

Review of Ameletidae (Ephemeroptera) of Russia and adjacent lands

Обзор Ameletidae (Ephemeroptera) России и сопредельных стран

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KEY WORDS: Ephemeroptera, Ameletidae, *Metreletus*, *Ameletus*, *Metreletus micus* **comb.n.**, *Ameletus altaicus* **sp.n.**, *Ameletus montanus rossicus* **ssp.n.**, *Ameletus montanus arlecchino* **ssp.n.**КЛЮЧЕВЫЕ СЛОВА: Ephemeroptera, Ameletidae, *Metreletus*, *Ameletus*, *Metreletus micus* **comb.n.**, *Ameletus altaicus* **sp.n.**, *Ameletus montanus rossicus* **ssp.n.**, *Ameletus montanus arlecchino* **ssp.n.**

ABSTRACT. Revised generic diagnoses of *Metreletus* and *Ameletus* are given. The species, originally described as *Ameletus micus*, is transferred to genus *Metreletus*. Basing on all stages of development, there are described a new species *Ameletus altaicus* **sp.n.**, as well as new subspecies *A. montanus rossicus* **ssp.n.** and *A. montanus arlecchino* **ssp.n.**, which inhabit in Siberia and Russian Far East. Brief characteristics of other species and subspecies, distributed on territory of Russia, are given. Characters of larval genital buds as such, are used in taxa diagnoses for the first time.

РЕЗЮМЕ. Уточнены родовые диагнозы *Metreletus* и *Ameletus*. Вид, исходно описанный как *Ameletus micus*, перенесен в род *Metreletus*. По всем стадиям развития описаны новый вид *Ameletus altaicus* **sp.n.**, а также новые подвиды *A. montanus rossicus* **ssp.n.** и *A. montanus arlecchino* **ssp.n.**, обитающие в Сибири и на Дальнем Востоке России. Даны краткие характеристики других видов и подвидов *Ameletus*, распространённых на территории России. В диагнозах таксонов впервые использованы признаки личиночных зачатков гениталий как таковых.

Introduction

For the long time, mayflies, which are recently attributed to Ameletidae, were attributed to a family Siphonuridae. In such wide sense, Siphonuridae s.l. represented a plesiomorphon [about this term — see Kluge, 2004]. Because of this, recently such taxon is not recognized, being splitted into several smaller holophyletic families — Siphonuridae s.str., Ameletidae and others [Kluge et al., 1995; Kluge, 2004].

Ameletidae are distributed in Holarctic and Oriental Region, having most number of species (about 30) in North America, less number of species in Asia and two species only in Europe. North American species were

recently revised by J. Zloty and G. Pritchard [Zloty, 1996; Zloty & Pritchard, 1997]. Asian species were described from Japan [Imanishi, 1932, 1933], Taiwan [Kang & Yang, 1994] and the former USSR [Bajkova, 1976; Brodsky, 1930; Kluge, 1979, 1982; Sinitshenkova, 1977, 1981; Sinitshenkova & Tshernova, 1976; Sinitshenkova & Varykhanova, 1989; Soldan, 1978; Ulmer, 1927]. The present paper contains descriptions of new taxa and a review of formerly known taxa from Siberia and Russian Far East.

All material examined is deposited in the Zoological Institute of Russian Academy of Sciences, in Saint-Petersburg; temporarily it locates in the department of entomology of Saint Petersburg University.

In the lists of material examined, the following arbitrary signs are used: **Im** — imago; **S** — subimago, **L** — larva, **L-S** — subimago reared from larva (with larval exuviae); **S-Im** — imago reared from subimago (with subimaginal exuviae); **L-S-Im** — imago reared from larva (with larval and subimaginal exuviae); **L/S** — mature larva with developed subimaginal cuticle.

Family Ameletidae McCafferty, 1991

Hierarchical name: Ameletus/fg1 (incl. *Metreletus*)

REFERENCES. Kluge et al., 1995: 111, Figs 18–22 (egg, larva, subimago, imago); Kluge, 2004: 80, Figs 11, 20, 21B–C (larva, subimago, imago).

Larva. Larva retains primary swimming siphonuroid specialization. Head hypognathous. Mouth apparatus has unique specialization: labrum elongate; mandibles elongate perpendicular to their axis of articulation, with thin weak incisor and kinetodontium, prosthema on left mandible setiform, on right mandible lost; superlinguae and hypopharynx elongate; maxilla elongate, with apical margin widened, pectinate setae of apical-ventral row elongate and form filtering apparatus, maxillary canines completely lost, only one vestigial dentiseta retained. Maxillary palp retains 3 segments. Unlike other mouthparts, labium not elongate; labial palp retains 3 segments. Patella-tibial suture retained on middle and hind legs. Claws slightly curved. Tergalii lost ability of

rhythmical respiratory movements. All three caudalii have subequal length, with dense primary swimming setae.

Subimago and imago. Mesonotal suture stretched backward and pointed medially. Both in imago and subimago, lateroparapsidal suture elongate; in subimago, lateral pigmented area of mesonotum includes entire sublateroscutum and submedioscutum up to medioparapsidal suture (similar form of this area in Isonychiidae only). Anterior paracoxal suture complete. Both in imago and subimago, epimeron of mesothorax with a unique membranous area between anepimeron and katepimeron. Furcasternal protuberances retain

contiguous condition. Fore wing with anastomosed veins in pterostigma. Hind wing well-developed, as long as 0.35–0.4 of fore wing length (even in *micus* [*Ameletus*], whose fore wing lost triangular shape). Tarsi 5-segmented, 1st segment fused with tibia. All claws ephemeropteroid. In male imago, styliger dorsally with a unique membranous area. Gonostylus retains 2 distal segments. Paracercus vestigial.

Composition and distribution. Distribution of Ameletidae is limited by Holarctic and Oriental Region. Ameletidae are divided into *Metreletus* and *Ameletus* (see below).

Table 1. Characters of species of *Ameletus* of Russian Federation, Kazakhstan and Mongolia.

Таблица 1. Признаки видов *Ameletus* Российской Федерации, Казахстана и Монголии.

	Egg				Larva								Subimago	Imago					
					Labrum	Mandible		Fc-mur	Abdomen			Wing		Penis					
	labrum length/width	proximal darkening	apical darkening	middle dark band		spine-like setae on terga	spine-like setae on sterna		tergalus II	tergalii III–VI	spots on crossveins		spots on crossveins	lateral lobe	Ventral plate				
					large denticle			small proximal denticles				small distal denticles							
	egg shape	papilla in polygonal cell	round cells	high polar cells															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	18
<i>A. inopinatus inopinatus</i>	O	+	-	-	0.8	-	±	±	-	-	s	(-	-	S	-	-	-	-
<i>A. inopinatus labiatus</i>	?	?	?	?	0.8	-	±	+	-	-	l	(-	-	S	-	-	-	-
<i>A. camtschaticus</i>	O	-	+	+	0.8	+	+	-	-	-	s	(-	-	(l	+	-	-
<i>A. altaicus</i>	O	-	-	±	0.6–0.7	±	+	-	-	-	s	(-	-	(-	+	-	-
<i>A. montanus montanus</i>	?	?	?	?	0.8–0.9	+	+	+	-	-	s	(+	-	l	-	+	-	-
<i>A. montanus rossicus</i>	l	-	+	+	0.8–0.9	+	-	+	-	-	s	(-	-	l	-	+	-	-
<i>A. montanus arlecchino</i>	l	-	+	+	0.8–0.9	+	-	+	-	-	l	(-	-	l	-	+	-	-
<i>A. parvus</i>	l	+	+	+	1.0	+	+	-	-	-	s	(-	-	l	-	-	+	-
<i>A. cedrensis</i>	l	-	+	+	0.8–0.9	+	+	-	-	-	s	(-	-	l)	-	-	-
<i>A. costalis</i>	l	-	+	+	0.9	+	+	-	-	-	s	(+	+	(l	-	-	-
grex <i>A. alexandrae</i>	O	+	+	+	0.8–0.9	+	+	-	±	+	s	(±	-	(-	-	-	-

Explanation for the Table 1:

1. Egg shape: "O" — ellipsoid (not flattened) (Fig. 17); "l" — flattened, in a form of ellipse-like biconvex lens (Figs 18–19).
2. Each polygonal cell on egg surface: "+" — with papilla; "-" — without papilla (Fig. 17).
3. On egg surface round papilla-bearing cells (other than large papilla-bearing cells on one pole): "+" — prominent, with borders and papillae distinctly higher than polygonal cell (Figs 17–19); "-" — absent or not higher than polygonal cells.
4. On egg surface large papilla-bearing cells located on one pole: "+" — larger than other round cells and higher than all cells (Figs 17–19); "-" — absent or not larger than others.
5. Labrum: ratio of length to width.
6. Mandible: "+" — proximally with darkening or whole proximal part darkened; "-" — proximal part without cuticular pigment except for area close to mola.
7. Mandible: "+" — with arched darkening stretching from distal-lateral margin to mola, or at least with darkening adjacent to distal-lateral margin; "-" — distal half without cuticular pigment.
8. Middle dark band on larval femur: "+" — femur with a distinct dark band or with compact dark macula in middle; "-" — femur unicolour or with long dark macula.
9. Larval abdominal terga: "+" — with spine-like setae; "-" — without spine-like setae.
10. Larval abdominal sterna: "+" — with spine-like setae; "-" — without spine-like setae.
11. Tergalium II: "s" — larger than tergalium I, but smaller than tergalium III and next ones (Fig. 6); "l" — the longest, longer than tergalium Ø and others (Fig. 13).
12. Tergalium III–VI: "(") — with anal rib just on anal margin; "(l)" — with anal rib near anal margin (Fig. 7); "(l)" — with anal rib far from anal margin (Fig. 14).
13. Subimaginal wings: "+" — each crossvein bordered by dark; "-" — wings uniformly coloured.
14. Imaginal wings: "+" — each crossvein bordered by dark; "-" — wings uniformly coloured.
15. Lateral lobes of penis: "S" — sigmoid, i.e. curved dorsally, with apices somewhat curved ventrally; "(— distinctly bent medially (Fig. 11); "l" — in ventral view nearly straight or only slightly bent medially (but bent dorsally) (Fig. 16).
16. Ventral plate of penis: "l" — with large apical straight spine; "(— with large apical arched spine; "-" — without apical spine: either without spines or denticles, or with several equally small denticles (see 17–18).

Larval mouth apparatus. Mouth apparatus, being modified (see above), has rather uniform structure in all Ameletidae. Labrum length is species-specific and varies from 0.65 of width (in North American species *A. majusculus*) to equal to width (in *A. parvus*, *A. atratus* and *Metreletus*). Mandibles (see above) have uniform shape in all species. Zloty [1997] regarded relative length of denticles of incisor of left mandible as a species character: in *A. celer* and *A. majusculus* second denticle is the longest, while in other North American species first denticle is the longest; actually, in some of the species examined by me (*A. celer*, *A. altaicus*, *A. camtschaticus*) this character varies individually. Maxillae (see above) also have uniform shape in all species. Maxillary palp is 3-segmented; Sinitshenkova [1981] regarded shape of apical segment to be species-specific, but this character appeared to be individual [Kluge, 1995]. Labium somewhat differs in *Metreletus* and *Ameletus* (see below). Labial palps are 3-segmented; Sinitshenkova [1981] regarded relative length of segments to be species-specific, but this character appeared to be individual [Kluge, 1995].

Larval cuticular colour pattern. As in other insects, cuticular colour changes during moulting cycle (being lighter after moult and darker before moult); as in other mayflies, larval cuticular colour pattern does not pass to the next stages — subimago and imago. Usually the most part of larval cuticle is pigmented; this background pigmentation can be from light to dark brown, varying in different species, individuals and moulting phases of the same individual; here this pigmentation is called darkening. Some areas of cuticle lack pigmentation, and on living larva these places are light whitish or yellowish; here they are called blanks.

Antenna can have the following colour pattern: scapus (which is very short) and pedicellus are partly darkened; proximalmost and distalmost segments of flagellum are light, while middle segments of flagellum are darker or partly darkened. This pattern is expressed in those specimens of *Ameletus* whose cuticle has contrasting darkenings and blanks, but in specimens with non-contrasting cuticle antennae are uniformly coloured.

Anterior surface of mandible can have two darkened areas: proximal darkening occupies most part of proximal half of mandibles and adjoins its lateral margin; distal darkening is arched and stretches from lateral margin of distal half of mandible toward mola. Most species have the both darkened areas, which are often united into an integral darkening; *A. inopinatus* has no proximal darkening; *A. montanus arlecchino* **subsp.n.** and *A. m. rossicus* **subsp.n.** have no distal darkening (see Table 1).

In most species of *Ameletus*, certain abdominal terga have a pair of isolated roundish blanks and an unpaired blank on background darkening (Fig. 14). As in other mayflies, each abdominal tergite can bear a pair of oblique submedian stripes diverging posteriorly; in the cases when they are darker than the background darkening, they are visible as dark oblique stripes (Fig. 7).

Larval colour pattern of living tissues. Unlike some other mayfly larvae, larvae of Ameletidae have no marked hypodermal pigmentation. But in some species abdominal nerve ganglia are distinctly darkened and well-visible through hypoderm and cuticle as blackish spots. Like hypodermal colour, this nerve colour does not depend upon moulting cycle and passes from larva to subimago and imago.

Larval tergalii. In all *Ameletus*/fgl each tergalii III–VII has a strong costal rib on costal margin and a strong

17. Ventral plate of penis: “+” — with several small denticles in proximal part (Figs 11–12, 15–16); “–” — without small denticles in proximal part.

18. Ventral plate of penis: “+” — with several small denticles in distal part (Fig. 20); “–” — without small denticles in distal part.

Пояснение к таблице 1:

1. Форма яйца: **O** — эллипсоидная (не уплощённая) (рис. 17); **I** — уплощённая, в виде эллипсоидной двояковыпуклой линзы (рис. 18–19).

2. Каждая многоугольная ячейка на поверхности яйца: “+” — с папиллой; “–” — без папиллы (рис. 17).

3. На поверхности яйца круглые папиллоносные ячейки (кроме крупных папиллоносных ячеек на одном полюсе): “+” — выступающие, с бортами и папиллами явственно выше, чем многоугольные ячейки (рис. 17–19); “–” — отсутствуют или не выше многоугольных ячеек.

4. На поверхности яйца крупные папиллоносные ячейки, расположенные на одном полюсе: “+” — крупнее прочих круглых ячеек и крупнее всех ячеек (Figs 17–19); “–” — отсутствуют или не крупнее других.

5. Верхняя губа: отношение длины к ширине.

6. Мандибула: “+” — проксимально с затемнением или вся проксимальная часть затемнена; “–” — проксимальная часть без кутикулярного пигмента кроме области, примыкающей к моле.

7. Мандибула: “+” — с дуговидным затемнением, тянущимся от дистально-латерального края к моле, или по крайней мере с затемнением, примыкающим к дистально-латеральному краю; “–” — дистальная половина без кутикулярного пигмента.

8. Срединная тёмная перевязь на личиночном бедре: “+” — бедро с ясной тёмной перевязью или с компактным тёмным пятном посередине; “–” — бедро одноцветное или с длинным тёмным пятном.

9. Тергиты брюшка личинки: “+” — с шиповидными щетинками; “–” — без шиповидных щетинок.

10. Стерниты брюшка личинки: “+” — с шиповидными щетинками; “–” — без шиповидных щетинок.

11. Тергалия II: “s” — больше, чем тергалия I, но меньше, чем тергалия III и следующие (рис. 6); “I” — самая длинная, длиннее тергалии III и следующих (рис. 13).

12. Тергалии III–VI: “(O)” — с анальным ребром на самом анальном крае; “(O)” — с анальным ребром около анального края (рис. 7); “(I)” — с анальным ребром далеко от анального края (рис. 14).

13. Крылья субимаго: “+” — каждая поперечная жилка окаймлена тёмным; “–” — крылья однородно окрашены.

14. Крылья имаго: “+” — каждая поперечная жилка окаймлена тёмным; “–” — крылья однородно окрашены.

15. Латеральные доли пениса: “S” — s-образные, т.е. изогнуты дорсально, а вершины несколько изогнуты вентрально; “(“ — явственно изогнуты медиально (рис. 11); “I” — при взгляде с вентральной стороны почти прямые или лишь слегка изогнуты медиально (но изогнуты дорсально) (рис. 16).

16. Вентральная пластинка пениса: “I” — с большим апикальным прямым шипом; “)” — с большим апикальным изогнутым шипом; “–” — без апикального шипа: либо без шипов или зубчиков, либо с несколькими одинаково мелкими зубчиками (см. 17–18).

17. Вентральная пластинка пениса: “+” — с несколькими мелкими зубчиками в проксимальной части (рис. 11–12, 15–16); “–” — без мелких зубчиков в проксимальной части.

18. Вентральная пластинка пениса: “+” — с несколькими мелкими зубчиками в дистальной части (рис. 20); “–” — без мелких зубчиков в дистальной части.

anal rib either at a distance from anal margin, or on anal margin (Figs 7, 14). Tergalii I and II are weaker than others, with costal and anal ribs vestigial or lacking. In most species tergalium I is the smallest, tergalium II is larger, but much smaller than tergalium III and next ones (Fig. 6). In two subspecies — *A. inopinatus labiatus* and *A. montanus arlecchino* **subsp.n.** — tergalium II is strongly elongated, being the longest, but retains its weak consistency (Fig. 13).

Male genitals. In imago and subimago, styliger has wide median incision and a pair of widely diverging lateral projections (Figs 9, 16). In *Metreletus*, larval styliger has shape similar to imaginal one (Figs 1, 2). In all *Ameletus* larval styliger differs from imaginal one — its median incision is much narrower, and lateral projections are less diverging, more prominent, pointed and sometimes serrate (compare Figs 8 and 9).

In imago and subimago, each gonostylus has two distal segments (plesiomorphy among Ephemeroptera); in larva each gonostylus has one indistinctly separated distal segment, which corresponds to two distal segments of winged stages (compare Figs 8 and 9).

Important species characters are found in penis structure. Imaginal penis bears a pair of sclerotized lateral lobes located laterad-distad of gonopores, and a pair of membranous or sclerotized ventral plates located proximad of gonopores [Zloty, 1996, 1997]; by sclerotized penial arms the penis is articulated with corners of styliger and with IX abdominal tergite [Kluge, 2004]. Subimaginal penis is non-sclerotized; it has lateral lobes of the same size and shape as imaginal ones; as in other mayflies, it lacks penial arms. Larval penis is evenly sclerotized, much shorter than imaginal and subimaginal. Shape of larval penis is more simple than in imaginal one and differs in *Metreletus* and *Ameletus* (Figs 1–2, 10). Ventral plates in various species are either smooth, or bear characteristic denticles. Each such denticle develops on a place where subimago has a small stout spine-like seta. Thus, subimaginal penis bears spine-like setae in the same number and arrangement as imaginal denticles; these subimaginal spine-like setae are heavily sclerotized and well-visible on background of the rest subimaginal penis cuticle, which is non-sclerotized. Larval penis also can bear spine-like setae, which correspond to the subimaginal spine-like setae; number of the spine-like setae on larval penis is either the same as in subimago, or less (compare Figs 10 and 11, 20 and 21). The presence of complete set of spine-like setae in subimaginal stage allows to know out arrangement of denticles on imaginal penis, studying subimagoes or mature nymphs which have developed subimaginal cuticle inside. Other features of penis structure, especially shape of its lateral lobes, are so strongly changed during transformation from larva to subimago and than to imago, that examination of larvae and subimagoes does not allow to determine their imaginal condition.

Egg. Egg surface has reticulation consisting of 2 kinds of cells — polygonal and round ones; inside each round cell locates a papilla (Fig. 18); bottom of polygonal cell can be either flat, or produced to a more or less prominent protuberance or papilla. Size of cells and papillae varies among species. Most species have eggs of a usual ellipsoid shape (Fig. 17); in some species eggs are flat (Figs 18–19) — these are East Asian species *A. montanus*, *A. cedrensis* and *A. parvus*, and North American species *A. celer*, *A. cooki*, *A. sparsatus*, *A. suffusus*.

I. Genus *Metreletus* Demoulin, 1951

Hierarchical name: *Metreletus*/g(1)

REFERENCE. Kluge, 2004: 81, Fig. 20D (larva, imago).

CHARACTERISTICS. Till recently, *Metreletus* was known as a single species *balcanicus* [*Metretopus*] and was separated from *Ameletus* by the following characters: (1) In cubital field of fore wing, instead of veins going from CuA to wing margin, there are one or two intercalaries (Fig. 4). (2) Larval claw has a regular row of denticles. (3) Glossae are not truncate, apically-ventrally with numerous irregular pointed setae. Now I am placing here a second species — *micus* [*Ameletus*]. It also has 2 intercalary-like veins in cubital field of fore wing (Fig. 4). But structure of claws and glossae of *M. micus* are unknown, because all legs and labium of the single known specimen (holotype) were detached and lost. So it is not quite clear, if the second and the third characters really belong to the whole genus *Metreletus*, or they occur only in *M. balcanicus*.

In addition to the three characters listed above, now we can add the following characters common for the both species of *Metreletus*: (4) Imaginal penis has ventral plates very long and blunt (this is reliably known for *M. balcanicus* only); each lobe of larval penis has a prominent ventral plate separated by incision from lateral lobe (Figs 1–2) (unlike larval *Ameletus*, whose ventral plates are not separated from lateral lobes — Figs. 10, 21). Ventral plates of penis have no denticles or spine-like setae (unlike some *Ameletus*). (5) Labrum has a deep apical incision (Fig. 3) (unlike *Ameletus*, whose labrum has a shallow apical incision). (6) Larval abdominal cuticle has no blanks and dark stripes: terga have only diffuse median darkenings, sterna colourless.

COMPOSITION AND DISTRIBUTION. *Metreletus* has Trans-Palaearctic distribution and includes two species: (1) West-European mountain species *balcanicus* Ulmer, 1920 [*Metretopus*] (= *hessei* Fizaïne, 1931 [*Ameletus*] = *goetghebuergi* Lestage, 1938 [*Metretopus*] = *hungaricus* Ujhelyi, 1960 [*Metreletus*]) and (2) Far-Eastern species *micus* Bajkova, 1976 [*Ameletus*].

I.1. *Metreletus micus* (Bajkova, 1976), **comb.n.** (Figs 2–5)

REFERENCES. Bajkova, 1976, 583, Figs 8–10 (larva); Kluge, 1995: 9, Figs 4–5 (genital buds).

MATERIAL EXAMINED. **RUSSIA:** basin of river Ussuri, river Vak, 3.VIII.1958 (O. Bajkova) — 1 L/S♂ (holotypus).

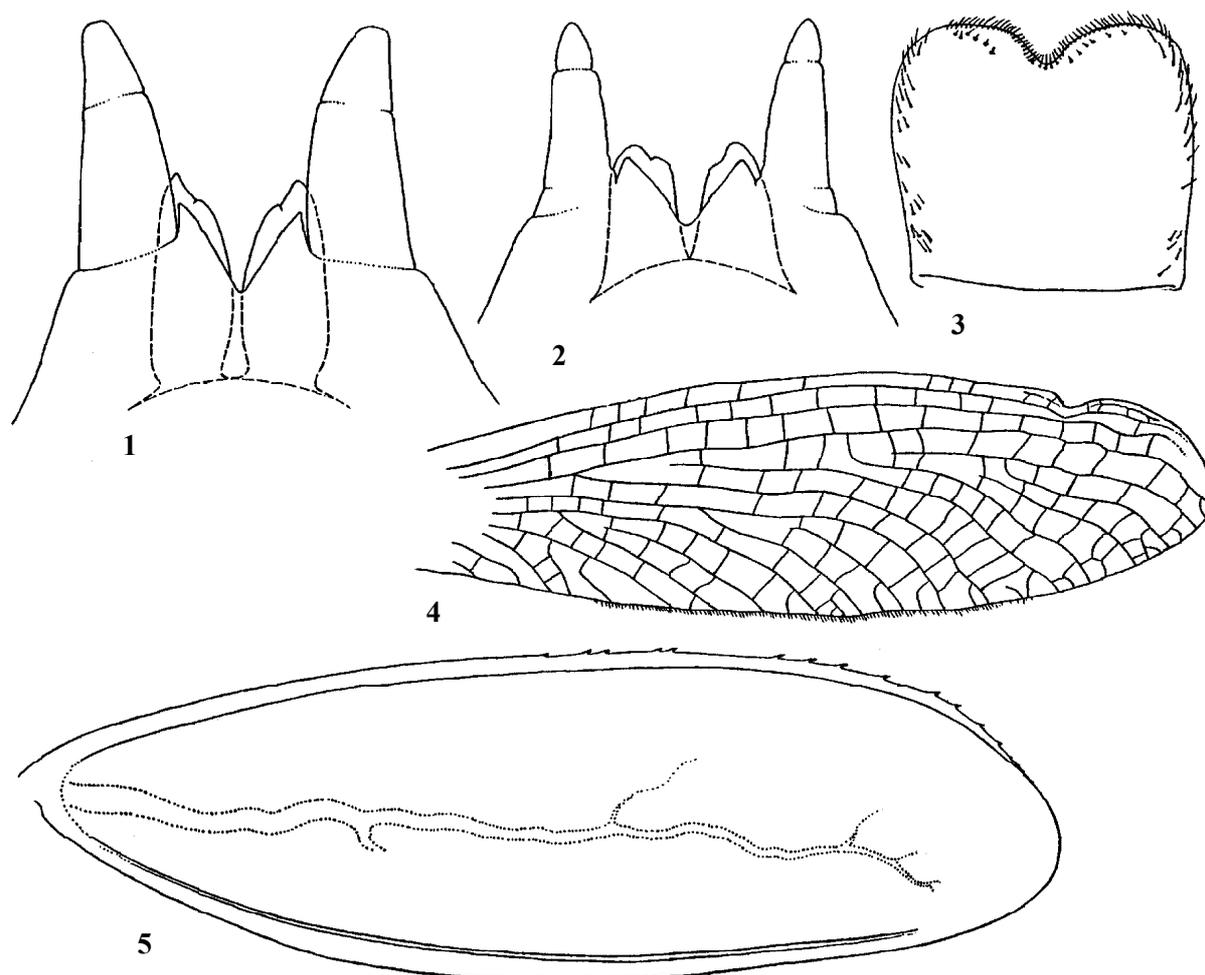
Larva. All abdominal terga and sterna without denticles on posterior margins; posterolateral spines absent on all segments (unlike all other Ameletidae, which have posterior tergal denticles and posterolateral spines at least on posterior-most abdominal terga). Tergalii (at least V–VI) very long and slender, each longer than two segments, with length three times exceeding width (unlike all other known species of Ameletidae, whose tergalii have length 1.5–2.5 times exceeding width); anal rib very slender, separated by a small distance from anal margin (Fig. 5).

Subimago and imago (basing on wings extracted from mature larva). Fore wing oval, without prominent tornus (Fig. 4) (unlike all other Ameletidae). Hind wing has shape and size usual for Ameletidae — triangular, with length slightly less than 1/2 of fore wing length. Subimaginal wings unicolour.

Egg. Unknown.

Size. Small: length of mature larva 7 mm.

DISTRIBUTION. Known as a single specimen from a single locality in Russian Far East.



Figs 1–5 — *Metreletus* spp.: 1 — *M. balcanicus*, male larval genital buds, ventral view. 2–5 — *M. micus* (holotype): 2 — male larval genital buds, ventral view; 3 — labrum; 4 — subimaginal fore wing extracted from larva; 5 — tergite VI.

Рис. 1–5 — *Metreletus* spp.: 1 — *M. balcanicus*, зачатки гениталий личинки самца, вентрально. 2–5 — *M. micus* (голотип): 2 — зачатки гениталий личинки самца, вентрально; 3 — верхняя губа; 4 — субимагинальное переднее крыло, извлеченное из личинки; 5 — тергалия VI.

II. Genus *Ameletus* Eaton, 1885

Hierarchical name: *Ameletus*/g2 (sine *Metreletus*; incl. *Chimura*, *Paleoameletus*)

REFERENCE. Kluge, 2004: 82, Fig. 20A (larva, imago).

CHARACTERISTICS. Till recently, *Ameletus* was separated from *Metreletus* by the following characters: (1) Cubital field of fore wing retains several (4–8) veins going from CuA to basitornal margin. (2) Larval claws have no denticles. (3) Glossae truncate; all apical setae are flat, widened toward apex, rounded apically and form a single regular apical-ventral row.

Now the following character can be added: (4) Larval penis has simple shape: each lobe is triangular or conic, with rounded apex and without incision between lateral lobe and ventral plate (Figs 10, 21); apex of this larval penis lobe corresponds to the apex of imaginal lateral lobe. It is important to note, that this shape of larval penis is retained not only in species whose imaginal lateral lobes are long, but also in *A. oregonensis*, whose imaginal lateral lobes are shorter than median plates and strongly divergent.

COMPOSITION AND DISTRIBUTION. *Ameletus* is distributed in Holarctic and Oriental Region. It includes the following species:

One Trans-Holarctic species — *A. inopinatus* Eaton, 1887 (= *A. alpinus* Bengtsson, 1913 = *A. eugenii* Smitshenkova & Varykhanova, 1989) (see below).

33 other North American species (Zloty, 1996) — *A. amador* Mayo, 1939; *A. andersoni* Zloty, 1996; *A. bellus* Zloty, 1996; *A. browni* McDunnough, 1933; *A. celer* McDunnough, 1934 (= *A. alticolus* McDunnough, 1934 = *A. celeroides* McDunnough, 1934 = *A. tuberculatus* McDunnough, 1939); *A. cooki* McDunnough, 1929; *A. cryptostimulus* Carle, 1978; *A. dissitus* Eaton, 1885; *A. doddsianus* Zloty, 1996; *A. edmundsi* Zloty, 1996; *A. exquisitus* Eaton, 1885; *A. falsus* McDunnough, 1938; *A. imbellis* Day, 1952; *A. lineatus* Traver, 1932; *A. ludens* Needham, 1905; *A. majusculus* Zloty, 1996; *A. minimus* Zloty & Harper, 1999; *A. oregonensis* McDunnough, 1933; *A. pritchardi* Zloty, 1996; *A. quadratus* Zloty & Harper, 1999; *A. shepherdi* Traver, 1934 (= *A. querulus* McDunnough, 1938); *A. similor* McDunnough, 1928 (= *A. monta* Mayo, 1952); *A. sparsatus* McDunnough, 1931 (= *A. aequivocus* McDunnough, 1934); *A. subnotatus* Eaton, 1885; *A. suffusus* McDunnough, 1936; *A. tarteri* Burrows, 1987; *A. tertius* McDunnough, 1938; *A. tolae* Zloty, 1996; *A. validus* McDunnough, 1932; *A. vancouverensis* McDunnough, 1933 (= *A. facilis* Day, 1952);

A. velox Dodds, 1923 (= *A. connectus* McDunnough, 1936 = *A. connectina* McDunnough, 1939); *A. vernalis* McDunnough, 1924; *A. walleyi* Harper, 1970.

Several species are known from Central Asia — *A. primitivus* Traver, 1939; *A. dodecus* (Dubey, 1971 [*Ichthybotus*]) and a group *A. alexandrae* (see below).

Three species are known from Taiwan only — *A. atratus* Kang & Yang, 1994; *A. formosus* Kang & Yang, 1994 and *A. montivagus* Kang & Yang, 1994.

Four species are known from Japan only — *A. aetherea* (Navas, 1915 [*Chimura*]); *A. crocerus* Imanishi, 1931; *A. kyotoensis* Imanishi, 1931 and *A. subalpinus* Imanishi, 1931.

Several other species and subspecies are distributed in eastern part of Asia (see below) — *A. inopinatus labiatus* Sinitshenkova, 1981; *A. camtschaticus* Ulmer, 1927 (= *A. pilatus* Sinitshenkova, 1981); *A. altaicus* sp.n.; *A. montanus montanus* Imanishi, 1930; *A. montanus rossicus* subsp.n.; *A. montanus arlecchino* subsp.n.; *A. parvus* Kluge 1979; *A. cedrensis* Sinitshenkova, 1977; *A. costalis* (Matsumura, 1931 [*Chimura*]) (= *A. longulus* Sinitshenkova, 1981).

Below, there are described the species found on the territory of the former USSR (Russian Federation, republics of Central Asia and Caucasus).

II.1. *Ameletus inopinatus* Eaton 1887

= *A. alpinus* Bengtssoná 1913 (synonymized with *A. inopinatus* by Brekke [1965])

= *A. labiatus* Sinitshenkovaá 1981

= *A. eugenii* Sinitshenkova & Varychanovaá 1989 (synonymized with *A. inopinatus* by Kluge [1995])

REFERENCES. See separately for *A. i. inopinatus* and *A. i. labiatus*.

Larva. Labrum length 0.76–0.82 of width (9 specimens measured) (unlike shorter in *A. altaicus* and longer in *A. parvus*). Abdominal terga and sterna without spine-like setae (unlike group *A. alexandrae*). Tergalii I and II without anal ribs (unlike *A. costalis*, *A. formosus* and *A. atratus*); tergalium I smallest, tergalium II varies among subspecies (see below). Tergalii III–VII with anal rib on anal margin (the same in *A. camtschaticus*).

Subimago. Wings light brownish, unicolour.

Imago. Wings non-coloured.

Male genitalis. In imago and subimago, lateral penis lobes bent S-shapely (unlike all other species). In imago, ventral plates non-developed, denticles absent. Subimaginal and larval penis without spine-like setae.

Egg. Ellipsoid (not flattened). Reticulation: each polygonal and round cell bears distinct papilla; all cells and papillae similar, so egg looks as evenly reticulated.

Size. Medium: fore wing length 9–11 mm.

DISTRIBUTION. Selected areas of Holarctic (see below, *A. i. inopinatus* and *A. i. labiatus*).

Subspecies. The species *A. inopinatus* can be divided into 2 subspecies (or forms) which differ only by length of larval 2nd tergalium. Areas of the both forms overlap in the Russian Far East. Similar forms exist in *A. montanus* (see below).

II.1.a. *Ameletus inopinatus inopinatus* Eaton, 1887

= *A. alpinus* Bengtsson, 1913

= *A. eugenii* Sinitshenkova & Varychanova, 1989

REFERENCES. Sinitshenkova & Varychanova, 1989: 576, Figs 1–20 (mole and female imago, subimago, larva; as *A. eugenii*); Zloty & Pritchard, 1997: 261, Figs 1, 6, 18A, 22E (larva, imago).

MATERIAL EXAMINED. RUSSIA: MURMANSKAYA OBLAST' (= Murmansk Prov.): Kolskiy Zaliv, 28.VI.1915 (A.

Djakonov) — 1 Im ♂; Khibiny, lake Vud-Yavr, 1930–1937 (Fridolin) — many imagoes and subimagoes. KOMI REPUBLIC, Northern and Subpolar Urals (E. Novikova et al.) — many L-S-I, larvae, subimagoes and imagoes. TUMENSKAYA OBLAST' (= Tumen' Prov.): basin of river Voikar, 19.VIII.1925 (Fridolin) — 2 Im ♂; river Malaya Sos'va, 1985 (T. Zaguzova) — 1 L; Verkhne-Tazovskiy Natural Reserve, river Pokol'ka, 1988 (T. Zaguzova) — 6 L. TAYMYRSKIY AUTONOMY ORRUG (Taymyr Autonomous Prov.): river Kotuy, mouth of river Ekhlilakh, 26.VII.1979 (N. Kluge) — 1 larval exuvia; NW of Plato Putorana, 22.VII.1982 (O. Antropova) — 5 L. KHABAROVSKIY KRAY (= Khabarovsk Prov.), Tuguro-Chumikanskiy Region, river Uda, 4–5 km above mouth, 27–28.VIII.2000 (T. Tiunova) — 3 Im ♂ (deposited in Vladivostok). MAGADANSKAYA OBLAST' (= Magadan Prov.), river Yama, 21.VIII.1980 (I. Zasykina) — 9 Im ♂. MONGOLIA: northern shore of lake Hubsugul (K. Varykhanova) — many imagoes and larvae [see Sinitshenkova & Varychanova, 1989 as *A. eugenii*].

Larva. Tergalium II not elongated, not longer (either equal or shorter) than tergalium III and next ones.

In most specimens from Siberia and Urals, abdominal darkening and blanks are contrasting and distinctly outlined, but in some specimens they are non-contrasting and diffuse, as in specimens from Great Britain [Macan, 1961: Fig. 17d]. Such larvae with non-contrasting coloration can be confused with *A. camtschaticus*.

Subimago, imago, male genitalis and egg. See *A. inopinatus*.

DISTRIBUTION. Selected areas of Holarctic: in Europe — Great Britain, Jura Mountains, Alps, Carpathians, Scandinavia, Kolskiy Peninsula, north of Ural Mountains; in Asia — Mountains Putorana (to the south from Taimyr Peninsula), northern tributaries of Lake Hubsugul (= Hövs-göl Nuur) (in Mongolia), mountains to the north-vest from Sea of Okhotsk; in North America — Alaska and Northwest Territories of Canada [Zloty, 1996].

II.1.b. *Ameletus inopinatus labiatus* Sinitshenkova, 1981

= *Ameletus labiatus* Sinitshenkova, 1981

= *Ameletus procerus*: Kluge, 1982 (non *Ameletus procerus* Bajkova, 1976)

REFERENCES. Sinitshenkova, 1981: 75, Fig. 2 (larva); Kluge, 1982: 113, Fig. 2 (male imago, subimago, larva; as *A. procerus*); Tshernova et al., 1986: 126, Figs 57: 9, 10 (male imago, as *A. procerus*); Kluge, 1995: 9, Figs 2–3 (larva).

MATERIAL EXAMINED. RUSSIA: BURYATIYA: 13.VI.2002 (V. Ivanov, S. Melnitsky) — 1 L/S ♂, 1 L ♀; river Snezhnaya (southern tributary of Lake Baikal), 24.VI.1998 (N. Rozhkova) — 2 L; natural reserve Barguzinskiy: river Davsha, 1 km from Lake Baikal, 29.VI.1998 (N. Rozhkova, O. Rusinek) — 1 L; ibid., mouth of river Osinovka, 22.VII.1998 (N. Rozhkova) — 2 L; natural reserve Baikalskiy, river Malinovka, 24.VII.1998 (N. Rozhkova) — 1 L. KHABAROVSKIY KRAY (= Khabarovsk Prov.): river Nikita, 10 km N railway station Bira, 4.VI.1980 (N. Kluge) — 2 L-S-Im ♂; 50 L. PRIMORSKIY KRAY, natural reserve Sikhote-Alinskiy: stream near Terney, 14.IV.1974 (L. Nadezhdina) — 1 L (holotypus of *A. labiatus*); river Yasnaya, 19.IV.1974 (L. Nadezhdina) — 1 L; river Zabolochennaya, 18.IV.1974 (L. Nadezhdina) — 1 L.

Larva. Tergalium II elongated, longer than tergalium III–VII [Kluge, 1982: Fig. 2: 4].

Abdominal terga and sterna usually with contrasting darkening and blanks, so that dark oblique stripes are indistinct or non-expressed on background of darkening.

Subimago, imago, male genitalis and egg. See *A. inopinatus*.

DISTRIBUTION. From Transbaikalia to Russian Far East.

COMMENT. Kluge [1982] described this species under the name *A. procerus* Bajkova, 1976, basing on a wrong museum label “holotype” which was placed by Bajkova on

the specimen which is actually paratype. The true holotype of *A. procerus* belongs either to *A. cedrensis*, or to *A. montanus rossicus*; the name *A. procerus* should be regarded as nomen dubium (see below).

II.2. *Ameletus camtschaticus* Ulmer, 1927

= *Ameletus pilatus* Sinitshenkova, 1981 (synonymized with *A. camtschaticus* by Kluge [1995])

REFERENCES. Ulmer, 1927: 12, Figs 10–12 (male imago); Sinitshenkova & Tshernova, 1976: 13, Figs 3–9 (male subimago, larva); Sinitshenkova, 1981: 73, Fig. 1 (larva, as *A. pilatus*); Tshernova et al., 1986: 126, Figs 57:7–8 (male imago); Kluge, 2004: Figs 11:A–D (genitals of male imago).

MATERIAL EXAMINED. RUSSIA: KHABAROVSKIY KRAY (= Khabarovsk Prov.), 6 km E Obluch'ye, 28.VII–3.VIII.1984 (N. Kluge) — 3 L-S-Im ♂, 1 L-S/Im ♂, 4 L-S-Im ♀, 1 L-S ♀. PRIMORSKIY KRAY, Sikhote-Alin' Natural Reserve: stream Kedrovyy, 30.VI–6.VII.1982 (E. Potikha, L. Nesterova, I. Sohan') — 7 L/S, 1 L; stream Yasnyi, 12.VI.1981 (E. Potikha) — 3 L/S; stream Spornyy, 13.VI.1990 (E. Potikha) — 2 S-Im ♀, 5 S ♀, 3 S ♂, 1 L/S ♀, exuviae LL. MAGADANSKAYA OBLAST' (= Magadan Province): river Khasyn near Khasyn, 28.VIII.1978 (V. Zherikhin, N. Sinitshenkova) — 1 Im ♂; near Sibit-Tellakh, streams Olen' and Osernyi, 2–21.VII.1977 (L. Zhiltzova) — 2 Im ♂, 1 Im ♀, 7 S ♂, 20 S ♀, 4 L/S, 8 L.

Larva. Labrum length 0.78–0.81 of width (5 specimens measured) (unlike shorter in *A. altaicus* and longer in *A. parvus*). Abdominal terga usually without contrasting darkenings, with a pair of diffuse dark oblique submedian stripes and diffuse blanks. Abdominal terga and sterna without spine-like setae (unlike group *A. alexandrae*). Tergalii I and II without anal ribs (unlike *A. costalis*, *A. formosus* and *A. atratus*), smaller than others. Tergalii III–VII with anal rib on anal margin (the same in *A. inopinatus*).

Subimago. Wings brownish, unicolour.

Imago. Wings non-coloured.

Male genitalis. In imago, lateral penis lobes with apices moderately bent medially and not bent dorsally; each ventral plate bears a large apical denticle and several small denticles proximad of it. Subimaginal penis with the same number of spine-like setae: one pair of large sclerotized ones and several smaller ones proximad of each large one. Larval penis with one pair of spine-like setae (which correspond to large ones in subimago), rarely with one more pair of smaller spine-like setae proximad of them.

Egg. Ellipsoid (not flattened). Reticulation: each polygonal cell with flat bottom lacking protuberance, with borders lower and narrower than borders of round cells, so round cells (each bearing papilla) are prominent; round cells small and sparse on most surface, denser and larger on pole.

Size. Medium: fore wing length 9–12 mm.

DISTRIBUTION. Russian Far East.

II.3. *Ameletus altaicus* Kluge, sp.n. (Figs 6–12, 17)

REFERENCES. See separately for *A. m. montanus* and *A. m. rossicus* subsp.n.

MATERIAL EXAMINED. RUSSIA: ALTAY: 10 km N Kosh-Agach, mountain stream running from ridge Kurayskiy, 4.VIII.1987 (N. Kluge) — L-S-Im ♂ (**holotypus**); ibid., 2–5.VIII.1987 (N. Kluge) — 3 L-S-Im ♂, 3 L-S-Im ♀, 4 L; river Tekelushka near its falling to river Kucherda (tributary of Katun'), 24–25.VII.1996 (S. Melnitsky) — 1 L. TUVA, river Balyktyg-Uem, 26.VI.1996 (V. Zaika) — 1 Im ♂; IRKUTSKAYA OBLAST' (= Irkutsk Prov.): Bolshie Koty, rivers Sennaya and Kotinka (western tributaries of Lake Baikal), 9–11.VIII.1994 (N. Kluge) — 9 L-S-Im ♂, 1 L-S-Im ♀. BURYATIYA: natural reserve Baikalskiy, river Kurkavka, 23.VII.1998 (N. Rozhkova) — 1 L; river Snezhnaya (southern tributary of Lake Baikal), 24.VI.1998 (N. Rozhkova) — 2 L.

Larva. Cuticle light, with non-contrasting, diffuse blanks and darkenings. Head capsule and clypeus with diffuse darkenings. Labrum shorter than in other species, its length 0.59–0.68 of width (6 specimens measured). Labrum with diffuse darkening in a form of triangle or a pair of oblique bends which stretch from anterior-medial incision to posterior-lateral corners. Mandibles can have more or less expressed diffuse distal and proximal darkenings. Thorax light, with diffuse ornament of blanks and darkenings. Legs mostly light, with darkened apex of tarsus and sometimes with more or less expressed darkenings on joints. Abdominal terga light, with darkenings non-contrasting and diffuse; most terga have uniform pattern of a pair of diffuse dark oblique submedian stripes and diffuse blanks (Figs 6–7). Abdominal nerve ganglia as in imago. Abdominal terga and sterna without spine-like setae (unlike group *A. alexandrae*). Tergalii I and II without anal ribs (unlike *A. costalis*, *A. formosus* and *A. atratus*), small. Tergalii III–VI with anal rib separated from anal margin (unlike *A. inopinatus* and *A. camtschaticus*), but located near anal margin (unlike *A. montanus* and other species); tergalium VII with anal rib just on anal margin (Fig. 1). Caudalii either nearly unicolour, or with diffuse colour pattern — proximal blank, middle darkening, distal blank and darkening on extreme apex.

Subimago. Wings brownish, unicolour.

Imago, male. Head brown. Thorax: sclerites brown (from dark to light brown), membranes pale; in each specimen all sclerites (notum, pleural sclerites and sternum) have similar colour (unlike *A. montanus*). Fore legs brownish. Middle and hind legs pale; coxa, trochanter and articulations brownish. Wings with membrane colourless, veins brownish; pterostigma without distinct coloration. Abdomen: Segment I brown. Segment II in most part light brownish, posterior margin pale. Segments III–VI translucent, in most part pale; on each of them tergum with diffuse brownish stripes along lateral margins, diffuse brownish submedian stripes and diffuse brownish transverse band parallel to posterior margin (posterior margin pale). Segments VII–VIII non-translucent, with the same brownish maculation. Segments IX–X darker. Last abdominal nerve ganglion dark brown, other ganglia either as pale as sterna, or partly brown. Cerci pale, sometimes with brownish articulations.

Male genitalis. In imago, lateral penis lobes with apices strongly bent medially and somewhat dorsally; each ventral plate with several (4–10) equally small denticles (Figs 9, 11, 12). Subimaginal penis with the same number of spine-like setae which correspond to the imaginal denticles. Larval penis with less number (0–5) of spine-like setae (Fig. 10).

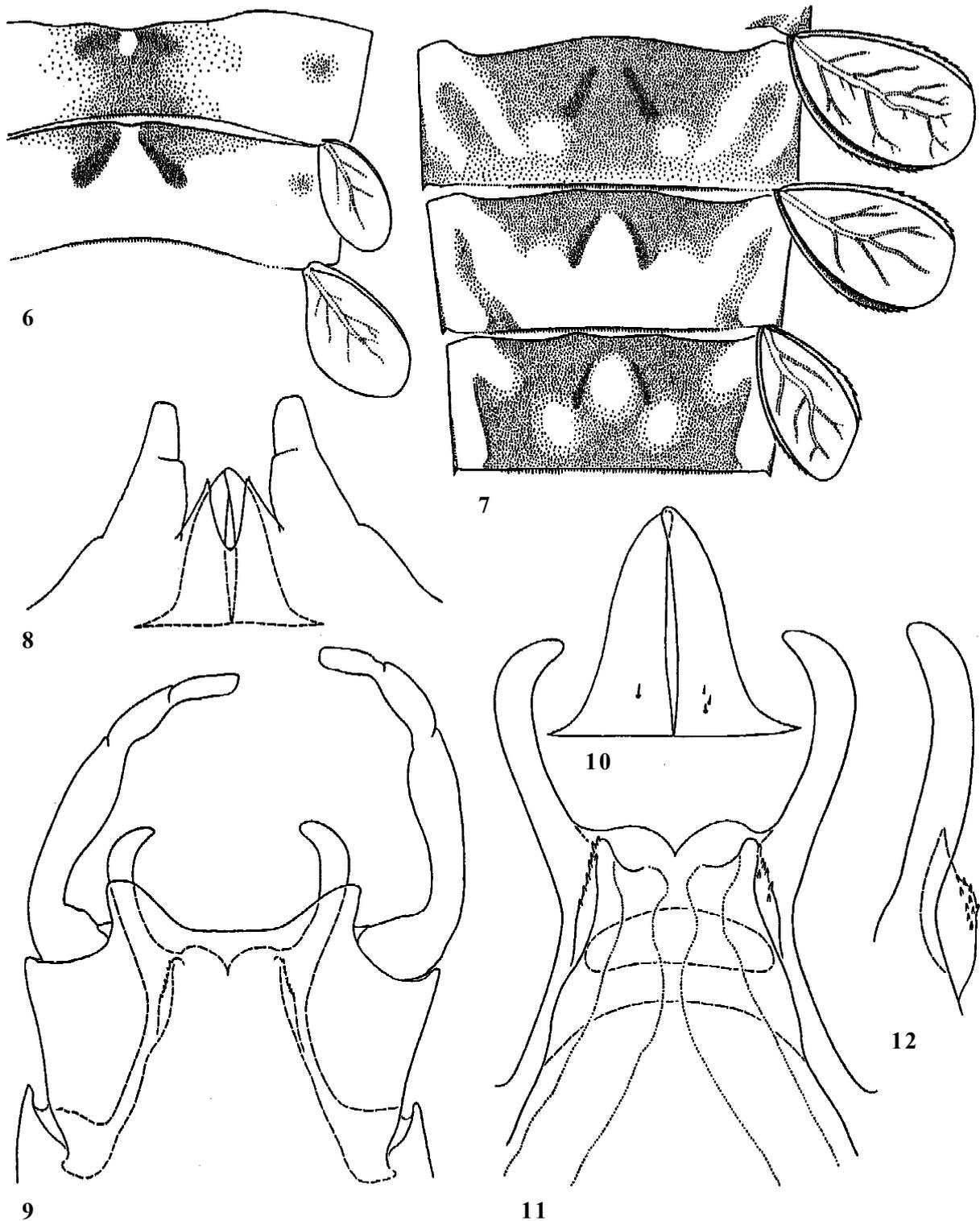
Imago, female. Head pale. Thorax with sclerites pale or light brownish. All legs pale. Wings with membrane colourless, veins brownish; pterostigma without distinct coloration, with anastomosed veins. Abdomen either entirely pale, or with brownish pattern on terga and ganglia pigmentation as in male. Cerci pale, sometimes with brownish articulations.

Egg. Ellipsoid (not flattened). Reticulation: polygonal cells with bottoms either flat or bearing a small protuberance, with borders prominent; round cells either absent, or a few large prominent round cells (each bearing papilla) exist on one pole only (Fig. 17).

Size. Medium: fore wing length 9–10 mm.

DISTRIBUTION. Siberia, at least from Altay Mountains to Baikal Lake.

COMPARISON. The new species resembles North American species *A. celer* in structure of male imaginal genitalis, larval cuticular colour pattern of abdomen and position of



Figs 6-12 — *Ameletus altaicus*, sp.n., holotype: 6 — larval terga I-II with right tergalii I-II; 7 — larval terga VI-VIII with right tergalii V-VII; 8 — male larval genital buds, ventral view; 9 — male imaginal genitals, ventral view, the same magnification; 10 — enlarged male larval penis buds, ventral view; 11 — male imaginal penis, ventral view, the same magnification; 12 — male imaginal penis, lateral view.

Рис. 6-12 — *Ameletus altaicus*, sp.n., голотип: 6 — личиночные тергиты I-II с правыми тергалиями I-II; 7 — личиночные тергиты VI-VIII с правыми тергалиями V-VII; 8 — зачатки гениталий личинки самца, вентрально; 9 — гениталии имаго самца, вентрально, то же увеличение; 10 — увеличенные зачатки пениса личинки самца, вентрально; 11 — пенис имаго самца, вентрально, то же увеличение; 12 — пенис имаго самца, латерально.

anal rib on tergalii [Zloty & Pritchard, 1997: Figs 4, 17B, 22C]; unlike *A. celer*, the new species has eggs not flattened.

II.4. *Ameletus montanus* Imanishi, 1930 (Figs 13–16, 18–19)

Larva. Labrum length 0.78–0.92 of width (9 specimens measured) (unlike shorter in *A. altaicus* and longer in *A. parvus*). Abdominal terga and sterna usually with contrasting darkenings and blanks (varying among subspecies — see below), so that dark oblique stripes indistinct or non-expressed on background of darkenings. Abdominal terga and sterna without spine-like setae (unlike group *A. alexandrae*). Tergalii I and II without anal ribs (unlike *A. costalis*, *A. formosus* and *A. atratus*); tergalii I smallest, tergalii II varies among subspecies (see below). Tergalii III–VI with anal rib well separated from anal margin (unlike *A. inopinatus*, *A. camtschaticus* and *A. altaicus*); only tergalii VII with anal rib on anal margin.

Subimago. Wing colour varies among subspecies (see below).

Male genitals. In imago, lateral penis lobes with apices straight in ventral view, bent dorsally; each ventral plate with several (1–7) equally small denticles (Figs 15–16). Subimaginal penis with the same number of spine-like setae corresponding to the imaginal denticles. Larval penis with less number (0–3) of spine-like setae (as in Fig. 10).

Egg. Flattened, in a form of ellipse-like biconvex lens (Figs 18–19). Reticulation: each polygonal cell with flat bottom lacking protuberance, with borders much lower and narrower than borders of round cells, so round cells (each bearing papilla) are prominent; round cells small and sparse on most surface, dense and large on one pole (the same in *A. cedrensis* and *A. costalis*).

Size. Variable: from 7 to 10.5 mm (see below).

DISTRIBUTION. Altay, East Siberia, Russian Far East, Japan.

COMMENT. *Ameletus procerus* Bajkova, 1976 was synonymized with *A. montanus* by Kluge [1995]. Actually, the holotype of *A. procerus* can belong either to *A. cedrensis*, or to *A. montanus rossicus*, so the species name *A. procerus* should be regarded as nomen dubium (see below).

Subspecies. The species *A. montanus* can be divided into three subspecies (or forms) which differ mainly by length of larval 2nd tergalii (the same in two subspecies of *A. inopinatus* — see below) and coloration of subimaginal wings (the same in forms of group *A. alexandrae*).

II.4.a. *Ameletus montanus montanus* Imanishi, 1930

REFERENCE. Imanishi 1930: 265, Figs 3–5.

MATERIAL EXAMINED. **RUSSIA:** KURIL ISLANDS, Shikotan, Malo-Kurilsk, 14.VII.1971 (Ermolenko) — 1 S ♂. **JAPAN:** Nagano Pref., Komagane City, Nakagosha Valley, Higyrashi waterfalls, 24.IX.2002 (I. Tatarenko) — 1 L/S ♂, 2 L/S ♀, 4 L.

Larva. Tergalii II not elongate, oval, smaller than tergalii III (as in *A. m. rossicus* subsp.n., unlike *A. m. arlecchino* subsp.n.).

Subimago. Wings brown, crossveins bordered by darker brown.

Egg. Unknown; probably, as in other *A. montanus* (see above).

Size. Medium: fore wing length 9–10.5 mm.

DISTRIBUTION. Japan and Kuril Islands.

II.4.b. *Ameletus montanus rossicus* Kluge, subsp.n.

= *Ameletus montanus*: Bajkova, 1976; Sinitshenkova & Tshernova, 1976; Tshernova et al., 1986

REFERENCES. Bajkova, 1976: 582, Figs 1–7 (male and female imago and larva); Sinitshenkova & Tshernova, 1976: 17, Figs 18–21 (male subimago, larva); Tshernova et al., 1986: 126, Figs 57: 5, 6 (male imago).

MATERIAL EXAMINED. **RUSSIA:** ALTAY, Turachak, river Biya, 10–31.VII.1937 (L. Gorbunov) — 1 L/S ♂, 1 L. **BURYATIYA:** natural reserve Baikalskiy, river Pereemnaya, 23.VII.1998 (N. Rozhkova) — 11 L/S. **PRIMORSKIY KRAY:** natural reserve Kedrovaya Pad', stream Bolshoy Zolotoy, 22–23.VII.1980 (N. Kluge) — 1 L-S-Im ♂ (**holotypus**); ibid, 20–26.VII.1980 (N. Kluge) — 1 L-S-Im ♂, 1 L-S-Im ♀, 5 L/S; river Narva (= Sidime), 20–21.VII.1980 — 2 L-S-Im ♂, 1 L-S ♂.

Larva. Tergalii II not elongate, oval, smaller than tergalii III (as in *A. m. montanus*, unlike *A. m. arlecchino* subsp.n.).

Cuticle often has contrasting blanks and darkenings, but usually not so pronounced as in *A. m. arlecchino* subsp.n. Head capsule mostly darkened (except blanks on eyes and ocelli); clypeus completely darkened. Labrum coloration variable — either mostly light with non-contrasting darkening basally, or with more or less contrasting distal-median blank and proximal-lateral darkening (Bajkova, 1976: Figs 4–6; Sinitshenkova & Tshernova, 1976: Fig. 19), or mostly darkened. Mandible without distal darkening: whole distal half is occupied by blank, darkening present on proximal part only (like *A. m. arlecchino* subsp.n., unlike other species). Maxilla with darkening on proximal part of stipes. Antennal pedicellus partly darkened, flagellum darker in middle part, lighter proximally and apically. Thorax with ornament of blanks and darkenings. Legs mostly light, with darkened apex of tarsus and with more or less expressed other darkenings — on coxa, on trochanter (or on trochantero-femoral joint), on middle of femur, on base of tibia, on base of tarsus (or on tibio-tarsal joint). Abdominal cuticle has colour pattern usually with 4 middle terga III–VI distinctly darker than previous and next ones [Bajkova, 1976: Fig. 7] (unlike *A. m. arlecchino* subsp.n., like *A. cedrensis* and some others): Tergum I mostly darkened. Tergum II mostly occupied by blank, with a small medio-anterior darkening. Tergum III either also mostly light, or with some other darkenings resembling terga IV–VI. Terga IV–VI mostly occupied by darkening, with a pair of isolated, large or small blanks, sometimes with isolated, unpaired blank between them. Terga VII–VIII mostly occupied by blank, with small darkenings. Terga IX–X mostly occupied by darkenings, with small blanks. Sterna I–II mostly or completely occupied by blank. Sterna III–VI either the same, or with some darkenings. Sterna VII–VIII, with more or less expressed median darkenings and lateral blanks. Sternum IX mostly occupied by darkening. Abdominal nerve ganglia non-coloured. Caudalii with proximal blank (of variable length), middle darkening (terminating distad of midlength), distal blank and darkening on extreme apex.

For other characters — see *A. montanus*.

Subimago. Wings uniformly brown (unlike *A. m. montanus*).

Imago, male. Head brown. Thorax: Pleural sclerites and sternum brown, pleural membranes pale; mesonotum lighter than pleurites and sternite, only antelateroparapsidal suture brown. Fore legs brownish. Middle and hind legs pale; coxa, trochanter and articulations brownish. Wings with membrane colourless, veins brownish; pterostigma tinged with brownish, with crossveins in distal parts of costal and subcostal fields narrowly bordered by brown. Abdomen: Segment I brown. Segments II–VI translucent, in most part pale; on each of them tergum with diffuse brownish stripes along lateral margins connected with diffuse brownish transverse band parallel to posterior margin (posterior margin pale); sterna either uniformly pale, or with diffuse median brownish makings. Segments VII–IX non-translucent, with the same

brownish maculation. Segment X darker. Abdominal nerve ganglia non-coloured.

Male genitals. See *A. montanus*.

Imago, female. Head pale. Thorax as in male. All legs pale. Wings as in male. Abdomen pale, with diffuse markings as in male.

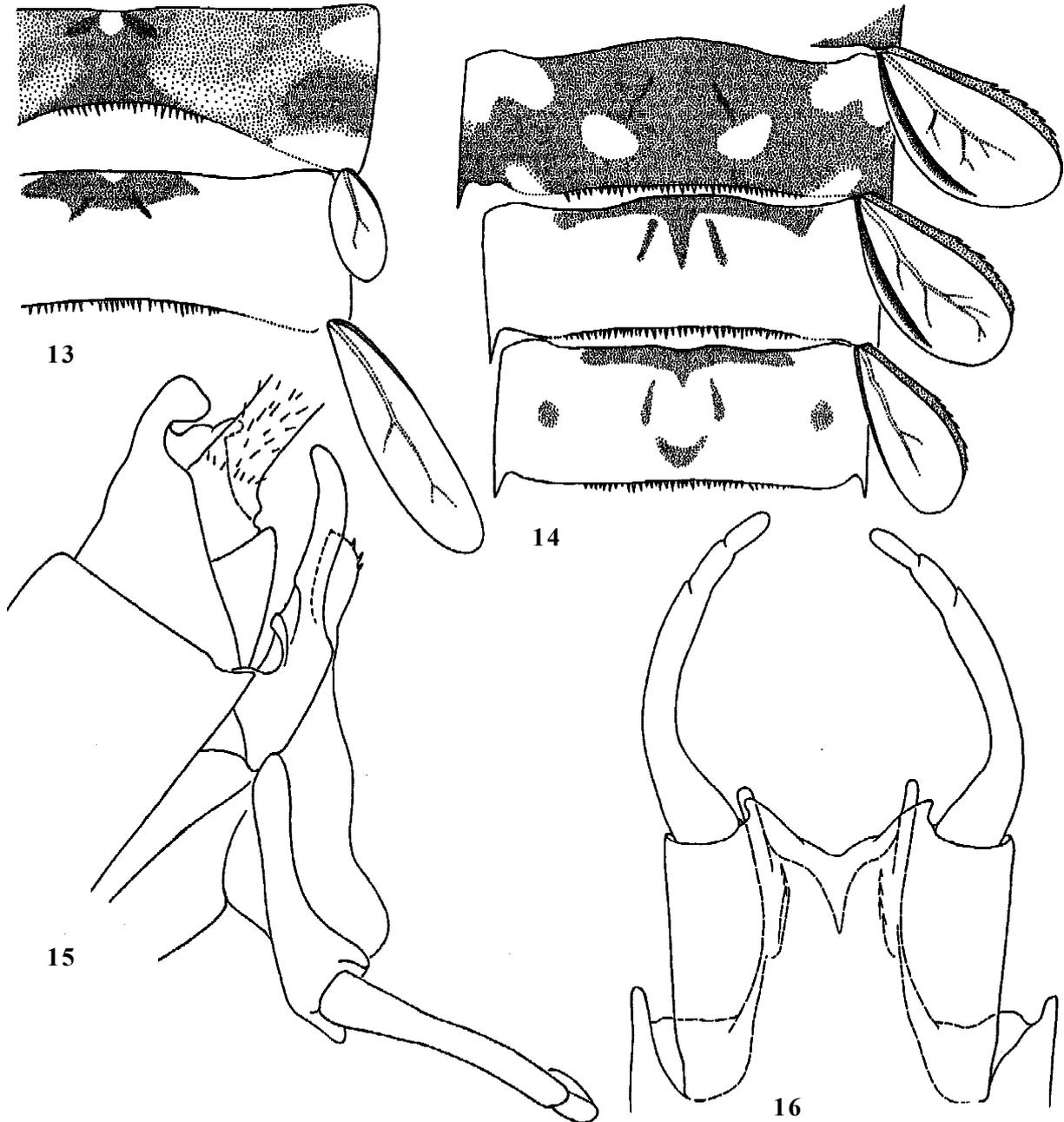
Egg. See *A. montanus*.

Size. Medium: fore wing length 8–9 mm.

DISTRIBUTION. Altay, East Siberia and Russian Far East.

II.4.c. *Ameletus montanus arlecchino* Kluge, **subsp.n.**
(Figs 13–16, 18–19)

MATERIAL EXAMINED. RUSSIA: Primorskiy Kray, Terney and Sikhote-Alinskiy natural reserve: Terney, river Serebryanka, 18.VIII.1990 (N. Kluge) — 1 L-S ♂, 1 L/S ♂; river Maysa (= Yasnaya), 4.VIII.1990 (N. Kluge) — 1-L-S-Im ♂ (**holotypus**); ibid., 9–15.VIII.1990 (N. Kluge) — 8 L-S-Im ♂, 3 L-S-Im ♀, 30 L; ibid., 14.VII.1982 (E. Potikha) — 1 L/S ♂, 1 L; river Zabolochennaya, 13.VII.1982 (E. Potikha) — 1 L/S ♂; stream Kedrovyi, 13.VIII.1990 (N. Kluge) — L-Im ♂; Blagodatnoe, VII.1990 (N. Kluge) — 1 L/S ♂.



Figs 13–16 — *Ameletus montanus arlecchino*, **sp.n.**: 13 — larval terga I–II with right tergallii I–II; 14 — larval terga VI–VIII with right tergallii V–VII; 15 — male imaginal apex of abdomen with genitals, lateral view; 16 — male imaginal genitals, ventral view (13–15 — holotype).

Рис. 13–16 — *Ameletus montanus arlecchino*, **sp.n.**: 13 — личиночные тергиты I–II с правыми тергаллиями I–II; 14 — личиночные тергиты VI–VIII с правыми тергаллиями V–VII; 15 — вершина брюшка имаго самца с гениталиями, латерально; 16 — гениталии имаго самца, вентрально (13–15 — голотип).

Larva. Tergalium II elongated, longer than tergalium III–VII (unlike *A. m. montanus* and *A. m. rossicus* subsp.n.).

Cuticle often has contrasting blanks and darkenings. Head capsule mostly darkened (except blanks on eyes and ocelli); clypeus completely darkened. Labrum has distal 1/3 completely occupied by blank; proximal 2/3 either completely occupied by contrasting darkening, or with pair of contrasting darkenings separated by a median longitudinal blank. Mandible without distal darkening; whole distal half is occupied by blank, contrasting darkening is limited by proximal half (like *A. m. rossicus* subsp.n., unlike other species). Maxilla with darkening on proximal part of stipes. Antennal pedicellus partly darkened, flagellum darker in middle part, lighter proximally and apically. Thorax with composite ornament of contrasting blanks and darkenings; in last larval instar, each fore prothorax has darker proximal part (which overlaps dark abdominal tergum I) and lighter apical part (which overlaps light abdominal terga II–III). Each leg mostly occupied by blank, with several contrasting darkenings (which can be larger or smaller) — on coxa, on trochanter (or on trochantero-femoral joint), on middle of femur, on base of tibia, on base of tarsus (or on tibio-tarsal joint) and on apex of tarsus; claw non-darkened. Abdominal cuticle has characteristic colour pattern, strongly different on different segments, usually with 3 middle terga IV–VI much darker than previous and next ones (Figs 13–14): Tergum I mostly darkened. Tergum II mostly occupied by blank, with a small medio-anterior darkening. Tergum III either the same, or with some other darkenings. Terga IV–VI mostly occupied by darkening, with a pair of isolated, contrasting, large (Fig. 14) or small blanks, sometimes with isolated, unpaired blank between them. Terga VII–VIII mostly occupied by blank, with small darkenings. Terga IX–X mostly occupied by darkenings, with small blanks. Sterna I–II mostly or completely occupied by blank. Sterna III–VI either the same, or with median blanks and lateral darkenings; from segment III to segment VI blanks become smaller and darkenings larger. Sterna VII–VIII, vice versa, with median darkenings (sometimes non-developed) and large lateral blanks. Sternum IX mostly occupied by darkening. Abdominal nerve ganglia non-coloured. Caudalium with contrasting proximal blank (of variable length), middle darkening (terminating distad of midlength), distal blank and darkening on extreme apex.

For other characters — see *A. montanus*.

Subimago. Wings uniformly brown (unlike *A. m. montanus*).

Imago, male. Head brown. Thorax: Pleural sclerites and sternum brown, pleural membranes pale; mesonotum lighter than pleurites and sternite, only antelateroparapsidal suture brown. Fore legs brownish or reddish. Middle and hind legs pale; sometimes femur indistinctly tinged with reddish near middle. Wings with membrane colourless, veins brownish; pterostigma tinged with brownish, with crossveins in distal parts of costal and subcostal fields narrowly bordered by brown. Abdomen: Segment I brown. Segments II–VI translucent, in most part pale; on each of them tergum with diffuse brownish or reddish pattern — pair of stripes along lateral margins connected with transverse band parallel to posterior margin (posterior margin pale); sterna either uniformly pale, or with diffuse median brownish markings. Segments VII–IX non-translucent, with the same brownish maculation. Segment X darker. Abdominal nerve ganglia non-coloured.

Male genitalis. See *A. montanus*.

Imago, female. Head pale. Thorax as in male. All legs pale. Wings as in male. Abdomen pale or with diffuse markings as in male.

Egg. See *A. montanus*.

Size. Small: fore wing length 7–8 mm.

DISTRIBUTION. Known from one area on the eastern slope of Sikhote-Alin' Mountains.

II.5. *Ameletus parvus* Kluge, 1979 (Figs 20–21)

REFERENCE. Kluge, 1979: 807, Figs 1–15 (male and female imago, subimago, larva).

MATERIAL EXAMINED. KAZAKHSTAN: VOSTOCHNO-KAZAKHSTANSKAYA OBLAST' (= East-Kazakhstan Prov.), 90 km S Ust'-Kamenogorsk, mountain ridge Kalbinskiy Khrebet, 6–8.VIII.1978 (N. Kluge) — 2 L-S-Im ♂, 2 L-S-Im ♀, 26 L (holotypus & paratypi).

Larva. Labrum longer than in most other species, its length 1.0–1.03 of width (3 specimens measured). Abdomen nearly unicolourly darkened, without blanks and with indistinct dark oblique stripes. Abdominal terga and sterna without spine-like setae (unlike group *A. alexandrae*). Tergalium I and II without anal ribs (unlike *A. costalis*, *A. formosus* and *A. atratus*), small. Tergalium III–VI with anal rib well separated from anal margin (unlike *A. inopinatus*, *A. camtschaticus* and *A. altaicus* sp.n.); tergalium VII with anal rib nearer to anal margin.

Subimago. Wings brownish, unicolour.

Imago. Wings non-coloured.

Male genitalis. In imago, lateral penis lobes with apices nearly straight in ventral view, slightly bent dorsally; ventral plates non-sclerotized, in distal part with a few (3–4) small denticles (Fig. 20) (unlike *A. montanus*, *A. altaicus* sp.n. and *A. camtschaticus* which have denticles in proximal part of ventral plate); these denticles are pale and poorly visible, so in the original description they were overlooked. Subimaginal penis with the same number of denticles or spine-like setae corresponding to imaginal ones. Larval penis with less number (0–1) of spine-like setae in middle part (Fig. 21) (unlike *A. altaicus* sp.n., *A. montanus* and *A. cedrensis*, whose larval penis has spine-like setae in proximal part — Fig. 10).

Egg. Flattened, in a form of ellipse-like biconvex lens (as in *A. montanus* and *A. cedrensis*). Reticulation: each polygonal cell with bottom bearing a protuberance (unlike *A. montanus* and *A. cedrensis*), with borders lower than borders of round cells, so round cells (each bearing papilla) are prominent; round cells are small and sparse on most surface, dense and large on one pole.

Size. Small: fore wing length 7 mm.

DISTRIBUTION. Altay (known as type series from the single locality).

II.6. *Ameletus cedrensis* Sinitshenkova, 1977

REFERENCES. Sinitshenkova, 1977: 44, Figs 1–2 (male and female imago, larva); Tshernova et al., 1986: 126, Figs 57: 3, 4 (male imago).

MATERIAL EXAMINED. RUSSIA: ALTAY: river Biya, 1.VII–25.VIII.1937 (L. Gorbunov) — 40 L; river Koldor near its falling into lake Teletskoe, 15.VIII.1987 (N. Kluge) — 3 L-S-Im ♂, 4 L-S-Im ♀, 1 L-S ♂; natural reserve Altayskiy: river Korbu near its falling into lake Teletskoe, 19–22.VIII.1987 (N. Kluge) — 5 L-S-Im ♂, 2 L-S-Im ♀, 2 L-S ♂, 1 L-S ♀; ibid., Yailyu, 13.VIII.1987 (N. Kluge) — 1 L-S-Im ♀, 1 L. IRKUTSKAYA OBLAST' (= Irkutsk Prov.): Bolshie Koty, rivers Sennaya and Kotinka (western tributaries of Lake Baikal), 7–13.VIII.1994 (N. Kluge) — 20 L-S-Im ♂, 11 L-S-Im ♀, 3 L-S ♀. Khabarovskiy KRAY (= Khabarovsk Prov.): 6 km E railway station Obluch'e, railway station "Udarnyi", 27.VII–3.VIII.1984 (N. Kluge) — 6 L-S-Im ♂, 3 L-S-Im ♀, 2 L-S ♂, 6 L. PRIMORSKIY KRAY: Upper-Ussuri research station of Biological-Soil Institute, 35 km SE Chuguevka, 1.VIII.1980 (N. Kluge) — 2 L-S-Im ♂, 12 L; ibid., 7 VII 1975 (L. Zhiltzova) — 1 S ♂;

ibid., 26–27.VI.1975 — 3 Im ♂, 6 Im ♀, 6 L (holotypus & paratypi); natural research Sikhote-Alinskiy, stream Kedrovyy, 10.VIII.1980 (N. Kluge) — 2 L-S-Im ♂, 2 L-S-Im ♀, 1 L-S ♂, 3 L-S ♀; ibid., river Yasnaya, 13.VIII.1990 (N. Kluge) — 1 L-S-Im ♂; stream Sikhote, 21.VIII.1979 (Timoshkin) — 1 Im ♂; natural research Kedrovaya Pad', 1 Im ♂, 12 L (paratypi).

Larva. Labrum length 0.85–0.90 of width (3 specimens measured) (unlike shorter in *A. altaicus* and longer in *A. parvus*). Abdominal terga and sterna usually with contrasting darkenings and blanks, so that dark oblique stripes indistinct or non-expressed on background of darkenings. Abdominal terga and sterna without spine-like setae (unlike group *A. alexandrae*). Tergalium I and II without anal ribs (unlike *A. costalis*), small. Tergalium III–VI with anal rib well separated from anal margin (unlike *A. inopinatus*, *A. camtschaticus* and *A. altaicus sp.n.*); only tergalium VII with anal rib on anal margin.

Subimago. Wings brownish, unicolour.

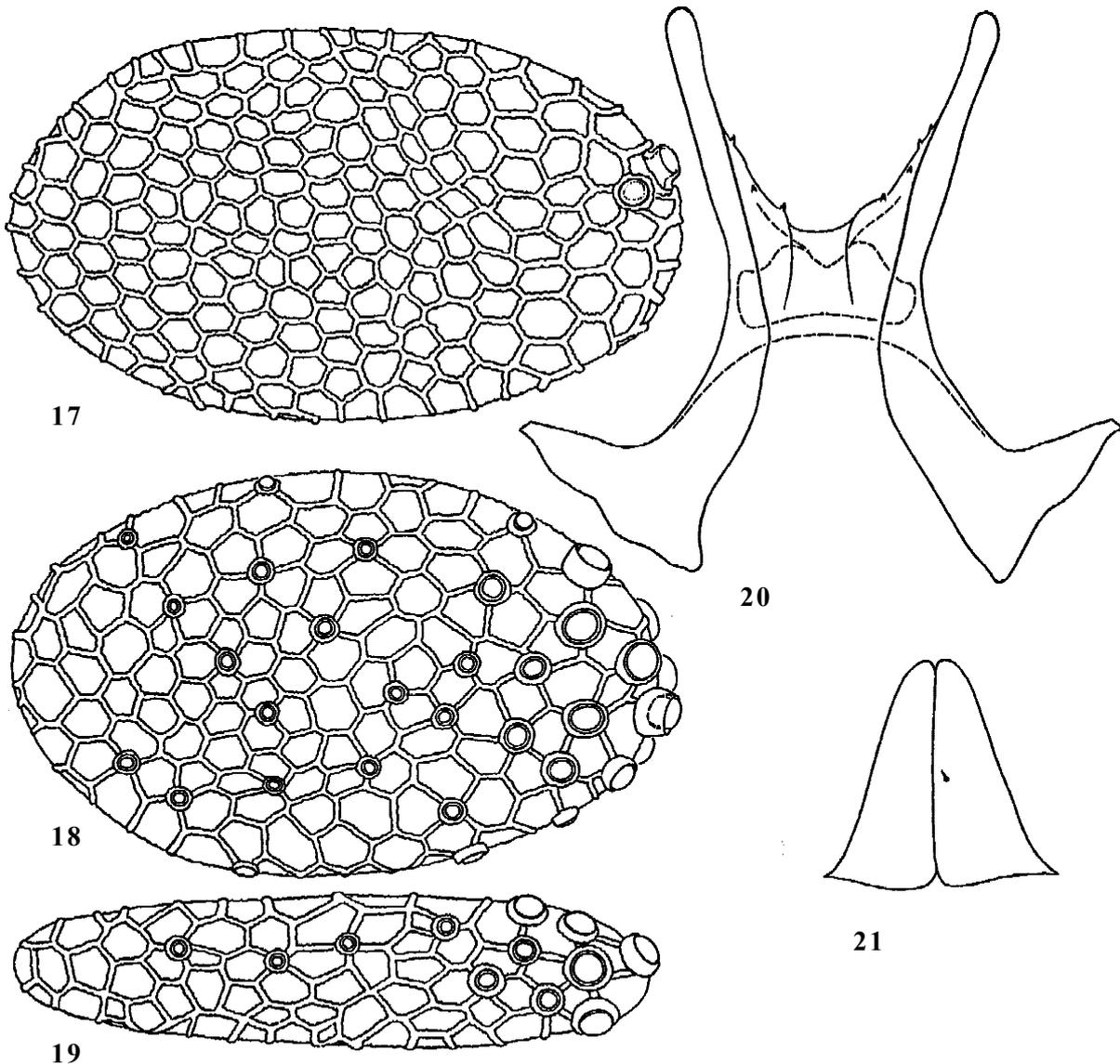
Imago. Wings non-coloured.

Male genitals. In imago, lateral penis lobes with apices straight in ventral view, bent dorsally; each ventral plate projects far ventrally, with a single long apical denticle, without small denticles. Subimaginal penis also has one pair of large denticles corresponding to imaginal ones. Larval penis has one pair of spine-like setae corresponding to imaginal and subimaginal denticles.

Egg. Flattened, in a form of ellipse-like biconvex lens. Reticulation: each polygonal cell with flat bottom lacking protuberance, with borders much lower and narrower than borders of round cells, so round cells (each bearing papilla) are prominent; round cells are small and sparse on most surface, dense and large on one pole (the same in *A. montanus* and *A. costalis*).

Size. Medium: fore wing length 12–14 mm.

DISTRIBUTION. Siberia (from Altay at the west) and Far East.



Figs 17–21 — *Ameletus* spp: 17 — *A. altaicus*, sp.n., egg; 18–19 — *A. montanus arlecchino*, subsp.n., egg in two views; 20–21 — *A. parvus*. 20 — male imaginal penis, ventral view; 21 — male larval penis buds, ventral view, the same magnification.

Рис. 17–21 — *Ameletus* spp: 17 — *A. altaicus*, sp.n., яйцо; 18–19 — *A. montanus arlecchino*, subsp.n., яйцо в разных ракурсах; 20–21 — *A. parvus*. 20 — penis имаго самца, вентрально; 21 — зачатки пениса личинки самца, вентрально, то же увеличение.

II.7. *Ameletus costalis* (Matsumura, 1931 [*Chimura*])

= *Ameletus longulus* Sinitshenkova, 1981

= *Ameletus sapporensis*: Imanishi, 1932 (non *Siphylurus sapporensis* Matsumura, 1904)

REFERENCES. Imanishi, 1932: 526, Pl.31: Fig. 1, Pl. 32: Figs 2–3 (male and female imagoes, as *Ameletus sapporensis*); Imanishi, 1933: 65, Figs 3, 5 (larva); Sinitshenkova & Tshernova, 1976: 16, Figs 10–17 (male and female imago, male subimago, larva); Sinitshenkova, 1981: 77, Fig. 3 (larva, as *A. longulus*); Tshernova et al., 1986: 126, Figs 57: 1, 2 (male imago).

MATERIAL EXAMINED. Among the specimens listed by Sinitshenkova & Tshernova [1976], the following ones are re-determined by me as *A. costalis*: RUSSIA: PRIMORSKIY KRAY: Olginskiy Rayon (= Olgino Distr.), Furmanovo, 15.VI.1972 (A. Rasnitsyn) — 1 Im ♂; Kavalerovskiy Rayon (= Kavalerovo Distr.), Pereval'noye, 29.VI.1972 (A. Ponomarenko) — 1 Im ♂, 1 Im ♀; river Kamenka, tributary of river Suputinka, 3.VI.1972 (I. Levandova) — 1 S ♂, 1 larval exuvia. Systematic position of other species (larvae) is doubtful.

Lava. Labrum length 0.93–0.94 of width (2 specimens measured) (unlike shorter in *A. altaicus* and longer in *A. parvus*). Abdominal terga and sterna without spine-like setae (unlike group *A. alexandrae*). Tergalii I and II with vestigial anal ribs (the same in *A. formosus* and *A. atratus*, unlike other species), small. Tergalii III–VI with anal rib far from anal margin (unlike *A. inopinatus*, *A. camtschaticus* and *A. altaicus*).

Subimago. Wings brownish, with crossveins bordered by darker brown.

Imago. Wings mostly colourless, in anterior part crossveins darkened and bordered by brownish.

Male genitals. In imago, lateral penis lobes with apices slightly bent medially-dorsally; each ventral plate bears a single long denticle which stretched closely parallel to the lateral lobe (unlike all other Palaearctic species). Subimaginal penis also has one pair of large denticles corresponding to imaginal ones.

Egg. Flattened, in a form of ellipse-like biconvex lens. Reticulation: each polygonal cell with flat bottom lacking protuberance, with borders much lower and narrower than that of round cells, so round cells (each bearing papilla) prominent; round cells are small and sparse on most surface, dense and large on one pole (the same in *A. montanus* and *A. cedrensis*).

Size. Large: fore wing length 15–18 mm.

DISTRIBUTION. Russian Far East and Japan.

COMMENTS. The species *Ameletus longulus* was described as larvae only; the description was based on two specimens [Sinitshenkova, 1981]. According to the original description, *A. longulus* differs from *A. costalis* by longer vestiges of ribs on tergalii I, longer tergalii II and some other characters. Possibly, these characters vary individually.

The name *Siphylurus sapporensis* Matsumura, 1904 was wrongly applied to this species by Imanishi [1932], while actually it is an older synonym of *Cinygmula grandifolia* Tshernova, 1952 [Ishiwata, 2001].

II.8. Group *Ameletus alexandrae* Brodsky, 1930 (incl. *A. asiacentralis* Soldan, 1978)

REFERENCES. Brodsky, 1930: 697, Figs 20–23 (male and female imago, egg); Sinitshenkova & Tshernova, 1976: 13, Figs 1–2 (larva); Soldan, 1978: 379, 380, Figs 1–18 (*A. alexandrae* and *A. asiacentralis*; larvae); Kluge, 1995: 7, Fig. 1 (larval lectotype).

MATERIAL EXAMINED. KAZAKHSTAN, UZBEKISTAN, KYRGYZSTAN and TADJIKISTAN — many L-S-Im, larvae, subimagoes and imagoes.

Lava. Labrum length 0.77–0.93. of width (19 specimens measured) (unlike shorter in *A. altaicus* sp.n. and longer in *A. parvus*). Abdominal terga and sterna with spine-like setae (unlike other Ameletidae). Tergalii I and II without anal ribs (unlike *A. costalis*), small. Tergalii III–VI with anal rib far from anal margin (unlike *A. inopinatus*, *A. camtschaticus* and *A. altaicus* sp.n.).

Subimago. Wings brownish, either unicolour, or with crossveins narrowly bordered by darker brown, or with darker brown maculae on crossveins.

Imago. Wings non-coloured.

Male genitals. In imago, lateral penis lobes with apices moderately bent medially-dorsally; ventral plates without denticles.

Egg. Ellipsoid (not flattened). Reticulation: each polygonal cell with bottom bearing a protuberance, with borders lower than borders of round cells, so round cells (each bearing papilla) are prominent; round cells are small and sparse on most surface, dense and large on one pole.

Size. Medium: fore wing length 8–13 mm.

DISTRIBUTION. Mountains of Central Asia.

TAXONOMIC COMPOSITION. Within the group '*alexandrae*', there are forms which differ one from another by some subimaginal and larval characters — coloration of subimaginal wings (uniform or with bordered crossveins), development of spine-like setae on abdominal terga, sterna and tergalii, et al. Probably, some of these forms have reproductive isolation, because inhabit in neighboring biotops in the same area. Complete revision of this group is rather difficult.

NOMINA DUBIA

Ameletus procerus Bajkova, 1976 — nomen dubium

The species was described by Bajkova [1976] as larvae and female subimago basing on two specimens — one larva and one female subimago with its larval exuvia. The subimago with larval exuvia was designated as holotype [Bajkova, 1976: 586]. In the collection of Zoological Institute RAS (S.-Petersburg), there are deposited two specimens — the larva and the larval exuvia, while the female subimago reared from this exuvia was not passed to the Zoological Institute and probably is lost. The larva was labeled by Bajkova as “holotype” and the larval exuvia — as “paratype” (while actually the larva is paratype and the exuvia is holotype, according to the publication). These two specimens belong to two different species. The larva (true paratype) has tergalii II longer than next ones [Bajkova, 1976: Fig. 19] and tergalii III–VI with anal rib on anal margin; it belongs to the species later described as *A. labiatus* Sinitshenkova 1981 (see above, *A. inopinatus labiatus*). The larval exuvia (true holotype) has tergalii II shorter than next ones and tergalii III–VI with anal rib far from anal margin [Bajkova, 1976: Fig. 20]; it belong either to the species later described as *A. cedrensis* Sinitshenkova 1977, or the subspecies described here as *A. montanus rossicus* subsp.n.; these two forms are hardly distinguishable by larval characters. The original description of *A. procerus* was based on the both specimens, so it is wrong.

The disagreement between holotype designation and museum labels provoked confusion. Kluge [1982], basing on the museum labels, redescribed under the name “*A. procerus*” the species which actually represents *A. inopinatus labiatus*. Later this error was revealed, and basing on the holotype designation Kluge [1995] synonymized *A. procerus* with *A. montanus* Imanishi, 1930.

Actually, larval exuvia which represent the holotype of *A. procerus*, can belong either to *A. cedrensis*, or *A. montanus rossicus* subsp.n., because the both species can be found in

this area and have the same larval structure. So the species name *Ameletus procerus* Bajkova 1976 should be regarded as nomen dubium.

***Ameletus cristatus* Bajkova, 1976 — nomen dubium**

The species was described by Bajkova [1976] as male and female imagoes, subimagoes and larvae; in the list of material examined, there are referred only 2 male imagoes (including holotype) and 2 larvae (but no females and subimagoes!). Attributing of all these specimens to one species was not grounded. The types should be deposited in the Zoological Institute of Russian Academy of Sciences in S-Petersburg [Bajkova, 1976: 582], but no one specimen was passed to this institute. Probably, the holotype and all paratype are lost. The description does not allow to determine on which species it was based; most probably, this is one of the species described above.

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