

INTERSEXUALITY AND HOMEOTIC MANIFESTATION OF SECONDARY SEXUAL CHARACTERS IN *BAETODES* (EPHEMEROPTERA: BAETIDAE: BAETINAE)

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ABSTRACT

Several specimens of an undescribed species of *Baetodes* from a single locality in Panama exhibit teratologies of secondary sexual characteristics. Seven specimens display the morphological characteristics of intersexes. One specimen, a male imago, displays a supernumerary clasper on the eighth abdominal segment.

This homeotic manifestation of male gonopods (supernumerary forceps) is consistent with the data from an Upper Carboniferous nymph that originally abdominal segments one to nine carried telopodites and now only those on segment nine normally develop (as gonopods) except in cases of developmental anomaly caused by genetic or unknown environmental factors. It is impossible to tell what might be causing the high frequency of morphological aberrations in these *Baetodes*.

INTRODUCTION

A number of Ephemeroptera which were collected by Dr. Henk Wolda in a light trap run from January to May, 1980, as part of an environmental impact assessment of a hydroelectric project on the Río Changuinola at Corriente Grande, Bocas del Toro Province, Republic of Panama were sent to us for identification. Among these Ephemeroptera were 65 specimens of an undescribed species of *Baetodes* Needham and Murphy, 1924 (Baetidae: Baetinae).

These specimens, collected from 13–II to 22–IV, 1980, by H. Wolda, can be placed in the genus *Baetodes* based on extensive rearing efforts (by RWF) in Panama. Because the taxonomy of this genus is somewhat confused and is based largely on the morphology of the nymphs, most adults cannot yet be placed to species. These specimens do not prove to be exceptions and must be placed simply as *Baetodes* sp. at this time.

DISCUSSION

The genus *Baetodes* is distributed throughout the Neotropical Region and extends northward into Texas and Arizona, USA. The species under discussion, from Río Changuinola, is known only from Panama, and can be characterized by the following combinations of characters:

Normal male. Turbinate eyes cylindrical; height equal to diameter, apex and base of equal diameter (Fig. 2). Thorax dark reddish brown. Abdomen slender with segments 1–6 hyaline white, washed with tan; segments 7–10 dark reddish brown. Genitalia reddish tan, forceps paler apically. Basal segment of forceps produced on the inner apical margin, as is characteristic of adult *Baetodes* (Flowers 1986).

Normal female. Head lacking turbinate eyes (Fig. 3). Thorax and abdomen reddish brown. Abdomen robust, broader at base than apex.

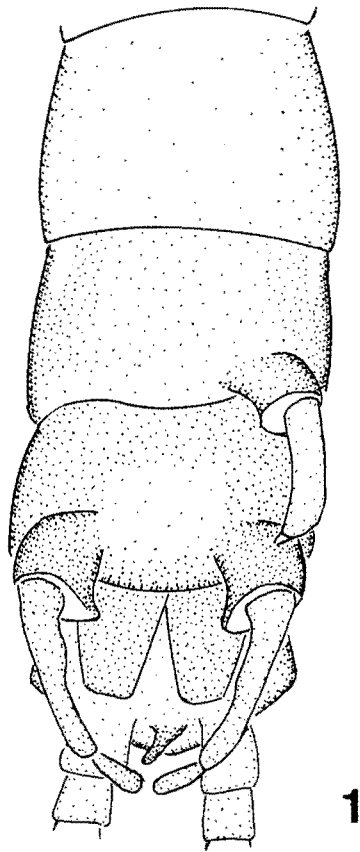


Fig. 1. Supernumerary male (*Baetodes* sp. from Changuinola); ventral view of abdomen.

The genus *Baetodes* was characterized and described in more detail and illustrated by Edmunds, Jensen, and Berner (1976) and by Flowers (1986).

Eight of these specimens of *Baetodes* were found to be morphologically aberrant and exhibit various teratologies of secondary sexual characteristics. One of the specimens, a male imago, bears one extra, supernumerary, clasper on the eighth abdominal segment. Seven other specimens display some of the morphological characteristics of intersexes. All of these specimens are deposited in the collections of the Entomology Department of Florida A&M University in Tallahassee, Florida, USA.

Male imagoes of Ephemeroptera are characterized by the presence of a pair of gonopods (often referred to as "forceps" or "claspers") on the ninth abdominal segment. These gonopods, typi-

cally of two to four segments, are used by the male to grasp and hold the female during copulation and intromission in flight. One male specimen of these Panamanian *Baetodes* bears a supernumerary gonopod on the left side of the eighth abdominal segment. This extra, or supernumerary, forceps half can be considered a homeotic (or "atavistic") manifestation of the primitive state in which forceps appeared on multiple segments of the abdomen of the male.

Supernumerary male. 12-18-III-1980. Head, thorax and basal half of abdomen developed as in normal male. Color pattern as in normal male. Genitalia with normally developed forceps on segment 9 and third gonopod on the left apical angle of segment 8. This supernumerary gonopod has three distinct segments but is three-fifths the length of the normal forceps. The first segment is expanded medially (resembling the condition on the normal forceps); the second segment is cylindrical, narrowed at apex; and the third segment is greatly reduced, present as a minute knob (Fig. 1). Homeotic manifestation of male gonopods (or "supernumerary forceps") has been reported only three times before in Recent Ephemeroptera.

Tiensuu (1937) reported a Finnish specimen of *Leptophlebia marginata* (Linnaeus, 1767) collected by J. E. Aro which bore a moderately well-developed left gonopod on abdominal segment eight. Tiensuu discussed the possibility that this supernumerary gonopod represented an "atavism", or partial manifestation of the primitive condition of appendages on all segments of the abdomen.

Codreanu and Codreanu (1938) reported two male imagoes of *Baetis melanonyx* (Pictet, 1843) [which they reported as *Baetis kulindrophthalmus* Bogoescu, 1933 and Soldán and Landa (1981) referred to as *Baetis alpinus* (Pictet, 1843)] from the Carpathian Mountains of Romania with supernumerary forceps on the eighth abdominal segment.

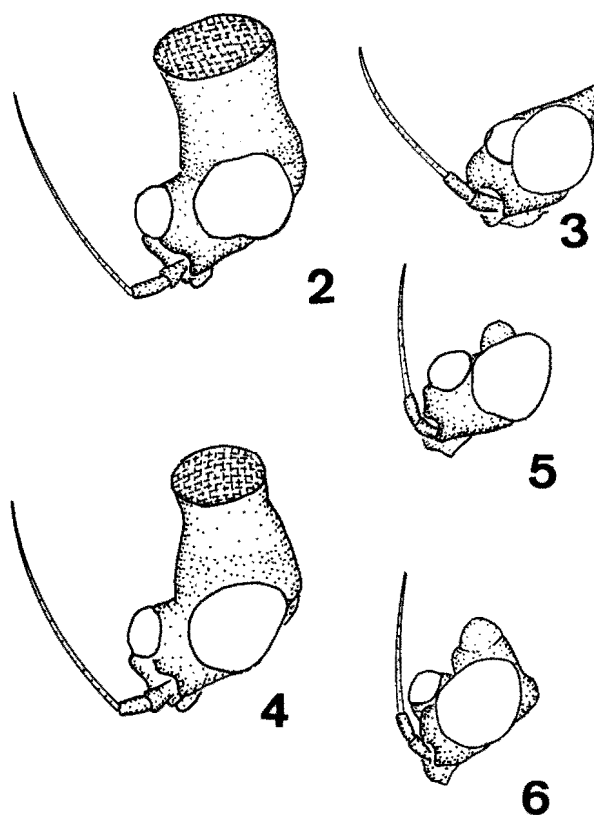
Soldán and Landa (1981) also reported a specimen of *Baetis vernus* (Curtis) from central Bohemia, Czechoslovakia, with a reduced left gonopod on abdominal sternum eight, in addition to the normal pair on sternum nine.

The ten serially homologous abdominal segments of Ephemeroptera appear to share an initially common pattern of development, after which differentiating influences switch development into one of several paths. Homeotic development, defined as the condition in which one body part is replaced by another having the same evolutionary or developmental origin (c.f., Bateson 1894, Postlethwait and Schneiderman 1973, Futuyma 1979, Gould 1980, 1985), is usually considered to be caused by a mutation. However, in practice there is often no way, without rearing subsequent generations, to determine if there is a mutation or simply an alternative scheme of development caused by some environmental factor. It is the physiology of animals, including their hormonal activity, that is first and inevitably affected by environmental changes (Matsuda 1982).

Kukalová-Peck (1985) reported the presence of serial abdominal telopodites which she found on the fossil nymph of *Bojophlebia prokopi* Kukalová-Peck (1985) a gigantic (nymph known with 92 mm body length; adult known with wingspread of 45 cm!) Upper Carboniferous mayfly from Bohemia, Czechoslovakia. These serial abdominal telopodites, composed of probably seven segments, occurred on the first nine of the ten abdominal segments, were segmented and stylus-like, and the last pair was transformed into claspers. The nine abdominal segments also bore plate-like gills. The presence of telopodites on abdominal segments one through nine of very early mayflies is strong evidence that the gonopods of present mayflies were derived from the abdominal legs of primitive Ephemeroptera and that gills were not.

The homeotic manifestation of male gonopods (supernumerary forceps) reported here is consistent with the findings of Kukalová-Peck (1985) that originally abdominal segments one to nine carried telopodites. At present day, in Recent Ephemeroptera, only those telopodites on segment nine normally develop (as gonopods, or forceps) except in cases of developmental anomaly (homeosis) caused by genetic or unknown environmental factors.

It has been suggested by some (e.g. Handlirsch



Figs 2-6. Head of specimens of *Baetodes* sp. from Changuinola. 2, normal male. 3, normal female. 4, intersex 1. 5, intersex 6. 6, intersex 7.

1921) that the Thysanura are closely related to the Ephemeroptera due to the close similarity of the mouthparts. Interestingly, the Thysanura are the only Recent Insecta which have representatives with paired styli and a pair of gonapophyses on the eighth abdominal segment of the male.

It is interesting that four of the five known specimens of Recent mayflies with supernumerary forceps belong to the family Baetidae, which is first known from as long ago as the lower Jurassic, more than 175 million years B.P. (Tshernova 1980). The fifth known mayfly with a supernumerary forceps belongs to the Leptophlebiidae, a family known from at least 50 million years B.P. (Hubbard and Savage 1981).

Seven other of these *Baetodes* specimens appear to be intersexes. Five are predominately male and 2 are predominantly female.

These intersex individuals deviate from normal

males and females of *Baetodes* in the variable development of the turbinate eyes, the size of the abdomen, the color of the abdomen, the presence of eggs, and the development of the male genitalia. In the descriptions below individuals are characterized as predominantly male or female based on their overall appearances.

Intersex 1: 12-18-III-1980. Predominantly male. Turbinate eyes constricted in apical 1/3: apical diameter approx. 3/4 basal diameter (Fig. 4). Thorax as in normal male. Abdomen stouter than in normal male; segments 1-4 hyaline; segments 5-10 bearing eggs, reddish brown. Male genitalia present, normally developed.

Intersex 2: 2-8-IV-1980. Predominantly male (?). Right tuberculate eye normal, left tuberculate eye 2/3 height of right eye, dome shaped, facets missing. Thorax as in normal male. Abdomen with segments 1-6 hyaline, segments 7-10 broken off and missing.

Intersex 3: 5-11-III-1980. Predominantly female. Head with turbinate eyes reduced to small tubercles. Thorax normal. Abdomen tan, filled with eggs; segments 7-10 reddish brown. Male genitalia present; forceps length somewhat reduced from normal length.

Intersex 4: 19-25-III-1980. Predominantly female. Head shrivelled but traces of turbinate eyes as in Intersex 3. Abdomen more slender than normal female, remnants of egg mass present. Male genitalia present; forceps strongly reduced.

Intersex 5: 16-22-IV-1980. Predominantly male. Head with turbinate eyes reduced to low conical tubercles (as in Intersex 6, Fig. 5). Abdomen tan, filled with eggs; segments 7-10 scarcely darker than preceding segments. Male genitalia present; forceps broken off and missing.

Intersex 6: 12-18-III-1980. Predominantly male. Head with turbinate eyes reduced to very small dome-shaped tubercles (Fig. 5). Abdomen with segments 1-5 opaque tan; segments 6-10 bearing eggs, reddish brown. Male genitalia pres-

ent; forceps with apical segment reduced, otherwise normally developed.

Intersex 7: 13-19-II-1980. Predominantly male. Head with turbinate eyes reduced to conical tubercles of 1/2 normal height (Fig. 6). Normal appearing foreleg present. Abdomen with segments 1-6 pale opaque tan; segments 7-10 reddish brown. Segments 4-10 bearing eggs. Male genitalia present, normally developed.

Soldán and Landa (1981) presented a comprehensive and cogent discussion of gynandromorphism and intersexuality in Ephemeroptera, along with an extensive literature review, and we see little reason to repeat their discussion here. However, the demarcation drawn by them between intersexuals and true gynandromorphs appears to be somewhat obscure.

We consider true gynandromorphs to be genetic sexual mosaics and, as such, they should exhibit distinct male and female characters, not intergrades between them. Intersexuals, on the other hand, are the result of developmental anomalies caused by parasitism, temperature extremes, hormones, hybridization of species or races (*c.f.* Brust 1966), or other factors, and should be expected to exhibit many characters intermediate, or on a grade or cline, between male and female characters. We characterize the seven specimens described here as intersexes.

Because no collections of nymphs were made of the *Baetodes* from Corriente Grande and ecological and climatic conditions at this locality have not been studied, it is impossible to tell what might be causing the high frequency (12.3%) of morphological aberrations of secondary sexual characteristics in these *Baetodes*. However, mayfly collections from other areas of Panama which we have examined do not contain aberrant specimens of either *Baetodes* or any other genera.

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