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Contribution to the understanding of the Fennoscandian *Baetis vernus* group: *B. subalpinus* and *B. vernus* [Ephemeroptera]

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Fennoscandia is home to six species in the *Baetis vernus* group. Three of them (*Baetis macani*, *B. bundyae*, and *B. tracheatus*) have long gills and are discussed by ENGBLOM (2019a) along with *Baetis jaervii*. The other three have short gills. *B. liebenauae*, which is generally regarded as easily recognized because of its extreme mandibles, will be discussed in a separate paper. The remaining two species are frequently but unnecessarily mistaken for each other: *B. subalpinus* Bengtsson, 1917 and *B. vernus* Curtis, 1834, "the two nomads".

Contribution à la compréhension du groupe finno-scandinave *Baetis vernus*: *B. subalpinus* et *B. vernus* [Ephemeroptera]

Mots-clés : Ephemeroptera, écologie, morphologie, distribution, migration, *B. subalpinus*, *B. vernus,* Finno-Scandinavie.

Six espèces du groupe *Baetis vernus* sont présentes en Finno-scandinavie. Trois d'entre elles (*B. macani*, *B. bundyae* et *B. tracheatus),* aux longues branchies, ont été précédemment présentées, ainsi que *B. jaervii* (cf. ENGBLOM 2019a). Les trois autres espèces de ce groupe possèdent des branchies courtes. *B. liebenauae*, généralement reconnue pour être aisément identifiable sur le caractère de la forme de ses mandibules, sera examinée ultérieurement. Les deux espèces restantes sont fréquemment confondues: *B. subalpinus* Bengtsson, 1917 et *B. vernus* Curtis, 1834, les "deux nomades".

1. Introduction

Many species of Ephemeroptera remain in the same habitat for hundreds or even thousands of years, provided that the habitat conditions continue to comply with their needs. Within the *Baetis vernus* group, *B. macani* and *B. bundyae* are known to be stationary. *B. tracheatus* and *B. liebenauae* are long-distance flyers, but the latter at least seems to settle down permanently once a good site is found. Conversely, females of *B. subalpinus* frequently lay their eggs in waters different from where they hatched themselves, and *B. vernus* females have a similar behaviour.

SAVOLAINEN et al. (2007) state that *Baetis* adults "*swarm close to the water, where the nymphs live, so that swarming either next to flowing or stagnant water results in ethological isolation*." This might be true for males, but females with fertilized eggs can fly long distances; in the cases of *B. subalpinus* and *B. vernus*, even several kilometres. When a river has been damaged and then

restored, for example by acidification and subsequent liming, the first mayfly species to arrive after restoration is often either the "settler" *Rhodobaetis* or *B. subalpinus*, which as early as the following season can be replaced by *B. vernus*. These two species are known to also swap habitats in waters untouched by human impact, such as the river Liukattijoki (TO) at 67.39°N, 20.58°E, where *B. subalpinus* was found in 1980 and *B. vernus* in 1983.

SAVOLAINEN et al. (2007) conducted an electrophoresis study in which they sampled sites repeatedly in order to study sympatric populations. Their clustering (Fig. 2 in that article) showed that the larvae of *B. subalpinus* collected from site 11 in 1997 were in a different place on the cluster from those collected from the same site in 1998, and the same was true for those from site 12 collected in 1995 and 1998; similarly, *B. vernus* collected from site 21 in 1995, 1997, and 1998 were spread out over three places in the clustering. The explanation given for this outcome was gene flow across species boundaries, but as *B. vernus* group species do what they can to steer clear of each other, I am more inclined to consider it the result of human error, as expressed by STÅHLS & SAVOLAINEN (2008): "In particular, the nymphs of *B. vernus* and *B. subalpinus* are difficult to separate."

However, confusion between *B. subalpinus* and *B. vernus* is not inevitable; as I explain below, there are characteristics that identify these two species quite easily.

2. *Baetis subalpinus* Bengtsson

2.1. A misidentification by Müller-Liebenau in 1969

BAUERNFEIND & SOLDÁN (2012: 134) state that *B. subalpinus* is frequent in still water habitats, and JACOB (2003) also mentions still water in connection with *B. subalpinus*. However, the *B. subalpinus* records at Limnodata HB for Sweden and Kola Peninsula, plus a few Norwegian findings, are all collected from running waters. The literature also refers to running water only, regarding Norway (AANES 1980, ARNEKLEIV 1996), Sweden (ULFSTRAND 1967), and Finland (MÜLLER-LIEBENAU & SAVOLAINEN 1975, SOLDÁN 1981, SAVOLAINEN & SAARISTO 1981, 1984, SAVOLAINEN et al. 2007). To my knowledge, the only reference to still water is for *B. saliens*; MÜLLER-LIEBENAU (1969) assigned this species to *B. subalpinus* from the pinned and dried male type and referring to Figure 8 in TIENSUU (1939: 112-113). However, from the same figure, which shows a hindwing with the third vein half as long as the wing, and from the descriptions of adults and larvae, I believe that *Baetis saliens* Tiensuu, 1939 is rather *B. macani* Kimmins, 1957 and not *B. subalpinus* Bengtsson, 1917.

2.2. Distribution and material

Baetis subalpinus is a Fennoscandian species known from Norway, Sweden, Finland, and the Kola Peninsula. BAUERNFEIND & SOLDÁN (2012) place it in ecoregions 20-23, but region 14 should be added to these; or, more precisely, ILLIES (1978) draws the border between 22 and 14 too far northwards. Boreo-tundra (HAYBACH & JACOB 2010) is an adequate faunistic element; in samples from all over Sweden, larvae have only been collected sixteen times in water temperatures exceeding 18°C.

The first Norwegian *B. subalpinus* record came from Sør-Varanger in Finnmark (TIENSUU 1937). In Norway it has been found at, from north to south, Finnmark (FI, FN, FØ), Troms (TRI),

Nordland (NSI), Nord-Trøndelag (NTI), Sør-Trøndelag (STY, STI), and Opland (ON) (BRITTAIN 1999). In addition imagos were collected by the river Tufsinga in Hedmark (HEN) at 62.13°N, 14.46°E on 5 August 1974 (Limnodata HB), and one male imago was found in Telemark (TE) on 4 August 2001 (OLSEN & SOLVANG 2006),

BENGTSSON (1917) described *B. subalpinus* from Nattavaara (LU) at 66.44°N, 20.56°E, collected in August 1909. For Sweden (Limnodata HB), there are 2419 register records from taiga and tundra at altitudes of 3-920 m a.s.l., mainly distributed from Virkaljåkko (TO) at 68.43°N, 20.25°E down to 60.30°N. In 1980 *B. subalpinus* was collected outside the species ordinary distribution in the two rivers Svartån (SM) at 57.59°N, 14.54°E, 160 m a.s.l. and Solgen (SM) at 57.32°N, 14.54°E, 205 m a.s.l. (Limnodata HB).

The first Finnish record came from Petsamo, Tavastia (Ta) (TIENSUU 1939). The distribution map in SAVOLAINEN (2009) shows Lapponia (Lkv, Lke, Le, Li), Kuusamo (Ks), Savonia borealis (Sb), Ostrobottnia borealis (ObS, ObN), Ostrobottnia kajanensis (Ok), Ostrobottnia media (Om), Karelia borealis (Kb), Savonia australis (Sa), Tavastia borealis (Tb), Ostrobottnia australis (Oe), Satakunta (St), and Aboensis (Ab).

From Kola Peninsula there are 26 register records with a total of 3247 specimens, from both tundra and taiga (Limnodata HB). Håkan Söderberg collected from the following taiga rivers (from west to east) in August 1995 and August 1997: Indel (66.59°N, 35.41°E), Pana, Ilma, Punyi, Vartzuga, Piatka, Falaley, Turma, Krivets, Yapoma, Melga, Arenga, Serga, and Western creek (66.24°N, 36.33°E) (BERGENGREN et al. 2004). Jan Åslund and Anders Dahlen performed their collections in August 1998, covering the taiga rivers Kuzreka, Ruma, and Viala and the tundra river Kharlovka, which was the northernmost collection point at 68.32°N, 36.52°E.

2.3. Identification of larva

The larvae of *B. subalpinus* are 5-8 mm long, usually chestnut brown but sometimes yellow, or greyish speckled as in MÜLLER-LIEBENAU (1969 Abb. 82). Dark larvae might have two round light spots at each tergite, compared to diffuse irregular spots for *vernus*; the fifth tergite is the lightest. The body shape resembles that of *vernus*, but is distinguished from that species by the unique light V-shaped area along the forewing pads (Fig. 1). This V-shape might even be visible on very young larvae; it is also visible on the larva drawing Abb. 3a by MÜLLER-LIEBENAU (1966). The rounded oblong gills resemble those of *B. buceratus*; the third gill is at most 1.6 times as long as broad, and is usually shorter and less pointed than that of *vernus*. The statement by BAUERNFEIND & SOLDÁN (2012) that the gills are "as in *B. vernus*" is misleading. The tail is half as long as the body, and the pale cerci have dark tips as for *vernus*.

The labrum has 1+3-5 bristles. The left mandible has the apical tooth as broad as the second tooth (SVENSSON 1986, KUUSELA 1993, ENGBLOM 1996, 2019b). The third segment of the labial palp is longer and more symmetric than in *vernus*. The outmost maxillary palp segment is semilong (ENGBLOM 1996 fig. 227, 2019b), as for *vernus* and *buceratus*. The female frons is broad and distally rounded; this is the most commonly used feature in Fennoscandian larva keys to separate *subalpinus* and *vernus* (JENSEN 1984, SVENSSON 1986, KUUSELA 1993, ARNEKLEIV 1995). Young larvae males have frons like the females, but as the turbinate eyes grow wider the frons is pressed together until it is triangular and bluntly pointed as for *vernus*. The denticles (conical bristles) of the tergal surface are not as densely placed as for *vernus* (MÜLLER-LIEBENAU 1969 Abb. 85). Along the posterior margin of the femora there is a row of club-shaped bristles, longer than for

vernus. The innermost of these bristles are densely situated and can form a veritable tuft, which is missing in *vernus*.

2.4. Identification of subimago

The subimago male turbinate eyes are dark apricot at the base with light yellow above, and the top surface is apricot. The rounded frons and the maxillary palp are still present on subimago females. Thorax and terga are light brown in males and grey-brown in females. The sterna are even lighter, and in both males and females have the same pattern of dots and lines as for imago females, only white. The wings are a smoky grey-brown. The femur is yellowish with brown-grey flecks, and the tibia and tarsus are yellow-white.

2.5. Identification of imago

Imago body length and forewing length are 5-7 mm in males and 6-8 mm in females. The male turbinate eyes are pale yellowish at the base, with chestnut brown and then yellow above, and the top surface is brownish orange. The pronotum and thorax are dark brown in males and lighter brown in females. Body colour is the same as for the larvae: chestnut brown, dirty yellow, or speckled greyish. Sometimes the last three male tergites are orange brown, in that case all females from the same population have tergites in the same colour but lighter. The female sterna pattern, resembling two dark "eyes" with "eyebrows", is nearly identical for *subalpinus*, *vernus*, and *macani*, though different from other *Baetis* species (ENGBLOM 1996 fig. 223, 2019b). The hyaline forewing might have brownish costal veins. The third vein of the hindwing appears to be a third as long as the wing; that is, this is the length that is visible, and the rest of the vein is fused with the posterior margin. BENGTSSON (1917: 187) described the hindwing as "Hinterflügel mit drei einfachen Längsadern, die 3. ganz kurz, nur etwa 1/3 der Länge des Flügels," and although he did not publish the drawing he made of this wing, it is reproduced in MÜLLER-LIEBENAU (1965 Abb. 16:b). The legs are yellow-white with grey feet. The male fore femur is yellow-brown and grey, the tibia is yellow-grey, and the tarsus is smoky grey. The female fore femur is yellow-grey. The first segment of forceps is conical and slightly concave, and the third segment is more than twice as long as broad. The cerci are white, sometimes ringed with orange in their basal part, and are up to 14 mm long for males and 12 mm for females.

2.6. Frozen eggs

In February 1996, when the temperature fell below -30°C, the new owner of the hydropower plant at Gunnilbo River (VS) had left the dam lids in a nearly closed position. They were soon ice bound, and the streaming parts of the river ran out of water. This river, which is usually open all through the winter, was frozen solid in no time. Two weeks later the dam lids were opened wide, and two weeks after that the ice had melted and the river was back to normal, except that 97% of the bottom fauna at site VS140 had been wiped out (LINGDELL & ENGBLOM 2007). Two of the 16 mayfly species in the river never noticed the disaster: *B. subalpinus* and *Serratella ignita lactata*. Larvae of *B. subalpinus* started to crawl out of the eggs on 2 May, and by 7 June all the larvae of this ordinary-sized population had left the water. This full-scale "experiment" is proof that the eggs of *B. subalpinus* (and *Serratella ignita lactata*) can survive being not only frozen but even "freeze-dried".

The oval white eggs of *B. subalpinus* are 0.17- 0.18 mm long, which is above-average for Baetidae. KOPELKE & MÜLLER-LIEBENAU (1981) state that *B. subalpinus* eggs have a length of 0.19 mm compared to the 0.14 mm in *vernus*, but do not say where these specimens originated. One 6 mm long female imago from Gunnilbo River had 913 eggs.

2.6. Life cycle and ecology

In northern Sweden (climate zones 6-9) *B. subalpinus* has one generation a year during August–September; this has been described, for example, at Ammarnäs 65.57°N, 16.13°E (ULFSTRAND 1967, 1968) and Kaltisjokk 66.42°N, 20.26°E (LINGDELL & MÜLLER 1980). In central Sweden and up the coast of the Baltic Sea (climate zones 4-5), there are two generations, as described at Ängerån 63.35°N, 19.50°E during June–July and September–October (ENGBLOM et al.1981). Although the categorisation of climate into zones 1-9 was originally developed for gardeners, it is also useful when studying mayflies. Despite climate change, these zones can still help to explain species distributions, such as whether there are one or two generations a year, or if there is overwintering as larvae or eggs.

According to current knowledge, *B. subalpinus* is univoltine in Norway, as described for the river Sagelva 63.21°N, 10.38°E with larvae in June–July (ARNEKLEIV 1996). However, a second generation seems likely in the south-eastern areas of Norway.

Collections made at Kola Peninsula in 1998 comprised 6.2- 6.5 mm long nymphs at Kharlovka Camp 7 (68.32°N, 36.52°E) on 14 August, and one subimago by a small tributary to the Kharlovka River at 68.17°N, 36.17°E on 4 August.

At Gunnilbo River site VS140 (59.48°N, 15.51°E; 80 m a.s.l.; climate zone 4), the larvae of the spring generation can be present from late April, when the water temperature is about 7°C. The larvae hatch during the first week of June, in water temperatures around 14-16°C, around 7pm. The subimago stage lasts for about 12 hours. Swarming takes place in the evening around 7pm–8pm, some hundred meters away from the water. One observation on 6 June reported about 100 males swarming 5-10 m over a road in the rain at an air temperature of 14.7°C. In the chillier tributaries, hatching can be delayed by a month. The autumn generation in this area fly during late August and early September, or even as late as mid-October.

The fast-swimming *B. subalpinus* inhabits riffles which are mainly 5-10 m broad and frequently shallow with a moderate to fast current, stony bottom, and green algae and mosses. *B. subalpinus* also feeds from mosses, though in aquarium the larvae are content with vegetarian fish food or green algae. In a rapid part of Gunnilbo River (Figs 1-2), *B. subalpinus* clings tight to boulders overgrown with the moss *Fontinalis dalecarlica* and the red alga *Lemanea*, syntopic with *Rhodobaetis* (true *B. rhodani* as described in GATTOLLIAT & SARTORI 2008).

In Sweden, *B. subalpinus* has been collected with up to 15 other mayfly species on the same occasion, and with 38 species in total; the most common are *Rhodobaetis* (76%), *Heptagenia dalecarlica* (49%), *B. fuscatus* group (41%), *Ephemerella aurivillii* (40%), *Alainites muticus* (32%), *Nigrobaetis niger* (31%), *Ameletus (alpinus)* (24%), and *Paracinygmula joernensis* (19%).

At Kola Peninsula, *B. subalpinus* has been collected with 24 other mayfly species: *Heptagenia dalecarlica* (85% of the sampling occasions), *Ephemerella aurivillii* (81%), *B. fuscatus* (73%), *Serratella ignita lactata* and *Rhodobaetis* (69%), *Paracinygmula joernensis* (61%), *Nigrobaetis niger* (58%), and *Caenis rivulorum* (50%).

Figures 1-2. Station VS140 at Gunnilbo River, home for *Baetis subalpinus*. Left: bottom frozen in 1992 (February 11); right: normal torrent in 2014 (February 27).

Figures 1-2. Station VS140 de Gunnilbo River, colonisée par *Baetis subalpinus* ; ruisseau gelé le 11 février 1992 (à gauche) ; ruisseau en eau libre le 27 février 2014 (à doite).

B. subalpinus avoid the company of other *B. vernus* group species; in the Swedish *subalpinus* material, *B. bundyae* was present in 1.9% of collections, *B. vernus* was present in 0.4%, and *B. macani* was seen at only two sites. At Kola, *B. subalpinus* was collected once with *B. vernus* and twice with *B. liebenauae*. In light of this, the statement by BAUERNFEIND & SOLDÁN (2012) that "*B. subalpinus* often occur syntopic with *B. macani*" is quite amazing.

B. subalpinus is very important as fish food. Larvae have been found in the stomachs of brown trout *Salmo trutta*, rainbow trout *Oncorhynchus mykiss*, grayling *Thymallus thymallus*, pike *Esox lucius*, minnow *Phoxinus phoxinus*, and the two bullheads *Cottus gobio* and *Cottus poecilopus* (ENGBLOM 2019b).

3. *Baetis vernus* Curtis

Specimens referred to *B. vernus* in older Fennoscandian literature from Denmark (ESBEN-PETERSEN 1910), Norway (TIENSUU 1937, BREKKE 1938), and Finland (ARO 1928, TIENSUU 1939) are most likely always *Baetis vernus* Curtis, 1834.

3.1. Distribution and material

B. vernus is widely spread. In northern Europe, it is found in Schleswig-Holstein, Denmark, Sweden, and the Kola Peninsula (Limnodata HB); BRITTAIN (1999) gives the distribution for provinces in Norway; and SAVOLAINEN (2009) gives a distribution map for Finland. In Denmark, Bornholm included, *B. vernus* is said to be the most common *Baetis* next to *Rhodobaetis.*

In Sweden (Limnodata HB) there are 250 register records at altitudes ranging from 0.5 to 500 m a.s.l. The distribution is scattered; it is not common in the southern half of the country, and sparse in the northern half. The northernmost find in Sweden is from the river Liukattijoki (TO) at 67.39°N, 20.58°E.

At Kola Peninsula, *B. vernus* was collected on 18 August 1995 in the river Krivetz at 66.42°N, 36.00°E by Håkan Söderberg (BERGENGREN et al. 2004).

3.2. Identification of larva

When all variations are included, the nymphs of *B. vernus* are 6-10 mm long. The body is uniformly light yellow or greyish speckled, and the back of the head is speckled like *B. subalpinus* and the *B. fuscatus* group. Gills are oval and semi-long, and the third gill is at most 1.8 times as long as broad (twice as long for "long-gilled *vernus*"). Sometimes the gills are slightly milky, and perhaps only a yellow mid vein is visible. The legs are almost white with grey feet. The cerci are pale yellowish or greyish, with darker tips.

The labrum has 1+3-8 bristles. The left mandible has an the apical tooth 1.5 times as broad as the second tooth (MÜLLER-LIEBENAU 1969 Abb. 71b, ENGBLOM 1996, 2019b) and twice as broad in the "Danish" variant. If the first tooth is said to be between 1.5 and 3.5 times as broad as the second (STÅHLS & SAVOLAINEN 2008), *B. vernus* only is not likely; here, *B. tracheatus* must be involved. It should be noted that if the widths of the teeth in the outer incisor group are measured along an imaginary line that cuts the dividing points between the teeth, it is irrelevant if the mandible is worn or not (ENGBLOM 2019b p. 16). The labial palp has an acute angle between the terminal segment and the protrusion on the sub terminal segment, and the inner margin of the third segment is more rounded than for *subalpinus*. The frons is triangular and bluntly pointed. Over most of the larval surface there are densely placed denticles that are sparse or absent in *subalpinus*, for example on the terga (MÜLLER-LIEBENAU 1969 Abb. 72).

3.3. Identification of imago

Imago body and forewing length are 5.5-9 mm in males and 6-10 mm in females. The wings of the subimago are smoky grey, and those of the imago are hyaline with colourless or pale brownish veins. The third vein of the hindwing is half as long as the wing. Male turbinate eyes are red-brown or yellow. Seen from above, the eyes are oval and slightly flattened on the inner side, but not as oblong as described by MÜLLER-LIEBENAU (1969 Abb. 65) or "*twice as long as broad*" (JACOB 2003). Male tergites 2-6 are green-brown and 7-9 red-brown like the fore body. Legs are green-grey with yellow tibiae, and the male first leg is white-grey. The first segment of the forceps is conical and has a small process; the third segment is less than twice as long as broad (ENGBLOM 1996, 2019b). The cerci are grey-white and 1.5-3 times as long as the body in males and 1-1.5 times as long in females. The eggs of Swedish *B. vernus* are 0.16-0.17 mm long.

***Baetis vernus* variations**:

1. I have reared the ordinary or "big yellow *vernus*" in aquarium several times. The adults are identical with "long-gilled *vernus*", and have forceps as shown by ENGBLOM (1996 fig. 211b, 2019b). They are found all over Sweden.

2. Reared males of "little speckled *vernus*" have forceps (ENGBLOM 1996 fig. 211a, 2019b) slightly different from those of "big yellow *vernus*", and their turbinate eyes are rounder when seen from above than for the larger variations. They are found all over Sweden.

3. The "long-gilled *vernus*" is practically a "big yellow *vernus*" with longer gills, found in three Swedish slow-running waters. Further details are given by ENGBLOM (2019a).

4. I have not reared the "Danish *vernus*" from Skåne (SK). Similar larvae are found in Denmark and Schleswig-Holstein (Limnodata HB). The left mandible of the larva has the apical tooth twice as broad as the second tooth, like the drawings by SVENSSON (1986 fig. 25r) and ELLIOTT et al. (1988 fig. 21b); the mandible in the key for Finland (KUUSELA 1993) is copied from SVENSSON (1986).

3.4. Life cycle and ecology

In Sweden, *B. vernus* inhabits assorted running waters, chiefly forest streams with stone bottoms and of medium current, but also muddy ditches or slow-running rivers rich in vegetation. Larvae are found from late April in the southern part. In the central part, there are two generations a year with imagines in June-July and in September-October, while in the northern part, with one generation a year, larvae have been collected in July-August.

In Norway there might be only one generation, as for the Ekse River 60.15N, 6.15E, with larvae in June–July and adults in August-September (ANDERSEN et al. 1978).

According to JENSEN (1984), *vernus* is univoltine in Denmark, but large larvae have been found in the autumn. On 8 November 1986, Limnodata HB collected full-grown larvae at Lilleå in West Jutland, Denmark (WJ) at 56.20°N, 8.21°E. It is possible that "Swedish *vernus"* and "Danish *vernus"* are two different species.

B. vernus in Sweden has been collected with up to 11 other mayfly species on the same occasion and 33 species in total. *Rhodobaetis* was present at 59% of the *vernus* sites, *Nigrobaetis niger* at 33%, *Heptagenia sulphurea* at 30%, *Centroptilum luteolum* at 25%, *B. fuscatus* group at 19%, and *Leptophlebia vespertina* and *L. marginata* both at 18%.

The only *B. vernus* group species that *B. vernus* has ever been collected with in Sweden is *B. subalpinus*, present at 8% of the sampling occasions. *B. subalpinus* was also present in the river Krivetz at Kola Peninsula. In Finland, it has been collected with *B. tracheatus* (later renamed *B. jaervii*) in the Jeesiöjoki River (Lkv) (SAVOLAINEN & SAURA 1996).

Larvae have been found in stomachs from brown trout *Salmo trutta*, pike *Esox lucius*, minnow *Phoxinus phoxinus*, burbot *Lota lota*, and perch *Perca fluviatilis* (ENGBLOM 2019b).

4. The nomads *Baetis subalpinus* and *B. vernus*

In northern Fennoscandia, *B. subalpinus* is one of the most abundant mayfly species; scarcely any suitable habitat is left empty, and so it may come as a surprise to learn that *B. subalpinus* is

frequently on the move, with any given generation seldom being the progeny of the previous generation at the same site. This becomes clear at the outskirts of the species distribution where there are few populations, or in cases where rivers have been damaged and subsequently restored.

When a river becomes available for recolonization after restoration, the first mayfly species to arrive is usually *B. subalpinus* or *Rhodobaetis*; eventually *B. vernus* will also arrive, as for the 2 m broad forest brook Prästvallsbäcken (HS) at 61.38°N, 16.39°E. The yearly autumn sample after liming showed that *Leptophlebia marginata* and *L. vespertina*, which until then had been the only two mayfly species in the river, had received company: *B. subalpinus* was present in 1987 and 1988; *B. vernus* in 1989; *Rhodobaetis* in 1990; *B. vernus*, *Rhodobaetis* and *Nigrobaetis niger* in 1991; *Rhodobaetis* and *N. niger* in 1992.

Two km downstream from that site, Prästvallsbäcken was sampled for bottom fauna every month during the years 1987-1992, revealing that *B. subalpinus* was present every autumn but not in the spring. The existence of two generations in this area was demonstrated by samples from the 8 m broad Tolbo River at 61.44°N, 16.36°E, where *B. subalpinus* was present in both spring and autumn in 1994 and in 1995.

In the 3-15 m broad Gunnilbo River, site VS140 (59.48°N, 15.51°E) is the south-eastern outpost for both *B. subalpinus* and *Serratella ignita lactata*. There are seemingly good places even downstream, but for these two species those places are definitely on the wrong side of the climate border. Samples taken every month at VS140 from January 1992 for many subsequent years showed that *B. subalpinus* was present in the spring but never in the autumn; it was present in 1993, 1996, 1998, 2001, and 2003 and has continued to appear every second or third spring ever since. *B. vernus* has also been seen at VS140, but only once in the autumn of 1992.

Obviously *subalpinus* females from the spring generation in the Gunnilbo basin main river lay their eggs in tributaries, and they seem to fly in all directions; upstream, downstream, or perhaps to other river basins. In this source stream area of about 290 km^2, 19 places that *B. subalpinus* can find acceptable have been identified at distances of 4-18 km from VS140. The larvae have a characteristic chestnut brown colour and are therefore easy to recognise in the field. Some of these populations are small enough to be the result of a single female. The number of habitats for the species is larger than the number of populations, which leaves a few habitats empty every spring, but several more habitats empty in the autumn. It is worth asking whether females from the spring generation fly over the forest to find places for their autumn offspring.

In the two rivers parallel to Gunnilbo River, suitable places are sparse. *B. subalpinus* larvae with familiar chestnut-brown colour have been found in the autumn at one site in each of these two rivers, at distances of 30 km and 36 km from VS 140. One might wonder if 30 km is too long a distance for such a small creature, but *B. liebenauae* proved that this and more was possible in the 1980s, when it took only a decade to invade south-west Sweden up to the Hornborga River at 58.17°N, 13.35°E. This is 300 km even if it had travelled in a straight line, which it did not.

However, in August 2016 a different kind of *B. subalpinus* was seen in the canalized part of a small tributary in the Gunnilbo area at 59.45°N, 15.51°E. The lower part of Utterdal Brook is a shallow grassy-bordered ditch of medium current, 1 m broad, and home to *Gammarus pulex*. Upstream the spring water ravine is home to species including *Nigrobaetis niger*. These *B. subalpinus* larvae were not the ordinary chestnut-brown sort, but yellow-brown, and the apical tooth of the left mandible was twice as broad as the second tooth. Such *subalpinus* mandibles are not found

elsewhere in Sweden, so it is unclear from where they originated; Southern Norway is one possibility. Aside from the yellow-brown colour, the reared imagos (21 August) looked like ordinary *B. subalpinus.*

B. subalpinus has specific demands, and potential habitats can be detected on a good map (scale 1:50000). This is not possible for *B. vernus*; its presence is always a surprise, and its absence is just as puzzling. In an attempt to study morphological differences between first and second generation, the spring generation of "little speckled *vernus*" was reared from a forest stream (VS), but in the autumn it was found to have been replaced by an abundant population of "big yellow *vernus*". In other seasons there have been no *B. vernus* at all in this stream.

5. How to separate *Baetis subalpinus* from *B. vernus*

When the left mandible apical tooth is not more than twice as broad as the second tooth, and the body shape and labial palp of the larva suggest it belongs to the *vernus* group, take a look at the dorsal side, and examine the …

1. … thorax. Is there a thick light V just above the forewing pads (Fig. 3)? If so, then this is *subalpinus.*

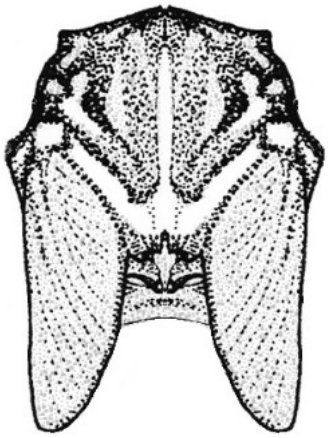

Figure 3. Thorax of *Baetis subalpinus* with a thick light V.

Figure 3. Thorax de *Baetis subalpinus* avec un épais motif en forme de V clair

If the larva is small or very pale, or the wing pads are black, the V can be difficult to discern. In this case, it might be *vernus,* so take a look at the …

2. … gills. Are they short; is the third gill at most 1.6 times as long as it is broad? Does it look as if the larva has borrowed its gills from a younger sibling? If so, then this is *subalpinus* (or *buceratus* if you did not check the labial palp). If the larva has no gills, it can still be *vernus*, so check the …

3. … frons. Is it clearly rounder than in *Rhodobaetis*, for example? If so, then this is *subalpinus* (or *buceratus* if you did not check the labial palp). However, examining the frons is difficult, so to be sure it is not *vernus* take a look at high magnitude at the …

4. … terga. There are small conical denticles scattered over the surface. Is the distance between these denticles at least the width of 2–3 denticles? If so, then this is *subalpinus*. If the distance is more like 1–2 denticles, this is *vernus*. Unfortunately the inter-denticle distance in *buceratus* is in

between the distances for *subalpinus* and for *vernus*, but since *subalpinus* usually has the light V and *buceratus* a different labial palp, this is a minor problem.

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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 are taken from Google Earth; http://earth.google.com

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