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LÉG ABCISSION AND ADULT *DOLANIA* (EPHEMEROPTERA: BEHNINGIIDAE)

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ABSTRACT

Legs of male imagos and female subimagos of *Dolania americana* Edmunds and Traver are described. Distal segments of meso- and metathoracic legs of males break during the subimaginal molt and remain in the cast exuviae. Leg abscission is probably a method to ensure rapid completion of the subimaginal stage in this short-lived mayfly.

RESUMEN

Se describen las patas de los imagos machos y los subimagos hembras de *Dolania americana* Edmunds y Traver. Los segmentos distales de las patas meso- y metatorácicas de los machos se rompen durante la muda subimaginal y permanecen en la exuvia. La abscisión de las patas es probablemente un método que asegura la conclusión rápida del estado subimaginal en esta efímera de vida de la mosca de mayo.

The descriptions of male imagos and female subimagos of *Dolania americana* Edmunds and Traver, the only North American member of the Behningiidae, have been published in parts. The wings, male genitalia, and female subimaginal head are illustrated in Edmunds *et al.* (1976), and the female abdomen and fore legs in Peters & Peters (1977). The only formal description of any adult behningiid is that for *Behningia lestagei* (?) Motas and Bacesco by Keffermüller (1959).

Herein, we describe the legs of subimagos and imagos of *Dolania*. Interestingly, the tarsi and claws of the meso- and metathoracic legs of the male imago are rarely attached

to the mayfly. They can be found in subimaginal exuviae, having broken off during the molt (parts of cerci may also break off). Fore legs are intact and functional in all stages. Descriptions of the reconstructed legs follow based on specimens in alcohol:

Male imago (Fig. 1-2). Prothoracic legs (Fig. 1-Im-I): tibiae a little longer than femora; tarsi one-segmented, sometimes with annulated appearance, a little less than 0.5 length of tibiae. Mesothoracic legs (Fig. 1-Im-II): tibiae a little shorter than femora; tarsi 2-segmented, segment one a little longer than tibiae, segment 2 about 0.25 length of segment 1. Metathoracic legs (Fig. 1-Im-III A): coxae well developed, elongated; tibiae small, less than 0.25 length of femora; tarsi 2-segmented, segment one 5-6 times length of tibiae, segment 2 about equal length of tibiae. Claws of all legs consisting of very small dactyl only (Fig. 2). Coxae, trochanters and base of femora of pro- and mesothoracic legs with well sclerotized areas, sclerotized rod along mid-line of coxae-trochanters of metathoracic legs weak in some specimens; femora of prothoracic legs with a well sclerotized macula at apex, remaining segments weakly sclerotized; femora and remaining segments of meso- and metathoracic legs variable, weakly sclerotized to membranous, tarsi and claws often flagellar, tarsi and claws usually separated from tibiae near base of tarsi; *if abscised*, tibiae and femora of mesothoracic legs and all remaining segments of metathoracic legs contracted, sometimes distorted to unrecognizable (Fig. 1-Im-III B).

Male subimago (Fig. 1-Sb). Legs similar to those of male imago except: tibiae and tarsi of prothoracic legs shorter, a membranous extension present on mesothoracic tibiae, and claws of meso- and metathoracic legs bulbous. All segments distinct and sclerotized to some degree.

Female subimago (Fig. 3). Coxae, trochanters, and femora of all legs similar to those of male imago; tibiae of prothoracic legs less than 0.25 length of femora, sometimes appearing fused with tarsi; tibiae of mesothoracic legs shorter than femora, membranous except at base, with apical membranous extension; tibiae of metathoracic legs less than 0.33 length of femora; tarsi of all legs membranous, flagellar, variable; claws absent or appearing as weak annulation at apex of membranous tarsi in some specimens.

Recent studies by Dr. E. L. Smith have homologized insect leg segments with those of other arthropods (Snodgrass 1935). Kukulová-Peek (1983, 1985) used this terminology for Paleodictyoptera and fossil mayflies; in fact, the patella was first discovered in fossil insects by Kukulová (1970, 1971). Some terms are applicable to recent mayflies, particularly the segmentation of the fused patello-tibia (commonly called the tibia). The separation of the male leg segments of *Dolania* occurs either at the patello-tibial suture or distal to the tibia (basitarsus is fused to tibia). Dr. Smith (pers. comm.) also notes that "claws" of male imagos and subimagos consist only of dactyls, and that annulations of the male prothoracic tarsi represent vestiges of tarsal segmentation.

We examined meso- and metathoracic legs of 324 male imagos collected in 8 samples on 6 days and found 5.6% ($5.7 \pm 4.6\%$) had one intact leg: 4 retained a mesothoracic leg and 14 retained a metathoracic leg, but none had more than 1. Quantitative exuvial results are not included because the exuviae of subimagos are fragile and many legs were broken off.

From the description by Keffermüller (1959) and specimens we have seen, the abscission of the meso- and metathoracic tarsi and claws also occurs in male imagos of *Behningia* and may be a derived character of the family; however, imagos of a 3rd genus, *Protobehningia*, are unknown (Tshernova & Bajkova 1960). Leg abscission does not occur in males of most other genera of short-lived adult mayflies examined (*Homoeoneuria*, *Tortopus*, *Ephoron*, *Caenis*, *Brachycercus*, *Tricorythodes*) although segments of these legs are sometimes membranous and apparently non-functional. However, as mentioned by Needham & Murphy (1924), the meso- and metathoracic legs of males and females of *Campsurus* are reduced to stubs showing the "coxa, trochanter,

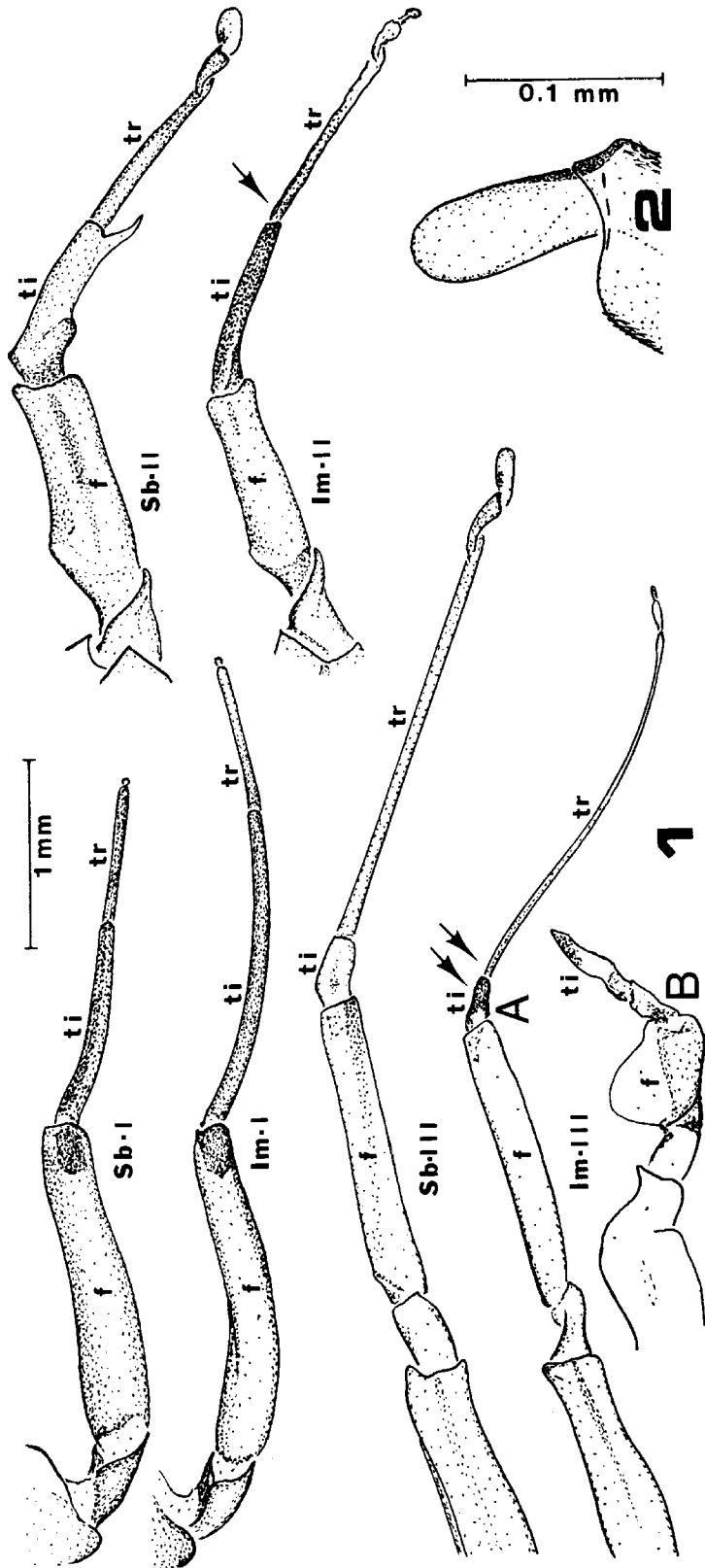


Fig. 1. Pro- (I), meso- (II), and metathoracic (III) legs of male *D. americana*. Sb, subimago; Im, imago. Arrows mark points of abscission. Abbreviations: f=femur, ti=tibia, tr=tarsal segments.

Fig. 2. Fore claw of male imago.

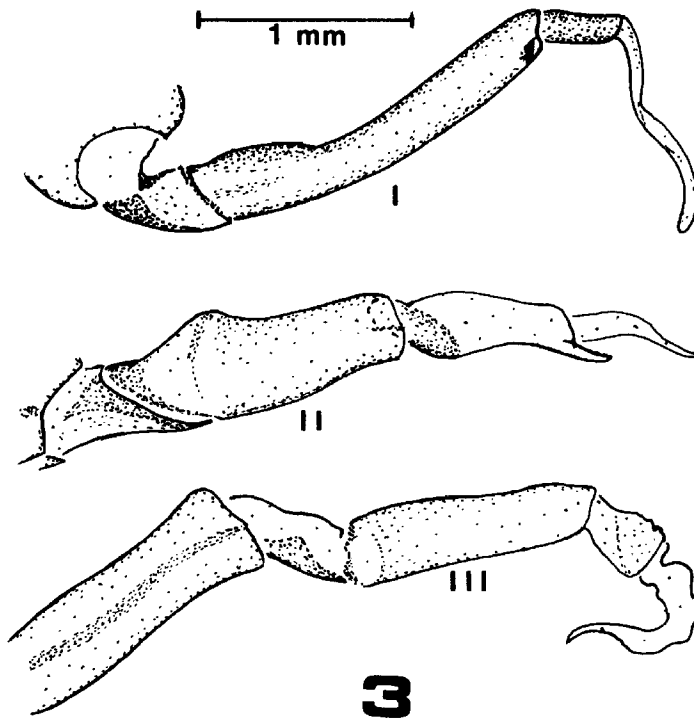


Fig. 3. Legs of female subimago of *D. americana*. Legend as in Fig. 1.

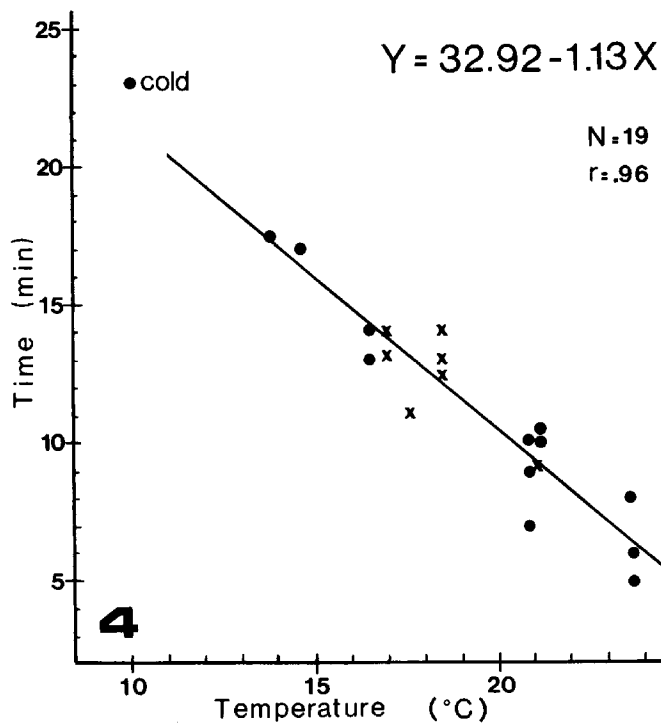


Fig. 4. Duration of male subimago of *D. americana*. Regression was computed from reared material (X) and 1983-1984 field-collected material (solid circles), except for molt labeled "cold" as discussed in text.

and a rudiment of the femur." The biology of *Campsurus* is little studied and it is not known if this condition results from abscission.

Functional segmented legs with full claws are the ancestral condition in mayflies (Kukalová 1968, Kukalová-Peck 1985). Legs of *Dolania* nymphs and female subimagos have either weak annulations at the apex of tarsi or no claws at all, and legs of females differ from those of nymphs mostly in the membranous condition of distal segments (Fig. 3). The fore legs of the male imago appear functional and all segments are present (tarsal segments fused); the male imago flies from completion of the subimaginal molt until death and has no apparent use for meso- and metathoracic legs however, we have no information on possible aerodynamic advantages resulting from abscission. Only the male subimago retains anything resembling the ancestral, functional, segmented leg.

The life span of subimagos is temperature dependent (Lyman 1944, Thomas 1969). The subimago of male *D. americana* lasts from 5 to 23 min. and is linearly correlated with temperature at temperatures above 11°C (Fig. 4). The regression line in Fig. 4 was computed for reared subimagos ("X" in Fig. 4) and for field-collected subimagos for 1983-1984 (solid circles) where temperatures were recorded by a thermometer with a small probe (accuracy $\pm 0.1^\circ\text{C}$) laid next to the molting mayfly and where specimens were not touched. Time was recorded from emergence to completion of the subimaginal molt, as measured as the time the imaginal wings came free from the exuviae. In general, the equation $[30 - X(\text{air temperature in } ^\circ\text{C})]$ will give duration of the subimago stage of males in minutes.

The molt labeled "cold" in Fig. 4 was not included in the regression line because molting success is greatly reduced at 10.2°C. Of 36 male subimagos observed, only 20 were able to complete the molt at that temperature. These males were on sand some distance from the river, the sand being warmer than the air (air temperature was 8°C). Another group of male subimagos (>70) attracted to light on wet sand at the shoreline molted successfully; there, the sand had been warmed by river water to 11.2 to >12°C.

Thus, in about 15 min. the male *Dolania* is in 3 life history stages. Male meso- and metathoracic legs progress from a derived nymphal state (no claws) to an ancestral subimaginal state (functional legs with claws) to a derived imaginal state (no legs). The retention of the ancestral condition in the intermediate instar suggests that functional male subimaginal legs are critical to the species. While the possibility of an in-flight molt for *Dolania* is not totally rejected (Peters & Peters 1977), it seems most improbable considering these morphological steps. Subimagos of most mayfly genera, except some Oligoneurinae, must interrupt flight to molt (Edmunds 1956).

When reared in the laboratory, *Dolania* subimagos flew from the water surface to the nearest perch and remained there until the imaginal molt. A shortage of supporting field observations of subimagos on vegetation results from inadequate light for observation, the subimago living sometime between 1.5 to 0.75 h before sunrise. Some males do molt on the water, but this is less common and may be accidental.

Speculation on an in-flight molt resulted from observations of subimaginal exuviae on trailing caudal filaments of imagos. This occurs because the male takes flight as soon as the wings are free (the exuvia will eventually fall off) and reflects not on subimaginal, but on male imaginal behavior.

Reproductive stages of *D. americana* emerge synchronously and mate in the air in mass swarms. Although many mayflies are capable of parthenogenesis (Degrange 1960), only fertilized eggs of *Dolania* can develop (unpubl. rearing data). For the individual, the mass swarm increases chances of finding mates and reduces probabilities that any individual will be consumed by predators before mating and oviposition (Sweeney & Vannote 1982).

Females of *Dolania* do not molt but mate immediately after emergence with available males. Timing of the emergence of male subimagos anticipates that of females so

that most males complete the subimaginal molt before female emergence (Peters & Peters 1977). Males that are already imagos when females emerge presumably have the first and the greatest number of mating opportunities. In this situation, time is critical and males might be expected to dispense with neat molts and useless legs and to take flight as soon as physically able. Reproductive success favors the male that is ready, or "a male in the air is worth two in the bush." This strategy is beneficial to both sexes, according to Wiklund & Fagerstrom (1979) who modeled early male emergence in Lepidoptera: males maximize the number of matings and females minimize the time between emergence and oviposition.

ACKNOWLEDGMENTS

We sincerely thank Dr. G. F. Edmunds, Jr. and Mr. T. J. Fink, University of Utah, Dr. E. L. Smith, California Academy of Sciences, and Dr. M. D. Hubbard, Florida A&M University, for critical review and suggestions on the manuscript, and Mr. G. J. Wibmer for translation of the abstract. We gratefully acknowledge the cooperation and assistance of the Florida Game and Freshwater Fish Commission and the Florida Division of Forestry. The research was supported by a research program (FLAX 79009) of CSRS, USDA, to Florida A&M University.

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