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NOVEL FEATURES OF REPRODUCTION IN THE DRAGONFLY GENUS *PROGOMPHUS* (ANISOPTERA: GOMPHIDAE)

S.W. DUNKLE
Bureau of Entomology, Division of Plant Industry, P.O. Box 1269, Gainesville, Florida 32602, United States

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Certain attributes of *Progomphus* are commented upon, including the: (1) Split male epiproct, — (2) Mid-ventral spine of the first abdominal segment, — (3) Mid--dorsal spine of the first abdominal segment in *P. borealis* McLachlan, — (4) Probable removal of previously deposited sperm during copulation, — (5) Forcible ejection of eggs, and — (6) Jet propulsion in second instar larvae.

INTRODUCTION

In spite of the fact that the genus *Progomphus* has been monographed twice (BYERS, 1939; BELLE, 1973), these and other authors have not remarked on some of its most interesting peculiarities. The following discussion is based on the examination of the *Progomphus* specimens in the Florida State Collection of Arthropods and the author's collection, and on a few field or laboratory observations.

DISCUSSION

SPLIT MALE EPIPROCT

The epiproct of adult male *Progomphus* is divided into 2 separate halves in most species I examined. It is only deeply forked, not split, in *P.geijskesi* Needham and *P. joergenseni* Ris. However, in life, at least in *P. bellei* Knopf and Tennessen, *P. borealis,* and *P. obscurus* (Rambur), each half of the epiproct is independently movable. The split epiproct is significant, because it shows the

evolution in the Anisoptera of 2 ventral grasping abdominal appendages, analogous with the 2 paraprocts of the Zygoptera, from which group the Anisoptera are presumed to have originated.

Scars on the vertex of mated female *Progomphus* indicate that during the tandem grip the halves of the split epiproct are diverged from their resting parallel position. The medial teeth of the epiproct grip on or near the anterior-lateral edge of the female's lateral ocelli, the lateral teeth at the edge of the compound eyes opposite the lateral ocelli. The medial lobe of the paraproct in male *Progomphus* is more developed than in females and appears to be inflatable. Possibly it expands to partly cover the lateral ocelli of the female during mating, giving her additional clues about whether a conspecific male is grasping her.

A split epiproct should make possible better adjustments of grip, resulting in a firmer tandem hold on the female than is feasible with a one-piece epiproct. A conceivable disadvantage of an adjustable epiproct is that it would be less useful as a species isolating mechanism, because it would more easily fit on the head of non-conspecific females.

MID-VENTRAL SPINE OF THE FIRST ABDOMINAL SEGMENT

Ten of the 12 *Progomphus* species found entirely north of South America have a small, median, finger-like spine with terminal denticles on the first abdominal sternum. A stouter but shorter process is found in the South American *P. brachycnemis* Needham (present in the 1 male but not the 1 female examined). Nine of the other 15 South American *Progomphus* species surveyed had a transverse ridge on abdominal sternum 1. This ridge is often highest medially and has posteriorly directed setae which are most numerous medially. The mid-ventral spine of the North American species probably evolved from such a transverse ridge. The assumed function of both ridges and spines is to prevent forward movement of the female abdomen during mating as discussed below.

In all species studied except *P. brachycnemis* the basal abdominal spine or ridge was equally developed in both sexes. Among those species with a mid-ventral spine, only 1 specimen, a female *P. obscurus,* lacked the spine. No indication of this spine is present in larvae. The mid-ventral spine has no obvious function in females, but in males it apparently helps position the female abdomen during copulation by fitting against the posterior edge of the female's abdominal sternum 10, possibly grasped between the female's paraprocts. Evidence that the spine functions in males but not females is that the spine was broken off in a number of mature males, but in only 1 mature female and no tenerals. In the most numerous species of the collections studied, *P. obscurus,* 11/308 or 3.6% had broken mid-ventral spines. A few of these may have been broken during previous examinations of the specimens, but certainly not all of them.

MID-DORSAL SPINE OF *PROGOMPHUS BOREALIS*

All specimens of both sexes of *P. borealis* seen had a straight, smooth, finger-like, nearly erect spine present mid-dorsally at the rear edge of the first abdominal tergite. This spine has no obvious function, and appears to be a persistent larval dorsal hook. A few individuals of *P. obscurus* had a short point on abdominal tergite 1, not tall enough to be called a spine. Except for spines on segment 10 associated with mating as in *Ischnura,* I am not aware of mid-dorsal spines in any other adult odonates.

SPERM REMOVAL DURING COPULATION

In a series of photographs taken a few minutes apart of a pair of *P. obscurus* in copulation for 14 minutes, a small white mass can be seen to appear at the rear ventral edge of tergite 2 of the male. This mass changes shape in successive photographs, and seems to be previously deposited sperm being hooked out of the female by the long flagella of the male penis. This is the first evidence of sperm removal in the Gomphidae.

EGG EJECTION

Females of all 4 species of U.S. *Progomphus* oviposit by flying low, fast, and erratically over the water, tapping the abdomen to the water to wash off eggs. In addition, on the headwaters of the Leaf River in Mississippi, I encountered a female *P. obscurus* hovering over a riffle at a height of 20 cm. She was probably dropping eggs although I could not see them against the background of moving water. After watching her for a few seconds she was netted. While she was held upside-down in the hand, she sprayed eggs vertically to a height of 1 cm. The eggs are large, round, and not sticky, quite like those of *Sympetrum* species which also exhibit non-contact flying oviposition. I do not know of forcible egg ejection in any other odonate, and it would be interesting to find out if the mechanism is direct muscular action of the vagina or indirectly by hydraulic pressure in the abdomen.

JET PROPULSION IN SECOND INSTAR *PROGOMPHUS*

Although jet propulsion is routine in late instar anisopteran larvae, it is rare in second instar larvae. Of many species of second instar larvae I have observed, included in all 7 Nearctic anisopteran families, only *Progomphus* (*P. bellei, P. obscurus*) and *Aphylla williamsoni* (Gloyd) demonstrated strong jet propulsion. Second instar Aeshnidae swim by a combination of weak rectal jets and running motions of the legs; other second instar anisopterans do not swim or do so only

with the legs. Strong rectal jets are undoubtedly useful to stream breeding *Progomphus,* and help them quickly re-burrow if they are dislodged from shifting sand. *Aphylla* breeds in quiet water, so rectal jetting would presumably be less useful for it. Perhaps other genera of Gomphoidinae also show strong rectal jetting in second instar larvae.

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