape of the ventral plates (Fig. 37C) distinguishes males of this species from all others except A. cryptostimulus, from which it differs in having a narrow lateral lobe with an acute apex (Fig. 37C), whereas the lateral lobe is broad and has a rounded apex in A. cryptostimulus (Fig. 38C); in having a wide base to the penis (narrow in A. cryptostimulus); and in having well-defined ganglionic markings on sternites 2–8 (ganglionic markings only on sternites 6–8 in A. cryptostimulus).

Distribution. Québec: Gaspé Peninsula (CNC, *); Maine (SWRC); Vermont: Bennington Co. (SWRC, UC); Pennsylvania (SWRC). VII–VIII.

Remarks. The larva was described by McDunnough (1933b).

Ameletus celer McDunnough

(Figs. 2, 11, 41, 45A)

Ameletus celer McDunnough 1934: 161; Needham et al. 1935: 451.

Ameletus alticolus McDunnough 1934: 163; Needham et al. 1935: 450. New synonymy.

Ameletus celeroides McDunnough 1934: 162; Needham et al. 1935: 451. New synonymy.

Ameletus tuberculatus McDunnough 1939: 50. New synonymy.

Type Material. Male holotype and female allotype of *A. celer*: Glacier Creek, Crowsnest Pass, Alberta, 25 June 1930, J.H. Pepper; No. 3762 in CNC. Male holotype of *A. alticolus*: Blairmore, Alberta, 23 June 1938, J.H. Pepper; No. 3764 in CNC. Male holotype and female allotype of *A. celeroides*: Shingle Creek, Penticton, B.C., 22 June 1933, A.N. Gartrell; No. 3763 in CNC. Male holotype of *A. tuberculatus*: Blue Lake, west of Lytton, B.C., 4 August 1938, J.K. Jacob; No. 4444 in CNC. I have examined the holotype of each form.

Diagnosis. Body length: 9–15 mm. Eyes dark brown. Mesonotum brown with yellow irregular patch in front of scutellum and sometimes in anterior area. Wings transparent with brown veins and yellowish cross-veins (Fig. 45A). Ganglionic markings on abdominal sternites 2–8 (Fig. 41B).

Ventral plates of the penis armored with 3–14 small accessory spines (Fig. 11E). This character will distinguish males of this form from all other species of *Ameletus* except A. edmundsi, A. tolae, and the eastern A. tertius. Ameletus edmundsi has a large number of minute accessory spicules on the ventral surface of the ventral plates (Fig. 13D) and dark patches at the centre of sternites 3–8 (Fig. 42). Ameletus tolae has only one small accessory spine at the apical end of the ventral plate (Fig. 19D) and is much smaller. Ameletus tertius has somewhat longer accessory spines (Fig. 18C) and lacks ganglionic markings.

Distribution (Map 2). Southern British Columbia (CNC, UC); southwestern Alberta (CNC, UC); Idaho: Blaine Co. (US), Valley Co. (GFE); Montana: Cascade Co. (UC), Gallatin Co. (MSU, UC); Utah: Salt Lake Co. (GFE), Utah Co. (TF); Colorado: Boulder Co. (CSU, UC), Jackson Co. (CSU, SWRC, UC), Larimer Co. (GFE). VI–VIII.

Remarks. Two species described by McDunnough (1934), A. alticolus and A. celeroides, do not show significant differences in morphology from A. celer. The only differences are in body size, which may be correlated with water temperature during larval development (Pritchard and Zloty 1994). Therefore, I am inclined to treat these two species as synonyms of A. celer.

Ameletus tuberculatus was described by McDunnough (1939) from a single specimen. The only morphological difference from A. celer is a large asymmetrical tubercle between the lateral lobes at the base of the penis. I believe that this specimen is an aberrant form of A. celer and should be considered as a synonym of this species. Further collecting around the type locality (Antimony Lake, B.C.) would help clarify the identity of A. tuberculatus.

The larva was described by McDunnough (1934). He also described larvae of *A. alti-colus* and *A. celeroides* (McDunnough 1934), which differed from *A. celer* mainly in size and coloration. However, McDunnough's descriptions were based on individuals collected at different times of year from different altitudes, and larval size is known to be influenced by emergence time and water temperature (Pritchard and Zloty 1994), and coloration by substrate characteristics (pers. obs.).

Life history data are provided by Zloty (1992), Zloty et al. (1993), and Pritchard and Zloty (1994).

Ameletus cooki McDunnough

(Fig. 12)

Ameletus cooki McDunnough 1929: 174; McDunnough 1931: 89; McDunnough 1935: 101; Needham et al. 1935: 452.

Type Material. Male holotype: Brackett Creek, near Bozeman, Montana, 7 August 1928, J. McDunnough; No. 3037 in CNC (examined).

Diagnosis. Body length: 7–9 mm. Living males with green eyes. Mesonotum yellowish with brown laterally; scutellum bright yellow. Wings transparent with faint amber tinge and with yellowish veins and white, faintly visible cross-veins. Abdominal sternites 2–6 with C-shaped markings that decrease in intensity posteriorly; ganglionic markings only on sternite 8.

This species can be easily identified by the shape of the ventral plates which has a broad base and a triangular apical process (Fig. 12C). Penis in lateral view somewhat resembles that of *A. pritchardi*, but the lack of accessory spines or teeth on the apical end of the ventral plate (Fig. 14C) diagnoses this species.

Distribution (Map 3). Southern British Columbia (CNC, UC); southwestern Alberta (UC); Washington: Skamania Co. (OSU); Oregon: Benton Co. (OSU), Lane Co. (UM, OSU), Union Co. (US); Idaho: Lemhi Co. (*); Montana: Gallatin Co. (MSU, UC); Colorado: Grand Co. (CSU), Larimer Co. (CSU). VII–VIII.

Remarks. The larva was described by McDunnough (1935).

Ameletus cryptostimulus Carle

(Fig. 38)

Ameletus cryptostimulus Carle 1978: 581; Davic 1983: 47.

Type Material. Male holotype and female allotype: Little Stony Creek, Giles County, Virginia, 10 April 1977, F. Carle; in USNM (not examined).

Diagnosis. Body length: 9–11 mm. Upper portion of eyes light green in living specimens. Mesonotum with yellow along median longitudinal suture and with brown laterally. Wings transparent with faint amber tinge and with brown veins and somewhat lighter cross-veins. Abdominal sternites 2–6 with C-shaped markings (Fig. 40C) that decrease in intensity posteriorly; ganglionic markings clearly visible only on sternites 7–8.

The characteristic shape of the ventral plates (Fig. 38D) distinguishes males of this species from all others except A. browni (see under A. browni).

Distribution. Vermont (SWRC); New York (SWRC); Pennsylvania: Susquehanna Co. (SWRC, UC); West Virginia (SWRC); Virginia: Giles Co. (SWRC, *); North Carolina: Macon Co. (*); South Carolina (SWRC). IV.

Remarks. The larva was described by Carle (1978).

Ameletus dissitus Eaton

(Figs. 4, 24)

Isonychia manca Eaton 1871: 134 (nomen nudum).

Ameletus dissitus Eaton 1885: 210; McDunnough 1929: 174; McDunnough 1931: 89; Needham et al. 1935: 452; Spieth 1941: 91; Day 1952: 29; Day 1956: 90.

Type Material. Male lectotype designated by Spieth (1941): San Geronimo, California, 20 April (year not provided); in BMNH (examined).

Diagnosis. Body length: 10-13 mm. Mesonotum light brown with darker shading laterally and posterolaterally. Wings transparent with brown veins and cross-veins. Ganglionic markings on abdominal sternites 2-8.

This species is closely related to A. andersoni, A. exquisitus, A. suffusus, A. vancouverensis, and A. vernalis, but the male genitalia are unique in having the apical ends of the titillators formed into inwardly twisted hooks (Fig. 24B).

Distribution (Map 2). California: Alameda Co. (*), Napa Co. (GFE); Oregon: Lane Co. (US). III-VI.

Ameletus doddsianus sp.nov.

(Figs. 23, 46A)

Ameletus subnotatus Eaton, 1885 sensu Dodds (misidentification), 1923: 105; sensu Needham et al. (misidentification), 1935: 457.

Description. Male imago (description based on specimens freshly preserved in alcohol): body length 13-15 mm, fore wings 11-12 mm. Upper two-thirds of compound eyes green to dark green in living individuals, lower portion gray with transverse green band; clypeus brown to dark brown, frons opaque white to amber; ocellar tubercles dark brown, ocelli opaque white; vertex opaque white to amber. Prothoracic tergum dark brown with opaque white shading at the posterior margin; mesotergum light brown with some dark brown shading on anterior and lateral areas and with an opaque white spot in front of scuto-scutellar impression; posterior scutal protuberance, scuto-scutellar impression and scutellum dark brown to black; metatergum dark brown with some lighter shading on subanterior margin; thoracic pleuron brown with extensive white at the base of legs and wings and between pleural plates. Fore legs dark brown to black; middle and hind legs light brown, the tibiae paler. Wings transparent; fore wings with light brown suffusion in stigmatic area, longitudinal veins and cross-veins dark brown, some cross-veins in the anterior portion narrowly margined with smoky brown (Fig. 46A). First abdominal tergite dark brown; tergites 2-7 opaque white with dark brown shadings along lateral margins that enlarge posteriorly, with submedian C-shaped dark brown markings (Fig. 40C), with a narrow brown transverse band near the hind margin, and with conspicuous tracheae; tergites 8-10 dark brown with some amber in anterolateral areas. Abdominal sternite 1 brown to dark brown; sternite 2-8 opaque white with brown ganglionic markings; sternite 9 dark brown on the anterior half and pale on the posterior half. Genitalia (Fig. 23A-D): basal plate and forceps dark brown, penis amber; lateral processes large with apices pointing laterally and with deep cleft between them (Fig. 8D); a number of small accessory spicules (seen under high magnification) on ventral surface of upper half of lateral lobes (Fig. 23A). Caudal filaments blackish at base, paling to brown distally.

Type Material. Male holotype and female allotype: Indian Creek, Route 211, Newspaper Rock State Park, San Juan Co., Utah, 5 June 1994, B. Kondratieff. Paratypes: same location, date, and collector as holotype (2♂♂, 1♀, 1♂ subimago, 1♀ subimago, 4 larvae); Skin Gulch, Stove Prairie Road, Larimer Co., Colorado, 8 May 1993, B. Kondratieff, R. Durfee (2♂♂, 1♀, 1 larva); Parowan Creek, 3 mi. E of Parowan, 6200' elevation, Iron Co., Utah, 14 June 1994, G.F. Edmunds (5♂♂, 2♂♂ subimagoes, 4♀♀ subimagoes, 6 larvae) (reared from larvae); South Boulder Creek, 250 m above Moffat Tunnel, Colorado, 22 August 1990 (reared from larvae collected on 7 July), J.K. Jackson (1♂, 1♀, 1 larva); Colorado (no other data), G.S. Dodds [genitalia and legs on one slide, ♀ abdominal segments 7–10 and a pair of wings on another; drawing of genitalia as "A. subnotatus" in Needham et al. (1935) was made from the first slide]. The holotype and the allotype will be deposited in CNC; paratypes will be housed in CAS, CSU, CU, UC, and UM.

Etymology. The name for this species was proposed by Edmunds in his unpublished Ph.D. dissertation (Edmunds 1952) in honour of G.S. Dodds, and I follow his choice.

Diagnosis. This species is closely related to A. bellulus from which it can be differentiated by the presence of ganglionic markings on sternites 2–8 (A. bellulus has ganglionic markings only on sternites 7 and 8), by the presence of spicules on the apical half of the lateral lobes of the penis (Fig. 23A), by the lack of large dark patches on the fore wings (Fig. 46A), and by the geographical distribution (Maps 1 and 4).

Distribution (Map 4). Colorado: Gilpin Co. (CSU, SWRC), Larimer Co. (CSU, UC), Saquache Co. (CSU); Utah: Iron Co. (GFE), San Juan Co. (GFE, CSU, UC); Arizona: Apache Co. (UC, *); New Mexico: Taos Co. (GFE). V–VII. Larvae collected from Nevada from Lander Co., Nye Co., and White Pine Co. (UC) by C. Murvosh may also belong to this species. According to G.F. Edmunds (pers. comm.), this is the most common *Ameletus* in southern Utah mountain streams.

Remarks. Needham et al. (1935) provided a description, based on specimens collected and identified by Dodds (1923) as *A. subnotatus*, and keyed this species. They also included drawings of the genitalia, and briefly pointed out differences between Dodds' specimens and Eaton's original description. Spieth (1941), after re-examining Eaton's types at BMNH, recognized Needham et al.'s mistake and included a diagram of the genitalia of the true *A. subnotatus*. Finally, Edmunds (1952, unpublished thesis), using Spieth's (1941) information, proposed the name, "*A. doddsianus*", for Dodds' material. Edmunds (1952) also included the description of a new species ("*A. chlorops*") from Utah (Red Rock Canyon, near Parowan, 7 June 1951, G.F. Edmunds, Jr.; Johnson Creek, near Blanding, 19–20 June 1946, S. Mulaik), which also proved to be *A. doddsianus* sp.nov.

The description of the larva provided by Allen and Chao (1981) under A. velox and collected at Greer, Arizona, is congruent with larvae of A. doddsianus sp.nov. reared by me from the same site.

Ameletus edmundsi sp.nov.

(Figs. 8B, 13, 42)

Description. Male imago (in alcohol): body length 14 mm, fore wings 12 mm. Head dark brown with opaque white around base and lateral to antennae; ocellar tubercles dark brown, ocelli opaque white; vertex opaque white, dark brown toward compound eyes; upper portion of compound eyes light brown, lower portion dark brown. Prothoracic tergum dark brown with some opaque white at lateral margins; mesotergum brown to dark brown with submedioscutum light brown and scuto-scutellar impression opaque white; scutellum dark brown; anterior half of metatergum opaque white extending mesally to posterior margin and with a pair of brown dots, posterior half of metatergum dark brown; thoracic pleuron light brown to brown with extensive white at the base of legs and wings and between pleural plates. Fore legs dark brown; middle and hind legs amber with brown tarsal segments. Wings transparent; fore wings with light suffusion in stigmatic area (best seen over a dark surface), longitudinal veins dark brown, cross-veins amber. First abdominal tergite brown to dark brown; tergites 2-9 opaque white with dark brown streaks along lateral margins and with paired submedian dark brown markings; tergite 10 opaque white with a pair of dark brown submedian markings. Abdominal sternites 2-8 with ganglionic markings; sternites 1-2 brown to dark brown; sternites 3-8 opaque white with dark brown patches at the centre and with narrow blackish streaks along lateral margins (Fig. 42); sternite 9 pale with extensive brown at anterior and lateral margins. Genitalia generally light amber; lateral processes large with apices pointing laterally and with a very shallow depression between them (Fig. 8B); penis with relatively narrow and straight lateral lobes (Fig. 13C); lateral plate with a small finger-shaped apical end (Fig. 13B); ventrolateral surface of ventral plates with a number of minute spinules (visible under high magnification) (Fig. 13D). Caudal filaments black at base, paling to amber distally.

Type Material. Male holotype: Emigration Canyon Creek, Salt Lake Co., Utah, 27 May 1989 (reared from larva collected on 25 May), G.F. Edmunds, Jr. Paratypes: Big Cottonwood Creek, Salt Lake Co., Utah, July (no other data) (1 °, 1 ° subimago), G.F. Edmunds, Jr. The holotype will be housed in CNC; paratypes will be deposited in UC.

Etymology. I name this species in honour of G.F. Edmunds, Jr., University of Utah, Salt Lake City, who has contributed greatly to mayfly taxonomy and biology. He also provided me with a large collection of *Ameletus*, without which this project would not have been feasible.

Diagnosis. Male genitalia resemble those of *A. celer, A. tolae*, and the eastern *A. tertius*, but the numerous minute spicules on the ventrolateral surface of the ventral plates (Fig. 13D) and the black patches at the centre of sternites 3–8 (Fig. 42) are diagnostic.

Distribution (Map 4). Currently known only from Salt Lake Co., Utah. V-VII.

Ameletus exquisitus Eaton

(Fig. 25)

Ameletus exquisitus Eaton 1885: 212; Needham et al. 1935: 453; Spieth 1941: 91.

Type Material. Male lectotype designated by Spieth (1941): Washington (no other data); in BMNH (examined).

Diagnosis. Body length: 14–16 mm. Mesonotum yellow with brown shading at the lateral and posterolateral areas; scutellum yellow brown. Wings transparent, faintly tinged with gray; venation dark brown. Ganglionic markings on abdominal sternites 2–7. Penis as in Figure 25A–C.

This species is closely related to A. andersoni, A. dissitus, A. suffusus, A. vancouverensis, and A. vernalis, but diagnostics given in the key will distinguish them.

Distribution (Map 4). Washington: Skamania Co. (*); Oregon: Benton Co. (CAS), Lane Co. (US); Lincoln Co. (OSU). IV-V.

Remarks. Spieth (1941) designated a lectotype and provided drawings of the genitalia.

Ameletus falsus McDunnough

(Fig. 26)

Ameletus falsus McDunnough 1938: 30; Spieth 1941: 91; Ameletus sp. C, Allen and Chao 1981: 449.

Type Material. Male holotype: Greer, Arizona, 14 June 1936, G.J. Sperry; No. 4293 in CNC (examined).

Diagnosis. Body length: 9–12 mm. Eyes with dark green pigmentation in living males. Mesonotum brown with dark brown to black at the periphery and with three yellow streaks running longitudinally from the anterior margin and joining together just before the blackish scuto-scutellar impression; scutellum dark brown to black. Fore wings transparent with dark brown veins and cross-veins and with some cross-veins narrowly bordered with brown. Dark brown ganglionic markings on abdominal sternite 8. Penis as in Figure 26A–C.

This species is closely related to A. amador, A. imbellis, and A. sparsatus, but the lack of pronounced suffusion around the cross-veins of the fore wings and the geographical distribution are diagnostic.

Distribution (Map 5). Arizona: Apache Co. (CNC, UC), Cochise Co. (UC), Pima Co. (GFE). VI.

Remarks. This species was described by McDunnough (1938) from a single individual from Greer, Arizona. The holotype is incomplete and the genitalia slide is missing. However, I have reared imagoes of this species from larvae collected at the type locality, and so a proper assessment of its relationship with other *Ameletus* species is possible. Figure 26A–C is drawn from the genitalia slide of this species collected from the Catalina Mts., near Tucson, Arizona, by V.K. Mayo. These genitalia are identical to those of the specimens reared from the type locality.

Larvae of A. falsus that I collected from the type locality fit the description of Allen and Chao's (1981) Ameletus sp. C. Also, it is possible that larvae collected from New Mexico (Canjilon Creek, Rio Arriba Co., 29 June 1964, R.K. Allen) and described as Ameletus sp. B (Allen and Chao 1981) belong to this species.

Ameletus imbellis Day

(Figs. 27, 8E)

Ameletus imbellis Day 1952: 23; Day 1956: 90.

Type Material. Male holotype and female allotype: Sage Creek, Napa Co., California, 4 April 1950; in CAS (examined).

Diagnosis. Body length: 11-12 mm. Mesonotum yellow brown with extensive dark in lateral areas; scutellum dark brown with two lighter dots in front of scuto-scutellar impression. Fore wings transparent with a few cross-veins lightly clouded with brown giving them a speckled appearance. Abdominal sternite 2 with a pair of brown median spots near anterior margin; ganglionic markings visible on sternites 2-7.

This species is likely to be confused with A. amador, but characteristics given in the key will distinguish these two forms. Male genitalia (Fig. 24A-C) and appearance of wings closely resemble those of A. sparsatus, but these two species appear to have allopatric distributions and different seasonal distributions. Male genitalia are also similar to those of A. falsus, but the strong inward bend of the second segment of the forceps (Fig. 8E) separates these two species.

Distribution (Map 6). This species is currently known only from California: Napa Co. and Colusa Co. (CAS, *). IV.

Remarks. A larval description was provided by Day (1952), but it was based on the cast skin and is inadequate for identification purposes.

Ameletus inopinatus Eaton

(Figs. 1, 9)

Ameletus inopinatus Eaton 1887: 307; Ulmer 1929: 27; Schoenemund 1930: 38, 88; Bengtsson 1930: 17; Kimmins 1954: 11; Landa 1969: 78; Studemann et al. 1988: 310. Ameletus alpinus Bengtsson 1913: 303; Bengtsson 1930: 17; Landa 1969: 80.

Type Material. The holotype of this species is housed in BMNH (not examined).

Diagnosis. Body length: 9–10 mm. Mesonotum completely brown. Wings transparent with light brown veins and faintly visible cross-veins. Ganglionic markings on abdominal sternites 2–8, but with diminishing pigmentation toward anterior sternites.

The lack of ventral plates suggests close affiliation with A. velox, but other characteristics including body size, details of the genitalia (Fig. 9A-C), emergence time, and distribution readily separate these two forms.

Distribution (Map 8). This species is widely distributed in Europe (Kimmins 1954; Landa 1969; Dahlby 1973; Brittain 1974, 1978; Sartori 1988), where it is the only species of *Ameletus*. It is the only species of the genus frequently found in lakes (Brittain 1974, 1978).

In North America it is known from only two locations in the Northwest Territories: the lake shore on Fortress Island, Great Slave Lake (10° and 2 exuviae; 24 July 1990, G.F. Edmunds, Jr.) and from the lake shore 6 miles north of Snowdrift (8 larvae; 10 July 1991, G.F. Edmunds, Jr.) (GFE). VII. A single larva collected from Alaska, West Fork Chena River, 27 June 1979, A.L. Howe (GFE) may also belong to this species.

Remarks. This is the first report of *A. inopinatus* from North America. It appears to be a species inhabiting northern lakes and so further collecting in northern Canada and Alaska may show that it is more widely distributed than is currently recognized.

Sinitshenkova and Varykhanova (1990) have described *A. eugenii* from Khubsugul

Sinitshenkova and Varykhanova (1990) have described A. eugenii from Khubsugul Lake, Mongolia, as differing from A. inopinatus only in body size and colour of the forceps. However, the body length of the holotype of A. eugenii is identical to the body length of the holotype of A. inopinatus and is very similar to the body length of specimens collected in North America. Also, the colour of the forceps can vary between individuals of the same species (pers. obs.) and should not be used as a species characteristic. I have not seen any material of A. eugenii, but based on the description of this species, its presence in lakes, the wide distribution of A. inopinatus, and comments from N. Kluge (pers. comm.), I strongly suspect that these are the same species.

The larva was described by Schoenemund (1930), and life history data were provided by Gledhill (1959), Larsen (1968), Ulfstrand (1968), and Brittain (1974).

Ameletus majusculus sp.nov.

(Figs. 3, 32, 43)

Description. Male imago (description based on specimens freshly preserved in alcohol): body length 17–21 mm, fore wings 14–17 mm. Head, including compound eyes, dark brown with extensive white area around and between antennae. Prothoracic tergum dark brown with white laterally and in some specimens also posteriorly; mesotergum dark brown changing to black at the scutellum, a pair of white markings in front of the scuto-scutellar impression and white streaks along the lateroparapsidal sutures; metatergum dark brown to black; thoracic pleuron brown to dark brown with extensive white at the base of legs and wings. Fore legs dark brown to black; middle and hind legs yellow with brown tarsal segments. Wings transparent with dark brown to black longitudinal veins and cross-veins, and with amber shading in stigmatic area of fore wings. First abdominal tergite dark brown to black; tergites 2–9 largely pale white, with dark brown shading on posterior margin extending to form triangular posterolateral patches, and U-shaped median markings; tergite 10 light brown with dark brown patch at the centre. Abdominal sternites without ganglionic markings except on sternite 8; sternite 1 brown; 2–8 largely pale white with dark brown patches at the centre (Fig. 43); sternites 2 and 3 also with a pair of submedian brown C-shaped markings (Fig. 40C) near anterior margin; sternite 9 pale with extensive brown at anterior and lateral margins. Genitalia generally dark brown; lateral processes relatively small with shallow depression between (Fig. 3); penis lobes twisted inwardly at tips and with distinct accessory spines on ventromesal surface of the apical half of each lobe (Fig. 32A). Caudal filaments dark brown to black basally, grading to reddish brown apically.

Type Material. Male holotype: Ford Creek, Alberta (50°48′N 114°51′W, elevation 1707 m), 2.7 km upstream from confluence with the Elbow River, 10 June 1992 (reared from larva), J.S. Zloty. Female allotype: same location and collector as holotype but collected on 22 June 1990. Paratypes: same location and collector as holotype but with following dates, 29 June 1988 (2°°), 22 June 1990 (2°°, 1 larva), 15 June 1992 (2°°), 18 June 1992 (6°°°, 1° subimago); Elbow River at Elbow Falls, Alberta (50°52′N 114°47′W), 20 June 1989, J.S. Zloty (1°°); Jumpingpound Creek, W of Calgary on Hwy 968 (51°02′N 114°44′W), Alberta, 5 June 1992, J.S. Zloty (2 larvae); Carbondale River, Crowsnest Pass, Alberta

(49°28′N 114°19′W), 12 June 1989, J.S. Zloty (2 ♂ ♂, 1 larva); Lynx Creek, Crowsnest Pass, Alberta (49°32′N 114°30′W), 8 June 1989, J.S. Zloty (2 larvae); South Castle River, Crowsnest Pass, Alberta (49°18′N 114°25′W), 8 June 1989, J.S. Zloty (1 ♂ subimago, 1 larva); Moose Creek, Gallatin Co., Montana, 12 June 1985, D.L. Gustafson (1 ♂, 1 ♀); Grasshopper Creek, Lane Co., Oregon, 23 May/4 June 1982 (1 ♂ subimago). The holotype and the allotype will be housed in CNC; paratypes listed above will be deposited in CAS, MSU, UC, and UM.

Etymology. majusculus = great, large, majestic (Latin), in reference to body size.

Diagnosis. Males of this species are easily separated from all others by the short, stout spines formed from the ventral plates (Fig. 32C) and the unique accessory spines on the ventroapical half of the lateral lobes (Fig. 32A). This is also the largest known species of *Ameletus*.

Distribution (Map 6). Southwestern Alberta (UC); Montana: Gallatin Co. (CSU, MSU); Washington: Pierce Co. (US); Oregon: Lane Co. (UM), Klamath Co. (OSU). V-VI. I also suspect that this species occurs in British Columbia and Idaho.

Remarks. Life cycle data were provided by Zloty et al. (1993). The larval stage will be described in a future publication on Alberta *Ameletus* larvae.

Ameletus oregonensis McDunnough

(Figs. 6, 33, 40, 44A)

Ameletus oregonensis McDunnough 1933a: 157; Needham et al. 1935: 455; McDunnough 1936: 208.

Type Material. Male holotype: Rock Creek, Philomath, Oregon, 19 March 1933, R.E. Dimmick; No. 3612 in CNC (examined).

Diagnosis. Body length: 9–11 mm. Eyes dark brown. Mesonotum brown with some yellow streaks that may vary between individuals. Wings transparent with dark brown veins and cross-veins and with pronounced suffusion at the base (Fig. 44A). Abdominal sternites 2–8 with C-shaped markings (Fig. 40C); no ganglionic markings. Penis with short and broad lateral lobes not reaching to the base of the forceps (Fig. 6), a character shared only with A. subnotatus, with which this species is broadly sympatric, and with the eastern A. walleyi from which it is well separated geographically. Ameletus oregonensis differs from these two species in having a penis with three apical processes (Fig. 33A) instead of two (Fig. 34A). The wings of A. oregonensis resemble those of A. walleyi but differ from those of A. subnotatus by the lack of brown pigmentation around the cross-veins. See also remarks under A. subnotatus.

Distribution (Map 7). Southern Alberta (CSU, UC, US, GFE); British Columbia (CNC, *); southwestern and northern Saskatchewan (US); Oregon: Benton Co. (CNC); Idaho: Benewah Co., Boise Co., Bonner Co., Bonneville Co., Boundary Co., Custer Co., Latah Co., Teton Co. (GFE, *); Montana: Gallatin Co. (MSU, UC), Meagher Co. (UC); Utah: Salt Lake Co. (CAS, GFE), Wasatch Co. (GFE). IV-V.

Remarks. The larva was described by McDunnough (1936). Edmunds (1952, unpublished thesis) described "A. needhami" from material (1 °, 1 °, 2 ° ° subimagoes) collected by A.R. Gaufin from the Provo River at Midway, Wasatch Co., Utah, 5 May 1948. I have not been successful in locating these specimens, but I have seen a male imago from Mt. Dell Creek, Salt Lake Co., Utah, May 1962, L.T. Nielson (CAS), identified by G.F. Edmunds as "A. needhami". This individual is identical to A. oregonensis.

Ameletus pritchardi sp.nov.

(Figs. 8C, 14)

Description. Male imago (description based on specimens freshly preserved in alcohol): body length 9-11 mm, fore wings 8-10 mm. Head dark brown, compound eyes dark green in living individuals. Prothoracic tergum dark brown with some opaque white in posterolateral area; mesotergum dark brown with a large opaque white spot in front of scuto-scutellar impression and with some light shading laterally to this spot; scutellum dark brown; metatergum dark brown; thoracic pleuron brown to dark brown with extensive white at the base of legs and wings and between pleural plates. Fore legs amber to brown; middle and hind legs amber-brown with darker shading at the base of each segment. Wings transparent; fore wings with milky white suffusion between costal and radial veins, more intense in stigmatic area (best seen over a dark surface); longitudinal veins amber; cross-veins white and faintly visible. First abdominal tergite brown to dark brown; tergites 2-7 opaque white anteriorly with gradual increase in brown pigmentation posteriorly and with conspicuous tracheae; tergites 8-10 brown to dark brown. Abdominal sternite 1 brown; sternites 2-8 largely pale white with a pair of C-shaped markings on anterior half of each segment (Fig. 40C) that decrease in pigmentation on the posterior segments; sternites 7 and 8 with black ganglionic markings; sternite 9 pale with extensive brown at anterior and lateral margins. Genitalia generally light amber; lateral processes large with apices pointing laterally and with a deep cleft between them (Fig. 8C); penis with narrow lateral lobes curved dorsally at tips (Fig. 14B, C); ventral plate formed into a small spine that is laterally bent at tip (Fig. 14B) and armed with two to six small saw-like teeth on the ventral edge (Fig. 14D). Caudal filaments uniformly opaque white.

Type Material. Male holotype and female allotype: Elbow River at Bragg Creek Provincial Park, Alberta (50°56′N 114°35′W), 20 August 1992 (reared from larvae collected on 14 August), J.S. Zloty. Paratypes: same location and collector as holotype but on following dates, 13 September 1988, reared from larvae collected on 8 August ($1 \circ, 1 \circ$), 9–28 August 1990, reared from larvae collected on 9–10 August ($4 \circ \circ, 1 \circ$ subimago, $7 \circ \circ$, 3 larvae); Jumpingpound Creek, Sibbald Creek Trail, Alberta ($51^{\circ}02'N$ 114°28′W), 15 August 1990, J.S. Zloty ($2 \circ \circ, 1 \circ$); Vermilion River, Kootenay National Park, Hwy 93, B.C. ($51^{\circ}11'N$ 116°08′W), 7 August 1990, J.S. Zloty ($1 \circ, 1 \circ$ subimago, $1 \circ$); Sheep Creek near Skookumchuck ($49^{\circ}54'N$ 115°43′W), B.C., 18 August 1990 (reared from larvae collected on 6 August), J.S. Zloty ($3 \circ \circ, 1 \circ$ subimago, $2 \circ \circ$, 1 larva). The holotype and the allotype will be housed in CNC; paratypes listed above will be deposited in CAS, UC, and UM.

Etymology. The species is named after my graduate supervisor Gordon Pritchard, University of Calgary, Alberta, who has contributed greatly to the biology of aquatic insects.

Diagnosis. Male genitalia of this species are most similar to those of the eastern *A. tarteri*, but differ in the number and form of accessory spines on the apical portion of the ventral plate and in the relative length of these spines (Figs. 14C and 17C). Also, *A. pritchardi* has transparent wings, whereas those of *A. tarteri* are lightly suffused with amber.

Distribution (Map 8). Southern British Columbia (UC); southwestern Alberta (UC). VII–IX. This species probably also occurs in Washington, Idaho, and Montana.

Remarks. The larval stage will be described in a future publication on *Ameletus* larvae from Alberta.

Ameletus shepherdi Traver

(Figs. 16, 47A)

Ameletus shepherdi Traver 1934: 238; Needham et al. 1935: 455; Day 1956: 90. Ameletus querulus McDunnough 1938: 29. New synonymy.

Type Material. Male holotype of *A. shepherdi*: Waddell Creek, Rancho del Oso, Santa Cruz Co., California (no date), D. Shepherd; No. 1282.1 in Cornell University (examined), but with missing genitalia. Male holotype of *A. querulus*: Trepanier Creek, Peachland, B.C., 20 July 1934, A.N. Gartrell; No. 4292 in CNC (examined).

Diagnosis. Body length: 7–8 mm. Eyes with green pigmentation on upper two-thirds in living specimens. Mesonotum dark brown with distinct yellow stripe formed by yellow shading of medioscutum, scuto-scutellar impression, and scutellum; infrascutellum dark brown. Fore wings lightly suffused with brown coloration, less at the apical area (Fig. 47A). No ganglionic markings on abdominal sternites.

This species is one of the smallest in the genus. The unique shape of the ventral plates (Fig. 16B-D) distinguishes males of this species from all other *Ameletus*.

Distribution (Map 9). British Columbia (CNC, UC); Montana: Beaverhead Co. (UC); Oregon: Union Co. (US); California: Alpine Co. (*), Redwood Belt (UC, *), Santa Cruz Co. (CU, *). VII–VIII.

Remarks. The terminal appendages of this species seem indistinguishable from those of *A. querulus*. Final-instar larvae that I collected at the type locality of *A. querulus* (Trepanier Cr., Peachland, B.C.) are identical to larvae collected from Smith River, Redwood National Park, California, from which I reared adult males of *A. shepherdi*. It seems to me that the reduced pigmentation on the fore wings in *A. querulus*, used by McDunnough (1938) as the species' diagnostic character, is merely interpopulation variation of *A. shepherdi*. Therefore, I strongly suspect that *A. querulus* can be treated as a synonym of *A. shepherdi*.

Ameletus similior McDunnough

(Fig. 15)

Ameletus similior McDunnough 1928: 9; McDunnough 1929: 174; McDunnough 1935: 102; Needham et al. 1935: 456.

Ameletus monta Mayo 1952: 93. New synonymy.

Type Material. Female holotype of *A. similior*: Jacques Lake, Jasper National Park, Alberta, 4 September 1926, F. Neave; No. 2665 in CNC (examined). Male allotype: Cameron Creek, Waterton Lakes National Park, Alberta, "late" August 1928; in CNC (examined). Holotype of *A. monta*: McGuigan Creek, near New Denver, B.C., 29 August 1940; presumed missing. Male paratype: same locality and date as holotype; in CAS (examined).

Diagnosis. Body length: 8–10 mm. Eyes dark brown. Mesonotum and scutellum brown with yellow shading in scuto-scutellar impression. Wings transparent with faint amber suffusion, brown veins and yellowish cross-veins. Ganglionic markings on abdominal sternites 2–8.

Well-defined spines on ventral plates (Fig. 15E-G) distinguish this species from all other North American Ameletus.

Distribution (Map 10). Southern British Columbia (CNC, UC); southwestern Alberta (CNC, UC, US); Oregon: Union Co. (US); Idaho: Valley Co. (GFE); Montana: Beaverhead Co. (UC), Gallatin Co. (MSU, UC). VIII–IX. Larvae collected by A.V. Provonsha from Emigration Creek, Salt Lake Co., Utah, 26 July 1972 (PU), may also belong to this species.

Remarks. I have not been successful in locating the holotype of *A. monta*, but in addition to examining the male paratype (CAS), I have collected specimens from McGuigan Creek, near New Denver, B.C., the type locality of *A. monta*. All of them are identical in regard to size, coloration, and details of the genitalia, and also in having a similar emergence time as *A. similior*. Accordingly, I consider *A. monta* a synonym of *A. similior*.

Jensen (1966) illustrated genitalia of A. similior based on a single individual collected at the beginning of August from the Lick Creek, Valley Co., Idaho. However, the genitalia of this specimen belong to A. celer and not to A. similior.

The larva was described by McDunnough (1935). Life history data are provided by Zloty (1992), Zloty et al. (1993), and Pritchard and Zloty (1994).

Ameletus sparsatus McDunnough

(Figs. 28, 46C)

Ameletus sparsatus McDunnough 1931: 89; Needham et al. 1935: 456.

Ameletus aequivocus McDunnough 1934: 164; Needham et al. 1935: 449. New synonymy.

Type Material. Male holotype and female allotype of *A. sparsatus*: Blairmore, Alberta, 15 July 1930, J.H. Pepper; No. 3271 in CNC (examined). Male holotype of *A. aequivocus*: Gunnison River, near Almont Co., 25 June 1925, A.W. Lindsey; No. 3765 in CNC (examined).

Diagnosis. Body length: 10–11 mm. Eyes with green pigmentation in living males. Mesonotum yellow with light brown at the periphery. Fore wings transparent with some cross-veins surrounded with smoky brown, giving them a speckled appearance (Fig. 46C). Abdominal sternite 2 with a pair of C-shaped markings (Fig. 40C); ganglionic markings may be visible on sternite 8.

This species is likely to be confused with A. amador and A. falsus. I have differentiated these three species under A. amador and A. falsus. The male genitalia (Fig. 28) also resemble those of A. imbellis (Fig. 27), but the diagnostic features in the key will separate them.

Distribution (Map 12). Southern British Columbia (CNC, UC); southwestern Alberta (CNC, UC); Montana: Gallatin Co. (MSU, UC); Idaho: Blaine Co., Valley Co. (CNC, GFE, SWRC); Colorado: Grand Co. (CSU), Larimer Co. (CNC, CSU). VI–VIII.

Remarks. Specimens of this species from British Columbia, Alberta, and Montana have well-defined dark patches on the fore wings. However, specimens from Colorado, including the type of *A. aequivocus*, have only lightly spotted fore wings, but otherwise closely resemble northern forms. The late emergers of *A. sparsatus* from Alberta are usually lighter in colour and have reduced pigmentation around the cross-veins. Because the lack of spots on the fore wings is the only diagnostic character (see also McDunnough 1935), I believe that *A. aequivocus* should be considered a synonym of *A. sparsatus*.

The drawing of the genitalia provided by Edmunds et al. (1976) is not that of A. sparsatus but resembles A. dissitus. Also, the drawing of the penis in Jensen (1966) is not of this form.

The larva was described by McDunnough (1935).

Ameletus subnotatus Eaton

(Figs. 34, 36C, 44B)

Ameletus subnotatus Eaton 1885: 211; McDunnough 1928: 9; McDunnough 1931: 89; Spieth 1941: 92.

Type Material. Male lectotype designated by Spieth (1941): Colorado (no other data); in BMNH (examined).

Diagnosis. Body length: 11–15 mm. Eyes dark brown. Mesonotum dark brown with some yellowish areas that may vary between individuals. Wings transparent but with at least three to four dark brown patches formed around some cross-veins (Fig. 44B). Abdominal sternites 2–8 with C-shaped markings (Fig. 40C); no ganglionic markings; penis as in Figures 34A, B, and 36C.

The male genitalia of this species have a distinctive form, shared only with A. oregonensis and the eastern A. walleyi (Fig. 6). Differences between A. subnotatus and A. oregonensis are discussed under the latter and below.

Distribution (Map 11). This is the only species of *Ameletus* known to occur in both eastern and western North America. Southeastern British Columbia (UC); Alberta (CNC, UC); southwestern Manitoba (JF, UC); northeastern Ontario (CNC); eastern and western Quebec (SWRC, UC, UM); New Brunswick (GFE); Newfoundland (UM); Utah: Uintah Co. (TF, GFE), Wasatch Co. (GFE, UC); Wyoming: Carbon Co. (CSU); Colorado: Grand Co. (CSU), Larimer Co. (CSU). IV-VI.

Remarks. Eaton (1885), in his original description of *A. subnotatus*, did not provide a description of the genitalia. Needham et al. (1935) provided a drawing from an individual that they believed belonged to this species, but which turned out to be an undescribed form (see remarks under *A. doddsianus*). This mistake was corrected by Spieth (1941) who also provided accurate drawings of the genitalia.

The Ameletus sp. in Flannagan et al. (1990) is A. subnotatus. The larval stage will be described in a future publication on Ameletus larvae of Alberta.

Ameletus suffusus McDunnough

(Figs. 29, 47B)

Ameletus suffusus McDunnough 1936: 210.

Type Material. Male holotype: Shingle Creek, Penticton, British Columbia, 3 May 1935, A.N. Gartrell; No. 4110 in CNC (examined).

Diagnosis. Body length: 9–10 mm. Eyes with green pigmentation in living males. Mesonotum yellow with brown shading at the lateral and posterolateral areas; scutellum yellow brown. Wings distinctly suffused with brown; veins brown and cross-veins surrounded by smoky brown (Fig. 47B). Ganglionic markings only on abdominal sternite 8. Penis as in Figure 29.

The male genitalia are similar to those of A. andersoni, A. dissitus, A. exquisitus, A. vancouverensis, and A. vernalis; their differences are given in the key. See also diagnosis under A. vancouverensis.

Distribution (Map 9). Southern British Columbia (CNC, UC, *); southwestern Alberta (UC). V-VII.

Ameletus tarteri Burrows

(Fig. 17)

Ameletus tarteri Burrows 1987: 284.

Type Material. Male holotype: Hamrick Run, near confluence with North Fork of Cherry River, Greenbrier County, West Virginia, 15 June 1983, W.L. Burrows; in USNM (not examined).

Diagnosis. Body length: 7.5–10 mm. Mesonotum light brown with lighter and darker shadings and streaks; scutellum of similar light colour. Fore wings transparent with some light amber suffusion in costal and subcostal area; veins and cross-veins with amber colour. Abdominal sternites 2–6 with C-shaped markings (Fig. 40C); ganglionic markings only on sternite 8; penis as in Figure 17.

This species is most similar to the western A. pritchardi, but the diagnostic features presented under that species readily separate them.

Distribution. West Virginia: Greenbrier Co. (SWRC, UC, *); Virginia: Giles Co. (*). VI-VII.

Remarks. The larva was described by Burrows (1987). Matthews and Tarter (1989) provided life history data for this species.

Ameletus tertius McDunnough

(Fig. 18)

Ameletus tertius McDunnough 1938: 27.

Type Material. Male holotype and female allotype: Baddeck Forks, Cape Breton Is., Nova Scotia, 13 July 1936, J. McDunnough; No. 4287 in CNC (examined).

Diagnosis. Body length: 9 mm. Mesonotum and scutellum dark brown. Wings transparent with a faint amber tinge; veins and cross-veins brown. Abdominal sternites 2–7 with a pair of C-shaped markings (Fig. 40C); ganglionic markings on sternite 8; penis as in Figure 18.

The male genitalia place this eastern form close to the western A. celer, A. edmundsi, and A. tolae. Differences between these species are presented under the account of A. celer.

Distribution. Eastern Quebec (SWRC, UC); Nova Scotia (CNC, *); Maine (SWRC); Vermont (SWRC); New York (SWRC). VII-VIII.

Remarks. The larva was described by McDunnough (1938).

Ameletus tolae sp.nov.

(Fig. 19)

Description. Male imago (in alcohol): body length 6.5–8 mm, fore wings 6–7 mm. Head generally brown with dark brown ocellar tubercles, ocelli opaque white; upper two-thirds of compound eyes grey, lower portion dark brown. Prothoracic tergum brown; mesotergum uniformly light brown; scutellum light brown, infrascutellum dark brown; metatergum brown; thoracic pleuron light brown to brown with extensive white at base of legs and wings and between pleural plates. Fore legs brown; middle and hind legs amber to yellow. Wings transparent; fore wings with milky suffusion in stigmatic area; longitudinal veins amber, cross-veins white, faintly visible. First abdominal tergite brown; tergites 2–9 opaque white, with light brown to brown shading in posterolateral and posterior areas; pigmentation increasing on posterior tergites. Abdominal sternite 1 brown; sternites 3–8 opaque white with dark brown ganglionic markings; sternite 9 pale with extensive brown at anterior and lateral margins. Genitalia generally light amber; lateral processes small, with shallow depression between them; penis with short lateral lobes (Fig. 19A); ventral plates with a single small spine on the apical portion (Fig. 19C). Caudal filaments uniformly golden brown.

Type Material. Male holotype and female allotype: Lick Creek, 6 mi. E of Medical Springs, Oregon, 8 August 1975, E. LaGasa. Paratypes: same data as holotype (3 ♂ ♂ subimagoes, 2 ♀ ♀, 1 ♀ subimago), and same data as holotype but collected on 25 July 1975 (1 ♂, 5 ♂ ♂ subimagoes, 2 ♀ ♀, 2 ♀ ♀ subimagoes); "National Forest near St. Maries", Idaho, 27 July 1966, A.R. Gaufin (1 ♂). The holotype will be deposited in CNC, and paratypes will be sent to collections of CAS and UC.

Etymology. The species is named after my mother, Tola Zloty.

Diagnosis. This species is near to *A. celer*, but is smaller and differs in details of the genitalia (Figs. 11 and 19).

Distribution (Map 11). Known from Idaho and Oregon: Union Co. VII-VIII.

Ameletus validus McDunnough

(Figs. 7, 39)

Ameletus validus McDunnough 1923: 50; McDunnough 1928: 9; Needham et al. 1935: 458; Day 1954: 24; Wigle and Thommasen 1990: 10.

Type Material. Male holotype: Banff, Alberta, 1 October 1922, C.B. Garrett; No. 526 in CNC (examined). Female allotype: same data as holotype, but collected on 20 September 1922; in CNC (examined).

Diagnosis. Body length: 9-11 mm. Eyes dark brown. Mesonotum dark brown with yellowish patch in front of scutellum. Wings strongly suffused with brown (Fig. 47B). No abdominal ganglionic markings.

This common, late season species is easily distinguished from all other *Ameletus* by the shape of the genitalia. Lateral lobes have outwardly twisted apices and small spines on the lateral surface (Fig. 39A); ventral plate formed into a small spine which bears two or more lateral accessory spines (Fig. 39C).

Distribution (Map 16). Northern and western Alaska (CNC, *); southern and southwestern British Columbia (CNC, UC, *); southwestern Alberta (CNC, UC, *); Washington: Skagit Co. (GFE); Oregon: Lane Co. (OSU, UM, US); Idaho: Boise Co. (*), Custer Co. (GFE); Montana: Beaverhead Co. (UC), Meagher Co. (UC), Missoula Co (US); California: El Dorado Co. (*), Mendocino Co. (*); Utah: Box Elder Co. (CSU), Salt Lake Co. (TF, GFE);

Colorado: Larimer Co. (CSU), Gunnison Co. (GFE). IX-XII.

Remarks. Ecological data were provided by Hill and Knight (1987), who stated that larvae were present most of the year. They also stated that this was the only species of *Ameletus* at their study site. However, my observations suggest that few, if any, western sites have only one species of *Ameletus*. Furthermore, *A. validus* has a univoltine life cycle with an overwintering egg diapause in Alberta, and small larvae do not appear before July (J. Zloty, unpubl. data). Thus, I suspect that the life history data of Hill and Knight (1987) may be questionable.

The larva of A. validus was described by McDunnough (1935).

Ameletus vancouverensis McDunnough

(Figs. 30, 47C)

Ameletus vancouverensis McDunnough 1933a: 157; Needham et al. 1935: 458. Ameletus facilis Day 1952: 24. New synonymy.

Type Material. Male holotype of *A. vancouverensis*: Pourtenay, Vancouver Island, B.C., 1 May 1931; J.W. Gregson; No. 3611 in CNC (examined). Male holotype of *A. facilis*: Sage Creek, Napa County, California, 22 April 1950, W.C. Day; in CAS (examined). Female allotype of *A. facilis*: Smith Creek, Clara County, California, 7 April 1951, W.C. Day; in CAS (examined).

Diagnosis. Body length: 9 mm. Eyes with green pigmentation. Colour of mesonotum varies from entirely yellow to light brown with yellow restricted to mesal area. Wings tinted with amber (Fig. 47C); longitudinal veins and cross-veins with brown. Ganglionic markings on abdominal sternites 7 and 8. Penis as in Figure 30A-D.

The suffused wings serve to separate this form from all other species that have titillators except A. suffusus, from which it is distinguished by the shape and length of the lateral lobes and the relative length of the titillators.

Distribution (Map 13). Southwestern British Columbia (CNC, *); Oregon: Benton Co. (US), Hood River Co. (*), Lane Co. (US, UM), Union Co. (US); California: Napa Co. (CAS), Santa Clara Co. (*), Siskiyou Co. (GFE). IV-VII.

Remarks. The genitalia of A. vancouverensis are identical to those of A. facilis, as are body coloration and flight period. The only difference is that wing pigmentation may be reduced in southern populations of A. facilis. Therefore, I regard A. facilis as a synonym of A. vancouverensis.

Ameletus vancouverensis differs from A. suffusus in the shape of lateral lobes and the relative length of titillators. In A. vancouverensis, the lateral lobes are short and club-shaped apically (Fig. 30B) and the titillators are relatively long (Fig. 30D); in A. suffusus, the lateral lobes are narrow apically (Fig. 29A) and the titillators are relatively short. However, both types of genitalia occur in a population in Oregon, and so more study is required to determine the status of these species.

Ameletus velox Dodds

(Fig. 10)

Ameletus velox Dodds 1923: 105; Dodds and Hisaw 1924: 139; Needham and Christenson 1927: 11; Seemann 1927: 47; McDunnough 1928: 9; McDunnough 1929: 174; McDunnough 1934: 163; Needham et al. 1935: 459; Edmunds 1954: 64; Day 1956: 90. Ameletus connectus McDunnough 1936: 209. New synonymy. Ameletus connectina McDunnough 1939: 50. New synonymy.

Type Material. Male holotype of *A. velox*: Tolland, Colorado, 1 July 1915; in ANSP (examined). Male holotype of *A. connectus*: Shingle Creek, Penticton, British Columbia, 5 May 1935, A.N. Gartrell; No. 4109 in CNC (examined). Male holotype of *A. connectina*: Blue Lake, W of Lytton, British Columbia, 6 August 1938, J.K. Jacob; No. 4443 in CNC (examined).

Diagnosis. Body length: 14–15 mm. Eyes dark brown. Mesonotum dark brown with small yellow spots in front of scutellum. Wings transparent; longitudinal veins dark brown and cross-veins brown. Ganglionic markings sometimes visible on abdominal sternites 2–8.

Males have reduced ventral plates (Fig. 10B), a character shared only with A. *inopinatus* (Fig. 9B). Other characters given under the diagnosis of A. *inopinatus* easily separate these two forms.

Distribution (Map 15). Southern British Columbia (CNC, *); southwestern Alberta (UC, *); Montana: Gallatin Co. (MSU, UC); Utah: Box Elder Co. (GFE, *), Cache Co (GFE, *), Davis Co. (GFE, *), Salt Lake Co. (GFE, *), Wasatch Co. (GFE, *); Colorado: Gilpin Co. (CSU), Saquache Co. (CSU); California: Los Angeles Co. (*), Riverside Co. (*). VI–VII. Jensen (1966) lists this species from Idaho. However, his record was based solely on larval material collected in early May and late November. I have not seen this material, but the larvae collected at the end of November would be too small for a positive identification.

Remarks. McDunnough (1936) diagnosed A. connectus by the lack of ganglionic markings. He could find no difference in the genitalia: "... the genitalia are distinctly reminiscent of the former [A. velox]." I have seen specimens with well-defined ganglionic markings, whereas in others they are only faintly visible or absent. These specimens otherwise differ in no significant way from A. velox.

Ameletus connectina was described by McDunnough (1939) on the basis of a single individual and differentiated from A. velox by its small size and the presence of ganglionic markings. He also stated: "According to genitalia ... the species is very close to connectus" However, size of individuals in a population is related to time of emergence, later emergers being smaller. The type specimen of A. connectina was collected in early August, quite late for A. velox. I could find no significant morphological differences between the two, and so I believe that both A. connectina and A. connectus are synonyms of A. velox.

Dodds (1923) and Edmunds (1952) described larvae as A. velox, but their specimens were A. doddsianus and A. edmundsi, respectively (Zloty and Pritchard, unpublished).

Ameletus vernalis McDunnough

(Figs. 31, 48, 45C)

Ameletus vernalis McDunnough 1924: 115; Needham et al. 1935: 459.

Type Material. Male holotype and female allotype: Oliver, British Columbia, 27 April 1923, C.B. Garrett; No. 749 in CNC (examined).

Diagnosis. Body length: 12–13 mm. Eyes dark green in living males. Mesonotum dark brown with characteristic yellowish markings at the posterior end (Fig. 48). Wings transparent; cross-veins of fore wings shaded with brown, more prominent along radial veins (Fig. 45C). Ganglionic markings clearly visible on abdominal sternites 7–8 and faintly so on sternite 6.

This species is close to A. andersoni, A. dissitus, A. exquisitus, A. suffusus, and A. vancouverensis. The transparent wings differentiate this form from A. vancouverensis and A. suffusus, and details of the genitalia separate it from the other three species (Fig. 31). The apical ends of the lateral lobes are pointed and strongly curved mediodorsally in A. andersoni (Fig. 21). In A. dissitus, the apical ends of titillators are inwardly twisted hooks (Fig. 24), and A. exquisitus is diagnosed by longer titillators that are bent ventrally at the tip (Fig. 25).

Distribution (Map 14). Southern British Columbia (CNC, *); southwestern Alberta (CNC, UC); Washington: Chelan Co. (*); Oregon: Benton Co. (US), Grant Co. (UC); Montana: Gallatin Co. (MSU, UC), Missoula Co. (US, GFE). IV–VI. Distribution of this species probably extends also to Idaho.

Remarks. The larva was described by McDunnough (1936).

Ameletus walleyi Harper

(Figs. 35, 36B)

Ameletus walleyi Harper 1970: 603.

Type Material. Male holotype and female allotype: Headwaters of the Eramosa River, Wellington Co., Ontario, 3 and 1 May 1969, respectively, P.P. Harper; in CNC (examined).

Diagnosis. Body length: 11–12 mm. Mesonotum and scutellum dark brown. Wings transparent with amber shading at the base and with dark brown veins and brown cross-veins (Fig. 44A). Abdominal sternites 2–8 without ganglionic markings, but with a pair of submedian C-shaped dashes (Fig. 40C). Genitalia as in Figures 35 and 36B.

This species, together with A. oregonensis and A. subnotatus, form a distinct group that is easily diagnosed by the unique shape of the male genitalia (Fig. 6). Ameletus walleyi is near to A. subnotatus in genitalic detail, but it shares wing characteristics with A. oregonensis. Differences between these species are also discussed under A. oregonensis.

Distribution. Known only from two locations in Wellington Co., Ontario. V.

ACKNOWLEDGMENTS

I am grateful to the following institutions and individuals who gave me information, loaned specimens, or allowed me to examine types in their collections: ANSP (D.H. Funk); BMNH (S.J. Brooks); CAS (W. Pulawski); CNC (J.T. Huber and R. Hutchinson); CSU (B.C. Kondratieff); CU (E.R. Hoebeke); MSU (D.L. Gustafson); OSU (N.H. Anderson); PU (W.P. McCafferty); SWRC (D.H. Funk); UF (D. Studemann); UM (F. Harper); US (D.M. Lehmkuhl); USNM (O.S. Flint); the late R.K. Allen, San Marcos, California; J. Brittain, Oslo, Norway; M. Dietrich, Kirchheim, Germany; G.F. Edmunds, Jr., Salt Lake City, Utah; T.G. Fink, DeKalb, Illinois; J.F. Flannagan, Winnipeg, Manitoba; R.L Hall, Gainesville, Florida; N.J. Kluge, St.-Petersburg, Russia; D.A. Lytle, Ithaca, New York; M.J. Wigle, Bella Coola, British Columbia. Also, I am grateful to N.H. Anderson, F. Harper, G.F. Edmunds, Jr., D.H. Funk, B.C. Kondratieff, and W.P. McCafferty for making suggestions that considerably improved the manuscript, and to G.E. Ball, University of Alberta, Edmonton, who made it possible for me to examine the CNC type material. In addition I thank Maria Zloty and Val Pritchard for being unpaid assistants on many field trips.

Particular thanks are due to Gordon Pritchard, Department of Biological Sciences, University of Calgary, for his guidance, criticism, and continuous support throughout the course of this study. The work was supported by an operating grant to G. Pritchard from the Natural Sciences and Engineering Research Council of Canada, and a Challenge Grant in Biodiversity from the Government of Alberta to J. Zloty.

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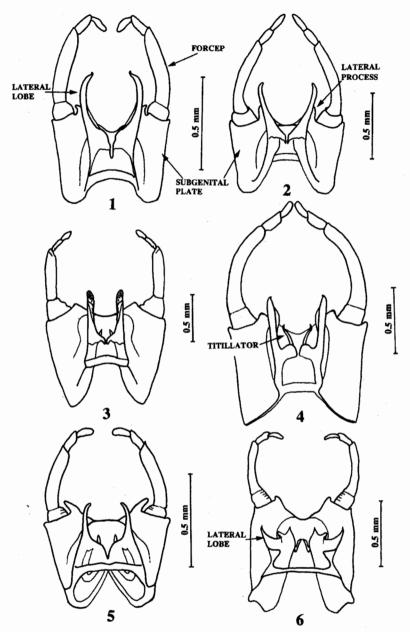
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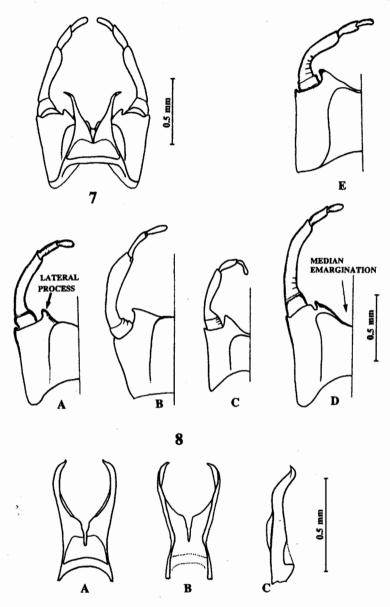
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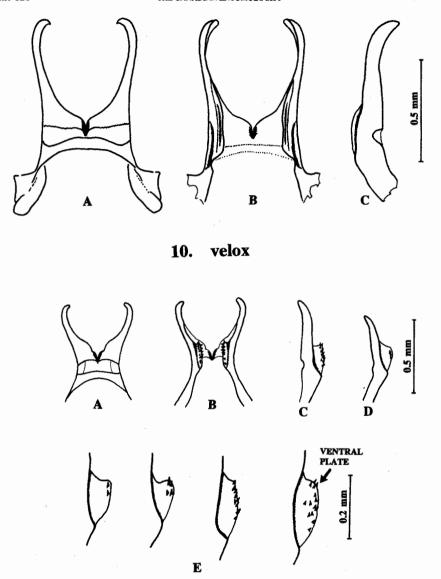


Figs. 1–6. 1, dorsal view of male genitalia of Ameletus inopinatus Eaton, Great Slave Lake, N.W.T.; 2, dorsal view of male genitalia of A. celer McDunnough, Ford Creek, Alberta; 3, dorsal view of male genitalia of A. majusculus sp.nov., Ford Creek, Alberta; 4, dorsal view of male genitalia of A. dissitus Eaton, Sage Creek, Napa Co., California; 5, dorsal view of male genitalia of A. browni McDunnough, Gilbert Brook, Bennington Co., Vermont; 6, dorsal view of male genitalia of A. oregonensis McDunnough, Jumpingpound Creek, Alberta.



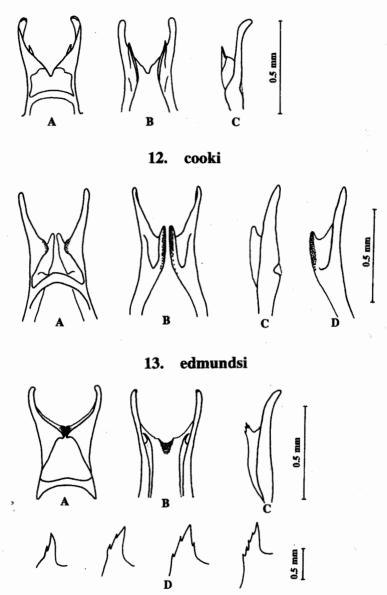
9. inopinatus

Figs. 7-9. 7, dorsal view of male genitalia of Ameletus validus McDunnough, Jumpingpound Creek, Alberta; 8, dorsal view of male subgenital plate (right half) of (A) A. amador Mayo, (B) A. edmundsi sp.nov., (C) A. pritchardi sp.nov., (D) A. andersoni sp.nov., (E) A. imbellis Day; 9, penis of male of A. inopinatus Eaton, Great Slave Lake, N.W.T.: (A) dorsal view, (B) ventral view, (C) lateral view.



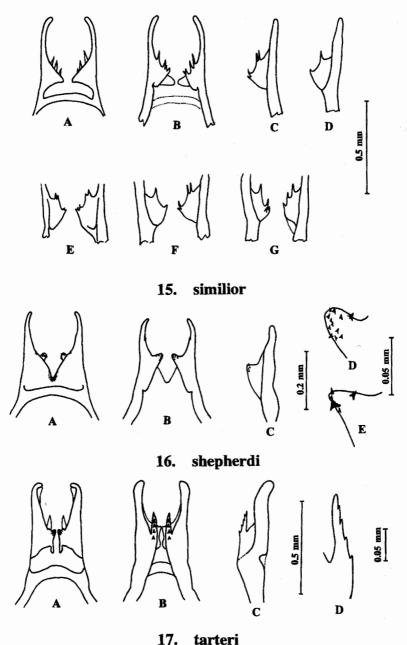
11. celer

Figs. 10–11. 10, penis of male of Ameletus velox Dodds, South Boulder Creek, Gilpin Co., Colorado: (A) dorsal view, (B) ventral view, (C) lateral view; 11, penis of male of A. celer McDunnough, Elbow River, Alberta: (A) dorsal view, (B) ventral view, (C) lateral view, (D) lateral view, holotype of A. celeroides, (E) ventral plates, ventrolateral view (from the left: Ford Creek, Alberta; Jumpingpound Creek, Alberta; Elbow River, Alberta; Lake Agnes, Jackson Co., Colorado).

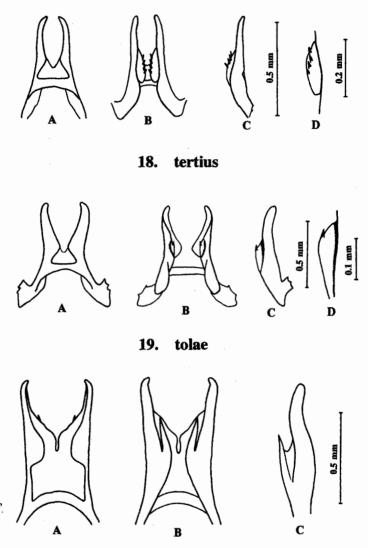


14. pritchardi

Figs. 12-14. 12, penis of male of Ameletus cooki McDunnough, Prairie Creek, Alberta: (A) dorsal view, (B) ventral view, (C) lateral view; 13, penis of male of A. edmundsi sp.nov., Emigration Canyon Creek, Salt Lake Co., Utah: (A) dorsal view, (B) ventral view, (C) lateral view, (D) ventrolateral view; 14, penis of male of A. pritchardi sp.nov., Elbow River, Alberta: (A) dorsal view, (B) ventral view, (C) lateral view, (D) apices of ventral plate, ventrolateral view.

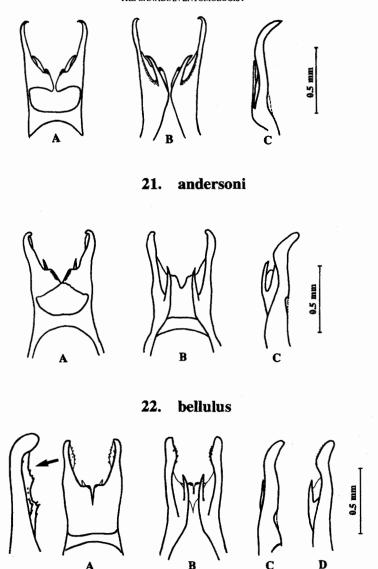


Figs. 15-17. 15, penis of male of Ameletus similior McDunnough, Ford Creek, Alberta: (A) dorsal view, (B) ventral view, (C) left lateral view, (D) right lateral view, (E-G) ventral plates, ventrolateral view (E, paratype of A. monta; F, Ford Creek, Alberta; G, Blackmore Creek, Gallatin Co., Montana); 16, penis of male of A. shepherdi Traver: (A) dorsal view, (B) ventral view, (C) lateral view, (D-E) apices of ventral plate, ventrolateral view (D, holotype of A. querulus; E, Prairie Creek, California); 17, penis of male of A. tarteri Burrows, Hamrick Run, Greenbriar Co., West Virginia: (A) dorsal view, (B) ventral view, (C) lateral view, (D) apex of ventral plate, lateral view.



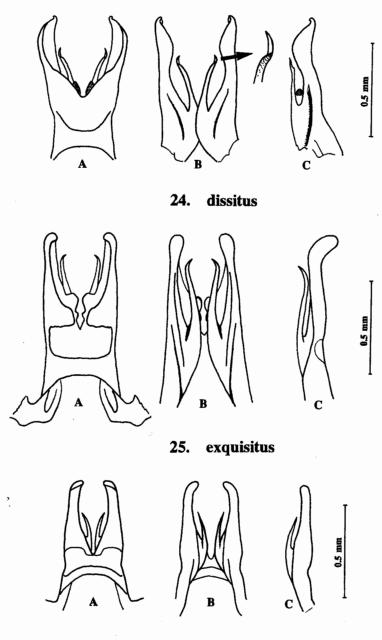
20. amador

Figs. 18-20. 18, penis of male of Ameletus tertius McDunnough, Rivière Pigou, Saguenay Co., Quebec: (A) dorsal view, (B) ventral view, (C) lateral view, (D) ventral plate, ventrolateral view; 19, penis of male of A. tolae sp.nov., Lick Creek, Union Co., Oregon: (A) dorsal view, (B) ventral view, (C) lateral view, (D) ventral plate, ventrolateral view; 20, penis of male of A. amador Mayo, Dry Creek, Amador Co., California, holotype: (A) dorsal view, (B) ventral view, (C) lateral view.



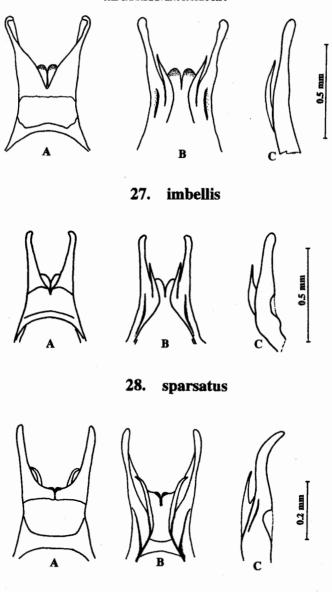
23. doddsianus

Figs. 21-23. 21, penis of male of Ameletus andersoni sp.nov., Oak Creek, Benton Co., Oregon: (A) dorsal view, (B) ventral view, (C) lateral view; 22, penis of male of A. bellulus sp.nov., Ford Creek, Alberta: (A) dorsal view, (B) ventral view, (C) lateral view; 23, penis of male of A. doddsianus sp.nov., South Boulder Creek, Gilpin Co., Colorado: (A) dorsal view, (B) ventral view, (C) lateral view, (D) ventrolateral view.



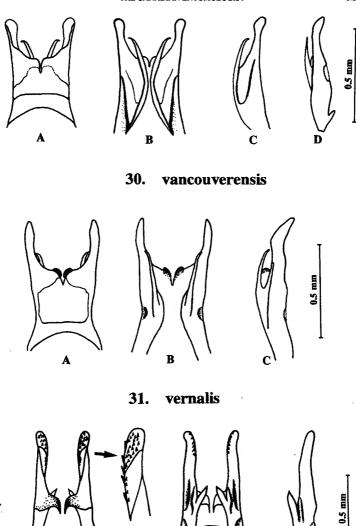
26. falsus

Figs. 24-26. 24, penis of male of Ameletus dissitus Eaton, Sage Creek, Napa Co., California: (A) dorsal view, (B) ventral view, (C) lateral view; 25, penis of male of A. exquisitus Eaton, Willamette River, Benton Co., Oregon: (A) dorsal view, (B) ventral view, (C) lateral view; 26, penis of male of A. falsus McDunnough, Catalina Mts., Pima Co., Arizona: (A) dorsal view, (B) ventral view, (C) lateral view.



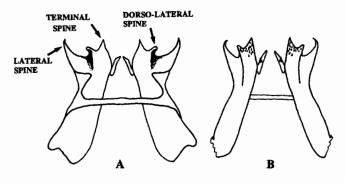
29. suffusus

Figs. 27-29. 27, penis of male of Ameletus imbellis Day, Sage Creek, Napa Co., California: (A) dorsal view, (B) ventral view, (C) lateral view; 28, penis of male of A. sparsatus McDunnough, Elk River, southeastern British Columbia: (A) dorsal view, (B) ventral view, (C) lateral view; 29, penis of male of A. suffusus McDunnough, Boundry Creek, southern British Columbia: (A) dorsal view, (B) ventral view, (C) lateral view.

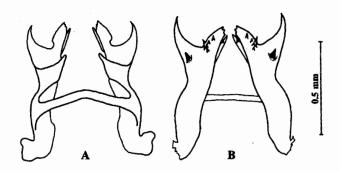


32. majusculus

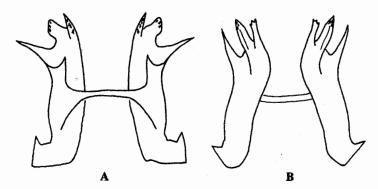
Figs. 30–32. 30, penis of male of *Ameletus vancouverensis* McDunnough, Courtenay, Vancouver Island, British Columbia, holotype: (A) dorsal view, (B) ventral view, (C) ventrolateral view, (D) lateral view; 31, penis of male of *A. vernalis* McDunnough, Bow River, Calgary, Alberta: (A) dorsal view, (B) ventral view, (C) lateral view; 32, penis of male of *A. majusculus* sp.nov., Ford Creek, southwestern Alberta: (A) dorsal view, (B) ventral view, (C) lateral view.



33. oregonensis



34. subnotatus



35. walleyi

Figs. 33-35. 33, penis of male of Ameletus oregonensis McDunnough, Jumpingpound Creek, southwestern Alberta:
(A) dorsal view, (B) ventral view; 34, penis of male of A. subnotatus Eaton, James River, southwestern Alberta:
(A) dorsal view, (B) ventral view; 35, penis of male of A. walleyi Harper, Lutteral Creek, Mimosa, Wellington Co.,
Ontario: (A) dorsal view, (B) ventral view.

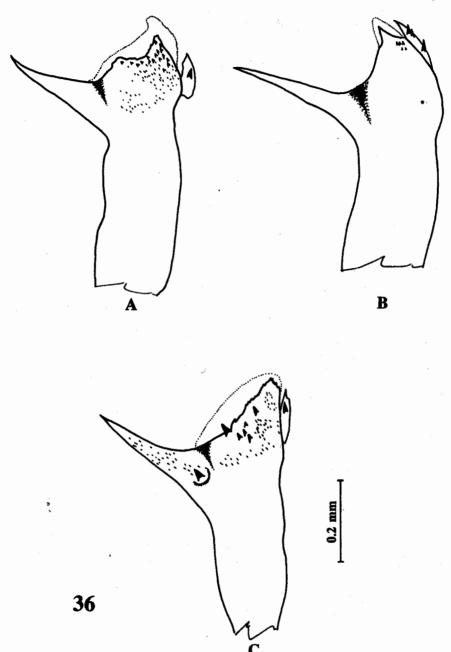
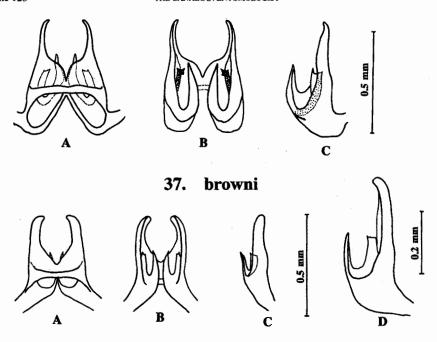
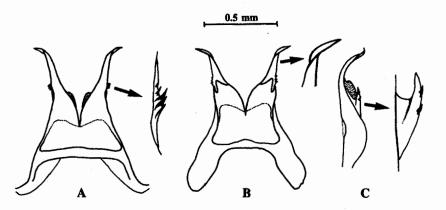


Fig. 36. Penis of male, lateral view: (A) Ameletus oregonensis McDunnough, (B) A. walleyi Harper, holotype, (C) A. subnotatus Eaton.

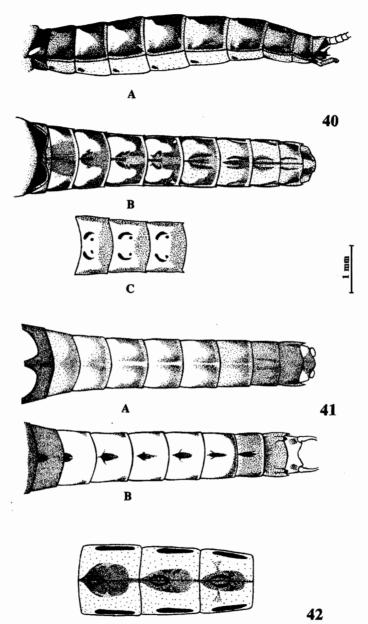


38. cryptostimulus

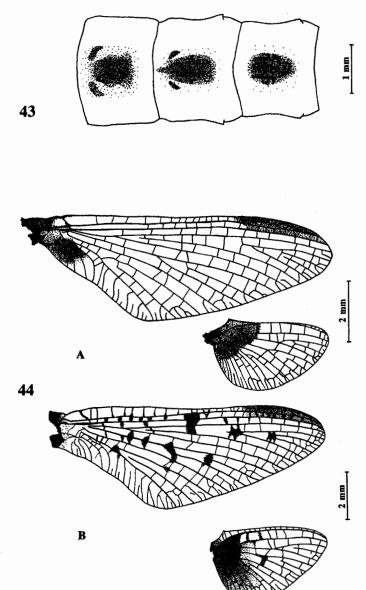


39. validus

Figs. 37–39. 37, penis of male of Ameletus browni McDunnough, Gilbert Brook, Bennington Co., Vermont: (A) dorsal view, (B) ventral view, (C) lateral view; 38, penis of male of A. cryptostimulus Carle, Little Stony Creek, south of Kire, Giles Co., Virginia: (A) dorsal view, (B) ventral view, (C) lateral view, (D) ventrolateral view; 39, penis of male of A. validus McDunnough, Jumpingpound Creek, southwestern Alberta: (A) dorsal view, (B) ventral view, (C) lateral view.



Figs. 40–42. Abdomen. 40, Ameletus oregonensis McDunnough: (A) lateral view, (B) dorsal view, (C) ventral view, sternites 3–5; 41, A. celer McDunnough: (A) dorsal view, (B) ventral view; 42, A. edmundsi sp.nov., sternites 3–5.



Figs. 43-44. 43, Ameletus majusculus sp.nov., sternites 2-4; 44, fore and hind wings: (A) A. oregonensis McDunnough, Belly River, Glacier National Park, Montana, (B) A. subnotatus Eaton, Clearwater River, southwestern Alberta.

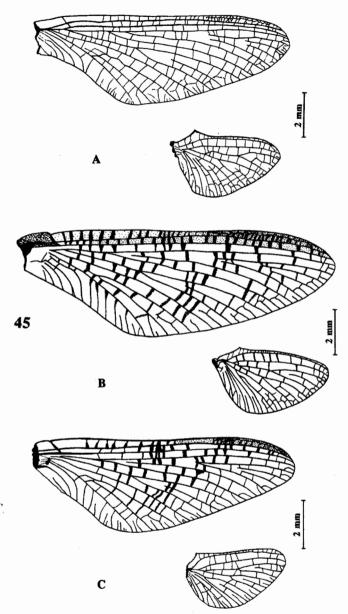


Fig. 45. Fore and hind wings: (A) Ameletus celer McDunnough, Ford Creek, southwestern Alberta, (B) A. andersoni sp.nov., Kalama Springs, Cowlitz Co., Washington, (C) A. vernalis McDunnough, Bow River, Calgary, Alberta.

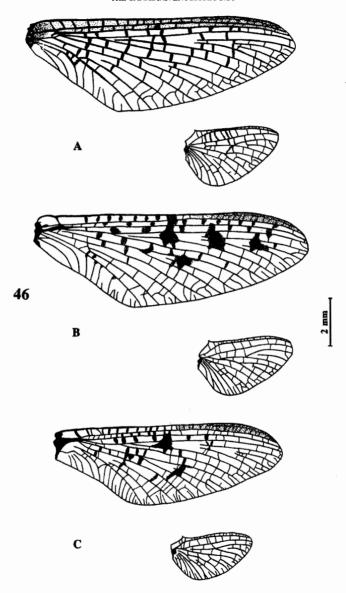


Fig. 46. Fore and hind wings: (A) Ameletus doddsianus sp.nov., Indian Creek, San Juan Co., Utah, (B) A. bellulus sp.nov., Ford Creek, southwestern Alberta, (C) A. sparsatus McDunnough, Bow River, Calgary, Alberta.

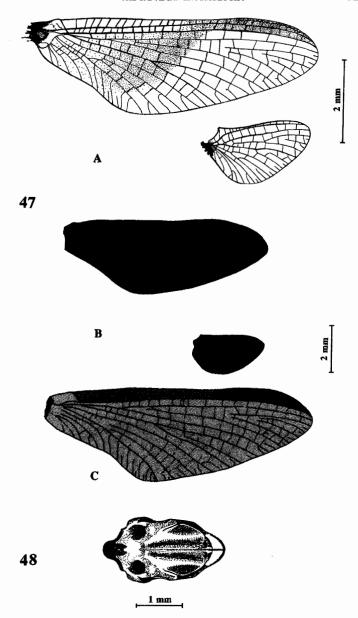


Fig. 47. Fore and hind wings, except as noted: (A) Ameletus shepherdi Traver, State Grove, Del Norte Co., California, (B) A. suffusus McDunnough, Manning Provincial Park, southern British Columbia, (C) A.vancouverensis McDunnough, Smith Creek, Mt. Hamilton, California (fore wing).

Fig. 48. Thorax of Ameletus vernalis McDunnough, Bow River, Calgary, Alberta.

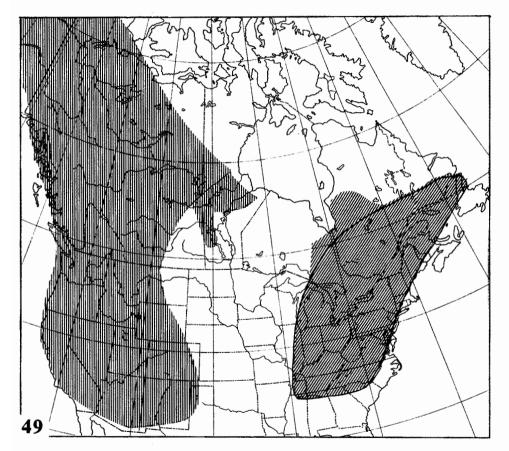
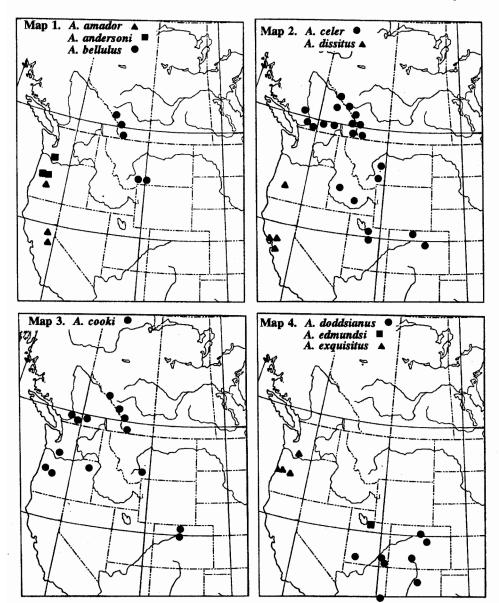


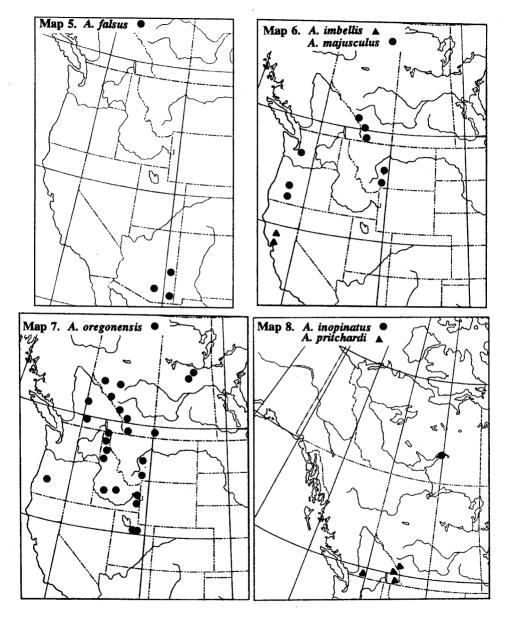
Fig. 49. Ranges of eastern and western North American species of Ameletus.

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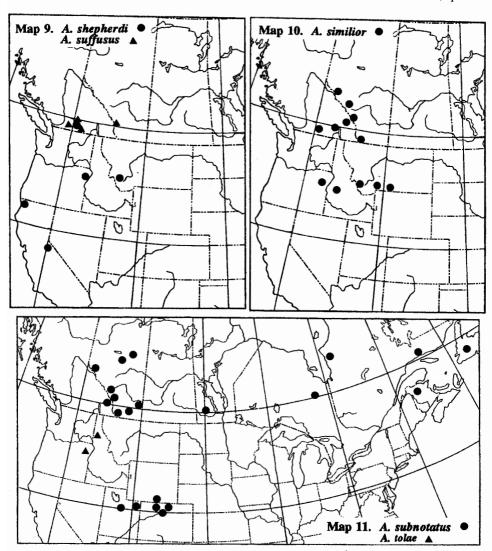
342



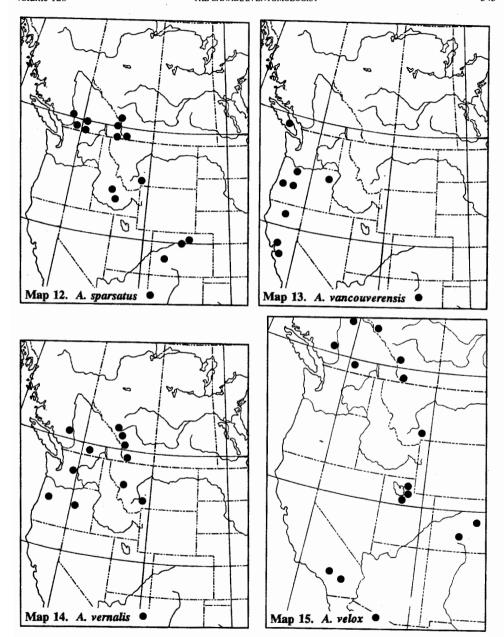
MAPS 1-4. 1, collection sites of Ameletus amador Mayo, A. andersoni sp.nov., and A. bellulus sp.nov.; 2, collection sites of A. celer McDunnough and A. dissitus Eaton; 3, collection sites of A. cooki McDunnough; 4, collection sites of A. doddsianus sp.nov., A. edmundsi sp.nov., and A. exquisitus Eaton.



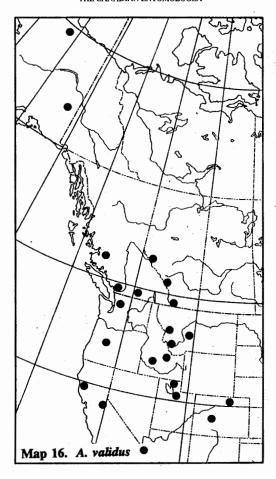
MAPS 5-8. 5, collection sites of Ameletus falsus McDunnough; 6, collection sites of A. imbellis Day and A. majusculus sp.nov.; 7, collection sites of A. oregonensis McDunnough; 8, collection sites of A. inopinatus Eaton and A. pritchardi sp.nov.



MAPS 9-11. 9, collection sites of *Ameletus shepherdi* Traver and *A. suffusus* McDunnough; 10, collection sites of *A. similior* McDunnough; 11, collection sites of *A. subnotatus* Eaton and *A. tolae* sp.nov.



MAPS 12–15. 12, collection sites of *Ameletus sparsatus* McDunnough; 13, collection sites of *A. vancouverensis* McDunnough; 14, collection sites of *A. vernalis* McDunnough; 15, collection sites of *A. velox* Dodds.



MAP 16. Collection sites of Ameletus validus McDunnough.