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THE SUBIMAGO OF EPHORON LEUKON WILL., AND A DISCUSSION OF THE IMAGO INSTAR. (EPHEM.)

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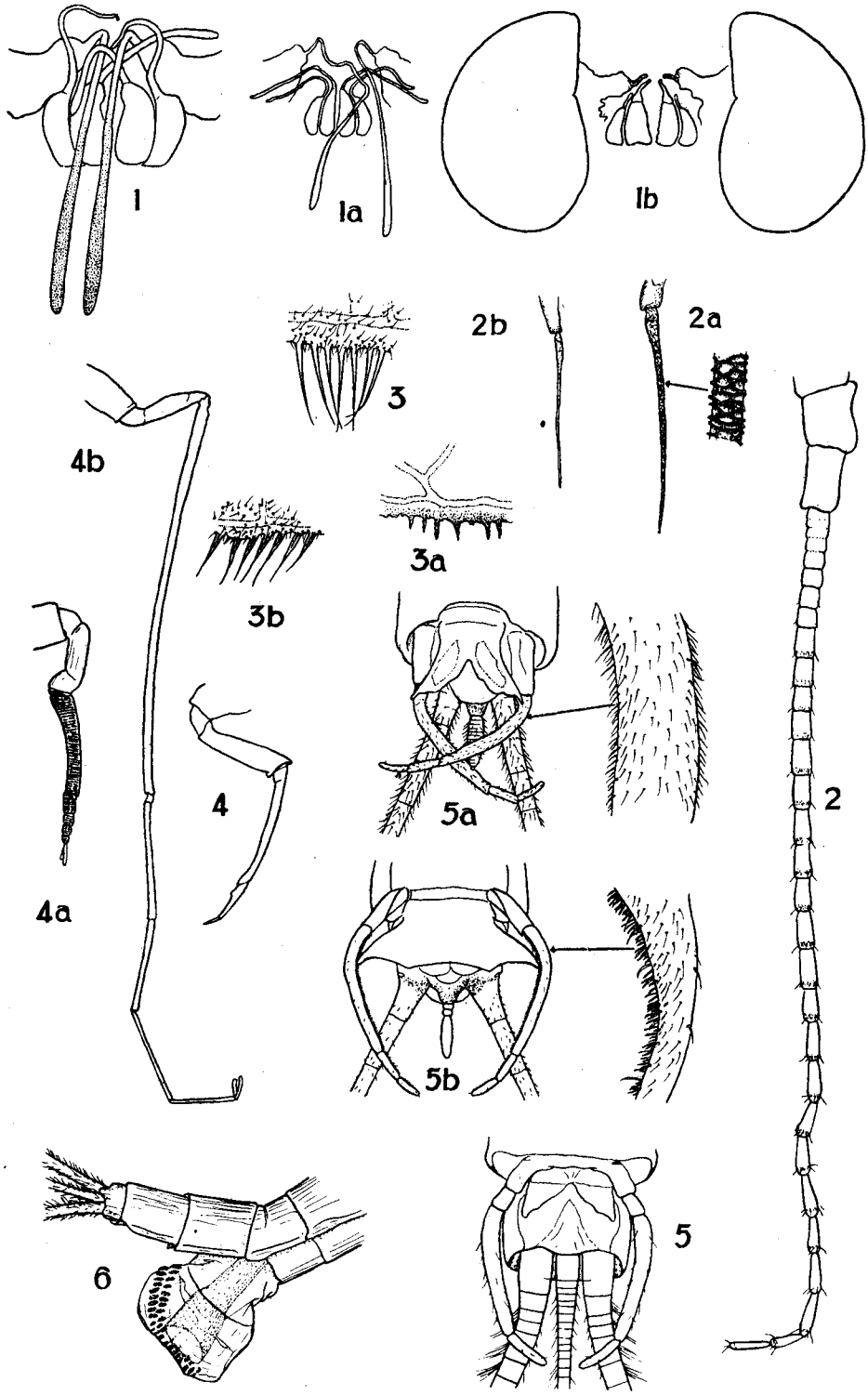
Lameere (1917), in a paper dealing with the evolution of mayflies recognizes the moult between subimago and imago as a mere delamination of the outer layer of cuticle resulting in a lighter more fragile imago. Needham (1935) agrees with this contention and states that the subimago "does not represent a growth period and is therefore not a true instar." Further, "It is only a casting of the delaminated, hairy outer cuticle." This is a recent view and at variance with the more conventional one that both the subimago and imago represent separate instars.

In a study of subimago and imago males and females of *Ephoron leukon* several points have been observed which would seem to be in disagreement with Lameere's and Needham's conclusions and support the more conventional view.

Mouth parts. In figs. 1, 1a and 1b are shown the mouth parts of the female, subimago male and imago male respectively. In the subimago male these parts are prominent as pendant filaments and in the female they are similar in form but of larger size. In the imago male all the parts are much aborted having very different proportions than in the subimago or female. There is some asymmetry in the mouth parts of certain individuals but not as marked as that described by Murphy (1922) for *Hexagenia recurvata* Morg.

Antennae. Figs. 2, 2a and 2b are of the antenna of nymph, subimago male and imago male respectively. In the subimago the antenna is much reduced from the condition found in the nymph, its surface is wrinkled or sculptured, as shown in the enlarged figure, and terminates in a scar. This scar is some of the material of the distal part of the nymphal antenna, which adheres when this part is dropped in the change from nymph to subimago in the manner described by Lubbock (1867). The antenna of the imago male is more slender than in the subimago, has a smoother surface and lacks the terminal scar.

Forelegs. These structures in the female, subimago male and imago male are shown in figs. 4, 4a and 4b, respectively. In the female the foreleg is like the foreleg of the nymph in having only one tarsal segment and a single tarsal claw. This peculiarity is found only in the foreleg, the other legs in the female being normal. The foreleg of the subimago male is a short thick appendage with five segmented tarsus and pair of tarsal claws. Within the tibia and tarsus may be seen the corresponding segment of the imago, greatly folded. In the imago there is a great elongation of the leg and this lengthening takes place in the tibial and tarsal segments and not in the femur. Two tarsal claws of much the same type as in the subimago are present and there are a few small setae particularly near the joints.



EPHORON LEUKON WILL.

Wings. Figs. 3, 3b and 3a illustrate a part of the posterior border of the mesothoracic wing of the female, subimago male and imago male respectively. The female and subimago male have minute setae (microtrichiae) scattered over the surface of the wing and over the general surface of the body. The wings also have a row of large processes along the posterior border of a similar type in both sexes. In the imago male the small setae are lacking on the surface of the wing but along the posterior border are processes with toothed edges corresponding in position with the longer processes of the previous instar.

Genitalia. The ventral aspects of the genitalia of the male nymph, subimago and imago respectively are shown in figs. 5, 5a and 5b.

In the change from nymph to subimago the median caudal filament is greatly shortened by the dropping of the distal portion. The resulting filament is indistinctly segmented, hairy and terminates in a scar which has the same significance as the scar at the end of the antenna of the subimago. In the imago this scar and the hairs are lost and the segmentation of the median filament is changed, two distinct segments appearing in the middle. The claspers of the imago are more slender than those of the subimago. Along the median border in the imago is a dense row of stout blade-like setae, with other small setae scattered over other parts of the clasper.

Fig. 6 is a lateral view of a female which has already discharged the eggs from the right ovary. A large sac has been extruded between the venters of segments 7 and 8 and this sac is continuous with the outer layers of the body wall. An oviduct leads down into this sac and the eggs are passed through the open end of the oviduct into the sac. By rupture of the sac wall the eggs escape to the exterior. In the specimen figured the rupture occurred on the medial or far side of the sac and is indicated by dotted lines in this position in the drawing.

There are a number of mayflies which it is known do not shed the subimago skin. The female of *Ephoron* does not moult in the winged condition whereas the male does moult a few moments after emerging from the nymphal exuvia. The female suggests in many ways a subimago. The long filamentous mouth parts are similar to the mouth parts of the subimago male and not to those of the imago; the wings are covered with small setae and are provided with a series of large setae along the posterior border as in the subimago male. The curious sac enclosing the opening of the oviduct is continuous with the outer cuticle and suggests that the outer layer of this sac is in reality the subimaginal cuticle through which the oviduct does not open thus necessitating the escape of the eggs by rupture of the sac. In most mayflies where the adult is definitely an imago the eggs issue freely from the open ends of the oviducts. The foreleg of the female is unlike the foreleg of either the subimago or imago male and more closely resembles the leg of the nymph in which there is also a single tarsal segment and one terminal claw. The mesothoracic and metathoracic legs of the female are normal. The evidence seems to indicate that the female of *Ephoron lukon* is a subimago.

The imago male is in the author's opinion a definite instar and is not arrived at merely by a delamination of the outer layer of cuticle of the subimago. It is quite true as Needham points out that there is no further growth but then

the subimago does not feed and its duration is so brief that growth could hardly be expected. On the other hand there are quite striking morphological changes which are better criteria of an instar than growth. One of these changes is the loss of most of the small setae from the surface of the insect including those of the wing. This fact has strongly influenced Lameere in his belief that the imago results merely from the delamination of the outer cuticle. There are other changes however which it would be very difficult to explain on this hypothesis. The great reduction of the mouth parts in the imago seems hardly explainable on the basis of the delamination hypothesis. If this were the case we would expect that these parts would retain much the same proportions. The change in the foreleg is very striking and it is significant that the tibia and tarsus change their proportions radically and not the femur. In the subimago the imaginal parts may be seen greatly folded within and it is hard to explain this by postulating delamination and subsequent stretching of the inner layer of cuticle. It is difficult to understand how turgor could account for this lengthening of the tibia and tarsus, as has been suggested. The lengthening has already taken place within the subimago cuticle and the elongated segments appear folded up inside. Turgor would explain the unfolding of the already lengthened segments but not the growth which has preceded the shedding of the cuticle. Further there are some small setae persistent on the foreleg in the imago.

The most convincing evidence, of the validity of the imago instar is found however in the structure of the male claspers. In the subimago these structures are provided with setae. In the imago there are still many setae present and these are particularly well developed and enlarged along the medial border. The change in the median caudal filament from subimago to imago is also fairly conclusive. The greater differentiation of segments and elimination of the terminal scar implies definite excuviation rather than delamination.

Lameere is of the opinion that the subimago is the real adult and that it is much closer to the ancestral adult of fossil relatives than is the imago. There seems to be a difficulty in accepting this statement in that the present day mayflies with very few exceptions have both subimago and imago stages; it is a universal phenomenon except in a few highly evolved types which remain as subimagos in one or both sexes, or which have only a partial shedding of the subimago cuticle. The primitive members of the order have both subimago and imago and if the imago were not a true instar one would expect that it would be absent in primitive rather than in highly specialized forms. It seems a more tenable hypothesis that the imago is the adult and that in a few highly specialized forms reproduction is possible in the subimago (e.g. female of *Ephoron*) by some special device and that in these species it is not necessary that the development proceed further than this point.

The number of instars in mayflies is large and each stage is extremely well adapted to its environment. The period of emergence from the water is a critical one in the life cycle and this takes place at the time of the emergence of the subimago. In some cases which are rather exceptional the nymph crawls out of the water before the subimago appears; in the majority of cases the nymph comes to the surface of the water and there the subimago emerges but in some, e.g.

Iron, the subimago leaves the nymphal exuvia some distance below the surface of the water and crawls to the surface with wings completely expanded. In such cases there must obviously be some device for preventing the wings and other fragile parts from becoming wet. Even in species which emerge at the surface there is the danger of the wings becoming wet particularly in taking flight. The hairy surface of the body, legs and wings of the subimago and the sculptured condition of the antennae in this stage would effectively prevent such wetting and enable the insect to successfully come through this hazardous period in its life cycle. The development of another instar after emergence from the water, with thinner cuticle and lacking the hairy covering is a distinct advantage for the mating flight, making the insect much more buoyant. More data should be gathered on this interesting phenomenon but the weight of the evidence so far seems to indicate that the subimago and imago are separate definite instars and that the subimago is especially adapted for emerging from the aquatic environment.

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EXPLANATION OF PLATE 2.

Figs. 1, 1a, 1b. Mouth parts of female, subimago male and imago male. Figs. 2, 2a, 2b. Antenna of male nymph, subimago and imago. Figs. 3, 3a, 3b. Posterior border of mesothoracic wing of female, subimago male and imago male. Figs. 4, 4a, 4b. Foreleg of female, subimago male and imago male. Figs. 5, 5a, 5b. Genitalia of male nymph, subimago and imago. Fig. 6. Female egg-sac extruded.