

## Secondary sexual characters in mayfly larvae and their evolutionary significance (Ephemeroptera)

TOMÁŠ SOLDÁN

Institute of Entomology, Czechoslovak Academy of Sciences, Praha

### Morphology, larval dimorphism, *Palingenia*, claws, ontogeny, subimago

**Abstract.** Secondary sexual characters occurring in the Ephemeroptera larvae are summarized and the differences between male and female larval claws in *Palingenia* are described and figured for the first time. The evolutionary significance of these characters in Ephemeroptera with respect to the subimaginal stage is discussed.

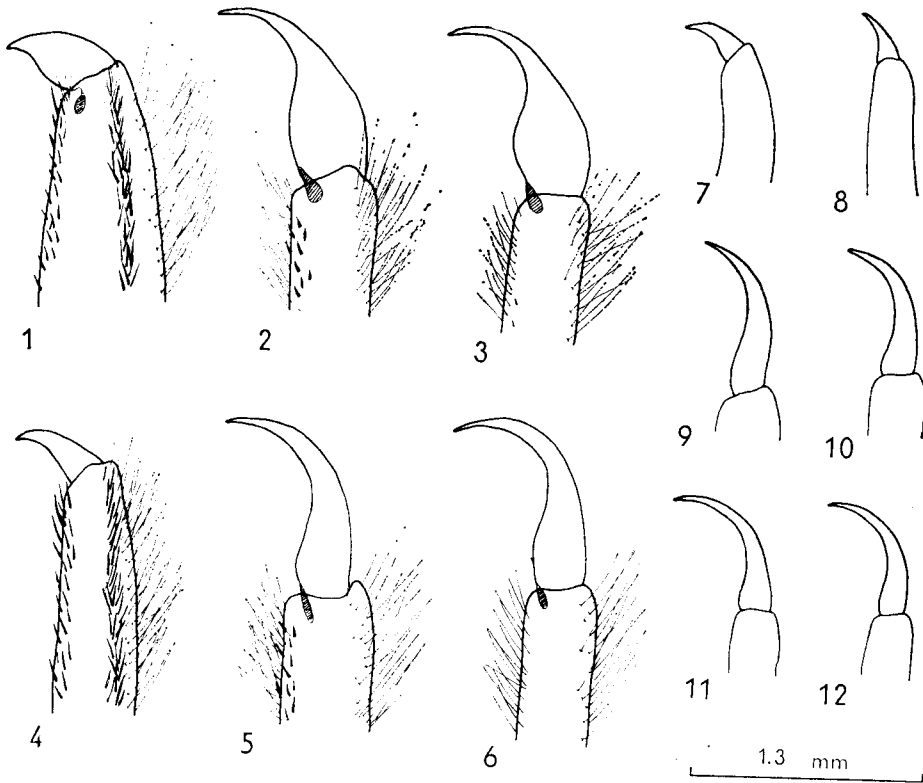
The sexual dimorphism of adults and subimagos is known to be well developed within the order Ephemeroptera. There are conspicuous differences in body size between males and females, besides the presence of turbinate eyes, size and colour of compound eyes and specialization of their dorsal portion, presence and shape of hind wings, arrangement of fore tarsi and claws, degree of degeneration of middle and hind legs, length of cerci and sometimes also in degree of the subimaginal moulting. Of course, some of these characters are more or less pronounced or even absent in individual families, e.g. in the Baetidae there are at least 5 secondary sexual characters developed (turbinate eyes in males, colour patterns of body and wings, arrangement of fore legs and length of cerci) while in the Caenidae only a single character is present (length of fore legs). For more details see monographs by NEEDHAM et al. (1935), LANDA (1969) and EDMUNDS et al. (1976).

Of the above adult and subimaginal secondary sexual characters, some characters are easily distinguishable even in the larval stage. Most larval characters are identical with those of adults. THIBAUT (1970) found distinct differences between male and female larvae of *Caenis* in the arrangement of bases of cerci which did not occur in adults. Larvae of remaining genera of the families Caenidae and Tricorythidae possess the same sexual dimorphism. Apart from some exceptions (e.g. undescribed genus of the Baetidae with males without turbinate eyes — Edmunds, pers. comm.) the sexual dimorphism in larvae is mostly manifested by differences in the arrangement or size of eyes. In adults the occurrence of these characters also varies from family to family and some of them are well pronounced in some families (e.g. female larvae are twice as long as males in the Euthyplociidae). The differences between male and female larvae in the arrangement of the eyes are often apparent even in younger larvae.

When studying the ecology and adult habits of *Palingenia fuliginosa* (GEORGI) in Eastern Slovakia I noticed a sexual differences in the arrangement of the larval claws. The claws of older male larvae are stout with considerably wide basis (fore legs) or considerably extended near the basis (middle and hind legs), claws are at most 2.5 times as long as wide. The claws of older female larvae are slender without any conspicuous extensions, about 3—4 times as long as wide (Figs. 1—6). Also, the tarsus of the fore legs of male larvae is about 1.5 times broader than that of female larvae. These differences begin to be apparent even in half-grown larvae although they are very slight (Figs. 7—12).

Most of the secondary sexual characters in mayflies evolved as an adaptation for mating flight and copulation. Since the male detects only those females approaching from above and does not show any reaction to females below, we can easily explain the specialization of the dorsal eye portion. The specialized eye area produces a superposition image useful especially in weak illumination. The specialized fore tarsi of males serve to clasp the female's thorax during copulation. Larger body size in females is undoubtedly due to the extremely high number of eggs. However, there is no explanation for the hindwing dimorphism in the Baetidae since the reduced hindwings are not functional in either males or females.

In mayflies, of which subimagos do not receive any nourishment and are extremely short-lived, the morphogenesis of secondary sexual characters is shifted into the larval stage. Since the compound eyes as well as the ocelli represent the definitive ones as in other exopterygotes, the specialization of the eyes begins early in the larval stages. Development of specialized male eyes



Figs. 1-13: Tarsal claws of larvae of *Palingenia fuliginosa* (Latorica river, Leles, East Slovakia). 1-6 - mature larvae. 7-12 - half grown larvae. 1-3, 7, 9, 11 - males. 4-6, 8, 10, 12 - females. 1, 4, 7, 8 - fore leg. 2, 5, 9, 10 - middle leg. 3, 6, 11, 12 - hind leg.

s completed before the subimaginal moult. As far as both male and female reproductive organs are concerned the same phenomenon has been observed (SOLDÁN, 1979).

On the other hand, the specialized male fore legs are formed in the last larval instars as those of pharate subimago, and especially in the subimago as those of pharate imago. Male fore legs may be as much as ten times longer. Based on data by ENDERS (1976), because of the relatively inelastic nature of the exoskeleton the usual growth increment between arthropod moults in a linear dimension ranges from 20% - 60%, MAIORANA (1979) proposes to explain the existence of subimaginal moult in the Ephemeroptera by the necessity of body appendages elongation (reproductive adaptation) which cannot be acquired during the larval stage. Contrary to growth of eyes, long male adult legs would presumably be disadvantageous to the larvae. This hypothesis (MAIORANA, 1979) concerning subimaginal moult in mayflies is in agreement with that of HINXON (1963) for the necessity of a pupal instar in endopterygotes - evagination and subsequent growth of wings cannot be completed in one moult.

The finding of differences in the arrangement of tarsal claws of *Palingenia* supports MAIORANA's (1979) hypothesis. In extremely short-lived *Palingenia* adults it is necessary to start the morphogenesis of male fore tarsi much earlier than in mayflies with relatively long-lived subimago (e.g. Heptageniidae, Leptophlebiidae, Ephemeridae, etc.). Wide claw bases and distal portions of fore tarsi in male larvae enable more effective folding of pharate subimaginal and imaginal tarsi during synthesis of a new cuticle before the subimaginal moulting because linear growth of the larval leg is impossible. Moreover, both subimaginal and imaginal structures of the legs develop nearly simultaneously (they can be dissected from mature larvae). Wider cerci bases in male larvae of *Caenis* (THIBAUT, 1970) are probably also due to more effective folding of pharate imaginal cerci which are at least 3-5 times longer than those of females. Contrary to *Palingenia*,

differences in the arrangement of male and female claws were not found in *Caenis* and *Oligoneuriella*, which also represent genera with extremely short-lived subimagos.

However, the existence of one subimaginal molt in the Ephemeroptera represents a complex problem. Mayfly Palaeozoic ancestors possessed several instars with functional wings and without reproductive morphological adaptations resembling those of recent Ephemeroptera, although the relationships between moulting and sexual maturity remained uncertain (KUKALOVA-PECK, 1978). Most probably also the ecological and behavioural factors formed the necessity of subimaginal stage retention (cf. SCHAEFFER, 1975).

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#### Вторичные половые признаки у личинок поденок и их эволюционное значение (Ephemeroptera)

Морфология, диморфизм, *Palingenia*, коготки, онтогенез, субимаго

**Резюме.** Дается обзор вторичных признаков, встречающихся у личинок поденок и впервые дается описание и изображение различий между коготками личинок самцов и самок рода *Palingenia*. Обсуждается эволюционное значение вторичных половых признаков поденок в особенности в отношении к стадии субимаго.

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*Author's address:* Dr. T. Soldán, Entomologický ústav ČSAV, Viničná 7, 128 00 Praha 2, Czechoslovakia.