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Contribution to the understanding of the Fennoscandian *Ameletus* Eaton, 1885 [Ephemeroptera, Ameletidae]

by Eva ENGBLOM

Gunnilbo 14, SE–739 92 Skinnskatteberg, Sweden

engblom.prasthammaren@telia.com

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Simon Bengtsson only knew *Ameletus inopinatus* from northern Norway, but on his sampling tours across Sweden a hundred years ago he found what he called *Ameletus alpinus* at several places in the mountains down to latitude 61.51°N. Today, the migrating *A. alpinus* is a characteristic species for ecoregion 22, and has a scattered distribution south to 56.26°N in ecoregion 14. These two *Ameletus*, which probably started as a single species that was split up by global climate change, are likely in the future to reunite into a single species as a result of interbreeding. However, for the time being, there are two *Ameletus* in Fennoscandia. This article aims to explain the differences between them.

Contribution à la connaissance du genre *Ameletus* Eaton, 1885 en Fennoscandie [Ephemeroptera, Ameletidae]

Mots clés: Ephemeroptera, distribution, morphologie, écologie, *Ameletus inopinatus* Eaton, 1887, *Ameletus alpinus* Bengtsson, 1913, Fennoscandie

Simon Bengtsson connaissait seulement *Ameletus inopinatus* de Norvège septentrionale, mais lors de ses voyages de récoltes entomologiques à travers la Suède, il y a une centaine d'années, il a trouvé ce qu'il a nommé *Ameletus alpinus* à plusieurs endroits dans les montagnes, mais à une latitude plus basse, jusqu'à 61.51°N. Aujourd'hui, le migrant *A. alpinus* est une espèce caractéristique de l'écorégion 22, et a une répartition dispersée au sud jusqu'à 56.26°N dans l'écorégion 14. Probablement issus d'une même espèce à l'origine et dédoublée par les effets du changement climatique global, ces deux *Ameletus* vont vraisemblablement dans le futur se réunir à nouveau en une espèce unique par croisement. Cependant, actuellement, il y a deux *Ameletus* en Fennoscandie. Le but de cet article est d'expliquer leurs différences.

1. *Ameletus* in Fennoscandia

The Holarctic *Ameletus inopinatus* is considered rare and endangered in Europe. It is spread over mountain areas in 22 European countries, and has been recorded from Turkey, Siberia, and Mongolia in Asia as well as the Northwest Territories, Nunavut, Yukon, and possibly Alaska in North America.

During the period lasting from the description of *A. alpinus* by BENGTSSON (1913) to the observations of BAGGE (1965), there were two *Ameletus* species in Fennoscandia. It was BREKKE

(1965) who suggested *alpinus* as a variety of *inopinatus*, for reasons explained below. This was adopted in Limnofauna Europea (ILLIES 1967), but because *inopinatus* was only recorded from ecoregion 21 (and not from ecoregion 22) and the name *alpinus* was no longer applicable, the genus *Ameletus* was later erased from region 22 in Limnofauna Europea (PUTHZ 1978). At the same time, another 16 Bengtsson species were removed from this area for similar reasons. BAUERNFEIND & SOLDÁN (2012 Table 1) correctly recorded "*Ameletus inopinatus*" for region 22, but unfortunately with the addition of 10 mayfly species that have never occurred in this area.

After 1965, except for the Limnodata HB reports, "*Ameletus inopinatus*" has been the only name used in Fennoscandia; for example, for larvae keys (ARNEKLEIV 1995, SVENSSON 1986) and for distribution in Norway (BRITTAIN et al. 1996, Norwegian Artsdatabanken [Internet]) and Finland (SAVOLAINEN 2009).

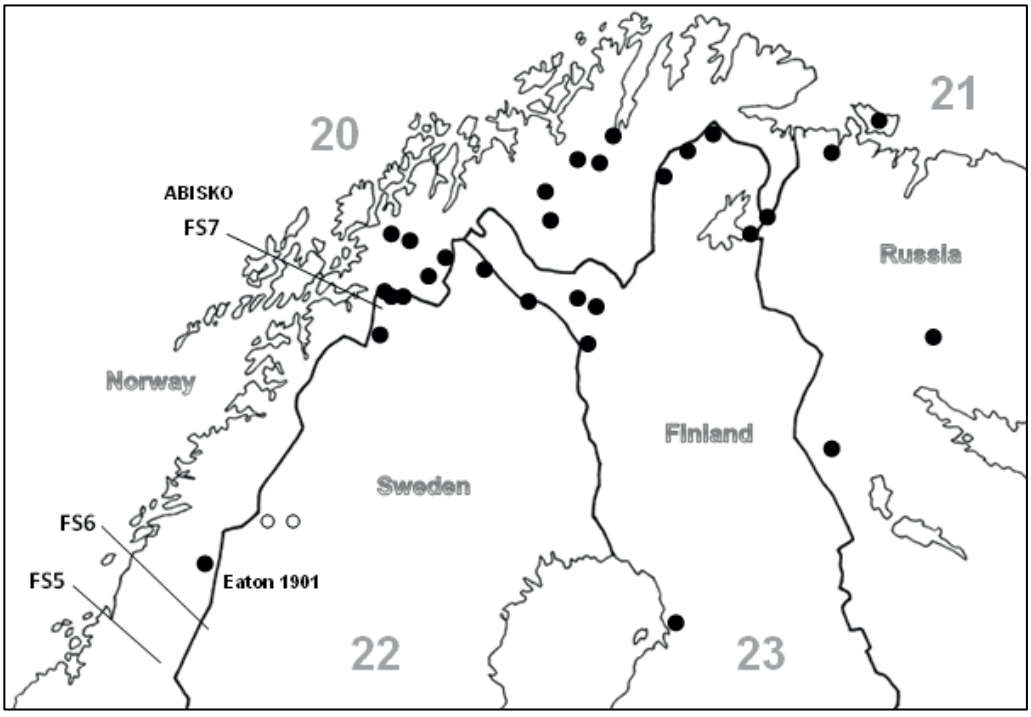

Figure 1. Known distribution of *Ameletus inopinatus* from Norway, Finland and Russia (EATON 1901, BENGTSSON 1930a, TIENSUU 1937 and 1939), from Sweden collections by Staffan Ulfstrand in 1961 and by Johan Hammar in 1982 and 1988. Open dots are doubtful *inopinatus.* FS5 – FS7 from TAUBMANN et al. (2011 Fig. 2) is explained below in Section 3. Eco regions 21–23 are found in e.g. BAUERNFEIND & SOLDÁN (2012).

Figure 1. Distribution connue d'*Ameletus inopinatus* en Norvège, Finlande et Russie (EATON 1901, BENGTSSON 1930a, TIENSUU 1937, 1939), en Suède selon les collectes de Staffan Ulfstrand en 1961 et Johan Hammar en 1982 et 1988. Les cercles blancs signalent une présence douteuse d'*A.inopinatus.* FS5-FS7 d'après TAUBMANN et al. (2011 Fig. 2) – voir chapitre 3-. Eco régions 21-23 : voir BAUERNFEIND &SOLDÁN (2012).

Since the reintroduction of *A. alpinus* in Sweden (ENGBLOM 1996), 2541 of the 3024 *Ameletus* registrations in the Limnodata HB database have been revised as *A. alpinus*. Only 0.4% of the samples had genuine *A. inopinatus*; these are combined with what is called "*Ameletus inopinatus*" in the Swedish ArtDatabanken and the Global Biodiversity Information Facility (GBIF), both of which mostly contain data points from the Limnodata HB database. The GBIF also contains "*Ameletus inopinatus*" from the Norwegian Artsdatabanken but not from Finland, which is in all probability the reason why the so-called current distribution for European *Ameletus* given by TAUBMANN et al. (2011 Fig. 1) does not include Finland, and also does not include what the GBIF labels as *A. alpinus* for Sweden.

The genus *Ameletus* is found in 15 of 19 provinces in Norway and 7 of 20 in Finland. Its distribution in Sweden remains the same as that presented by ENGBLOM (2003): one province for *A. inopinatus,* and 17 of 29 for *A. alpinus*. In both Norway and Finland, *A. alpinus* ought to be the more frequent species.

Norway: R, AA, TE, B, HO, SF, SF, O, MR, ST, NT, NS, TR, F, and in addition HE (Limnodata HB). Sweden: SK, HA, SM, VG, DR, HS, ME, HR, JÄ, ÅN, VB, NB, ÅS, LY, PI, LU, and TO. Finland: Sa, Ok, ObS, ObN, Ks, LkW, LkE, Li, and Le.

Ameletus inopinatus is also rare in Fennoscandia, but with *A. alpinus* included as a synonym for *A. inopinatus* is neither rare nor endangered in Europe.

2. Distribution of *Ameletus inopinatus* Eaton, 1885

Simon Bengtsson never found *A. inopinatus* in Sweden (BENGTSSON 1930b), but knew the species from the descriptions by EATON (1888) and ULMER (1929), and from specimens collected by Schoenemund from Tatra in the Carpathian Mountains. At Tromsø Museum in northern Norway, Bengtsson got the opportunity to examine the three winged specimens from Hattfjeldsdalen in Nord Trøndelag (Nn) collected by Strand in 1899 (BREKKE 1938) at about 65.35°N, 14.16°E and identified by EATON (1901 p. 253).

Norway. At Tromsø Museum, Bengtsson found several *A. inopinatus* from Troms and Finmark collected between 1908 and 1924 (BENGTSSON 1930a). Troms (TRi): Måselv Nordnes at 69.03°N, 18.35°E in 1908; Lille Ruostavand at 68.48°N, 20.13°N on 4 July 1922; Dividal Øvredal at 69.01°N, 19.16°E on 9 July 1922; and Frihetsli at 68.44°N, 19.22°E on 26 July 1922. Finmark (F): Lakselv Porsanger at 70.02°N, 24.55°E in 1908; Kautokeino Carasjjavre at 69.25°N, 22.52°E on 21 July 1922; Alta Bojobäske at 69.48°N, 24.12°E on 17 July 1924; Tsävdne on 27 July 1924; Fästningsstuen on 3 August 1924; and Jotkajavre at 69.46°N, 23.50°E on 25 July 1924. In addition, TIENSUU (1937) found *A. inopinatus* from Finmark in museum material collected from Puolmak (Ruija) at 69.33°N, 31.15°E in July 1905.

The specimens shown in Figs. 38–44 in STUDEMANN et al. (1988) originate from Jotunheimen in southern Norway, and seem to be true *A. inopinatus*; if so, there is information about this species from the same geographic area in BRITTAIN (1974).

Material from Sweden. The 11 registrations of *A. inopinatus* are all from Torne Lappmark (TO). Johan Hammar sampled larvae from eight waters north of Lake Torneträsk from 18.16°E to 18.59°E in August 1982, and on 2 August 1988 he sampled a 5 m broad brook to Pajep Snarapjaure at 68.10°N, 18.17°E and 1034 m a.s.l. Winged specimens from two tributaries to the border river

between Sweden and Finland were collected by Staffan Ulfstrand: Könkämä at 68.48°N, 21.24°E on 21 June 1961 and Muonio at 68.24°N, 22.21°E on 1 July 1961.

Twice I have come to the conclusion that examined specimens must be "less good *inopinatus*" rather than "less good *alpinus*" (see the discussion in Section 6); in both cases these were subimagos, collected by Björn Nagel on 22 July 1964 at Krabbsele Ammarnäs (LY) and by Staffan Ulfstrand on 16 July 1965 at Tjulån (LY). These locations are marked with open dots in Fig. 1.

Finland. TIENSUU (1939) reported Oulu from Ostrobottnia borealis (Ob), Muonio from Lapponia kemensis (Lk), Enontekiö Hetta Närpistöjoki and Koltapahta from Lapponia enontekiensis (Le), and Outakoski and Utsjoki Onnela from Lapponia inarensis (Li). Oulu at 65.01°N, 25.28°E seems outside the distribution to me, but is also mentioned by ARO (1928).

Russia. TIENSUU (1939) reported Petsamo (Storå), Paatsjoki (Pasvikälven), Haukilampi, Hoomanjoki, Nautsijoki, Pummanki, and Imantero (Imandra) from Murmansk or Lapponia rossica (Lr), and Salla Vuorijärvi from Karelia rossica (Kr).

Mongolia. SINITSHENKOVA & VARYKHANOVA (1990) described larvae and imago from the Khubsugul Lake as *A. eugenii*; these were in all probability *A. inopinatus*.

Canada. Specimens from two lakes in the Northwest Territories are, though nothing is said about the legs, very likely to be *A. inopinatus* (ZLOTY 1996).

3. Distribution of *Ameletus alpinus* Bengtsson, 1913

Bengtsson found his first *A. alpinus* (called *Parameletus affinis*) at Tärna (LY) at 65.44°N, 15.05°E (BENGTSSON 1904). He later found the species at other places in the mountains, such as Abisko (TO) (BENGTSSON 1931); his southernmost find (a subimago female named *A. inopinatus*) was near Idre (DR) (BENGTSSON 1908) at 61.51°N, 12.43°E. Until 1984, the southernmost known *Ameletus* was collected not far from there at 61.07°N (DR), and so the unambiguous finding of *A. alpinus* in the Gagnå River at 57.59°N, 14.08°E on 22 March 1984 caused quite a sensation. It is 400 km from Idre (DR) to Gagnån (VG), and another 200 km to Krusån (SK) at 56.26°N, 14.00°E, where the species was collected in 1998.

In 1991, *A. alpinus* was collected further south in Dalarna (DR) at 60.10°N, but there is still a gap from that site to the Gagnå River.

Material from Sweden. 2541 samples with more or less good *A. alpinus* + winged specimens + 472 non-revised records of *Ameletus* sp. and "*Ameletus inopinatus*" which is likely to also be *A. alpinus*.

THEISSINGER-THEOBALD (2011) collected material for her *A. inopinatus* study from two sites in Sweden: at 68.26°N, 18.11°E (FS7) and at 65.03°N, 14.22°E (FS6). All specimens from these two places in the Limnodata HB collection are more or less good *A. alpinus*: winged specimens collected from Abisko (FS7) by Björn Nagell in 1964, bottom fauna collected from several places by Limnodata HB in 1983 and by Lisa Lundstedt in 1991, and several bottom fauna samples from Gelvenåkko (FS6) collected by Limnodata HB in 1983.

Ecoregion 14: at the Gagnå River (VG), *A. alpinus* was first collected at two places by Göran Åström on 22 March 1984 (still present in 2007, collected by Ekologgruppen). On 19 May 1986, Limnodata HB found the species in the nearby river Rödån. The distribution map in LINGDELL & ENGBLOM (2013) does not include the finds collected by Ekologgruppen from Småland (SM) Gnyltån on 3 May 1995 and in 2000; from Halland (HA) Skillnadsbäcken, Dalabäcken, and

Truedsfällsbäcken on 11 April 1999 and Viskan at 5 m a.s.l. on 5 November 1999 (no *Ameletus* was present there on 19 May 1980); and from Skåne (SK) Krusån on 30 November 1998.

Norway. *A. alpinus* was collected in Finnmark at Maitokoski in 1928 (TIENSUU 1937).

Material from Norway. Four samples collected by Limnodata HB from Hedland (HEn): Ljördal in 1975, Bergåa in 1977 and 1983, and Gira in 1983; one sample from Randalselva (NL) in 1976; and one sample from Innerdalsån (NT) in 1978. All these samples, with more or less good *A. alpinus,* are from close to the Swedish border.

Finland. *A. alpinus* was first identified from Lapponia inarensis (Li) at Utsjoki in Outakoski (TIENSUU 1939), and in 1962 was collected at Utsjoki in Kevojoli River and in Lake Jomppalanjärvi (BAGGE 1965).

Carpathians. The *A. alpinus* larvae collected from Poland and Romania in 2003 look like nearly perfect copies of the Gagnå River larvae.

Material from Poland. Two larvae from a stony river surrounded by leafy wood with beech and fir in Bieszczady National Park, 0.7 m wide and 8.6°C at 800 m a.s.l., collected by Johan Törnblom on 18 May 2003.

Material from Romania. One larva from a stony river surrounded by arable and pasture land at Lieud-Sieu (north), 2 m wide and 11.5°C at 400 m a.s.l., collected by Johan Törnblom on 6 May 2003.

Russia. At Kola Peninsula or Lapponia rossica (Lr), *A. alpinus* was found in Petsamo, Salmijärvi in 1928 (TIENSUU 1939). The 7 mm long larvae collected from Kharlovka River in 1998 are *A. alpinus*, but the larvae from the other rivers are too young (about 2 mm long) for a safe determination.

Material from Kola Peninsula. One larva from Kharlovka River at 68.32°N, 36.52°E and about 200 m a.s.l., collected on 14 August 1998 by Jan Åslund and Anders Dahlen. In addition, 83 larvae of *Ameletus* sp. were found in another 9 samples from 7 rivers all entering the White Sea, collected by Håkan Söderberg in 1995 and 1997 (BERGENGREN et al. 2004): Piatka on 17 August 1995, Krivets on 18 August 1995, Varzuga on 21 August 1995 and 15 August 1997, Punyi on 6 August 1997, Yapoma on 11 August 1997, Melga on 12 August 1997, and Western creek on 15 August 1997.

Material from Lake Baikal. Twelve *A. alpinus* larvae were found by Solberga Gymnasium biology teacher Björn Oledal and his students on 28 May 2002 at Lake Baikal near the Silver Spring railroad station at 455 m a.s.l., on gravel and sand bottom in an open landscape sparse in trees. The coordinates given were N 51° 51.511′ and E 104° 46.106′, but these coordinates seem to be incorrect since they are located offshore in the lake. The Gagnå larvae look like nearly perfect copies of these Baikal larvae.

4. Identification of larvae

The characteristics given by Bengtsson for the maxilla can only be observed if it is removed from the larva; the other characteristics are visible with a good stereomicroscope. In *A. inopinatus*, the comb-like bristles at the apex of the maxilla are slightly bent, and the spines on each bristle are as long as the bristle is wide, or 2–3 times longer than broad. In *A. alpinus*, the bristles are more bent and the spines are twice as long as the bristles, or 4–5 times longer than broad. In other words, *A. inopinatus* has a neat “moustache” while *A. alpinus* could need some grooming.

Ameletus inopinatus (Fig. 2)

The *A. inopinatus* larva is 8.5–10.5 mm long, with a slim body and long legs. *A. inopinatus* can reach the rear edge of the second body segment with its front leg claw, which is impossible for *A. alpinus*. All gills, except sometimes the first gill, are longer than the body segments they sit on. The sixth gill is twice as long as broad (BENGTSSON 1930b Figs. 37–40) and so is the third gill (e.g. ELLIOTT et al. 1988 Fig. 7a, or STUDEMANN et al. 1992 Fig. 56).

The frontoclypeus might have a light round central spot like Fig. 6 in SINITSHENKOVA & VARYKHANOVA (1990). The front edge of the superlingua is without notch (e.g. SCHOENEMUND 1930a Fig. 153 or 1930b Fig. 1, LANDA 1969 Table 1). The apex of the second segment of the labial palp is distinctly enlarged (SOLDÁN 1978); the labial palp in SVENSSON (1986 Fig. 21) is too schematic to identify.

Ameletus alpinus (Fig. 3)

The body of *A. alpinus* is 9.5–11.5 mm long. The head is larger and the legs are shorter than for *A. inopinatus*. At least the first two gills, and possibly all of them, are shorter than the body segments they sit on. The sixth gill is 1.5 times as long as broad (BENGTSSON 1930b Figs 41–44), and the third gill 1.7 times. Gills 3–6 are somewhat truncated. The frontoclypeus is uniformly coloured. The front edge of the superlingua has a notch (BENGTSSON 1930b Fig. 34). The apex of the second segment of the labial palp is slightly enlarged (BENGTSSON 1930b Figs. 35–36, SOLDÁN 1978), and somewhat longer than for *A. inopinatus*. The inner margin of the maxilla has a few bristles; in *A. inopinatus* these are about as long as the apical comb bristles (e.g. ELLIOTT et al. 1988 Fig. 6c), while in *A. alpinus* they are more than twice as long

5. Identification of imagos and subimagos

BENGTSSON (1930b) suggests that the ratio between measured parts of the legs in *Ameletus* is the same for subimagos as for imagos; although this is generally true for mayflies, it is not so in this case. I have measured a great number of legs from *Metretopus* spp. and *Siphlonurus alternatus*, and found that the ratios agree with the statement by Bengtsson, but the legs of *Ameletus* function in a different way; the subimago legs are not fully developed until it is time to transform to imago, and the best imago legs are those from mating couples; it is possible that *Ameletus* has to fly up over the clouds before the legs are fully stabilised. The findings below regarding imagos are in agreement with Bengtsson; statements for subimagos within parentheses are from my measurements alone.

Ameletus inopinatus (in ENGBLOM 1996 Figs 235, 242, 248, 250)

The forewings are 9–11 mm long, and the imago legs are as shown by BENGTSSON (1930b Figs 24, 25, 28, and 29).

The male front leg might be longer than the body. The tarsus is twice as long as the tibia, the second tarsal segment is twice as long as the first segment (subimago male: 1.5 times as long), and the tarsus segment order is 2 or 3, 4, 1 or 5.

The male hind leg tarsus is slightly longer than the hind tibia. The second tarsal segment is about as long as the first segment, or at most 1.3 times, and the tarsus segment order is 2, 1, 5, 3, 4 (EATON 1888, ULMER 1929, ELLIOTT & HUMPESCH 1983).

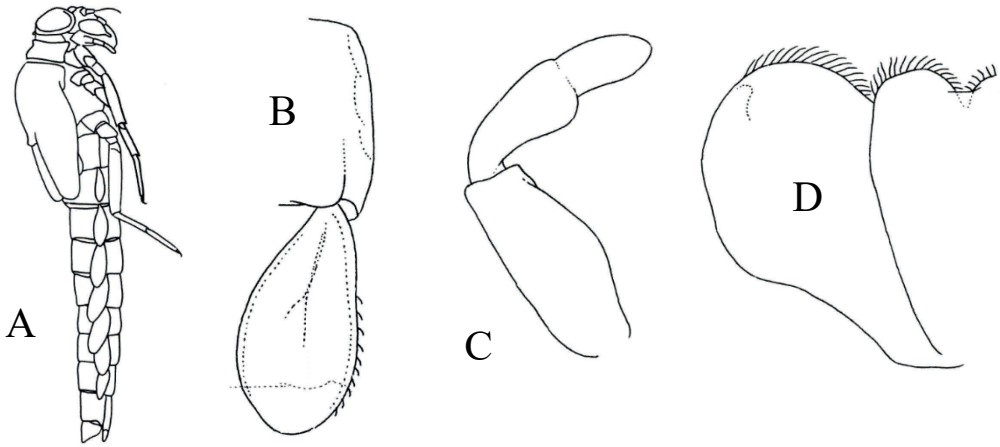

Fig. 2: *Ameletus inopinatus*. Snurrijåkka (TO) 68.30°N, 18.50°E. A. Larva. B. Third gill. C. Labial palp. D. Hypopharynx: superlingua.

Fig. 2: *Ameletus inopinatus*. Snurrijåkka (TO) 68.30°N, 18.50°E. A. Aspect de la larve. B. Troisième branchie. C. Palpe labial. D. Hypopharynx: superlingua.

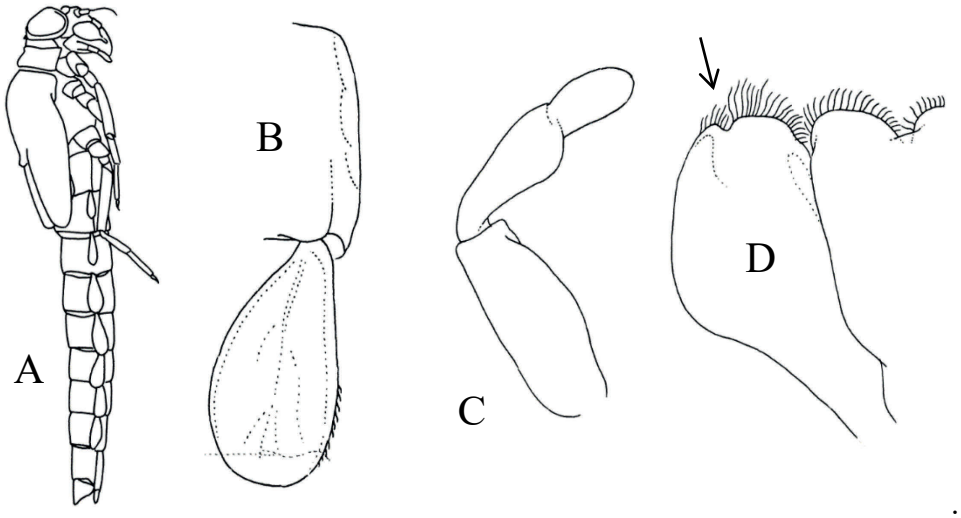

Fig. 3. *Ameletus alpinus*. Gagnå River (VG) 57.59°N, 14.08°E. A. Larva. B. Third gill. C. Labial palp. D. Hypopharynx : superlingua.

Fig. 3. *Ameletus alpinus*. Gagnå River (VG) 57.59°N, 14.08°E. A. Aspect de la larve. B. Troisième branchie. C. Palpe labial. D. Hypopharynx: superlingua.

The female front leg tarsus is clearly longer than the front tibia. The second tarsal segment is about 1.1–1.3 times longer than the first, and the tarsus segment order is 2, 1, 3, 5, 4. The second tarsal segment for female middle and hind legs is about 1.0–1.2 times as long as the first segment.

The male subanal plate has a U-shaped apical margin (EATON 1888, ULMER 1929, TSHERNOVA 1964, STUDEMANN et al. 1992, ZLOTY 1996 Figs. 1 and 9); the male genitalia shown in BAUERNFEIND & SOLDÁN (2012) are from an Austrian subimago. Male genitalia from specimens collected in Norway at Øvre Heimdal and Sjodalen in Jotunheimen (STUDEMANN et al. 1988 Figs 38–44) seem to be *A. inopinatus*, but unfortunately the legs are not described. The eggs from this area were 220 µm long and 140 µm wide, which is the same size as for *A. alpinus*.

In some literature, the *A. inopinatus* imago hind tarsus is said to be slightly shorter than the hind tibia (KIMMINS 1972, ELLIOTT & HUMPESCH 1983 Fig. 8b, SÖDERSTRÖM & NILSSON 1986, STUDEMANN et al. 1988 Fig. 50e, BAUERNFEIND & SOLDÁN 2012). It is possible that this is true for English *A. inopinatus*. In SCHOENEMUND (1930a) the female front leg tarsus is said to be as long as the tibia. However, an accurate statement is that segment 1 of the hind tarsus is longer than segment 5 for *inopinatus* and shorter for *alpinus* (SOLDÁN 1978).

***Ameletus alpinus* (in ENGBLOM 1996 Figs 247 and 249)**

The forewings are 10–12 mm long, and the imago legs are as shown by BENGTSSON (1930b Figs. 26, 27, 30, 31).

The male front leg is as long as or slightly shorter than the body. The tarsus is 2.0–2.5 times as long as the tibia, the second tarsal segment is 2.8–3.5 times as long as the first segment (subimago male: 1.9 times as long), and the tarsus segment order is 3, 2, 4, 5 or 1.

The male hind leg tarsus is as long as the hind tibia. The second tarsal segment is about 1.3 times as long as the first segment, and the tarsus segment order is 2, 5, 1, 3, 4.

The female front leg tarsus is somewhat longer than the front tibia. The second tarsal segment is 1.5–1.7 times as long as the first segment (1.3–1.4 times for subimago), and the tarsus segment order is 2, 3, 5, 1, 4. The second tarsal segment for female middle and hind legs is about 1.1–1.3 times as long as the first segment (both segments are of equal length for subimago).

The male subanal plate has a V-shaped incision at the apical margin, which Bengtsson compared to that of *Ameletus camtschaticus* and may also be said to resemble that of *Metreletus* (e.g. STUDEMANN et al. 1988 Fig. 48). The female subanal plate has a deeper median indentation than for *A. inopinatus*. According to BENGTSSON (1913), *A. alpinus* eggs are 227–231 µm long and 146 µm wide.

6. The "less good *alpinus*" in the Scandinavian mountains

Bengtsson described larva he collected in 1903 and in 1907 from several places in the Scandinavian mountain chain. Larvae I have seen, collected from the same areas on both side of the frontier from the 1960s onwards, do not fully correspond.

ULMER (1943), in his overambitious description of *A. alpinus* from material collected by Thienemann in Abisko in 1936–1938, points out that the median notch at each superlingua is not always present. This is true; in the mountains, there can be a notch on one side but not on the other, or there can be larvae without notches. There may also be other discrepancies, such as gills or legs that are a bit too long for *A. alpinus*. Nevertheless, in my opinion, if the population has aptitude for median notches then it may not be "good *alpinus*" but it is still *A. alpinus* and not *A. inopinatus*.

For winged specimens from the mountains, aside from the ordinary *Ameletus* leg problems the major problem is the implausible second tarsal segment of the male front leg.

On an inquiry from Tiensuu, who was surprised not to find *A. alpinus* in BREKKE (1938), Brekke told him about "intermediate forms between these two species", and stated that he had decided to regard *alpinus* as a variety of *inopinatus* (TIENSUU 1939). Brekke, who knew *A. alpinus* only from the Norwegian mountains, most likely never saw any "good *alpinus*", while both TIENSUU (1937, 1939) and BAGGE (1965) found specimens in Finland that agreed with Bengtsson's *A. alpinus* description.

7. Ecology

The European *A. inopinatus* is considered a high mountain species, inhabiting small to medium rivers or clear cold lakes. This is valid for the Swedish *A. inopinatus*, which is found in the tundra in climate zone 9 and at altitudes of 440–1034 m a.s.l., while *A. alpinus* is found in tundra, taiga, and low land in climate zones 2–9 and at altitudes of 5–1125 m a.s.l.; 700 of the *A. alpinus* registrations are from below 440 m a.s.l.

In the Limnodata HB database, *Ameletus* is recorded from 72 stony oligotrophic lakes with sparse vegetation, all situated in the mountains north of 63°N and at altitudes exceeding 300 m; 14 of the lakes had *A. alpinus* (JÄ, ÅS, LU, and TO) and 4 had *A. inopinatus* (TO). SOLDÁN (1981) collected *Ameletus* from 10 lakes in Finnish Utsjoki (Li); he also found *Ameletus* to be the most frequent mayfly in that area, although SAVOLAINEN & SAARISTO (1984) put *Ameletus* in the ninth place. However, *Ameletus* is one of the most frequent mayflies all over northern Fennoscandia.

In Aurland River at 60.51°N, 7.21°E in Western Norway, LARSEN (1968) had very few *Ameletus* larvae in his monthly samples, up to 32 specimens per m^2, but mentioned much denser populations further up the river. *Ameletus* is not evenly spread in a river, and less so in the autumn than in the spring. Under perfect circumstances, rivers in the Swedish taiga can have 500-1000 *A. alpinus* larvae per m^2.

Both species are fast swimmers. The rivers they inhabit have stone bottoms; slate, for *A. inopinatus*. *A. alpinus* at least likes to take a rest on top of stones or blocks. *A. inopinatus* is found in 0.75–10 m broad rivers and *A. alpinus* in 0.5–500 m broad rivers. The velocity is usually 0.5–1.0 m/sec, but can exceed 1.5 m/sec. There may be algae and mosses such as *Fontinalis*; the guts of *A. alpinus* have been seen to contain small pieces of green alga.

A. inopinatus is a cold water species, and measured water temperature for *A. alpinus* has never been over 20°C; however, it is not necessary for the entire river to be cold, as long as there are areas with cold ground water seeping up. A pH over 6 is preferred, but *A. alpinus* can stand a temporary dip to even pH 4.6; there are examples of *A. alpinus* colonizing limed waters in the north, and liming of waters at the Swedish west coast must have helped the species to spread further south. Both species prefer clear clean water, although *A. alpinus* has been collected in a conductivity of 94 µS/cm in an agricultural area, in lime-rich waters there have been conductivity exceeding 300 µS/cm, and even 500 µS/cm seemed tolerable in a well with a pH of 8.12 (LINGDELL & ENGBLOM 2013).

Figure 4. Two *Ameletus alpinus* rivers: To the left a brock to Potjujaure in Abisko National park at 68.16°N, 18.31°E and 800 m a.s.l. in Eco region 22. To the right Rödån at 58.02°N, 14.11°E and 110 m a.s.l. in Eco region 14.

Figure 4. Deux cours d'eau abritant *Ameletus alpinus*: à gauche, le ruisseau de Potjujaure dans le Parc national d'Abisko, 68.16°N, 18.31°E à 800 m d'altitude, éco-région 22. À droite le Rödån, 58.02°N, 14.11°E à 110 m d'altitude, éco-région 14.

Ameletus has a univoltine life cycle, with overwintering larvae proved with, for example, monthly samples in Ekse River at 60.15°N, 6.15°E in West Norway (ANDERSEN et al. 1978). At Ammarnäs there were larvae in May–June samples but not in the late autumn samples (ULFSTRAND 1968). Most of the growth takes place under the ice, and by the time the ice breaks the larvae are almost fully grown (ULFSTRAND 1968, BRITTAIN 1974, ARNEKLEIV 1996).

Emergence and swarming take place in daylight. In Sweden, *A. inopinatus* swarms in June, and *A. alpinus* in the north part of the country swarms in June to mid-August. They fly not fast but very high, usually out of the reach of a butterfly net. It is possible that this albatross amongst mayflies can also fly large distances. TAUBMANN et al. (2011) suggest that a 20 km radius can be reached during dispersal events, but since they found no significant differentiation in 70% of the populations that were up to 100 km apart, they believe 20 km to be toward the lower end of the distance *Ameletus* can fly.

A. alpinus has been collected with up to 17 other mayfly species, most frequently with *Rhodobaetis* and *Ephemerella aurivillii*. It has also been found with up to 20 different Trichoptera and Plecoptera, most commonly *Rhyacophila nubila* and *Diura nanseni*. Blackflies are usually present, and often Hydracarina are seen. At Kola Peninsula, all ten *Ameletus* samples were found with *Baetis fuscatus*, *Ephemerella aurivillii*, and the stoneflies *Leuctra fusca* and *Taeniopteryx nebulosa*.

Larvae of *A. alpinus* are important winter food for Salmonides, and have been found in stomachs of *Salmo trutta*, *Salvelinus alpinus*, and *Thymallus thymallus*; one of the graylings had consumed an imago male (ENGBLOM 2019).

THEISSINGER-THEOBALD (2011) also studied the European phylogeography of the stonefly *Arcynopteryx compacta*, suggested to have the same distribution as *A. inopinatus*. Only 4.7% of Swedish *Ameletus* samples show the presence of *Arcynopteryx compacta*, but it is very likely that *A. inopinatus* used to have the same distribution as *Arcynopteryx compacta* before *A. alpinus* arrived.

8. Discussion

THEISSINGER-THEOBALD (2011) states that the genetic diversity of *Ameletus* decreases along an east–west gradient in Central Europe and along a north–south gradient in Scandinavia, as illustrated with a dendrogram in TAUBMANN et al. (2011 Fig. 2): "There was strong differentiation between the Fennoscandian and all other populations, indicating that Fennoscandia was recolonized from a refugium not accounted for in our sampling. High degree of population genetic structure within the northern samples suggested that Fennoscandia was recolonized by more than one lineage." For these studies, material was collected at two places in Sweden (FS7 and FS6) and five places in Norway: Skorovatn at 64.39°N, 13.11°E (FS5); Dovrefjell at 62.33°N, 9.49°E (FS4) and 62.26°N, 9.45°E (FS3); and Jotunheimen at 61.28°N, 8.51°E (FS2) and 61.23°N, 8.53°E (FS1).

The Swedish and Norwegian material at Limnodata HB shows no visible gradient from north to south in ecoregion 20. There is more or less good *A. alpinus* at FS5–FS7. FS1–FS4 is unfortunately outside my knowledge area, but it is possible that *A. alpinus* has not yet occupied the entirety of southern Norway, and if the male genitalia in STUDEMANN et al. (1988 Figs. 38–44) are to be believed, there may still be populations of genuine *A. inopinatus* in Jotunheimen, which is the same area as FS1 in THEISSINGER-THEOBALD (2011).

Larvae of *A. alpinus* that perfectly fit the description by Bengtsson were found 400 kilometres south of the mountains in 1984. There are "good *alpinus*" in the taiga in the eastern half of Swedish ecoregion 22 and south along the Baltic Sea down to ecoregion 14, and the larvae collected from the Carpathians in 2003 are "good *alpinus*". The very best ("excellent") *A. alpinus* larvae are those from Lake Baikal in Russia.

My opinion about the mountain situation is that during the last ice age the Norwegian *A. inopinatus* survived in ecoregion 21 and spread down from there to the Scandinavian mountains. The larger intruder *A. alpinus*, which may have initially been identical with *A. inopinatus*, entered via Finland from Siberia and also spread down the Scandinavian mountain chain; the resulting interbreeding then caused the confusing pattern of legs and notches. Perhaps *A. alpinus* first arrived when the inland ice had newly melted, but this immigration is an ongoing process, and many more *A. alpinus* must have entered Sweden during the past hundred years, spreading all the way south

into ecoregion 14. If this migration is due to climate change, they seem to be flying in the wrong direction.

However, there is another possibility. Although THEISSINGER-THEOBALD (2011) interprets her material to reject the idea of an *Ameletus* recolonization of Fennoscandia from Central Europe, she is referring to the situation in the past. In the present time, it is possible that the *A. alpinus* in Swedish ecoregion 14 arrived from the Carpathian Mountains; the larvae I have seen from Poland and Romania are quite similar to those from southern Sweden. SOLDÁN (1978), in discussing what he regards as slight differences between *inopinatus* and *alpinus* as described by Bengtsson, says that "similar differences were observed from Hercynian and Carpathian mountain systems in Czechoslovakia". According to this author, "these differences are not considered to be of specific importance", but to *A. inopinatus*, which is threatened by both climate change and the risk of being driven out of business by the more robust *A. alpinus*, they are of considerable importance.

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References

Abbreviations for the provinces: Sweden (ENGBLOM 2003), Norway, Denmark and Finland in e.g. Fauna Entomologica Scandinavica. E.J. Brill / Scandinavian Science Press Ltd. Latitudes and longitudes (grades, minutes, seconds) are taken from Google Earth; http://earth.google.com
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