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The Female and Male Coupling Apparatus in *Tortopus* Mayflies[1]

by

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A unique coupling system and its associated morphology are described for mayflies of the genus *Tortopus*. In addition to styli, the styliger of male *Tortopus* includes lateral, paired claw-like parastyli that are derived from the basal segment of the styli. A pair of distinct, grooved excavations was discovered on the eighth abdominal sternite of female *Tortopus*, and these features are termed parastylus receptors because the parastyli evidently hook into them during copulation. This coupling system may have evolved as a compensation for the highly reduced styli, which are unable to clasp the females as in most other mayflies. Dense papilla-like structures at the apices of the styli suggest some other reproductive function for the styli.

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Tortopus Needham and Murphy (family Polymitarcyidae) is a relatively poorly known genus of Western Hemisphere mayflies that currently consists of three Nearctic and six Neotropical species. It, like its sister genus *Campsurus* Eaton, is unusual in a number of ways. Notably, the winged stages are extremely short-lived and possess highly atrophied legs. In addition, *Tortopus* is representative of one of four highly specialized mayfly lineages in which the adult stage of the female has been eliminated and the subimago mates and oviposits (Edmunds and McCafferty, 1988). Thus, subsequent references herein to *Tortopus* males are to adults, and those to *Tortopus* females are to reproductive subimagos.

In North America, *Tortopus* is restricted to southeastern and central areas including Texas and Mexico. Larvae live burrowed in clay substrates of rivers and canals (McCafferty, 1975). In South America, where the genus may have evolved (McCafferty et al., 1989), *Tortopus* was recently reported as far south as Argentina (Dominguez, 1985). Larvae have not been taken in Neotropical areas despite concerted effort by the senior author in Costa Rica and Colombia.

Originally, the concept of *Tortopus* was rather weakly based on leg and venational characters of females (Needham and Murphy, 1924). However, this was considerably reinforced with the subsequent discovery of males and their strikingly unique genitalia (Ulmer, 1932), particularly the pair of "claw-like" structures discussed by Ulmer (1942) and Traver (1950). During our review of

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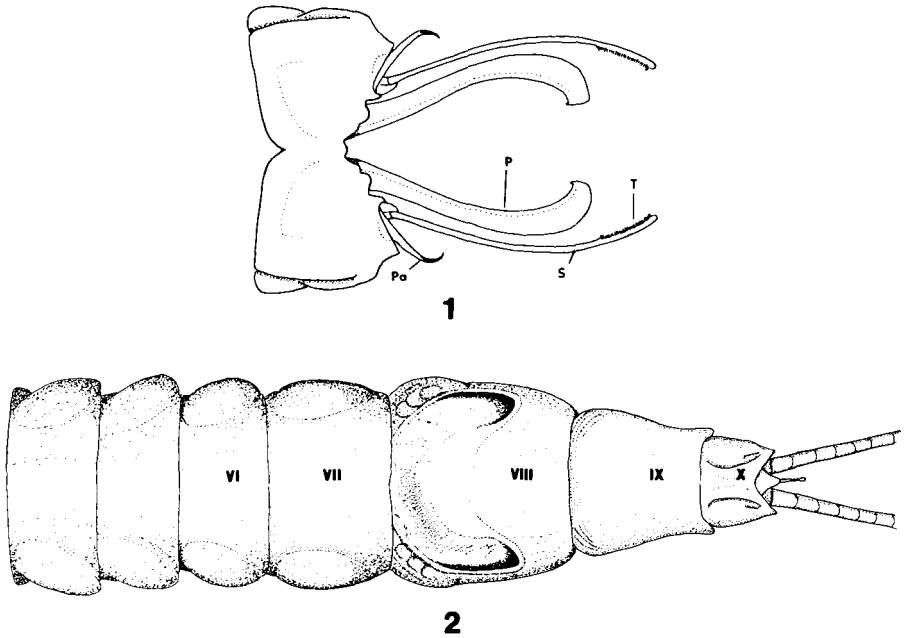
the genus, we discovered that females possess distinctive external features on the eighth abdominal sternite that, as far as we know, are unique to *Tortopus*. There appear to be no similar modifications of the abdominal sternites in any other Ephemeroptera, including other polymitarcyids, although the apex of the seventh sternite and sometimes the base of the eighth sternite in females of some Leptophlebiidae is formed into a totally unrelated structure that evidently functions as an egg guide (Morrison, 1919; Peters, pers. comm.). Detailed examination of these newly found female features of *Tortopus*, along with the genitalia of males of the same, has led to the conclusion that these female features actually aid coupling of the sexes during copulation.

In this report we describe and illustrate the coupling apparatus and assign terminology to the unique structures. We also discuss the functional morphology of coupling. Males and females of at least five species of *Tortopus* have been examined from the following areas: Southeastern U.S., Central U.S. and Texas, Mexico, Hondurus, Belize, Guatemala, Costa Rica, Peru, Brazil, Argentina, and Paraguay. Illustrations are of *Tortopus incertus* (Traver). We consider the styliger of the male to include the fused coxites of the ninth sternum and their associated appendages that are referred to as styli or gonostyli (forceps in other papers of the senior author). For a comparison of the various nomenclatural systems used for Ephemeropteran genitalia see Brinck (1956) and Needham et al. (1935).

Male. – Male genitalia typical of *Tortopus* are diagrammed in Figure 1. Penes tend to be elongate and gradually and slightly hooked medially. The posterior margin of the styliger (subgenital) plate is variously shaped, whereas the appendages of the styliger are highly distinctive. The styli proper are small and narrow compared to those of most Ephemeroptera. There is a distinct apicomedial area on each stylus (Fig. 1 and 3) made up of numerous papilla-like filaments (Fig. 3 and 4). We refer to this as the *terminal pad of the stylus*. Papilla-like structures, although usually shorter, occur commonly on the styli of several mayfly genera, but the density and development of these into a distinct terminal pad in *Tortopus* (and somewhat similarly in *Campsurus*) is atypical. Although the styli may appear unsegmented, which is also unusual for Ephemeroptera, there is a slight, somewhat diagonal segmentation line very near the base of each stylus that can be seen clearly with the scanning electron microscope (Fig. 5). In addition, a small cap-like or scale-like structure originates near the medial base of each stylus and extends over the base of segment 2. We refer to this structure as the *basal knob of the stylus* (Fig. 5).

The claw-like structures of *Tortopus* genitalia referred to by other authors can also be seen in Figures 1 and 5. These structures, which we call *parastyli*, are derived from the basal segment of the styli and project laterad and somewhat dorsad of the elongate second segment of the styli. A sclerotized ridge extends from around the medial aspect of the basal segment of the stylus to across the face of the parastylus (Fig. 5). This should not be confused with the segmentation line between segments 1 and 2 of the stylus, which is slightly distad

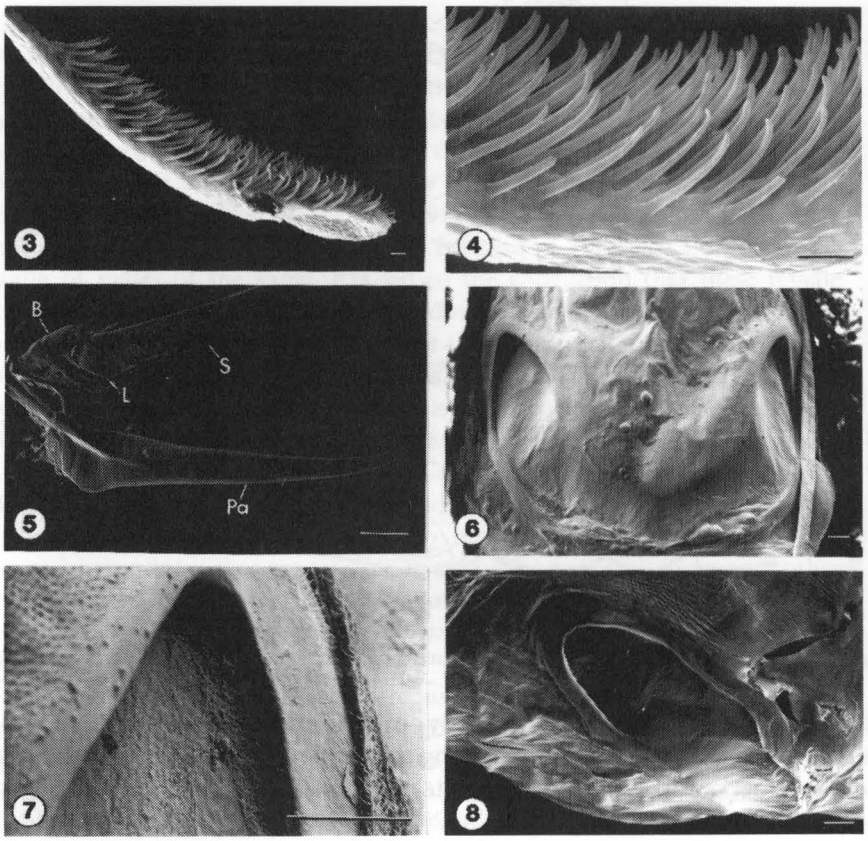


Figs. 1-2. *Tortopus incertus:* 1, ventral styliger and penes; 2, female abdominal sternites 4-10. P – penis, PA – Parastylus, S – stylus, T – terminal pad of the stylus.

of this ridge on the stylus proper, directly opposite the basal knob (Fig. 5). Also, the basal segment of the stylus, including the parastylus, does not appear to be clearly demarked from the styliger plate when viewed with normal dissecting microscope magnifications (Fig. 1), but becomes evident with higher magnifications (Fig. 5).

The parastyli are rigidly sclerotized but vary somewhat in the degree of hooking apically and in overall size among different species (e.g. see Traver, 1950). Such structures are not found in other Ephemeroptera, although they may be homologous with the more rudimentary lateral processes appressed to the side of the styli in certain species of the related genus *Povilla* (see Fig. 7-12 of Hubbard, 1984).

Female. – The ventral aspect of the terminal abdominal segments of *Tortopus* is shown in Figure 2. The seventh sternite is not extended posteriorly as in some mayflies and there is no evidence of a so-called subgenital plate or egg valve. The eighth sternite is, however, uniquely modified to possess a pair of lateral excavations, with grooves deepening and forming an attenuation of the excavation posteriorly (Fig. 6-8). The excavation is less developed anteriorly (Fig. 7), but it and its ridge-like lateral borders, which are best seen in the lateral aspect (Fig. 8), are continuous medially near the anterior base of the sternite, giving a somewhat horseshoe shaped impression (Fig. 2 and 6). We refer to these features as the *parastylus receptors*. The cuticular surface of the deeply excavated regions of the parastylus receptors is distinctly roughened (Fig. 7).



Figs. 3-8. Scanning electron micrographs, *Tortopus incertus:* 3, terminal pad of the stylus (bar = 10 μm); 4, papilla-like filaments of terminal pad (bar = 10 μm); 5, right parastylus and base of stylus (bar = 100 μm); 6, ventral sternite 8 with parastylus receptors (bar = 100 μm); 7, apex of left parastylus receptor (bar = 100 μm); 8, lateral parastylus receptor (bar = 100 μm). B – basal knob of the stylus, L – segmentation line, Pa – parastylus, S – stylus.

Although we have found the parastylus receptors in all *Tortopus* females examined, the degree of excavation varies somewhat among species.

Functional Morphology. – Coupling and the facilitation of mating in Ephemeroptera has been detailed by Brinck (1956). This general knowledge of mating behavior, our observations of mating in the closely related genus *Ephoron*, and manipulations of fluid preserved specimens are together highly suggestive of a unique coupling system in *Tortopus*. The relative positions of the female and male in mating mayflies are shown in Figure 9. Penes are inserted into the female gonopores just inside the posterior margin of the seventh sternite as the male abdomen is bent up and forward. In this position the styli, or forceps, of the male contact the eighth abdominal segment of the female. In most mayflies, which have relatively more developed styli that are commonly

segmented apically, the male's styli surround or nearly surround the female's abdomen, thus securing the abdominal positions during copulation. Note, as illustrated in Figure 9, however, that when males and females of the appropriate size relationship (collected from the same population) are positioned in-copula, the styli are unable to reach around the female's abdomen. Given the frail structure and smallness of the styli of *Tortopus*, their clasping ability apparently is not equivalent to that of most mayflies.

The parastyli do appear to have a major function in coupling and holding the female and male together during copulation. Because the stylus and parastylus share a common base, they move together. When we rotated the elongate second segment of the styli ventrally and anteriorly to the usual clasping position, the parastyli also rotated in this direction and were positioned to fit perfectly into the parastylus receptors. (The basal knob of the stylus appears to act as a brace preventing articulation at the segmentation line between segments 1 and 2 of the stylus.) The pointed apices of the parastyli can thus hook into the deep posterior grooves of the parastylus receptors. The developed ridges of the parastylus receptors likely serve as a guide for the parastyli and may prevent them from slipping outside the receptors upon initial contact. The roughened

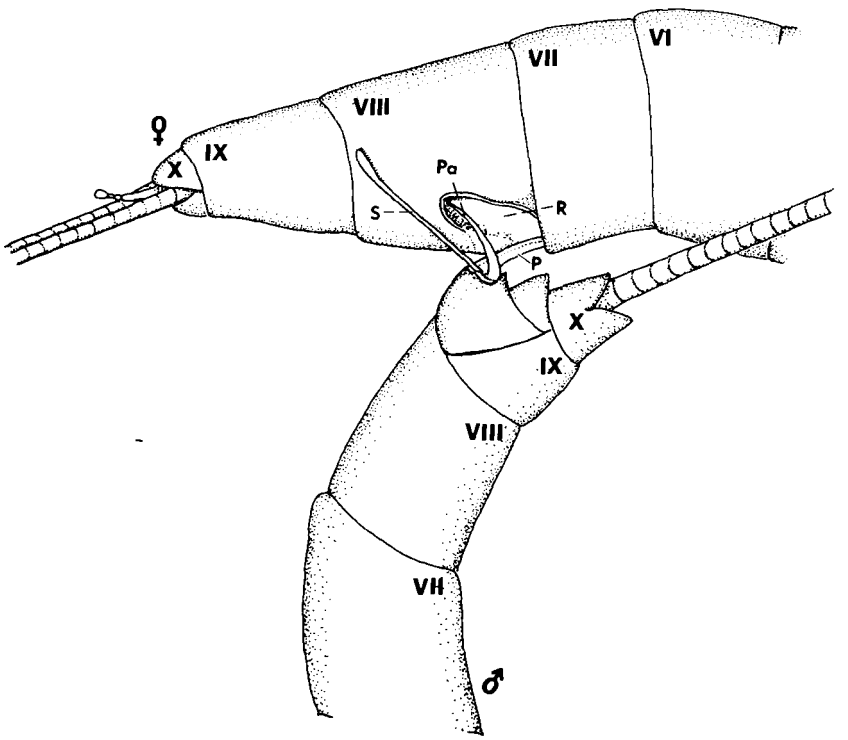


Fig. 9. Diagrammatic lateral and posterior aspect of in-copula pair of *Tortopus*. P – penis, Pa – parastylus, R – parastylus receptor, S – stylus.

cuticle within the parastylus receptors would also aid in securing the parastyli. This novel coupling system is apparently unique to *Tortopus*.

We do not know the function of the terminal pad of the stylus, although there may be a number of possible explanations. Perhaps it functions in physical coupling by also providing some adhesion or cohesion with the cuticle or posterior edge of the eighth segment of the female. Perhaps, even more likely, given the nature of the papilla-like structures, the pad is sensory or stimulatory in function. Observations that *Campsurus* and *Tortopus* mate at night (McCafferty, unpublished) and the fact that males have relatively small eyes could lead to the speculation that a pheromone is used for attracting males and is detected by possibly chemosensory terminal pads of the styli.

The adaptive significance of such an unusual and intricate coupling system in *Tortopus* will not be known until more data on the reproductive behavior of the group are gathered. The parastyli and their hooking mechanism may have evolved as a compensation for the loss of clasping ability in the styli. However, the presence of similar styli, but absence of parastyli in *Campsurus*, would appear to argue against this idea. Alternatively, the coupling of *Tortopus* may be related to the way the mating pair fly while in-copula. For example, rapid female flight might require extra anchoring of the male in the posterior direction, which the parastyli would seem to facilitate. In any case, any attribute that improves mating ability would, in theory, be strongly selected.

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