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On the identity of Heptagenia sulphurea (Müller, 1776) and H. dalecarlica Bengtsson, 1912 (Ephemeroptera)

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Abstract

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Heptagenia dalecarlica is shown to be a good species, with several constant characters distinguishing it from *H. sulphurea* in both the winged and nymph stages. *H. dalecarlica* is known from Fennoscandia and apparently from Siberia; possibly also from North America. The ecological differentation of the two species is discussed.

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In 1912, BENGTSSON described a new heptagenid species, *Heptagenia dalecarlica* from Sweden, Dalarna Elfdalen. He declared it as differing from its close relative *Heptagenia sulphurea* (Müller, 1776) in the following respects: colouration darker, median longitudinal line on hind body double, first tarsal joint of the third leg of male only slightly shorter than the second, and the lower part of the double eyes of the male much smaller than the upper. Later, BENGTSSON (1917) also described the nymph of the new species, stating that it differed from that of *H. sulphurea* in that its mandibles appeared as mirror images of those of the latter.

Although Fennoscandian authors have recognized the two species since Bengtssons description of *H. dalecarlica,* difficulties have been encountered in differentiating the winged stages of *H. dalecarlica* from those of *H. sulphurea* (e.g. ULFSTRAND 1968a:175 and 1969:152). This provoked the present authors to study the problem, and the aim of this paper is to show the existence of two distinct species and to give certain relatively easy methods of determining them in all of their life-cycles.

There is probably an older name available for *H. dalecarlica* among the specific names listed as synonyms of *H. sulphurea.* However, to establish this would necessitate the examination of the types with older names (even if they exist) and no attempt has been made to check the synonymies of either of the species.

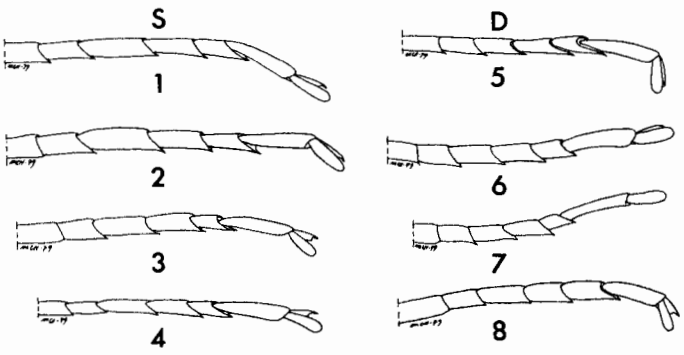
Material and methods

Apart from ca. 1500 specimens of all life-cycle stages of *H. sulphurea* and *H. dalecarlica* from various parts of Finland, Sweden, and Norway, our material also includes one male, one female, and some nymphs of *H. sulphurea* from both the USSR and the Federal Republic of Germany and four males and several nymphs of *H. dalecarlica* from the USSR.

To determine the various stages of the two species, several more or less easily recognizable characters have been chosen for more precise discussion. These characters are drawn as accurate as possible in order to avoid any generalization. Thus all figures represent certain individuals. Therefore, in order to describe the infraspecific variation and, to a certain extent, the effect of preserving fluid, more than one drawing of a particular character is usually presented. All corresponding figures are to the same scale.

Comparative description of the species

No attempt has been made to study coloura-



FIGS. 1—8. Hind tarsus of *H. sulphurea* (S) and *H. dalecarlica* (D). — 1 = Finland, Rovaniemi, river Ounasjoki. 2 = Sweden, Skåne Brömolla. 3 = GDR. 4 = U.S.S.R. 5 = Finland, Rovaniemi, river Ounasjoki. 6 = Sweden, Dalarna Elfdalen (type locality). 7, 8 = U.S.S.R, — Orig.

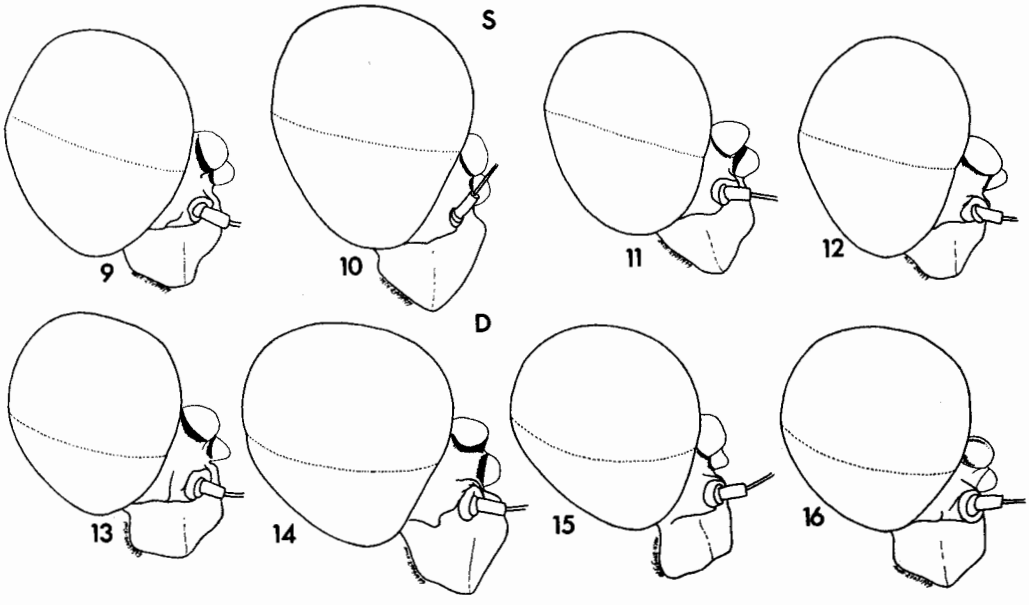
tion because this is not very suitable for determination due to rapid fading in preserved material. Moreover, certain morphological characters are also affected by preserving fluids. This problem is discussed more closely in connection with corresponding characters.

Imago and subimago

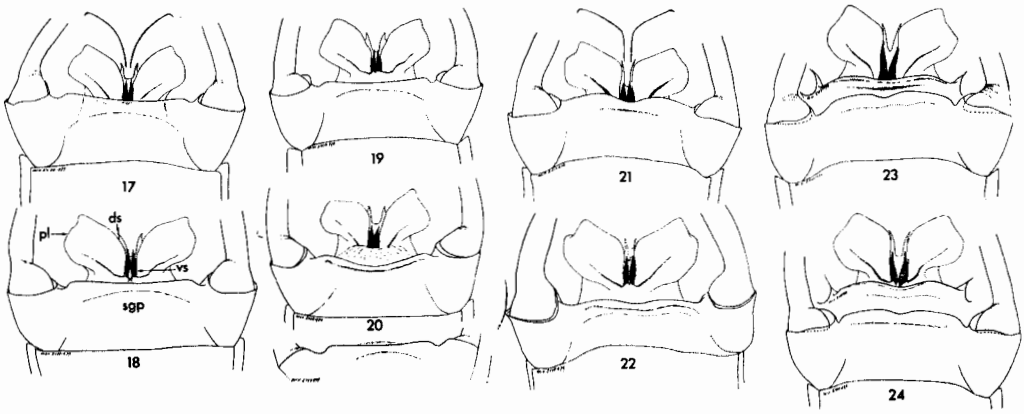
Hind tarsus (Figs. 1—8). — In *H. sulphurea* the first segment is distinctly shorter than the second, ca. half as long as the second segment. In *H. dalecarlica* the first segment is as long as the second or only slightly shorter. There seems to be considerable variation in the length and thickness of the segments of the last tarsi, though the relation between the two most proximal segments is as stated above. This character is visible in both subimagos and imagos of both sexes.

Compound eyes of males (Figs. 9—16). — Laterally viewed these eyes are higher than wide in *H. sulphurea,* while in *H. dalecarlica,* they are almost as wide as high or more often wider than high. Furthermore, the upper and lower parts of compound eyes are approximately of equal size in *H. sulphurea* but in *H. dalecarlica* the lower part is much smaller than the upper. These differences are visible in both imagos and subimagos.

Male genitals (Figs. 17—24). — When viewed ventrally, the free end of the subgenital plate (sgp) of *H. sulphurea* is slightly concave, evenly curving. In *H. dalecarlica* it is decidedly convex with a notch in the centre. However, the posterior part is quite often bent, usually



FIGS. 9—16. Male head of *H. sulphurea* (S) and *H. dalecarlica* (D). — Corresponding specimens to Figs. 1—8. — Orig.



FIGS. 17—24. Penis lobes and subgenital plate of *H. sulphurea* (17—20) and *H. dalecarlica* (21—24). — Corresponding specimens to Figs. 1—8, except Fig. 22 (corresponds to Fig. 6) which is from a lectotype of *H. dalecarlica*. Abbreviations: ds = dorsal spine. pl = penis lobe. sgp = subgenital plate. vs = ventral spine. — Orig.

almost at a right angle to the rest of the plate. In these cases the actual shape of the edge of the subgenital plate is only seen when viewed more or less anteriorly (Figs. 20, 23, 24). Differences in penis lobes (pl) are not so easy to establish as there were virtually no two specimens in which they occupied the same position. This was due to the effect of the preserving fluid. However, in *H. sulphurea* the inner sides of the lobes are more or less evenly curved from their bases towards the apex, while in *H. dalecarlica* there is a blunt angle approximately at the middle of the inner sides. Therefore, the penis lobes of *H. sulphurea* seem to form a more open structure, while in *H. dalecarlica* they appear to be more compact. To illustrate this, simplified subfigures of the inner sides of the penis lobes have been presented in Figs. 17 and 21. There seem to be no apparent differences in the ventral spines (vs) of penis lobes but dorsal spines (da) of *H. sulphurea* are wider apart and have relatively thicker and shorter free ends than those of *H. dalecarlica*. On the other hand, ventral spines are quite often displaced from their normal positions due to the effect of preserving fluid and may even point anteriorly. The same phenomenon is also known from *Heptagenia fuscogrisea*, at least, and ARO (1928:54) described such a specimen as *Ecdyurus convergens*. It should also be mentioned that at least the shape of the edge of the subgenital plate and usually the form of the penis lobes can be observed in subimagos, too.

Subanal plate and egg valve (Figs. 25—32). — In *H. sulphurea* the sides of the subanal plate (sap) are, before curving medially, parallel, while in *H. dalecarlica* they diverge. Moreover, the notch in the free end of the subanal plate of *H. sulphurea* is shallower than that of *H. dalecarlica*. The edge of the egg valve (ev) of *H. sulphurea* forms a half circle while in *H. dalecarlica* it forms a blunt-tipped triangle.

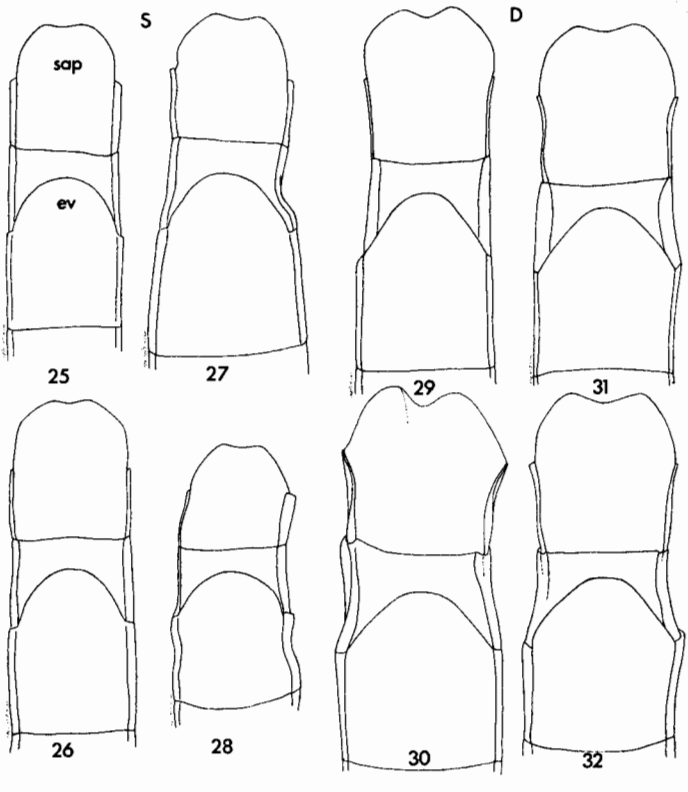
Nymphal stage

Mouth parts (Figs. 33—36). — The most convenient way to determine the nymphs of these two species is to observe the mandibles which, in *H. dalecarlica*, are like mirror images of those of *H. sulphurea*. This situation is called reverse asymmetry by Ulfstrand (1969). Mandibles are easily revealed by gently pressing the hind margin of the labium towards the cranium with a needle and the nymph on its back. There are also other differences between the mouth parts, but they are less significant and difficult to use for determination.

Gills (Figs. 37, 38). — The distal end of the gills are rounded in *sulphurea*, while in *dalecarlica* they are more or less pointed; this is best seen in the last gill.

Discussion

The species pair *Heptagenia sulphurea* and *H. dalecarlica* have been regarded as one of the most difficult taxonomic problems among mayflies in Northern Europe. Thus e.g. ULFSTRAND (1968a and b, 1969) has maintained that the imagos of these species are impossible to differentiate while the nymphs, on the other hand, are easy to determine according to the reverse asymmetry of the mandibles.

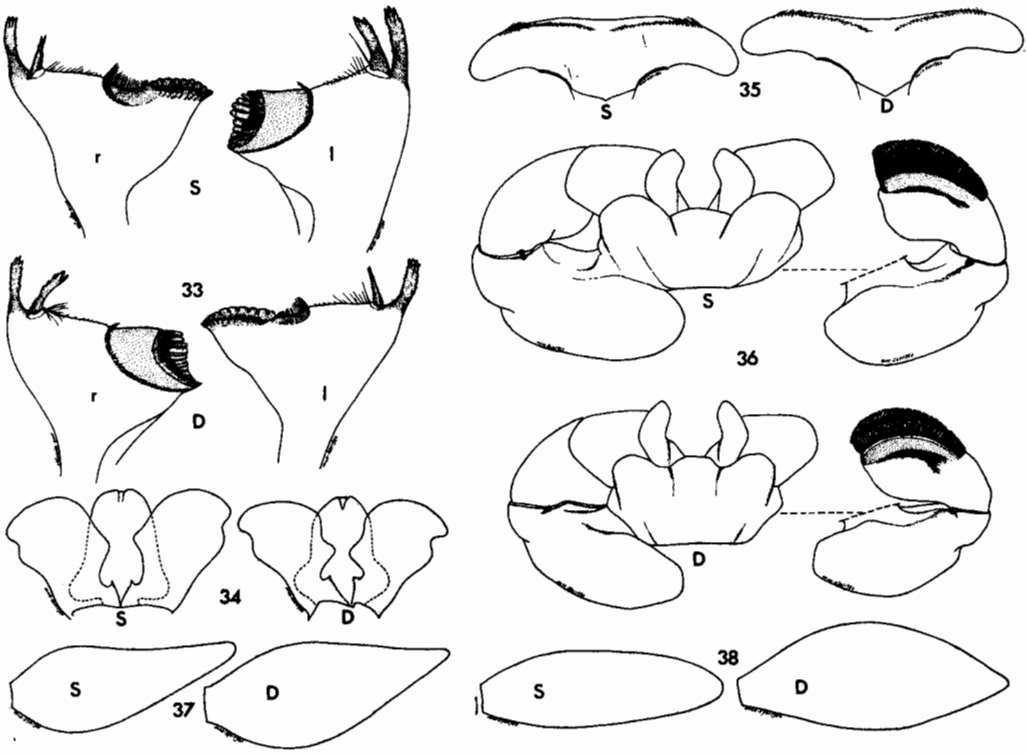


FIGS. 25—32. Subanal plate and egg valva of *H. sulphurea* (S) and *H. dalecarlica* (D). 25 = Finland, Rovaniemi, river Ounasjoki. 26 = Sweden, Skåne Brömolla. 27 = GFR. 28 = U.S.S.R. 29 = Rovaniemi, river Ounasjoki. 30 = Finland, Sääminki, lake Haukivesi. 31, 32 = Sweden, Dalarna Elfdalen. Abbreviations: ev = egg valva. sap = subanal plate. — Orig.

However, he doubted the taxonomic value of this character. It is also obvious that although both species seems to have a wide distribution eastwards, only Scandinavian authors have recognized the existence of *H. dalecarlica*. TSHERNOVA (1964) does not mention it from the European part of the USSR, although TIENSUU (1935, 1939) reported it from the Karelian Isthmus, Ladogan Karelia, East Karelia, and Petsamo. PUTHZ (1978), however, has retained the species in Limnofauna Europaea.

The results of this study show that there are two distinct species which are rather easy to differentiate morphologically in all life-cycle stages. This is further supported by initial electrophoretic studies on the enzymes of the two species. There seem to be enzymatic differences between morphologically different populations, although the size of these differences has not yet been determined (SAVOLAINEN, unpublished). As to the taxonomic value of the morphological characters used in this study, it can be said that, barring the reverse asymmetry of the mandibles, all of them have been commonly used on family, genus, and species levels in mayfly taxonomy and, barring the male eyes, they have also been used in determination of *Heptagenia* species (PETERSEN 1910, SCHOENEMUND 1930, NEEDHAM, TRAVER & HSU 1935, TSHERNOVA 1964, LANDA 1969, KIMMINS 1972). The reverse asymmetry of the mandibles also seem to be a stable character; there were no exception in our material. This is also easy to observe even in very young nymphs.

The identification keys are usually illustrated with drawings of the penis lobes, gonopods, and subgenital plate of *Heptagenia* males. Closer examination of these drawings of *H. sulphurea* shows that some of them are good re-



FIGS. 33—38. Mouth parts and gills of *H. sulphurea* (S) and *H. dalecarlica* (D). 33 = right (r) and left (l) mandibula ventrally. 34 = hypopharynx dorsally. 35 = labium ventrally. 36 = labrum ventrally. 37 = first gill. 38 = seventh gill. — Orig.

presentations of this species (EATON 1883—88, PETERSEN 1910, REMM 1970) while others seem to be mixtures of *H. sulphurea* and *H. dalecarlica.* Thus the penis lobes may appear similar to those of *H. sulphurea* and the subgenital plate to that of *H. dalecarlica* (SCHOENEMUND 1930, GRANDI 1960, KIMMINS 1972) or vice versa (TSHERNOVA 1964). This is probably due to the distorsion caused by the preserving fluid and/or because of somewhat schematic styles and figures have really been drawn from *H. sulphurea* specimens. On the other hand there are also drawings which clearly represent *H. dalecarlica* (ARO 1928, BAJKOVA 1972). The drawing of a North American species, *Heptagenia pulla* Clemens, 1913, in NEEDHAM, TRAVER & HSU (1935) may also represent *H. dalecarlica.*

H. sulphurea is found almost throughout Europe from the Mediterranean coasts up to the Arctic Ocean and from England to Ural (PUTHZ 1978). However, its range most probably extends from Ural still further eastwards. In Finland the species is found from Åland up to Lapland. TIENSUU (1939) mentions Sodankylä (E 26°30′, N 67°30′) and Muonio (E 23°30′, N 68°00′) as the northernmost localities of the species in Finland. The northernmost samples of this study come from Inari, river Lemmenjoki (E 26°00′, N 68°45′) and river Vaskojoki (E 25°20′, N 68°45′). According to the present study, the range of *H. sulphurea* seems to more southern than that of *H. dalecarlica.*

All information in the literature about the occurrence of *H. dalecarlica* is restricted to Fennoscandia (PUTHZ 1978). TIENSUU (1939) placed the species in his group "Fennoscandic species" and according to him it is found

in northern, central, and eastern Finland. The material of this study shows that the species occurs throughout the lake district of Finland; the southernmost samples coming from Nastola (E 26°00′, N 61°00′) and Lammi, lake Pääjärvi (E 25°00′, N 61°00′). BRANDER (1966) has recorded the species from Tammela (E 23°45′, N 60°45′). In the north the species is found in the rivers discharging into the Arctic Ocean. The northernmost samples of this study were from Nesseby (E 29° 00′, N 70°00′) and Lebesby (E 27° 00′, N 70°30′) in Finnmarken, Norway. The distribution of the species seems to be more northern and eastern than that of *H. sulphurea*. Although the records of *H. dalecarlica* are restricted to Fennoscandia, the species most probably has a wide range eastwards as far as to Asia. This assumption is based on BAJKOVA's drawing of *H. sulphurea* collected from the river Amur because it seems to represent *H. dalecarlica*. Thus the possible range of the species includes all northern parts of Eurasia, Taiga and at least a part of the Arctic. It is also possible that the North American species, *H. pulla*, is conspecific with *H. dalecarlica*.

According to PUTHZ (1978), *H. sulphurea* is found in rivers and streams and *H. dalecarlica* in small streams and brooks. According to TIENSUU (1935), the nymphs of *H. sulphurea* thrive only in lotic waters while those of *H. dalecarlica* live both in lotic waters and on stony lake shores. Among the material of this study all the nymph specimens of *H. sulphurea* were from lotic waters; from small brooks to rivers. On the other hand, all specimens of *H. dalecarlica* from southern Finland up to the northern parts of North Savo (N 63°—64°) were from oligotrophic lakes with stony shores while more northern samples came from different-sized lotic waterbodies as well as from oligotrophic lakes. According to ULFSTRAND (1968a and b, 1969), *H. sulphurea* and *H. dalecarlica* have different local distribution patterns in Swedish Lapland: *H. sulphurea* prefered the lake outlets while *H. dalecarlica* was more abundant in other lotic sites and had a wider local distribution range. He also noted that the two species were often found together, but they never dominated at the same localities. According to this study, too, the species are often found together in northern Finland: Kuusamo, river Oulankajoki (E 29°20′, N 66°20′), Kolari, river Äkäsjoki (E 23°50′, N 67°30′), Rovaniemi, river Ounasjoki (E 25°00′, N 67°10′), Inari, river Vaskojoki (E 25°20′, N 68°45′). The nymphs of these two species most probably have different microhabitats, though it has not been possible to establish this.

In the whole genus *Heptagenia* the swarming of imagos is principally the same (for *H. fuscogrisea*, see SAVOLAINEN 1978). Swarming takes place mainly in the evening above rivers or lake shores near the shore line, but also during day time during cloudy or chilly weather. The individuals fly horizontally backwards and forwards parallel to the shore line. Stagnant swarming is also typical. Swarms are relatively dispersed but they can be very large, consisting of huge numbers of specimens continuing several kilometres along the shore line or above the river.

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