The Ecdyonurus helveticus (Eaton) Complex (Ephemeroptera)

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(With 23 figures)

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In 1942 (pp. 123-5) I had occasion to discuss the status of three species of Ecdyonurus described by Eaton, E. helveticus, E. italicus and E. zelleri, and to designate lectotypes for them. At that time, the material at my disposal suggested that all three were conspecific, as such differences as occurred in the male genitalia were rather indefinite and tended to intergrade one into another. Recently Dr. G. Pleškot, of the Zoological Institute, University Vienna, has been working in the Department of Entomology, British Museum (Nat. Hist.) and has shown me some specimens of Ecdyonurus which she has bred from nymphs collected in Austria. The male imagines all have the basal segment of the fore tarsus about one-third as long as the second, a characteristic of E. helveticus (Eaton), but they have been bred from two quite distinct forms of nymph, and the sub-imagines are also easily separable. In general appearance and genital structure the male imagines are very similar.

It thus becomes necessary to re-consider the status of the three species listed above, and at the same time to endeavour to decide which of Dr. Pleskot's two types of sub-imago represents the true helveticus of Eaton. Since the sub-imagines show better distinctions than the imagines, they will be dealt with first. In Dr. Pleškot's material, one type has both wings unicolorous greyish (fig. 19). The other has the fore wing dark grey with a distinct, whitish, zigzag, transverse pattern and the hind wing is greyish at the base and the apical border, the centre whitish (fig. 1). Eaton writes of the living sub-imago of helveticus (1887, p. 282), "fore wing marked with the usual dark stripes; terminal margin of the hind wing broadly bordered with dark grey" (fig. 9). The sub-imaginal material determined as E. helveticus in the British Museum (Nat. Hist.) is rather limited (7 specimens). The pinned sub-imagines of the type-series of E. helveticus show only faint dark stripes on the fore wing, now brownish rather than grey. Amongst the unidentified accessions in the McLachlan collection is a Swiss sub-imago from Bergün in the Canton of Grisons, which has the strongly marked zigzag pattern of Dr. Pleškot's second sub-imaginal type. This specimen is approximately the same age as the helveticus types and suggests that the paler markings of the latter are not due to fading with age. In addition, I do not believe that Eaton, had he been describing the strongly patterned form, would have dismissed it with the bare statement "the usual dark stripes", since the strongly patterned form is certainly not usual.

A sub-imago of the type-series of E. zelleri from Carinthia has unicolorous wings, and this led me to re-examine the ♂ genitalia of the type, and to compare it with males of the unicolorous form from Austria. Allowing for differences due to methods of preservation (the type having been pinned, the genitalia cleared in caustic potash and examined in glycerine, Dr. Pleškot's material being in alcohol), I am satisfied that the two are conspecific. At the same time there are certain differences between the ♂ genitalia of zelleri and helveticus, mostly not very definite and subject to some variation. Had there
been no difference in the sub-imaginal form, I should have adhered to my original view, but I am now of the opinion that we are dealing with two closely allied species. It must be admitted that the differences are not such as one would suppose to be necessary to prevent interbreeding, but it is quite possible that there is some ecological barrier present. The greater part of the material over the label "helveticus" in the British Museum (Nat. Hist.) appears to be correctly identified. In Dr. Pleskot’s material there is only one ♂ imago which I consider can be assigned to helveticus Eaton. Unfortunately this specimen was not collected by her and there is no information as to the type of sub-imago from which it originated. The strongly patterned sub-imago does not appear to belong to any described species and a full description is given below.

_Ecdyonurus austriacus_ spec. nov. (Figs. 1—8)

♂ imago (in alcohol). Eyes light grey. Head above dark brown, with a paler, transverse line beneath the ocelli, which are whitish, antennae fuscous, terminal style shading to whitish apically. Pronotum dark fuscous, meso- and metanota shining dark castaneous, somewhat paler on the sides. Fore leg fuscous, basal segment slightly less than one-third as long as the

Fig. 1—5. _Ecdyonurus austriacus_ spec. nov. (Austria, R. Ybbs).
Fig. 1. Wings of sub-imago. — Fig. 2—4. ♂ Genitalia (specimen in alcohol). — Fig. 2. Ventral. — Fig. 3. Penis, ventral. — Fig. 4. Penis, dorsal. — Fig. 5. Inner apical sclerite of penis, from another example (after treatment in caustic potash solution).

Wings faintly smoky hyaline, slightly yellowish at the base, pterostigma pale fuscous. Venation fuscous.

♂ Genitalia. Forceps-base more or less strongly toothed, the teeth often appearing as lateral productions from the attachment of the forceps. The margin of the forceps-base between the teeth only slightly produced, not reaching the level of a line between the apices of the teeth. Ventral surface of forceps-base moderately convex at centre. Forceps of usual form. Lobes of penis out-turned and rounded, only lightly sclerotized. Penis about as long as broad, stem less pigmented than in helveticus, more or less parallel-sided. (When detached from the forceps-base for figuring, the base of the stem tends to spread and give the false appearance of a tapering stem. Maceration in caustic potash solution also alters the relative proportions of the penis.) In ventral view, the inner margins of the basal sclerites are distinctly sinuous. The basal margin of the penis-lobe overlaps the lateral margin of the stem. In dorsal view, the upper apical margin of the basal sclerite is armed with a short, acute, inturned tooth and some setae. Outer sclerite curved, moderately long. Apical sclerite armed with numerous small teeth of uniform size along the apical margin from inner angle to at least half way. Basal margin of sclerite usually with two small teeth.

♀. There is at present insufficient bred material from which to make satisfactory descriptions.
♂ Sub-imago (in alcohol). Head pale ochraceous, fuscous between the ocelli, eyes lavender-grey, antennae pale fuscous. Pronotum pale ochraceous, faintly shaded with pale fuscous. Meso- and metanota pale ochraceous, with fuscous markings. Legs pale ochraceous, coxae and trochanters marked with fuscous, femora with a fuscous line along the ventral surface, anterior tibia fuscous, all tibiae fuscous at base, apices of tarsal segments finely bordered with fuscous. Abdomen above pale fuscous, joinings ochraceous, each segment with three pairs of small ochraceous spots — one pair at base near middle, one longitudinal spot near each lateral margin and one oblique spot on each side near the base of the lateral spot. Ventrally also pale fuscous, each segment with two pairs of ochraceous spots near the base, one pair elongate, oblique and divergent, the other pair smaller, circular, situated between the divergent spots. Cerci fuscous, penis ochraceous, forceps-base pale fuscous.

Fore wing medium fuscous, with a curved, transverse, zigzag pattern of whitish hyaline. Venation ochraceous. Hind wing medium fuscous, with a curved, transverse, hyaline band across the centre of the wing. (The specimen figured is a well-marked one.)

♀ Sub-imago. Resembling the male but with the head and pronotum more shaded with pale reddish fuscous. Abdomen distinctly tinged with reddish, apical margins of tergites faintly fuscous, basal spots not conspicuous.

Length of fore wing 13—16 mm.

♂ Type (Austria, Brodingbach, 700 m., 25. VIII. 1955, imago with nymph skin), ♂ paratype, sub-imago (Austria, Lunz, Rotmoosbach, 3. IX. 1955), ♀ paratype, sub-imago (Austria, Ybbs, Ois-Klaus, 26. VIII. 1955), in the British Museum (Nat. Hist.), presented by Dr. G. Pleskot. Paratypes also in the Naturhistorisches Museum in Vienna.

In the British Museum (Nat. Hist.), I have found only two examples of this species, a rather damaged ♂ imago from Switzerland, Pontresina, VII. 1911, T. A. Chapman and a ♀ sub-imago from Bergün, (Grisons), 24. VI. Dr. Pleskot has examples from the following localities in Austria: Lunz (Niederösterreich), Seebach, up to 900 metres, III—VIII.; R. Ois (upper part of R. Ybbs, ca. 900 m., 26. VIII. 1955; Brodingbach, 700 m., 25. VIII. 1955; Rotmoosbach, 1100 m., VII—IX; Herrnalm, 1300 m., 20. VIII. 1955, all collected by Dr. G. Pleskot. Niedere Tauern and Gesäuse, R. Enns and tributaries, 11 records, VI-IX, 1942—50, H. Franz.

The most satisfactory method of comparing this species with the others of the helveticus group seems to set out the differences in tabular form:

<table>
<thead>
<tr>
<th>Species</th>
<th>Sub-imaginal wings</th>
<th>Fore wing</th>
<th>Hind wing</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. zelleri</td>
<td>unicolorous grey.</td>
<td>faintly banded with brownish (? grey in life).</td>
<td>heavily margined with grey.</td>
</tr>
<tr>
<td>E. helveticus</td>
<td></td>
<td>faintly bordered with brownish (? greyish).</td>
<td></td>
</tr>
<tr>
<td>E. austriacus</td>
<td></td>
<td>grey, with a transverse, zigzag, white pattern.</td>
<td>pale, greyish at base, and heavily margined with grey.</td>
</tr>
</tbody>
</table>
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<table>
<thead>
<tr>
<th>E. zelleri</th>
<th>E. helveticus</th>
<th>E. austriacus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forceps-base usually toothed, space between the teeth not very wide, usually with a convex margin.</td>
<td>Forceps-base usually toothed, teeth often less developed than in zelleri, space between teeth a little wider, margin moderately to weakly convex.</td>
<td>Forceps-base strongly toothed, space between them wider, margin not or scarcely convex.</td>
</tr>
<tr>
<td>Stem of penis rather slender, longer than width of lobes.</td>
<td>Stouter, not longer than width of lobes.</td>
<td>as helveticus.</td>
</tr>
<tr>
<td>Ventral margins of stem of penis in ventral view straight or only slightly sinuous, converging from base to apex.</td>
<td>much as in zelleri.</td>
<td>strongly sinuous, converging strongly near base, then becoming more or less parallel.</td>
</tr>
<tr>
<td>Outer sclerite of penis usually rather short and broad, fairly strongly sclerotized and pigmented.</td>
<td>generally longer and narrower, usually less sclerotized.</td>
<td>generally longer, narrower and less sclerotized.</td>
</tr>
<tr>
<td>Armature of inner apical sclerite usually consisting of a few acute teeth, one generally larger than others.</td>
<td>teeth of varying size and number.</td>
<td>teeth usually more numerous and of uniform size.</td>
</tr>
<tr>
<td>Angle formed by outspread lobes and stem of penis smoothly rounded.</td>
<td>as in zelleri.</td>
<td>Angle abrupt.</td>
</tr>
<tr>
<td>Base of stem of penis on dorsal side with a somewhat triangular, hyaline area.</td>
<td>hyaline area short and transverse.</td>
<td>much as in zelleri.</td>
</tr>
</tbody>
</table>

It will be seen from the above table that no one imaginal character is entirely reliable to separate the three species, but the differences in the sub-imaginal wings and in the nymphs of the two species bred by Dr. Pleskot seem to me to indicate that we are dealing with three closely-allied species. Dr. Pleskot will be dealing with the nymphal characters in a separate paper. It is realised that the identification of imagines unaccompanied by sub-imagines or nymphs will offer considerable difficulties, but at present the only alternative would be to consider them as one species, which in view of the nymphal and sub-imaginal characters seems illogical.

Dr. Pleskot's imaginal material is preserved in alcohol, whereas that of the British Museum is pinned. This in itself makes comparison of the $\varphi$ genital structures difficult. At various times preparations have been made of the genitalia of a number of examples from the pinned collection, by clearing them in caustic potash solution. Some were mounted as microscope preparations in canada balsam and others are in glycerine. Unfortunately the drying and the maceration in caustic potash both cause a certain amount of distortion and, whilst the various sclerites can be examined fairly easily, the membranes between them tend to become stretched and the relative positions of the sclerites affected. In particular, the base of the penis may become appreciably wider and thus a normally parallel-sided stem may appear tapering. This fact must be
remembered when examining any of the figures given of the various type specimens. It is desirable therefore that continental students should make careful examination of alcohol-preserved specimens, bred from known sub-imagines, to see whether it will be possible to modify any of the qualified statements given in the above table.

It now becomes necessary to modify the synonymy of *E. helveticus* given in my 1942 paper.

_Ecdyonurus helveticus* (Eaton), (Figs. 9—12)


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Fig. 9—12. *Ecdyonurus helveticus* (Eaton).

Fig. 9. Wings of sub-imago (paratype, Switzerland, Valais, Val d’Illiez). — Fig. 10—12. ♂ Genitalia of type (treated with caustic potash solution and preserved in glycerine). — Fig. 10. Forceps and base, ventral. — Fig. 11. Penis, ventral. — Fig. 12. Penis, dorsal.

Fig. 13—15. *Ecdyonurus italicus* (Eaton). ♂ Genitalia of type (treated with caustic potash solution and mounted in Canada balsam).

Fig. 13. Forceps and base, ventral. — Fig. 14. Penis, ventral. — Fig. 15. Penis, dorsal.
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In the British Museum (Nat. Hist.) there are examples from the following localities:

Switzerland: Vaud, Vallorbe, 2500m., 3. VIII. 1908; Valais, Val d’Illiez, 3800–4000m., VIII. 1879, Dranse de Biot, Chardonnière, 4500–4830m., 1879; Bern, Interlaken, Habkern Tal, 2400m., 3. VIII. 1908; Grisons, Klosters, 12–20. VIII. 1927; Ticino, Lugano, VIII. 1925.

France: Puy-de-Dôme, Le Mont-Dore, 24. VI.–6. VIII. 1934; Basses Alpes, Digne, 8–11. VII. 1923; Hautes Alpes, Lauteret, 22. VIII. 1932; Haute Savoie, Samoëns, Chalets de Jouplane, 5100m., 29. VIII. 1879.

Italy: Tuscany, Apennino Pistojese, VII. 1882; Piedmont, Val Anzasca, VII. 1882.


Dr. Pleskot has a single ？imago from Austria: Gröbming (Ennstal), ca. 800 m., 26. VIII. 1949. H. Franz.

Ecdyonurus zelleri (Eaton) (Figs. 16–23)


Fig. 16–18. Ecdyonurus zelleri (Eaton). ？Genitalia of type (treated with caustic potash solution and preserved in glycerine).

Fig. 16. Forceps and base, ventral. — Fig. 17. Penis, ventral. — Fig. 18. Penis, dorsal.


In the British Museum (Nat. Hist.) there are the original type specimens from Carinthia and a rather broken male from France: Auvergne, 23. VII. 1879. Dr. Pleskot has examples from the following localities in Austria: Niederösterreich, Lunz,
Seebach, to 900 m., VI–IX (G. Pleskot); Oberösterreich, Salzkamergut, Traunstein, probably 1200 m., 28. IX. 1946 (H. Franz); Niedere Tauern, Ennstal, up to 1100 m., four localities, VII–IX. 1946–51. (H. Franz).

E. *epicordes* Demoulin from Greece appears to be synonymous with *E. zelleri* both in the form of the ♀ genitalia and in the nymph. In view of the poor condition and limited amount of the material, it might have been better to have left the specimen nameless.

Fig. 19–23. *Ecdyonurus zelleri* (Eaton) (Austria, Lunz).
Fig. 19. Wings of sub-imago. — Fig. 20–22. ♀ Genitalia (preserved in alcohol). — Fig. 20. Ventral. — Fig. 21. Penis, ventral. — Fig. 22. Penis, dorsal. — Fig. 23. Inner apical sclerite of penis, from another example (after treatment in caustic potash solution).