

Contribution to the understanding of the Fennoscandian *Baetis vernus* group: species with long gills [Ephemeroptera]

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This paper attempts to explain the status of the Fennoscandian species of the *Baetis vernus* group based on a substantial Swedish material. Several studies concerning the *Baetis vernus* group from Finland have been published during the last decade by Savolainen et al., necessitating a new description and distribution of the closely related and often confused *B. macani* Kimmins, 1957 and *B. bundyae* Lehmkuhl, 1973. *B. macani* and *B. bundyae* are considered well established species in Fennoscandia, occurring in both lakes and rivers. In Sweden *Baetis tracheatus* Keffermüller & Machel, 1967 is considered late immigrant, while the long gilled *Baetis vernus* might be an endemic variant. *Baetis jaervii* Savolainen, 2009 is not a member of the Swedish fauna.

Contribution à la compréhension du groupe finno-scandinave *Baetis vernus* : espèces à longues branchies [Ephemeroptera]

Mots-clés : Ephemeroptera, écologie, morphologie, distribution, *B. macani*, *B. bundyae*, *B. tracheatus*, *B. vernus*, *B. jaervii*, Finno-Scandinavie.

Cet article tente d'expliquer le statut des espèces Finno-scandinaves du groupe *Baetis vernus* sur la base d'un important matériel de Suède. Plusieurs études concernant le groupe *B. vernus* en Finlande ont été publiées durant la dernière décennie par Savolainen et al., rendant nécessaire de nouvelles description et distribution des espèces très proches et souvent confondues : *B. macani* Kimmins, 1957 et *B. bundyae* Lehmkuhl, 1973. *B. macani* and *B. bundyae* sont considérées comme bien établies en Finno-Scandinavie, se trouvant à la fois dans les lacs et les rivières. En Suède, l'espèce *B. tracheatus* Keffermüller & Machel, 1967 est tenue pour immigrante tardive, tandis que *B. vernus* aux longues branchies pourrait être une variation endémique. *B. jaervii* Savolainen, 2009 n'est pas connue de la faune de Suède.

1. Introduction

In the 1970s when Pär-Erik Lingdell collected mayflies in Sweden, he had the impression that there were two different forms of *Baetis macani*. In 1975 he sent larvae from Vallentuna Lake close to Stockholm to Ingrid Müller-Liebenau. He received the reply that there was only one *macani* in Scandinavia. In 1978 Lingdell also sent larvae collected in southern Greenland to Müller-Liebenau. This time he received the reply that they were probably a North American subspecies

of *Baetis macani*, and she sent the larvae on to Canada where it was confirmed as *Baetis macani bundyae*.

Some 15 years later Lingdell and Engblom, Limnodata HB, had thousands of computerized bottom fauna samples. At this time it appeared necessary to revise the “*macani*” material, because when Lingdell made computer plots for different associated chemical, hydrological, geological or biological parameters, the records for this “species” split up in two clusters, along with several outliers, while most other species gave one single cluster.

After removing errors in the database, three different clusters of “*macani*” became apparent. The most abundant “*macani*” from the Norwegian-Swedish Mountains, was found to be identical with the species collected on Greenland verified as *bundyae*. Consequently the other “*macani*”, verified as *macani* by Müller-Liebenau, was likely to be the true *Baetis macani*. The third “*macani*” cluster turned out to be a variation of *B. vernus*.

2. The background story of the two *macani*

SOLDÁN (1981) remarked that “some adults of *B. tenax* recorded from Utsjoki by TIENSUU (1939) might in fact belong to the closely related species, *B. macani*”, or rather *B. bundyae*. In earlier studies, what BENGTTSSON (e.g. 1912) and BREKKE (1938) called *tenax* is often likely, if not always, to be *bundyae*. However, outside Fennoscandia, from forceps figures in older literature it seems that *tenax* is usually *vernus*.

In 1943 ULMER described larvae, collected 1936-39 by Thienemann in the Abisko area in Swedish Torne Lapland (TO). Although they were named *vernus*, this is the most detailed description of *bundyae* ever done.

In 1957 KIMMINS described imagines of the new species *Baetis macani*, collected by Macan, from a lake on the mountain Saana, 800 m a.s.l., close to Kilpisjärvi in Northern Finland (Le) (at about 69.03°N, 20.52°E). Later on in 1957, MACAN described the larvae of the same species from the exuvia from Saana and larvae from Heinola in Southern Finland and Erken in Sweden. Erken (UP) is a lake 11 m a.s.l. surrounded by arable land and pasture for cows, located at 59.50°N, 18.38°E.

In 1973, LEHMKUHL described larvae of a new species, *Baetis bundyae*, from Canada, that “keys to *Baetis pavidus* in the European *Baetis* by MÜLLER-LIEBENAU (1969).” He referred to the couplet; “denticles along hind margin of abdominal tergites very short” or “longer”. The same is true for Scandinavian *bundyae* larvae, denticles at the posterior margin of the terga (Fig. 3B1) are pointed and identical to fig. 6 in LEHMKUHL (1973), although sometimes the denticles are blunt (Fig. 3B2) and then have a striking resemblance to Abb. 41 *pavidus* in MÜLLER-LIEBENAU (1969). On the contrary denticles from Swedish *macani* (Fig. 3M) correspond best to Abb. 73 *macani* in MÜLLER-LIEBENAU (1969).

Being familiar with the Brinck and Ulfstrand collections (partly in Limnodata HB collection) used in MÜLLER-LIEBENAU (1969), the large material she based her description on consisted of at mostly *bundyae*; although *macani* dominated in text and figures of larval mandibles, labial palps and tergite denticles, as well as adult male forceps and eyes. Most other features in this description are identical for both species; including what LEHMKUHL (1973) noticed about hairs and spines on

the legs and the fact that the small hairs on the tips of the claws are missing. *B. bundyae* in MÜLLER-LIEBENAU (1969) describes maximum gill-size and minimum body-size of 5 mm for both larvae and adults.

In 1979, MORIHARA & MCCAFFERTY described the imago male of *B. bundyae* from Canada, and compared the male with paratype *B. macani* male from Saana. They found no significant difference except for the eyes, since unfortunately they did not examine the legs. Then they compared *bundyae* larvae with Swedish larvae of true *macani* from the northern taiga, and found clear differences in the mouthparts, especially in the mandibles. In consequence they separated *macani* into two subspecies, the North American *B. macani bundyae* and the European *B. macani macani*.

As a result of *B. macani* and *B. bundyae* in ENGBLOM (1996) many vials of larvae were received from the mountain chain that forms the border between Norway and Sweden. All these specimens were allocated to *bundyae*. However, no vials were received from Finland. Long before the electrophoresis study in 2007, Savolainen et al. were apparently convinced that I had split up “*macani*” into two groups according to water velocity, as SAVOLAINEN & SAARISTO did in 1981. This must be the reason for the repeated sentence in, for example, STÄHLS & SAVOLAINEN (2008); “In her review of northern European mayflies, ENGBLOM (1996) called the form with broader gills in lentic waters, recognized by SAVOLAINEN & SAARISTO (1981), *B. macani* Kimmins, while she called the form with narrow gills and invisible tracheae living in lotic waters *B. bundyae* Lehmkuhl, 1973”.

From the coordinates Savolainen et al. were offered from Limnoda HB database in 1998, they studied larvae from one Swedish *macani* site, Bastuträsk at 64.47°N, 20.01°E, but not from a single *bundyae* site in either Norway or Sweden. “The Bastuträsk sample from central Sweden also differed from the northern Finnish ones far more than the Kallavesi population from central Finland did” (SAVOLAINEN et al. 2007). In 2014 the Kallavesi larvae were named *jaervii*, and three of the “northern Finnish ones”, from Paskalomaoja and Kaunispäänoja, were with molecular methods identified as *Baetis bundyae* (see SAVOLAINEN et al. 2014).

In 2009 SAVOLAINEN described the new species *Baetis jaervii* and also declared what in ENGBLOM (1996) was called *bundyae* to be *macani* Kimmins, 1957, and what was called *macani* and *tracheatus* to be *B. jaervii*. This statement is repeated in SAVOLAINEN et al. (2014).

3. Long gills

In the Swedish material, large gills rich in trachea indicate an ability to cope with pollution and low oxygenation, and are only to a certain degree result of low water velocity as suggested by SAVOLAINEN et al. (2007).

In Sweden *B. vernus* is found exclusively in running waters. The “ordinary” *vernus* with short gills favours clear forest streams while the long-gilled variation (Fig. 4V) is only found in slow running, muddy waters. Wastewater tolerant *vernus* larvae with long gills are also known from Germany (HAYBACH 1998).

The only lake with *B. tracheatus* in Sweden, Turingen (SÖ) at 59.13°N, 17.27°E, is polluted and mercury concentrations are high as a result of earlier industrial activities. Fig. 4 illustrates the third gill on the right side from four long-gilled species; Fig. 4T is the third gill of *tracheatus* from Jeesiöjoki in Finland.

White gills without or with barely visible trachea are characteristic for tundra species such as *Acentrella lapponica*. The white gilled *B. bundyae* (Fig. 4B) require clean water. Conductivity, measured on sampling ranges from 8 to 335 $\mu\text{S}/\text{cm}$ and mean 38 $\mu\text{S}/\text{cm}$. *Baetis macani* (Fig. 4M) with gills rich in brown coloured trachea occurs in more turbid habitats; 22-634 $\mu\text{S}/\text{cm}$ and mean 144 $\mu\text{S}/\text{cm}$. It should be noted that gill-colour may change with fixation. Gills of *Baetis macani* that have spent some years in ethanol often turn partly or even entirely white, and then the only visible trachea may be a purple mid-trachea. Sometimes the northern *macani* have white gills after only short time in alcohol, and perhaps even when still alive, as is the case with *Parameletus* spp. that have either white or hyaline gills.

4. “Long-gilled *Baetis vernus*”

Larvae of “long-gilled *vernus*” have been identified from three streams in central Sweden; Alby (SÖ), Lillån (UP) and Sorkan (VR). The streams are up to four meters wide with a clay bottom, muddy and slow running and surrounded by arable land and pasture. They are situated at similar latitudes between 59.14°N and 59.46°N at altitudes 15-45 m a.s.l., with a distance between the eastern and western sites of 244 km. At Alby, a suburb of Stockholm, the bottom substrate consisted largely of snails, such as the in Sweden rare *Physella acuta*.

These nymphs are 7-9 mm long, and the third gill is twice as long as broad, hyaline and with distinct trachea (Fig. 4V). The left mandible has its apical tooth 1.5 times as broad as the second tooth, and all other features are also identical to “ordinary” Swedish *Baetis vernus*: the denticles on the posterior margin of the terga are small and pointed (Fig. 3V), and the antenna and caudal filaments are considerably shorter than in either *Baetis bundyae* or *B. macani*.

From Alby nymphs were reared, while at the other two sites there were flying adults during sampling in early June and early September. The male forceps can be distinguished from “little speckled *vernus*” (ENGBLOM 1996, fig. 211a), but not from “large yellow *vernus*” (ENGBLOM op. cit., fig. 211b).

5. Larvae of *Baetis tracheatus* Keffermüller & Machel and *B. jaervii* Savolainen

Baetis tracheatus Keffermüller & Machel, 1967 seems to be a recent immigrant, and therefore not expected to be found in older material or literature. It was collected for the first time in the river, Jeesiöjoki, in Finland in 1994 (SAVOLAINEN & SAURA 1996) and in the lake Turingen, in Sweden in 1996 (LINGDELL et al. 1996). In 2009 the Finnish material identified as *tracheatus* was renamed as *Baetis jaervii*, and at that time was recorded from a further three lakes in Finland (SAVOLAINEN 2009).

According to SAVOLAINEN (2009) *B. jaervii* and *B. tracheatus* differ in their habitats; *B. jaervii* lives in “standing water”, although Savolainen earlier recorded this species from a “slowly-moderately” running part of the river Jeesiöjoki, *B. tracheatus* lives in “flowing water”, but appearing to neglect both the Swedish lake and the lake Piskie, in Poland (SOWA 1962).

From description of the *B. jaervii* nymph in SAVOLAINEN (2009), the apical tooth of the mandible is “up to 3 x or more broad than the second tooth”, and measured at the photo (fig. 1) nearly

6 times. This size span includes all *vernus* group species, and in consequence the mandibles at figs 40a *macani* and 40b *tracheatus* in ENGBLOM (1996) are both said to belong to *jaervii*, as well as fig. 2 in MORIHARA & MCCAFFERTY (1979) and Abb. 76b in MÜLLER-LIEBENAU (1969).

The main character SAVOLAINEN (2009) used to separate *jaervii* from *tracheatus* is the number of long setae just behind the anterior edge of the labrum; 1+4 or more for *jaervii* contra 1+2-3 for *tracheatus* as in MÜLLER-LIEBENAU (1969, Abb. 83a). 1+2-3 is a common configuration for the *vernus* group (*macani* and *subalpinus*), and as well for the *tracheatus* specimens from the Swedish lake Turingen (and fig. 1 in KEFFERMÜLLER & MACHEL 1967). *B. vernus* may have up to 8 long setae, while *bundyae* only has 1+1-2. The only *vernus* group species with long gills in Sweden that has more than 1+3 long setae is *B. vernus*.

However, there are other characters to consider, such as the rounded frons (Fig. 2T) similar to *subalpinus* females, and denticles on the posterior margin of the terga, which on the larvae from Turingen are larger and more acutely pointed than for *macani*, and corresponding to Abb. 84 *tracheatus* in MÜLLER-LIEBENAU (1969).

6. *Baetis bundyae* Lehmkuhl

Imago

Ephemera bioculata Ström, 1783 Norway (= *tenax* sensu BENGTTSSON 1912)

Ephemera culciformis Zetterstedt, 1840 Greenland (= *tenax* sensu BENGTTSSON 1912)

Baetis tenax Eaton, 1870 (TIENSUU 1939 Finland, BREKKE 1938 Norway)

Baetis macani bundyae Lehmkuhl, 1973 (MORIHARA & MCCAFFERTY 1979 Canada)

Baetis bundyae Lehmkuhl, 1973 (MCCAFFERTY 1994 Alaska, ENGBLOM 1996 Sweden-Norway)

Larva

Baetis vernus Curtis, 1834 (ULMER 1943 Sweden, BAGGE 1965 Finland)

Baetis macani Kimmins, 1957 (MÜLLER-LIEBENAU 1969 in part Sweden, BRITAIN 1974-1980 Norway, SVENSSON 1986 Sweden, ARNEKLEIV 1995 Norway)

Baetis macani bundyae Lehmkuhl, 1973 (MORIHARA & MCCAFFERTY 1979 Canada)

Baetis bundyae Lehmkuhl, 1973 Canada (MCCAFFERTY 1994 Alaska, ENGBLOM 1996 Sweden-Norway, SAVOLAINEN et al. 2014 Finland)

What Zetterstedt called *culciformis* from Greenland in 1840, is not necessarily the *culciformis* Linnéus had in mind in 1746. However, it is possible that Linnéus came across this rather common species during his journey to Lapland in 1732. From the sparse description of an imago male with black thorax (STRÖM 1783), *bioculata* seems to me as the most plausible name for the Holarctic *macani*.

Distribution and material

According to SAVOLAINEN (2014) trans-Atlantic dispersal seems unlikely for insects and JACOB (1997) stated that in northern Europe “all species (of mayflies) are immigrants, because during the Ice Age Fennoscandia was completely glaciated.” However, there is evidence that a number of species, possibly including *bundyae*, survived in northern Norway. COBB & FLANAGAN (1980)

mention *Acentrella lapponica* and *Baetis macani bundyae* as examples of species that dispersed via a North Atlantic route before continental drift separated Europe and North America.

Baetis bundyae inhabits Alaska (e.g. HARPER & HARPER 1981, RANDOLPH & MCCAFFERTY 2005), Canada (e.g. HARPER & HARPER 1997, GIBERSON et al. 2007), Greenland, Scandinavia and the Kola Peninsula (Limnodata HB) and Finland (SAVOLAINEN et al. 2014).

On Greenland in July 1978, Lingdell and Engblom collected hundreds of larvae in a brook 2 km W from Brattalid at 61.09°N, 45.33°W.

Figures of mouthparts and gills in ESBEN-PETERSEN (1916) from Siberian larvae collected at the Talota, Pyderata and Stschutschja Rivers on the tundra of Kara show some sort of “*macani*” that is possibly *bundyae*.

The *Baetis macani* in NOVIKOVA & KLUGE (1997) said to be sensitive to pollution and common in tundra lakes with clear water in Northern West Siberia, in Tumen Province at 60-68°N and 70-78°E, is most likely *bundyae*. The same species is as well found in the Lena delta at about 72°N and 127°E.

On the Kola Peninsula, 68.17°N, 36.17°E, Jan Åslund collected in 1998 (4 August), 13 immature 4-5 mm long female larvae of *B. bundyae* from a small tributary of the Kharlovka River that flows into the Barents Sea. The sparse fauna harboured no other mayfly species.

In Norway, *Baetis bundyae* (listed as *macani*) has been recorded in Telemark (TE), Hordaland (HO), Opland (O), Hedmak (HE), Sør-Trøndelag (ST), Nord-Trøndelag (NT), Nordland (NO), Troms (TR) and Finnmark (F) (BRITAIN 1999). The majority or perhaps all of Norwegian “*macani*” in the literature (e.g. BRITAIN 1974, 1975, 1978, 1979 and 1980 and KJÆRSTADT et al. 2012) are likely to be *bundyae*. In Norway the mountains extend far south and the species occurs to 59.45°N (BRITAIN 1975).

In Saskatchewan, Canada, *B. bundyae* is found as far south as 56.99°N (WEBB et al. 2004).

In Finland, the presence of *B. bundyae* was established from two brooks using DNA; Inari Kaunisäänoja 68.26°N, 27.24°E and Savukoski Paskalomaaja 67.52°N, 28.10°E (Ks) (SAVOLAINEN et al. 2014). On the same day in 1997 (5 August), Savolainen visited Paskalomaaja and also collected larvae in Karijoesta and in Savukoski Parakainen (sample number 4 *macani* in SAVOLAINEN et al. 2007). A few of these larvae were identified by me in April 1998 as *bundyae*. Furthermore, in 1963 Bagge collected what he called *vernus* in a small lake near Utsjoki church (Li) at 69.45°N, that from drawings of mandibles, labrum and gills in fig. 1 (BAGGE 1965) were definitely *bundyae*.

In Sweden there are 168 records of *B. bundyae* (Limnodata HB; species distribution in Table 1 in ENGBLOM 2003) at altitudes of mainly 210-1125 m a.s.l., mostly from the tundra and a few from the taiga, down to 60.53°N.

Limnodata HB stores most of the material from the Kaltisjokk-Messaure projects (LU), led by Professor Karl Müller in 1966-67. The “*Baetis macani*” in THOMAS (1970), is likely to be *bundyae*, but is not present in the preserved material.

Identification larvae

The nymphs are uniformly coloured, in general 6-8.5 mm long, and with the third gill 2.6-2.8 times as long as broad. Gills are milky white, parallel sided, and with no or barely visible trachea (Fig. 4B). The shape of the third gill resembles more the third gill in *Nigrobaetis* than in any other Baetidae species. The anterior surface of head capsule resembles *vernus*, but with rounder lateral

areas below the eyes (Fig. 2B). The apical tooth of the left mandible is as broad as the second tooth. Setae on the labrum are 1+1-2 long and a few small, as fig. 1 in BAGGE (1965). The terminal segment of the labial palp is longer than in *B. macani*, and the angle between the protrusion on the sub terminal segment is slightly acute or about 90° (Fig. 1B). Denticles on posterior margin of terga are short and pointed (fig. 6 LEHMKUHL 1973 and Fig. 3B1), although sometimes blunt (Fig. 3B2). Caudal filaments are very long, $\frac{3}{4}$ of the body length, with terminal filament markedly shorter as in *B. macani*, unlike the related Nearctic *B. hudsonicus* (IDE 1937), or the other Fennoscandian species in *vernus* group (*vernus*, *subalpinus*, *tracheatus*, *liebenauae*), with all three filaments subequal in length.

In Canada nymphs are only 5-6.5 mm long on the tundra, while in ponds with warmer and more nutrient waters at Rankin Inlet the nymphs are 6.5-7.5 mm long (GIBERSON et al. 2007). The slightly larger Scandinavian nymphs might be due to the temperate Gulf Stream and/or that the habitats often have filamentous algae. The largest Swedish nymphs from a lake at 600 m a.s.l. in Pieljekaise National Park (PI) (66.17° N, 16.52°E) were up to 9.5 mm long, with the third gill four times as long as it is broad. This lake had plenty of a very rare variation of *Nostoc*, and perhaps this alga is the reason for the nymphs reaching this unique size. The smallest nymphs, with males only 5.5 mm long were collected by Johan Hammar 1988 (2 August) in Bajip Snarapjauri, a lake with no visible algae at 1034 m a.s.l. in the Kebnekaise (TO).

GIBERSON et al. (2007) noticed that larvae in Nunavut could be separated into three groups on their body-shape; narrow, medium or wide. They also found populations without males. In Scandinavia larvae of *bundyae* are narrow to medium, while *macani* are narrow to wide; both species are sometimes slimmer than any other *Baetis*. In Sweden there are usually two females per male in *Baetis* and there is no reason to suspect a different ratio for *bundyae*. On the contrary, on Greenland no males were collected in 1979, and older adult records are only females (ZETTERSTEDT 1840, MOSELY 1929).

“*B. macani*” in larval keys by SVENSSON (1986) for Sweden and ARNEKLEIV (1995) for Norway are both illustrated with *bundyae* gills, while in Finland KUUSELA (1993) chose Abb. 70 from MÜLLER-LIEBENAU (1969), that correspond best with *macani* from southern Sweden.

Identification subimago and imago

Males of *B. bundyae* are distinguished from *B. macani* by legs, eyes and forceps, and females by legs, dots and lines on sterna and egg size (ENGBLOM 1996). Legs and turbinate eyes are discussed under “Identification subimago and imago” for *Baetis macani*. The preserved adult *bundyae* material in Limnodata HB collection has long since bleached, but there is a colour description of the male imago in MORIHARA & MCCAFFERTY (1979).

Ecology

In Sweden, as in Norway (BRITAIN 1975), *B. bundyae* spend the winter as eggs and there is a single generation per year. The larval stage last for about 4 weeks, though larvae can be found during an 8-10 week period. From mid-June larvae are present in the southern part of the distribution area, with adults emerging during August and early September, although further north in Sweden there are adults in July-August. In Canada with a harsher climate than in Europe, the larval stage can be as short as 2.5 weeks (GIBERSON et al. 2007).

The distribution of *Baetis bundyae* in Sweden is similar to those of other Holarctic species like *Metretopus alter*, *Parameletus chelififer*, *Acentrella lapponica*, *Ephemerella aurivillii* and *E. mucronata*.

On the Swedish tundra *B. bundyae* larvae inhabit small lakes and ponds (28% of the records), or streams up to 4 m wide (72%), many times just upstream lakes or large rivers. They are rarely found in large rivers. Close to the limits of their distributional area, at low altitudes in the taiga, the species is restricted to fast running and/or cool streams.

Vargbäcken (VB) (64.25°N 19.30°E) is a small, cool stream outside the species ordinary distribution, and at an altitude of only 160 m a.s.l. In warm summers the temperature may reach 14°C and it may even dry out then. In the winter the stream is covered with ice for at least five months, and partly frozen solid to the bottom (JOHANSSON & NILSSON 1994). This study is evidence that the eggs of *bundyae*, larger than for any other European *Baetis* (0.25-0.27 mm), can remain frozen during a major part of the winter. In contrast, this may not be the case with *B. macani*, whose eggs are of ordinary size (0.15 mm). The measured egg size, 0.25 mm long and “larger than for *B. vernus*” in BRITAIN (1975) is striking evidence that the “*macani*” from Finse, Norway, at 60.36°N, 7.30°E is really *Baetis bundyae*.

However, *B. bundyae* can endure relatively high water temperatures in the Arctic territories, and ponds in Rankin Inlet, Canada can reach 23°C (GIBERSON et al. 2007). In Scandinavia 17°C in the Norwegian river Gravelva close to the Sulitelma copper mine (67.10°N, 15.50°E), and 18.5°C in a small pond 934 m a.s.l. on a mountain plateau in Sweden (HR), have been recorded. This latter pond had no visible algae and no other mayflies.

B. bundyae is the sole mayfly species in about a quarter of the waters they inhabit, but has been recorded coexisting with 10 other mayfly species, and has in total been collected together with 28 mayfly species. The most abundant are *Rhodobaetis* 39%, *Siphonurus lacustris* 31%, *Baetis subalpinus* 30%, *Ameletus (alpinus)* 28%, *Acentrella lapponica* 23%, *Ephemerella aurivillii* 23%, and *Heptagenia dalecarlica* 14%. In Canada *Parameletus chelififer* is not uncommon together with *bundyae* (GIBERSON et al. 2007), but in Sweden in only 4% of the habitats. It is notable that *bundyae* was collected 3 times with *Heptagenia orbiticola* known from 15 localities in Sweden, and 3 times with *Paraleptophlebia weneri* known only from 8 localities. Species never recorded with *B. bundyae* are *Caenis* spp., and they have only once been collected with *Ephemerella*.

Baetis is in general very important as fish food, but *bundyae* is not a preferred item, due to the short larval stage. In a small lake in southern Norway at 1090 m a.s.l. it constituted 1.3 % of Ephemeroptera consumed by brown trout (*Salmo trutta*) over the year (BRITAIN & LIEN 1978). BAGGE (1965) found mandibles and gills in stomachs of grayling (*Thymallus thymallus*) and brown trout from a lake east of Utsjoki in Finland. In Sweden, out of more than 1000 examined stomachs from assorted fishes, one single larva was found in a 17 mm long bullhead *Cottus gobius* (pers. obs).

7. *Baetis macani* Kimmins

Imago

Baetis n. sp. Bengtsson 1907-1914 Sweden (= *macani* sensu MÜLLER-LIEBENAU 1965)

Baetis saliens Tiensuu, 1939 Karelia = NOT *B. subalpinus* Bengtsson, 1917

Baetis macani Kimmins, 1957 Finland (MÜLLER-LIEBENAU 1969 Sweden, MÜLLER-LIEBENAU & SAVOLAINEN 1975 Finland, ENGBLOM 1996 Sweden)

Baetis macani macani Kimmins, 1957 (MORIHARA & McCAFFERTY 1979 Finland)

Larva

Baetis n. sp. Bengtsson, 1907-1914 Sweden (= *macani* sensu MÜLLER-LIEBENAU 1965)

Baetis macani Kimmins, 1957 (MACAN 1957 Finland-Sweden, MÜLLER-LIEBENAU 1969 Sweden, SAVOLAINEN & SAARISTO 1981 (lentic and lotic forms) Finland, JENSEN 1984 Denmark, KUUSELA 1993 Finland, ENGBLOM 1996 Sweden-Norway, SAVOLAINEN & al 2014 Finland)

B. macani macani Kimmins, 1957 (MORIHARA & McCAFFERTY 1979 Sweden)

From the pinned and dried male type, and referring to fig. 8 (TIENSUU 1939), MÜLLER-LIEBENAU (1969) assigned *Baetis saliens* to *Baetis subalpinus* Bengtsson, 1917.

BAUERNFEIND & SOLDÁN (2012: 134), state that *B. subalpinus* is frequent in still water habitats (pools and oligotrophic lakes). The 2419 records of *B. subalpinus* in Limnodata HB database are exclusively from running waters, and the only record from lakes is for *B. saliens*.

From the description of *B. saliens* in TIENSUU (1939: 112-113), the hind-wing third vein is half as long as the wing, not 1/3 as in *B. subalpinus*. He also compared the larvae found in two lakes to *Centroptilum*, and as Tiensuu was the first to identify *B. subalpinus* from Norway in 1937 and Finland in 1939, I consider *Baetis saliens* Tiensuu, 1939 to be the correct name for *B. macani* Kimmins, 1957.

Distribution and material

Baetis macani is mainly a Fennoscandian species, but is also recorded from Hancza-See Poland, its southern limit in Europe at 54.15°N (HAYBACH 1998). In Denmark *B. macani* has been reported in South Jutland (SJ), West Jutland (WJ) and Jylland (J) (JENSEN 1984). However, the species is now regarded as extinct in Denmark (JENSEN 1998). What earlier was called *B. macani* in Schleswig-Holstein in Germany is now assigned to *B. tracheatus* (HAYBACH & MALZACHER 2002). The hitherto only record from Norway was collected by “Laxvattnet” (Laksåvatnet? 63.28°N, 8.41°E?) on the island Hitra in Sør-Trøndelag (ST) (Limnodata HB; collected by Allan Arvidsson 17 June 1977). In Finland *B. macani* is widespread between 62.52°N and 69.47°N (SAVOLAINEN et al. 2014). SAVOLAINEN (2009b) gave distribution maps for *Baetis macani* and *Baetis jaervii*.

In Sweden (Limnodata HB; species distribution in Table 1 in ENGBLOM 2003) there are 53 records at altitudes of 0.5-385 m a.s.l. in lowland and forest areas, in addition to a single record from a lake above the treeline, Salamasjärvi at 68.11°N, 21.48°E.

The collection of Björn Nagell, among the non-computerized material at Limnodata HB, includes *B. macani*, larvae and adults, from the surroundings of Uppsala University (UP).

Simon Bengtsson's unpublished *Baetis n. sp.* 1907, 1909 and 1914 from (HS), (JÄ) and Lapland (MÜLLER-LIEBENAU 1965 and 1969), is at least partly *B. macani*. HS is outside the distribution area for *B. bundyae* and moreover Bengtsson knew this species as *Baetis tenax*.

Identification larvae

Nymphs are 7-9 mm long and uniformly coloured. The third gill is 2.4-2.6 times as long as broad, hyaline drop-shaped with convex sides and distinct brown trachea (Fig. 4M). The anterior surface of the head capsule like *vernus* (2V), or more triangular (2M). The apical tooth of the left mandible is twice as broad as the second tooth. Setae on labrum like Abb. 76 in MÜLLER-

LIEBENAU (1969), i.e. 1+2-3 long +2-3 short. The labial palp has an acute angle between the terminal segment and the protrusion on the sub terminal segment (Fig. 1M). Denticles at posterior margin of terga are all large, triangular and pointed (Fig. 3M). I have never observed bidentate denticles as mentioned in BAUERNFEIND & SOLDÁN (2012).

The adults of *B. macani* always look identical, while the larvae in Sweden can be separated into four morphological groups:

1. *Extreme B. macani*; the largest nymphs of this species in Sweden, up to 9 mm long, with the largest gills and an unique triangular “face” (head capsule), found in the muddy river Nossan (VG) at 58.21°N, 12.38°E (Fig. 2M and 4Mb).

2. *Southern B. macani*; with *vernus*-type “faces” and shorter gills like Abb. 70 in MÜLLER-LIEBENAU (1969) or fig. 2 in JENSEN (1984), recorded from the southern part of Sweden (SM) and (SK).

3. *Standard B. macani*; with slightly triangular “faces” (2V), is found in lakes and rivers in central Sweden (SÖ), (UP), (NÄ), (GÄ), and on the island Hitra off the Norwegian coast.

4. *Northern B. macani*; with *vernus*-type “faces”, in lakes and rivers from about 63°N in (HS), (VB), (NB), (ÅS), (LU), and in (TO) only found in four lakes. The general appearance and size of larvae is very similar to that of *B. bundyae* except for the mandibles, the tergite denticles (Fig. 3M), and the hyaline gills (4Ma) resembling fig. 2 in MACAN (1957), i.e. not parallel sided. The two examined *Baetis macani macani* larvae from Siluluoberl and Koskats (LU), at 66.28°N, 20.18°E in MORIHARA & MCCAFFERTY (1979) belong to this form, as well as the “cryptic undescribed larvae lenitic” from the Swedish lake Bastuträsk (VB) (number 51 SAVOLAINEN et al. 2007). That lake is a representative habitat of the Northern *B. macani*, with e.g. *Utricularia*, *Potamogeton* and *Caenis horaria*.

Identification subimago and imago

Leg measurements are the most powerful method to distinguish *B. macani*, both subimago and imago, from other species of the *Baetis vernus* group; that is valid for all legs except male imago front legs. For *macani* the tibia is as long as or shorter than the femur, the tars is as long as half the femur and the first tarsal segment is about equal to the second segment (fig. 230 in ENGBLOM 1996). For *bundyae*, *vernus* and *subalpinus* the tibia is longer than the femur, the tarsus is shorter than half the femur and the first tarsal segment, especially for females, is clearly longer than the second segment (fig. 229 in ENGBLOM 1996).

Larvae with abdominal tergum uniquely grey with a median longitudinal white streak were collected from lake Hjälmarén (NÄ) at 59.15°N, 15.25°E in 2003 (2 September). Rearing as described below, showed these specimens to be ordinary *Baetis macani*.

Subimago

Turbinate eyes: base brown-yellow, top dull orange. Compound eye yellow. Antenna brown-grey. Thorax beige and white with brown lines. Legs: femur yellowish white, tibia pale greyish, tars grey. Body beige-white. Cerci pale greyish. Females are like the male, but femur on the first leg more yellow and thorax lighter, body segment 2-6 dorsally dark yellow. For both sexes, except dark lines on thorax, the feet are the darkest parts. The subimago stage lasted for about 12 hours.

Imago female

Thorax apricot. Legs light yellowish. Femur on first leg yellow-orange. Body yellow. Eggs 0.15 mm long. Forewing 7.5 mm. Cerci 9-10 mm. (In KOPELKE & MÜLLER-LIEBENAU (1981) the egg size is only 0.12 mm).

Imago male

Turbinate eyes from the base and up brilliant light yellow, a line of orange-brown, a line of grey-yellow, edge brilliant light yellow, top side brownish orange. Compound eye yellow. Thorax beige, light brown, darker brown, yellow and white. Legs yellowish white. Body dorsal: segment 1 brown, segment 2-6 white scattered with a little beige, segment 7-9 yellow-brown, segment 10 yellow. Body ventral: segment 2-6 white, segment 7-9 light beige-yellow. Cerci white with a yellow-brown ring at the base. Forceps white. Segment 3 slightly longer than it is broad. Forewing 7.0-7.2 mm. Cerci 13 mm.

Imago males of *B. macani*, compared to *B. bundyae* in ENGBLOM (1996, fig. 210) have a shorter segment three in the forceps, corresponding to Abb.75 in MÜLLER-LIEBENAU (1969) and fig. 2 in KIMMINS (1957), and similar to figure 14b in JACOB (2003). The illustrated segment three in the *jaervii* forceps (SAVOLAINEN 2009, fig. 2) is in between *macani* and *bundyae*, besides the bulbous inner margin of first segment has a striking likeness to *tracheatus* (e.g. fig. 1 in MOOL 1985).

Seen from above the eyes of *B. macani* imago males are evenly oval. Compared to Abb. 66 in MÜLLER-LIEBENAU (1969) Swedish subimago males have top side of turbinate eye with same proportions, 32 x 43 mm, and imago males 2 mm longer. *B. vernus* and *bundyae* with eyes slightly flattened on the inner side, are in between Abb. 65 and Abb. 66. No Swedish *vernus* have eyes as oblong as Abb. 65, or "twice as long as broad" (JACOB 2003).

In lateral view the turbinate eyes of *B. bundyae* and *B. vernus* from Sweden are almost identical, while the eyes of *B. macani* are slightly depressed. Adult *bundyae* males from Norwegian-Swedish Mountains have eyes similar to the Canadian male imago fig. 2 in MORIHARA & MCCAFFERTY (1979) and males of Swedish *macani* have eyes resembling of the male from the Finnish Saana (fig. 1 in both MORIHARA & MCCAFFERTY (1979) and KIMMINS (1957)).

Ecology

In Sweden, *B. macani* spend the winter as eggs, and hatching occurs over a 4-6 week period. In the southern half of its distribution, larvae have been collected in May-June and in August-September. There are two generations a year, and in the Vallentuna lake (UP) at 59.30°N, 18.03°E (Lingdell, pers. comm.) at least in one year a third generation. In the north, there is a single generation per year with larvae in July and adults in August.

The species is found in lakes (48% of the records), medium to large, or in deep slow running or fast streams which are at least 3 m wide (52%). The water can be rich in sediment or muddy, nutrient-rich and rather polluted.

B. macani dwell close to the surface in submerged vegetation such as *Potamogeton* spp., *Myriophyllum* spp. or *Menyanthes trifoliatum*. In 12% of the records it was the only mayfly species, there have been up to 7 other mayfly species on the same occasion and in total 24 different mayfly species: *Caenis horaria* 46%, *Caenis luctuosa* 28%, *Centroptilum luteolum* 28%, *Ephemera vulgata* 26%, and *Baetis fuscatus*-group 16%. In 71% of the *B. macani* localities *Caenis* and/or *Ephemera* was present.

8. How to distinguish larvae of the long-gilled species

SAVOLAINEN et al. (2007) suggest that the three distribution maps for *B. macani* and *B. bundyae* in DEGERMAN et al. (1994) demonstrated the difficulties in distinguishing the two species. However, the state of knowledge at that time arose from identifications by 28 persons over a 90-year period. At the time, the map *macani/bundyae* was based on non-revised material in the Limnoda HB collection plus other material of “*macani*” stored in other collections or perhaps even lost.

To distinguish *B. macani* and *B. bundyae* is easy with a good stereo microscope (e.g. Nikon SMZ 1500), and the same applies to *B. subalpinus* and *B. vernus*. These latter species are still often confused, with the consequence: “Morphological characters such as mandibles and gills overlap widely” (DROTZ et al. 2012), or can result in conflicting texts like in JACOB (2003) or BAURNFEIND & SOLDÁN (2012).

For an accurate species determination at least three unambiguous characters are required. For *Baetis vernus* group that is for instance gills, denticles on the terga and mandibles. Even if the mandibles are worn down, it is usually possible to estimate how broad the teeth are. Except for nymphs with black wing pads, the new mandibles are usually visible inside the old ones. To state if the first tooth on the left mandible is as broad as the second or twice as broad, is not difficult, especially when you have to look out for *vernus* with apical tooth 1.5 times the size of the second tooth.

Soft mouth parts, such as labial palps, are risky to use, but long-gilled species can be identified as: *bundyae* (Fig. 1B) frequently with the labial palp having an angle slightly acute or about 90° between the terminal segment and the protrusion on the sub terminal segment, contra *macani*, *vernus* and *tracheatus*, always with an acute angle (Fig. 1M). Compare Figs 3 and 4 in MORIHARA & MCCAFFERTY (1979).

In the field *B. bundyae* is easily recognized by their white parallel sided gills, while *B. macani* is recognized as “one of those long-gilled species”. *B. macani* and *tracheatus* hide under fresh or partly decayed vegetation, while *bundyae* is exposed on the surface of stones and often swim in open water.

9. Discussion and conclusion

Ever since the key (ENGBLOM 1996) was published, I have been concerned that what Macan collected at Saana Mountain was the “*holarctic macani*”. SAVOLAINEN et al. (2014) demonstrated using DNA barcoding that Kimmins species was different from *B. bundyae*, thus most pieces of the puzzle fell into place. Descriptions by MORIHARA & MCCAFFERTY (1979) confirmed this picture. Thus, in 1957 Kimmins described the Northern *B. macani*, Macan intended to do the same but included the Standard *B. macani* from Sweden and Standard *B. macani* or perhaps something else from southern Finland. Müller-Liebenau denied this mistake and also unfortunately involved the more common species *B. bundyae*, although she pointed in the right direction.

SAVOLAINEN et al. (2014) stated: “One of these forms (*B. macani*) is widespread in Finland while the other (*B. bundyae*) is restricted in small brooks in northernmost Finland”. In other words in Fennoscandia and Kola Peninsula *Baetis bundyae* (? *Baetis bioculata* Ström, 1783) thrives in small ponds and brooks on the tundra and in cold and fast-flowing streams in the boreal forest. In

contrast, *Baetis macani* (? *Baetis saliens* Tiensuu, 1939) occurs in lowland lakes and rivers in southern Fennoscandia, but has moved further north to lakes in the more continental climate on the eastern side of the Scandinavian Mountains.

Most important after all is not what names the “*macani*” species are assigned to, but that they are treated as different species, having been mistaken for each other for far too long.

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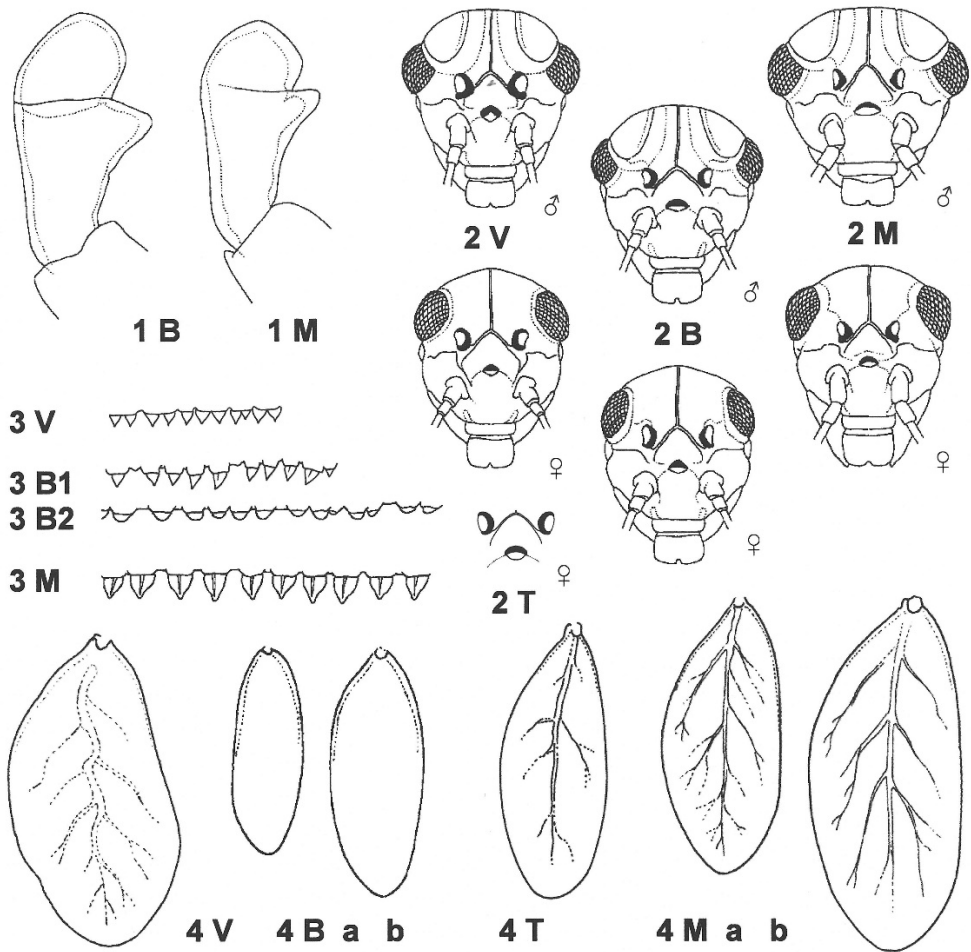
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Abbreviations for the provinces: Sweden (ENGBLOM 2003), and for Norway, Denmark and Finland in e.g. Fauna Entomologica Scandinavica. E.J. Brill /Scandinavian Science Press Ltd. Latitudes and longitudes are taken from Google Earth; <http://earth.google.com>

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Figures 1-4. Specimens from Sweden except 1B and 4Bb from Greenland, and 4T from Finland.

Labial palp: 1B *B. bundyae*; 1M *B. macani* (VG). Frons: 2T *B. tracheatus* (SÖ),

Heads, male and female: 2V *B. vernus*; 2B *B. bundyae* (ME); 2M *B. macani* Nossan (VG).

Denticles at posterior margin of terga: 3V *B. vernus*; 3B 1-2 *B. bundyae* (TO); 3M *B. macani* (UP).

Third gill on right side: *B. vernus* with long gills: 4V Alby (SÖ) 10 mm. *B. bundyae*: 4B a Vargbäcken (VB) 6 mm; 4B b 8.5 mm. *B. tracheatus* 4T Jeesiöjoki (Finland) 8 mm. *B. macani*: 4Ma Äijäjärvi (TO) 6.5 mm; 4M b Nossan (VG) 9 mm.

Figures 1-4. Spécimens de Suède, sauf 1B et 4Bb du Groenland, et 4T de Finlande.

Palpe labiale : 1B *B. bundyae* ; 1M *B. macani* (VG). Front : 2T *B. tracheatus* (SÖ),

Tête, mâle et femelle : 2V *B. vernus* ; 2B *B. bundyae* (ME) ; 2M *B. macani* Nossan (VG).

Denticules du bord postérieur des tergites : 3V *B. vernus* ; 3B 1-2 *B. bundyae* (TO) ; 3M *B. macani*

(UP). Troisième branchie du côté droit : *B. vernus* à longues branchies : 4V Alby (SÖ) 10 mm. *B. bundyae* : 4B a Vargbäcken (VB) 6 mm ; 4B b 8.5 mm. *B. tracheatus* 4T Jeesiöjoki (Finland) 8 mm. *B. macani* : 4Ma Äijäjärvi (TO) 6.5 mm ; 4M b Nossan (VG) 9 mm.