

Zeitschrift: Mitteilungen der Schweizerischen Entomologischen Gesellschaft =
Bulletin de la Société Entomologique Suisse = Journal of the Swiss
Entomological Society

Herausgeber: Schweizerische Entomologische Gesellschaft

Band: 60 (1987)

Heft: 1-2

Artikel: Notes on mayfly species belonging to the Ecdyonurus helveticus-group
(Heptageniidae, Ephemeroptera) and the description of *E. alpinus* sp.
nov.

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DOI: <https://doi.org/10.5169/seals-402264>

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Notes on mayfly species belonging to the *Ecdyonurus helveticus*-group (Heptageniidae, Ephemeroptera) and the description of *E. alpinus* sp. nov.¹

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This paper is the continuation of two previous works on the *Ecdyonurus helveticus*-group. The aim of these studies is the revision of the morphological features of the available species belonging to the *E. helveticus*-group on the basis of many populations from different areas. At first, a complete redescription of *E. helveticus* (EATON, 1885) is presented. It is based on a study of 30 populations from Switzerland, France, Austria and Italy. This species shows a wide distribution and a pronounced variability of morphological characteristics, especially in the nymphal stage. Then we present a complete redescription of *E. zelleri* (EATON, 1885), a species which we found in the Slovenian Alps, in the Austrian Alps and in the Valais (this last station provided the first record for Switzerland). Finally, this paper presents the description of a new member of this group, which we named *E. alpinus* because of its ecological distribution.

DESCRIPTIONS

Ecdyonurus helveticus (EATON, 1885)

Imago, male

Length of the body (without cerci): 12–14 mm

Length of the fore wings: 13–14 mm

Head: brown to fuscous, darker in the ocellar area. The facial keel is grey to brown. The scapus and the pedicellus are brownish clear. The distal parts of the ocelli are white and are separated from the darker surface of the cephalic part by a brown circular ring all around the stem. The eyes are grey clear with darker bands at the posterior borders. *Thorax*: general colour brown yellowish. It is darker on the notum and on the ventral face, paler laterally and at the level of the coxae. The fore legs are brown with some yellowish tinges and darker than the other ones. The middle and the hind legs are paler with the exception of the tarsi and the tibio-femoral articulations which exhibit some dark spots. The fore wings are hyaline with the exception of the opaque costal and subcostal zone. Venation homogenously brown. The pterostigmatic area is opaque, darker and well marked with anastomosed cross-veins. Hind wings hyaline with regular brownish venations, paler at the level of the costal projection. *Abdomen*: brown yellowish, generally paler than the thoracic coloration. The lateral tergites present the typical L-shaped pattern of the *E. helveticus*-group (fig. 1). Cerci fuscous to yellowish. *Genitalia*: in dorsal view (fig. 4), the penis lobes are widely extended laterally. The inner border of the apical sclerite forms a projection. The characteristic

¹ This work is supported by the Swiss National Science Foundation Grant no 3.551-0.83.

lateral sclerite is narrow with emargination of its lateral border near the distal end and it is situated in the basal part of the lobe. The basal sclerite often bears a slanting tooth oriented perpendicular to the direction of symmetry of the penis lobes in contrast to *E. picteti* (MEYER-DÜR, 1864). The forceps base is ventrally brown yellowish, generally with slight lateral protuberances (but we noted a broad range of variability of this last character). The forcipes are brown at their base, becoming progressively paler at the distal end.

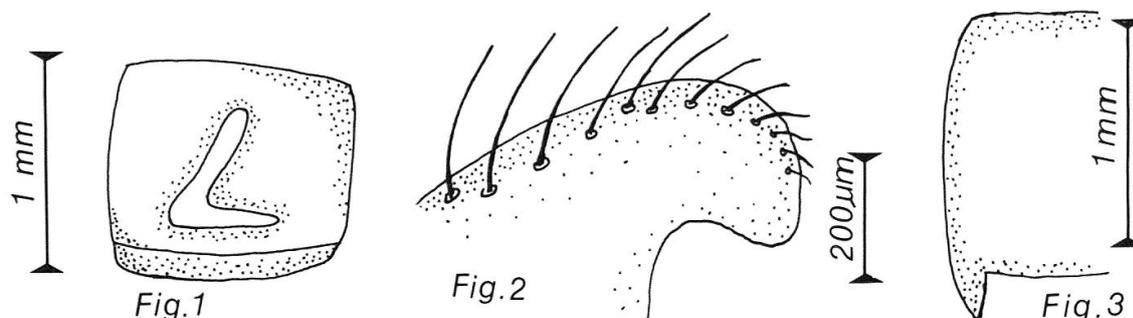


Fig. 1–3. Morphological characteristics of the species belonging to the *E. helveticus*-group. 1: Lateral abdominal tergite of the imago and the nymph. 2: Hypopharynx of the nymph. 3: Lateral expansion of the abdominal tergite of the nymph.

Imago, female

Length of the body (without cerci): 13–15 mm

Length of the fore wings: 14–16 mm

The general colour of the body is brown yellowish with some reddish and orange tinges on the lateral sclerites. The head is darker, especially in the ocellar area and on the facial keel. The thorax and the abdomen are similarly coloured with the notum slightly darker. The fore legs are darker than the other ones. The fore wings present a hyaline surface, with the exception of the opaque costal, subcostal and pterostigmatic zones.

Eggs

The ovoid and pale yellowish eggs of *E. helveticus* show an rough surface with multiple micropyles (fig. 5). A thin layer of granulated sculpture is concentrated at the two poles of the egg.

Subimago

The body is yellowish to brown, with some clear reddish tinges on the female's abdominal segments. The head is darker at the level of the ocelli. The fore legs are in both sexes darker than the other ones. The wing pattern shows slight brownish bands diffusely distributed on the wing's surface, contrasting with the darker stripes of *E. picteti*. Nevertheless we recorded some variability in this character.

Nymph

The coloration is yellowish to brown, very similar to that one of the subimago. The morphology of the hypopharynx (fig. 2), the lateral expansions of the abdo-

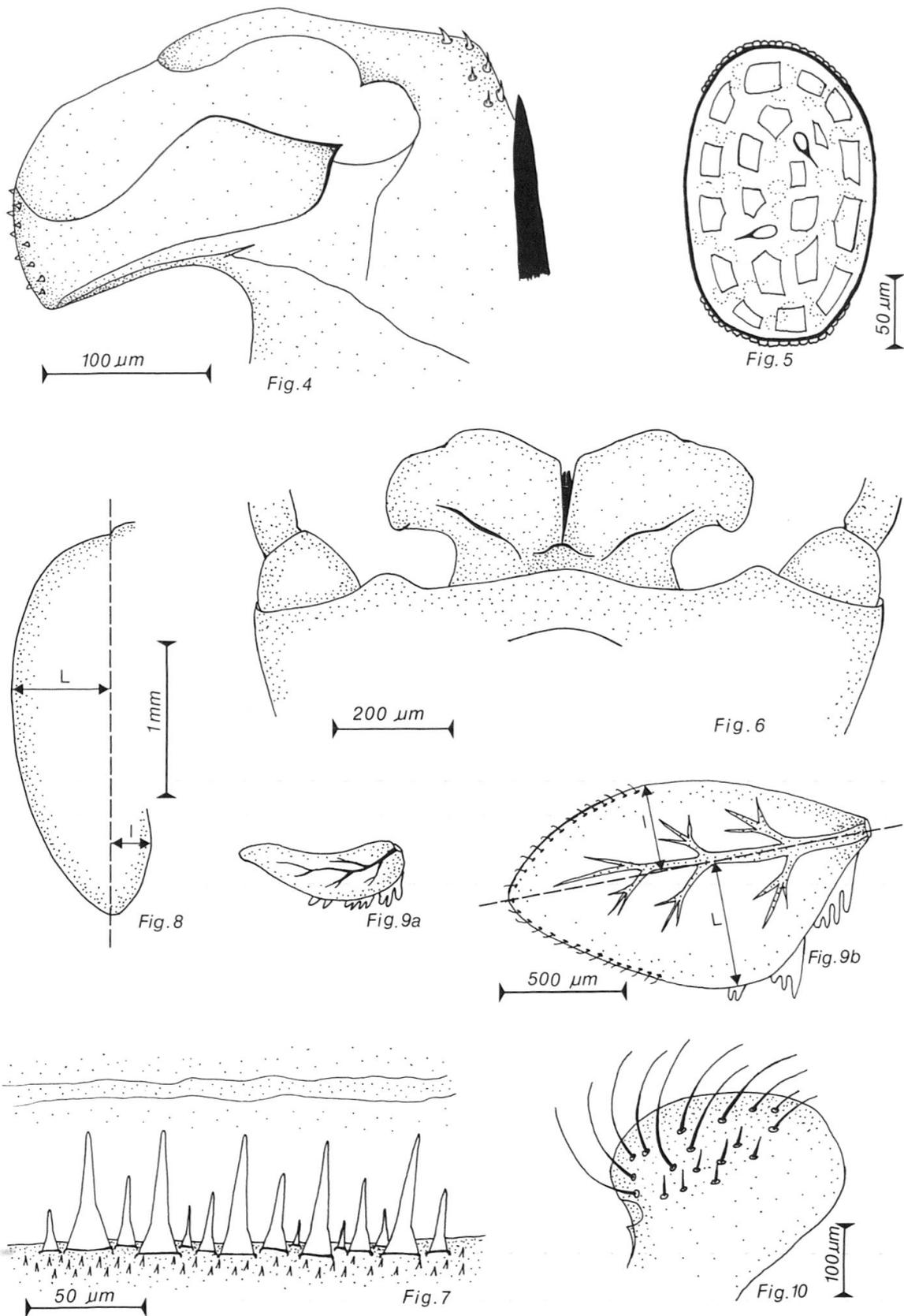


Fig. 4–10. Morphological characteristics of *E. helveticus*. 4: Penis lobe (dorsal view). 5: Egg. 6: Genitalia (ventral view) and forceps base. 7: Tergo-abdominal spines of the nymph. 8: Lateral expansion of the pronotum of the nymph. 9: First (9a) and fourth (9b) gill of the nymph. 10: Glossa of the nymph.

men (fig. 3), the drawing of the abdominal tergites (fig. 1) and the shape of the femoral teeth are all typical for the species belonging to the *E. helveticus*-group. The tergo-abdominal spines (fig. 7) are elongated and their length shows a broad distribution (similar to *E. picteti*). A twofold tarsal denticulation is generally present, but as stated in table 1, variability appears in this character. The pronotum expansions are slightly pointed at the apex and are directed parallel to the longitudinal axis of the body (fig. 8). Fourth gill is slightly asymmetrical (table 3). Its length to width ratio is less than two (fig. 9b).

Ecdyonurus zelleri (EATON, 1885)

Imago, male

Length of the body (without cerci): 10–12 mm

Length of the fore wings: 12–13 mm

Head: dark brown to black in the ocellar area. The facial keel is dark grey, slightly clearer at the base of the eyes. The scapus and the pedicellus are more homogeneously brownish grey. The ocelli are white at the top, their stem being bordered by a brownish clear ring. Eyes grey clear with darker basal and posterior borders.

Thorax: dorsally and ventrally brown clear to castaneous, the sclerotized parts being darker. The pleurites and the coxae are more yellowish. The fore legs are uniformly brown and darker than the other ones. The middle and the hind legs are whitish to yellowish with brownish tarsi and brownish spots on the tibio-femoral articulations. The fore wings are hyaline with the exception of the opaque costal and subcostal area. The pterostigmatic zone is opaque and brownish with some slight yellowish reflections. The hind wings are hyaline with lighter venations at the level of the costal projection. *Abdomen*: reddish to brown with yellow tinges. The lateral tergites exhibit the drawing typical for the *E. helveticus*-group (fig. 1). *Genitalia*: in dorsal view (fig. 11), the penis lobes are laterally less extended than those of *E. helveticus*. The inner border of the apical sclerite presents a clear projection (similar as in *E. helveticus*). The lateral sclerite of *E. zelleri* is situated in the middle of the lobe and presents an emargination or narrowing near its distal end. If the basal sclerite bears a visible tooth, this one is always directed perpendicular to the axis of symmetry of the penis lobes. The forceps base is brown ventrally and it shows two lateral protuberances (fig. 13). The forcipes, brown at the base, become progressively paler at the distal end.

Imago, female

Length of the body (without cerci): 11–13 mm

Length of the fore wings: 13–14 mm

The general colour of the body is brownish, with some reddish reflections on the abdominal sternites as in *E. helveticus*. The head and the thoracic notum present a darker coloration. Fore wings uniformly hyaline with exception of the costal, the subcostal and the pterostigmatic area.

Eggs

The ovoid yellowish eggs do not present any particular specific difference relative to those of *E. helveticus*, but the external granulated layers seem to be more irregularly distributed at the two poles (fig. 12).

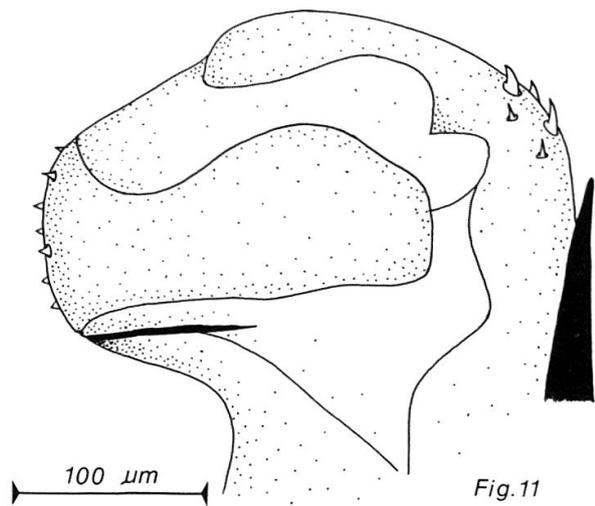


Fig. 11

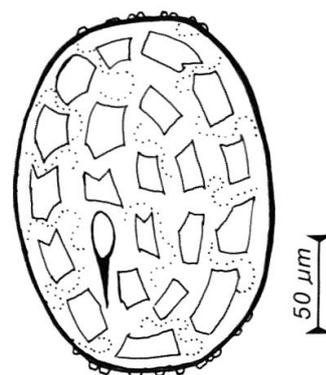


Fig. 12

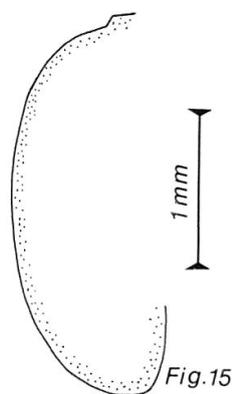


Fig. 15

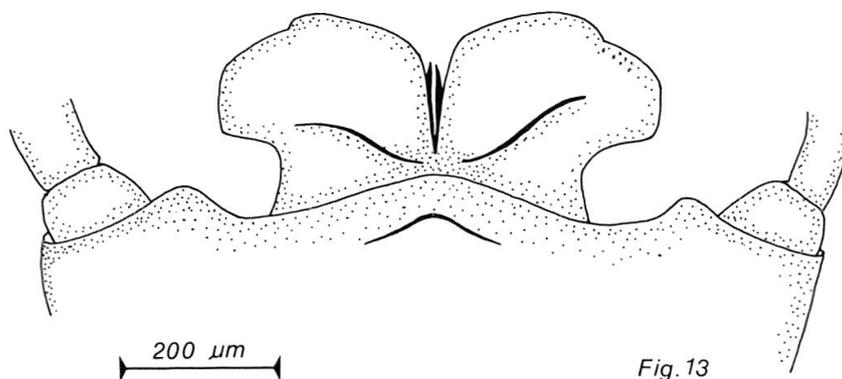


Fig. 13

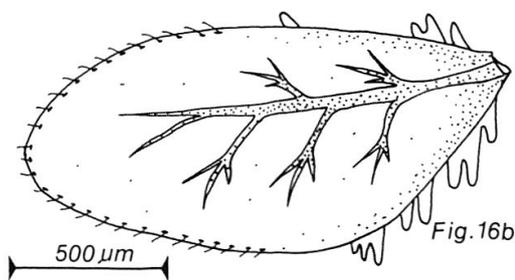


Fig. 16b

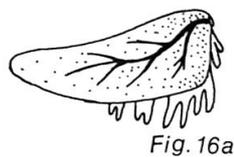


Fig. 16a

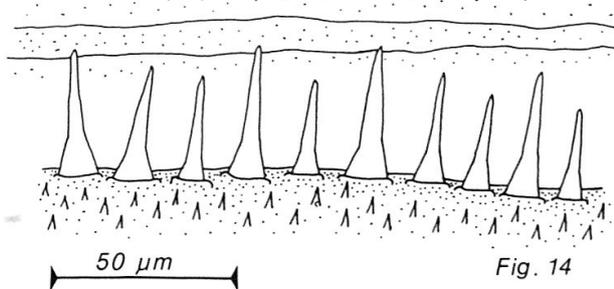


Fig. 14

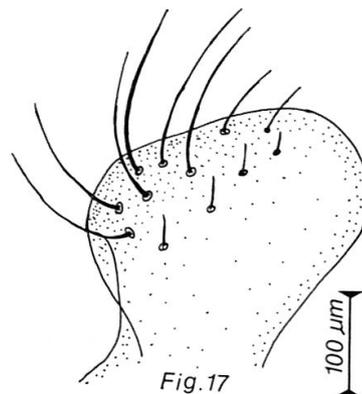


Fig. 17

Fig. 11–17. Morphological characteristics of *E. zelleri*. 11: Penis lobe (dorsal view). 12: Egg. 13: Genitalia (ventral view) and forceps base. 14: Tergo-abdominal spines of the nymph. 15: Lateral expansion of the pronotum of the nymph. 16: First (16a) and fourth (16b) gill of the nymph. 17: Glossa of the nymph.

Subimago

General colour of the body brown with some clear reddish reflections at the level of the lateral abdominal tergites (particularly well marked on the females). Head generally greyer. Fore legs browner than the other ones. The wing is of an uniformly black-grey coloration, in agreement with EATON's original description (1883–1888) and with KIMMINS' redescription of the species (1958). Nevertheless, this characteristic does not always have a good differential value (see previous redescription of *E. helveticus*).

Nymph

The general coloration of the body is brownish with yellowish tinges on the abdomen. The nymphs present all the typical characteristics of the *E. helveticus*-group (hypopharynx, lateral extensions of the abdomen, femoral teeth). The tergo-abdominal spines are elongated like those of *E. helveticus* (fig. 14) but they are all approximately of the same size. The tarsal denticulation is variable (table 1). Pronotum expansions asymmetrical, the external border strongly curved (fig. 15). Fourth gill longitudinally elongated, its ratio of length to width equals to two or more (fig. 16b).

Ecdyonurus alpinus sp. nov.

Imago, male

Length of the body (without cerci): 11–14 mm

Length of the fore wings: 12–15 mm

Head: brownish to black. The facial keel is grey with reticulated black spots. The scapus and the pedicellus are grey clear to brown, becoming clearer at the distal end of the pedicellus. The ocelli are white at the top, bordered by a brownish ring, becoming darker at the base of the stem. The front is black and the eyes are grey clear with darker bands in the basal borders. *Thorax*: notum fuscous to black, very contrasting to the more yellowish general colour of the abdomen. The coxae are slightly paler. The fore legs are homogeneously brown. The middle and the hind legs are yellowish with the exception of the tarsi and the tibio-femoral articulations, which exhibit some brownish spots. The fore wings are hyaline with the exception of the opaque venations of the costal and subcostal zone. The pterostigmatic area is opaque and darker. The hind wings are hyaline with paler transverse venations at the level of the costal projection. *Abdomen*: general colour brown to yellowish. The lateral tergites present sometimes some reddish reflections all around the typical drawing characterizing the *E. helveticus*-group. Dorsally every segment shows a dense pattern of tracheal arborization. *Genitalia*: in dorsal view (fig. 18), the penis lobes are not so far extended laterally as in *E. helveticus* but seem to be more slender than in *E. zelleri*. In contrast to the last species, the inner border of the apical sclerite of *E. alpinus*, presents only a slight projection. The lateral sclerite occupies a large proportion of the penis lobe and its distal part shows only a slight emargination (or no emargination at all, the distal and basal borders of the sclerite are subparallel). We generally noted on the basal sclerite the presence of a tooth, directed as in *E. zelleri* and *E. helveticus* perpendicular to the axis of symmetry of the penis lobes. The base of the penis stem often presents a little notch as in *E. austriacus* KIMMINS, 1958. Forceps base ventrally

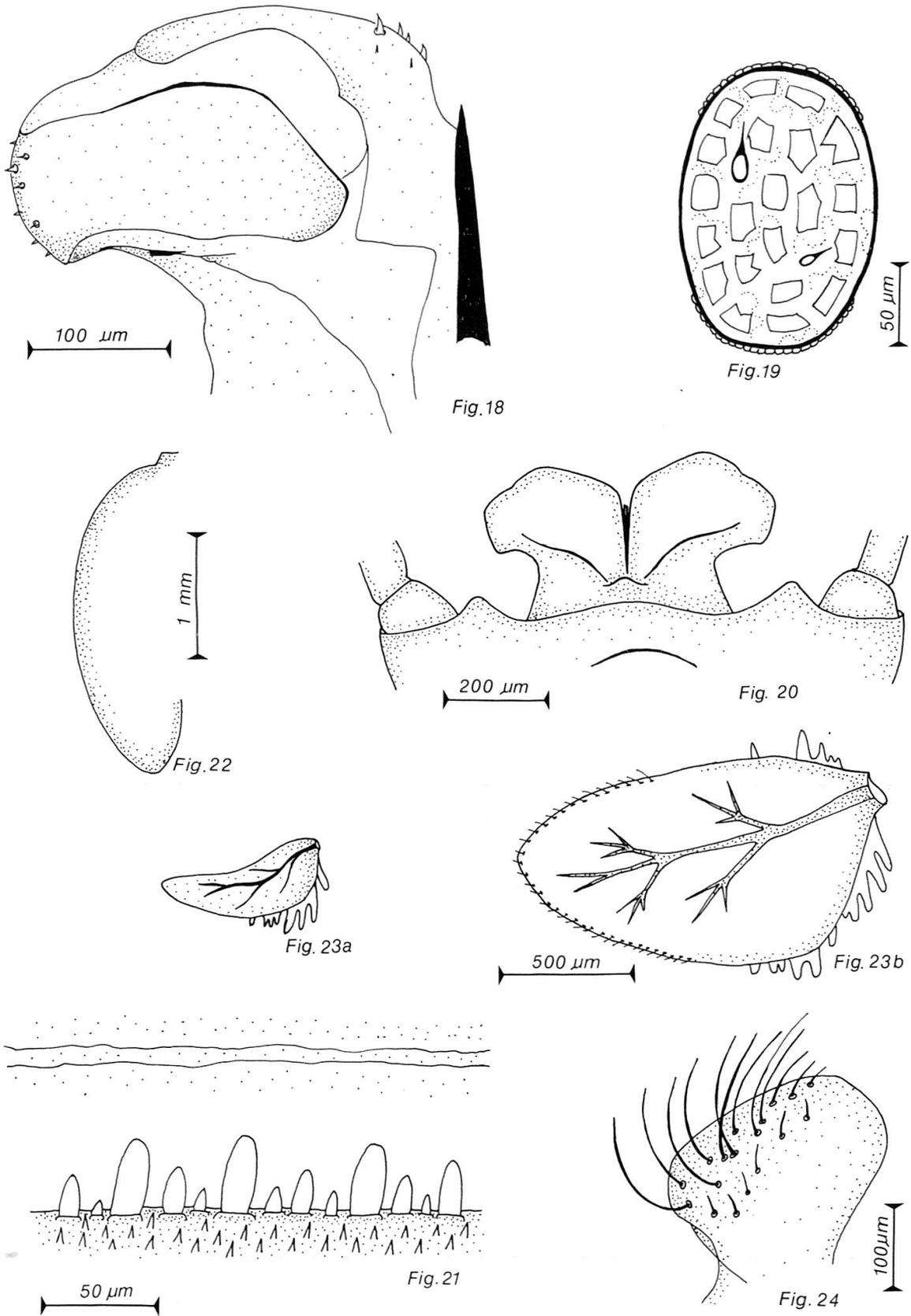


Fig. 18–24. Morphological characteristics of *E. alpinus*. 18: Penis lobe (dorsal view). 19: Egg. 20: Genitalia (ventral view) and forceps base. 21: Tergo-abdominal spines of the nymph. 22: Lateral expansion of the pronotum. 23: First (23a) and fourth (23b) gill of the nymph. 24: Glossa of the nymph.

brown with two strong lateral protuberances (fig. 20). The forcipis are dark brown at the base, becoming yellowish at the distal part.

Imago, female

Length of the body (without cerci): 12–14 mm

Length of the fore wings: 13–15 mm

General colour of the body brown to yellowish with some reddish tinges on the lateral part of the abdominal tergites. Head brown to black, darker on the front and at the level of the facial keel. The thoracic segments are brownish clear to fuscous on the dorsal notum, which does not present any net contrast with the coloration of the abdomen (in contrast to the male). The fore legs are brown, darker than the other ones. The fore wings are hyaline, only the costal, the subcostal and the pterostigmatic areas are slightly opaque and brownish. The hind wings are also hyaline. The cerci are brownish clear to yellow.

Eggs

The eggs of *E. alpinus* (fig. 19) are identical in shape and structure with those of *E. helveticus*, but the general colour is yellower.

Subimago

The general colour of the body is homogeneously brownish, with some slightly darker spots all around the typical drawing on the abdominal tergites. The front and the facial keel are grey. The thoracic nota are brownish pale like the abdomen. The fore legs are only slightly darker than the other ones. The fore wings are with the same pattern as in *E. helveticus*.

Nymph

The general colour of the body is brownish clear with yellowish tinge particularly well marked on the abdominal segments. The hypopharynx, the lateral extensions and the drawing on the abdominal tergites, as well as the shape of the femoral teeth are all characteristic for the *E. helveticus*-group. The tergo-abdominal spines are small (fig. 21), some of them being typically rounded at the apex as in *E. parahelveticus* HEFTI *et al.*, 1986. Tarsal denticulation variable (table 1). The pronotum expansions are more or less pointed, with a regularly curved external border (fig. 22). Fourth gill strongly asymmetrical, its length to width ratio is less than two (fig. 23b).

MATERIAL

Our material was collected in more than 50 stations and covers a large geographical and ecological range. A complete list of all the prospected stations in Switzerland is given in ZURWERRA & TOMKA (1984) for the species *E. helveticus*. Below are listed the stations outside Switzerland for *E. helveticus* and all the stations for *E. zelleri* and *E. alpinus*.

E. helveticus: Rio di Varzo/Varzo (I), 530 m, 6.83; Isorno/Masera (I), 400 m, 6.83; Ambro/Piedivalle (I), 595 m, 7.83; Carzola/Vaglia (I), 300 m, 5.85; Torre Sambro/Rioveggio-Valle (I), 480 m, 4.82; Barberine/Barberine (F), 1140 m,

6.83; Epierre/Arc (F), 400 m, 5.81; La Laysse/Pont des Callets (F), 590 m, 5.81; Torrent de Valentine/Col du Joux Plane (F), 1600 m, 7.83; Verdon/Allons-Argens (F), 900 m, 8.83; Issole/St-André (F), 900 m, 8.83; Le Clévieux/Samoens (F), 680 m, 7.83; Taurerbach/Untertauern (A), 930 m, 6.85.

E. zelleri: Radowna/Bled (YU) 650 m, 8.83; Kremsbach/Innerkrams (A), 1600 m, 9.85; Seebach/Lunz (A), 620 m, 8.85; Schreyerbach/Lunz (A), 800 m, 8.85; Saufla/Grand Paradis Val d'Illiez (CH), 1050 m, 9.85 (first record for Switzerland).

E. alpinus: Lochbach/Realp Uri (CH), 1550 m, 8.83, (Imago male holotype: no 1997 leg Zurwerra), 8.85 (paratypes). Splügen/Splügen (CH), 1500 m, 8.85; Ova dal Crot/Silser See (CH), 1820 m, 8.83, 8.84, 8.85; Ova dal Roda/Silser See (CH), 1830 m, 8.85.

The holotype is deposited in the Entomological Department, Institute of Zoology, University of Fribourg, Pérolles, 1700 Fribourg-Switzerland.

ECOLOGY

The ecological characteristics for *E. helveticus*, *E. zelleri* and *E. alpinus* are briefly summarized in table 2. Concerning the typical ecological specificity of *E. alpinus*, this species was only found in demineralized water at high altitudinal level with large substratum size and with a slope of the channel, characterizing turbulent ecosystems of the epirhithron.

DIFFERENTIAL DIAGNOSIS

Imago: *E. helveticus*, *E. zelleri* and *E. alpinus* each are separable from the other species belonging to the *E. helveticus*-group because of the shape and the structure of the dorsal sclerites of their penes. For *E. helveticus* are characteristic its laterally far extended penis lobes and its slender lateral sclerites situated in the basal half part of the lobes. *E. zelleri*, in contrast, presents laterally less extended penis lobes with broader lateral sclerites situated symmetrically in the middle of the lobes. A possible confusion might appear in the separation of *E. zelleri* from *E. alpinus*. While these two species are easily separable at the level of the subimaginal and nymphal stages, only a careful analysis of the dorsal sclerite's structure permits the determination at the imaginal stage. The inner border of the apical sclerite presents in *E. zelleri* a clear projection (like in *E. helveticus*), whereas

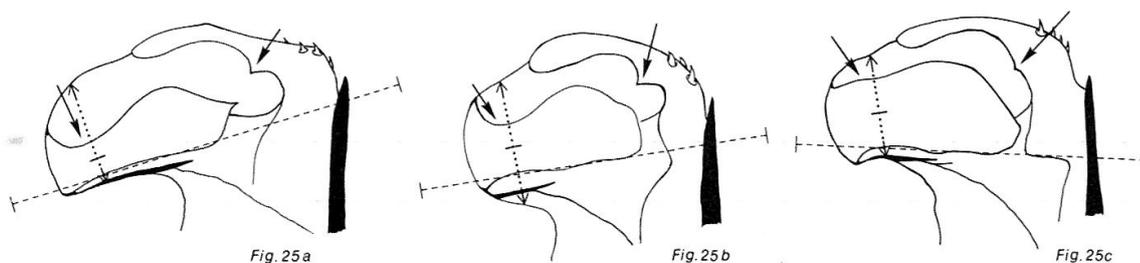


Fig. 25. Spatial orientation of the lateral sclerite for the species *E. helveticus* (25a), *E. zelleri* (25b) and *E. alpinus* (25c).

Tab. 2. Ecological characteristics of *E. helveticus*, *E. zelleri* and *E. alpinus*. Altitude (Alt.) in meters, temperature (Temp.) in centigrades, pH, alkalinity (Alc.) in mVal/l and electrical conductivity (C.E. 20°) in $\mu\text{S}/\text{cm}$. \bar{M} = mean, σ = standard deviation and n = number of measures.

	Alt.			Temp.			pH			Alc.			C.E. 20		
	\bar{M}	σ	n												
<i>E. helveticus</i>	1048	410	22	9.57	3.7	22	7.99	0.43	22	2.07	0.96	21	214	99	22
<i>E. zelleri</i>	775	243	3	6.80	1.4	3	7.97	0.20	3	2.03	0.46	3	197	32	3
<i>E. alpinus</i>	1672	171	4	8.26	1.3	3	7.22	0.72	3	0.76	0.58	3	81	61	3

Tab. 1. Number of teeth observed on the tarsal claw of *E. helveticus*, *E. zelleri* and *E. alpinus*.

a) 1/L of the fourth gill	\bar{x}	σ	n
<i>E. helveticus</i>	0.73	0.08	10
<i>E. picteti</i>	0.52	0.14	10
b) 1/L of the pronotum expansion	\bar{x}	σ	n
<i>E. helveticus</i>	0.32	0.08	14
<i>E. picteti</i>	0.44	0.66	20

Tab. 3. a) Measure of the asymmetry of the fourth gill for the species *E. helveticus* and *E. picteti*, calculating the ratio 1/L (cf. fig. 9b). b) Measure of the asymmetry of the pronotum expansion for *E. helveticus* and *E. picteti*, calculating the ratio 1/L (cf. fig. 8).

Nb. of teeth	0	1	2	3	more
<i>E. helveticus</i>	3	2	60	5	–
<i>E. zelleri</i>	4	8	3	–	–
<i>E. alpinus</i>	32	16	33	5	–

it shows only a slight broad protuberance in the case of *E. alpinus*. The lateral sclerite of *E. alpinus* is broader than in *E. zelleri* and occupies a large proportion of the penis lobe. It does not present any deep emargination on its distal part, the two borders of the sclerite being almost parallel each other. In contrast, the lateral sclerite of *E. zelleri* is more slender and always presents a net emargination in its distal part. Furthermore, the orientation of the lateral sclerite relative to the longitudinal axis of the penis lobe gives an additional discriminative character between *E. alpinus* and *E. zelleri*. (fig. 25).

Nymphs: Because of the shape of its tergo-abdominal spines, *E. alpinus* is clearly differentiable from *E. helveticus*, *E. zelleri*, *E. picteti* and from all the East European species: *E. krueperi* (STEIN, 1863), *E. carpathicus* SOWA, 1973 and *E. subalpinus* (KLAPALEK, 1907). *E. alpinus* is then separable from *E. austriacus* because of the constant twofold and asymmetrical claws of the legs of this last species. Until now it was not possible for us to find any good differentiating character between the species *E. alpinus* and *E. parahelveticus*, but investigations concerning this point are still running. *E. helveticus* and *E. zelleri* are both separable from *E. austriacus* and *E. parahelveticus* because of the shape of their tergo-abdominal spines, from *E. krueperi* and *E. carpathicus* because of the morphology of the glossa and from *E. subalpinus* because of its characteristic pointed pronotum expansion (SOWA, 1973). *E. zelleri* is then separable from *E. helveticus*, *E. picteti* and from all the above cited members of the *E. helveticus*-group because of the shape of the fourth gill (JACOB & BRAASCH, 1984). In addition the typical convex outline and rounded distal end of the pronotum expansion of *E. zelleri* (fig. 15) allows a separation from *E. helveticus* and *E. picteti*. But, as stated elsewhere (HEFTI & TOMKA, 1986), we could not confirm the differences cited in the paper of JACOB & BRAASCH (1984) between *E. helveticus* and *E. picteti* based on the shape of the fourth gill and of the pronotum. We never found a length-width ratio of the fourth gill which was «mindestens doppelt so lang wie hoch» for the species *E. helveticus*. It was nevertheless possible to detect a difference in the asymmetry of the fourth gill, calculating the ratio 1/L (fig. 9b) for the two species (table 3). The quoted differences in the shape of the pronotum described by JACOB & BRAASCH (1984) for the two species could not be verified within our material, but significant differences appear when calculating the ratio 1/L (fig. 8) between *E. helveticus* and *E. picteti* (table 3).

Tab. 4. relativ mobility values for three enzymes-loci showing the distinct character of *E. helveticus*, *E. zelleri* and *E. alpinus*.

	<i>E. helveticus</i>	<i>E. zelleri</i>	<i>E. alpinus</i>
Adenylate kinase (AK)	106	100	106
Arginine phosphokinase (APK)	98	100	98
Glutamate oxaloacetate transaminase-2 (GOT-2)	101	99	99

Biochemical data: All the morphological observations correlate with a biochemical analysis based on the specific electromorph mobilities of 16 enzyme-loci. Table 4 presents the relative mobility values of the discriminative enzyme-loci for the species *E. helveticus*, *E. zelleri* and *E. alpinus*. The biochemical results will be published later also for all the other members of the *E. helveticus*-group.

DISCUSSION

From the three discussed species, *E. helveticus* seems to be a widely distributed taxon. It is well recognizable at the imaginal stage, because of the morphology of its genitalia. The nymphs, in contrast, present a large range of morphological variability which does not always permit a sure distinction from *E. picteti*. The nymphal characteristic (based on the fourth gill) mentioned in the key of JACOB & BRAASCH (1984) for the species *E. helveticus* is not valid. The reason for this may be explained by the fact that the authors investigated only one population of nymphs (Rhodopoden, BG) and probably underestimated the broad range of variability that we recorded in the *E. helveticus* populations, particularly in the nymphs. Furthermore they used different populations to describe different developmental stages (the nymphal population coming from Bulgaria and the imaginal population from North Yugoslavia). Knowing the morphological variability recorded in *E. helveticus* populations (probably in response to their large ecological extension), it seems quite ambiguous to associate two specimens of different developmental stages from different populations under the same name.

With the exception of «one rather broken male» (KIMMINS, 1958), from the Auvergne (France), all the related stations for *E. zelleri* are restricted to the Alps. In spite of our careful investigations through all the Swiss Alps, *E. zelleri* was found in only one locality in the southern part of the Valais. This relict like biogeographical distribution is quite common in the Alps.

E. alpinus was found in a few stations in the middle east of the Swiss Alps and its occurrence seems to be restricted to high altitudinal stations characterized by a granitic substrate. This ecological specificity might be helpful in the difficult determination of the two morphologically closely related species *E. zelleri* and *E. alpinus* at the imaginal stage.

ACKNOWLEDGMENTS

We would like to thank Prof. G. Lampel for his help in the elaboration and in the correction of the paper. We further would like to thank Miss D. Studemann, Mrs. D. Janke and Mrs. L. Sygnarski for their help in the field as well as in the laboratory and Mr. Gachoud for his help in the graphism.

RESUME

Ce papier présente la redescription morphologique complète de deux espèces d'*Ecdyonurus* appartenant au groupe *helveticus*: *E. helveticus* et *E. zelleri*, ainsi que la description d'une nouvelle espèce du même groupe: *E. alpinus*. La caractérisation du biotope est donnée pour les trois espèces ainsi qu'un diagnostic différentiel permettant leur identification. Finalement, une discussion portant essentiellement sur la variabilité morphologique enregistrée chez les nymphes souligne la difficulté d'une approche taxonomique chez les Heptageniidae.

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(received February 27, 1987)

