

**SIMILARITIES IN THE GENITALIA AND REPRODUCTIVE
BEHAVIOUR OF MALE AND FEMALE *THOLYMIS TILLARGA* (FABR.),
PARAZYXOMMA FLAVICANS (MARTIN), *BRACHYTHEMIS
LACUSTRIS* KIRBY AND *B. LEUCOSTICTA* (BURM.) (ANISOPTERA:
LIBELLULIDAE)**

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The genera *Tholymis* Hagen and *Parazyxomma* Pinhey have been classified in the Trameinae (or Zyxommatinae), whereas *Brachythemis* Brauer is included in the Sympetrinae. In spite of this, however, the male secondary genitalia and the arrangement of the female's sperm storage organs in *T. tillarga*, *P. flavicans*, *B. lacustris* and *B. leucosticta* resemble each other much more closely than they do those of any other sp. so far examined in either subfamily. Moreover these spp. show several other structural similarities as well as having comparable reproductive behaviour. The structural and behavioural similarities are unlikely to be the result of evolutionary convergence and probably result from a recent common ancestor. It may, therefore, be appropriate to include them within one subfamily.

INTRODUCTION

The structure of the secondary genitalia of males and the arrangement of the sperm storage organs in females show much variability among different members of the Libellulidae, sometimes even between the species of one genus (e.g. *Trithemis*, *Libellula*, *Sympetrum*) (WAAGE, 1984; SIVA-JOTHY, 1984).

Brachythemis has been placed in the subfamily Sympetrinae, while *Parazyxomma* and *Tholymis* are normally thought to be members of the Zyxommatinae (FRASER, 1957; PINHEY, 1961, 1984), or of the tribe Zyxommatini in the Trameinae (DAVIES & TOBIN, 1985). Several features, including venational characteristics, head size and activity patterns have been used to separate the Zyxommatinae from other subfamilies, but PINHEY (1961) has drawn

attention to some puzzling similarities of size, shape, colour, wing markings and other features between *Brachythemis leucosticta* and *Parazyxomma flavicans*.

The secondary genitalia of the males and the form of the sperm storage organs of the females of *B. leucosticta*, *B. lacustris*, *T. tillarga* and *P. flavicans* are described here, and several striking resemblances between the species are discussed. Similarities in reproductive behaviour patterns and some other features, which are not shared with other species in the two subfamilies, have also been noted.

SPECIES EXAMINED

Tholymis tillarga (Fabr.), *Brachythemis leucosticta* (Burm.) and *B. lacustris* Kirby were all observed at and obtained from Hunter's Lodge in Kenya, (37° 32' 2° 15'S). *Parazyxomma flavicans* (Martin) was obtained from Entebbe, Uganda. Specimens were preserved in 70% alcohol or in 2% formaldehyde for subsequent examination.

GENITAL STRUCTURE

In all 4 species the second and third segments of the penis are fused. The 4th segment is a wedge-shaped structure somewhat longer in *T. tillarga* than in the other species (Fig. 1). The large lateral lobes meet distally in the resting penis and they rotate outwards with inflation, while at the same time a large apical lobe expands and swings downwards. A prominent central "housing", formed from a part of the medial complex and previously described in *B. lacustris* (MILLER, 1982), conceals the single,

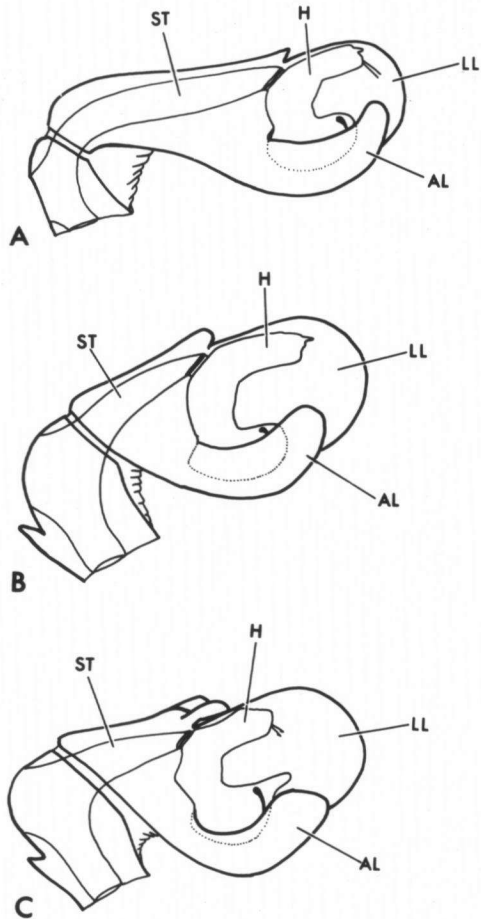


Fig. 1. The 4th segment of the uninflated penis, with the right lateral lobe removed: (A) *T. tillarga*; —(B) *B. leucosticta*; —(C) *P. flavicans*. — [ST: sperm tube (shown by transparency); — H: housing for the flagellum and cornua; — LL: left lateral lobe; — AL: apical lobe].

long flagellum and a pair of bristly cornua. These are expelled together from the upper end of the housing during inflation (Fig. 2). The mechanism of expulsion which is the same in all 4 species will be described in more detail elsewhere. This type of flagellate penis has been found in no other dragonfly species so far examined, although different types of flagellate penis are known in *Orthetrum* spp. and *Pantala flavescens* (MILLER, 1984).

There are small differences in the shape of the hamules and of the genital lobes, but otherwise the only major difference, so far detected, between the secondary genitalia of the four species is in the armature at the tip of the flagellum (Fig. 3). In *B. lacustris* this takes the form of a large double barb, 60 μ m long. In *B. leucosticta* and *P. flavicans*, the flagellum is bifurcated 200 μ m from the tip, each part ending in a cap 34-38 μ m long and bearing a small barb. In *T. tillarga* the flagellum is also bifurcated but the tips are not barbed and they terminate in broadened and flattened spatulate regions which bear small spines.

The female genitalia are also similar to each other in all four species. The sub-genital plates is large and bifurcated while the sternite of the 9th segment is modified in various ways. It forms an egg basket in *T. tillarga*, but in the other three species it is modified into a large rounded plate which probably facilitates the particular mode of oviposition known to occur in *B. lacustris* and *B. leucosticta* (MILLER & MILLER, 1985). In *B. lacustris* there is a small bursa and a common spermathecal duct which arises

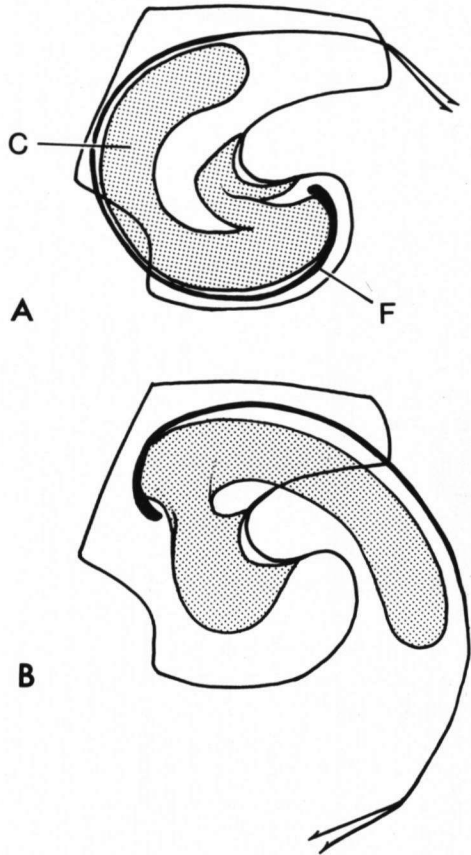


Fig. 2. Diagram of part of the medial process of the 4th penis segment of *B. leucosticta*: (A) The uninflated penis showing the housing which contains the flagellum (F) and cornua (C); — (B) The inflated penis with the flagellum and cornua partly expelled from the housing. — The mechanism in *T. tillarga*, *B. lacustris* and *P. flavicans* is identical.

posteriorly and immediately swells into a dilated sac. It then narrows and passes to one side of the bursa, normally the left, before dividing into left and right ducts (Fig. 4a). This marked asymmetry is believed to make it difficult for the penis flagellum to reach into one spermatheca (normally the left), whereas it may have access to the other. In *B. leucosticta* and *P. flavicans*, the common spermathecal duct lacks the initial dilatation: it runs anteriorly in a more or less medial position and then splits into right and left ducts (Fig. 4b). In *T. tillarga*, the arrangement is again asymmetrical with the common spermathecal duct also lacking the initial dilatation and running to the left of the bursa in those females so far examined (Fig. 4c). A T-shaped spermathecal duct, of the type described here, has also been found in *Potamarcha congener*.

BEHAVIOUR

Some behavioural similarities were also noted in these species when they were examined at Hunter's Lodge and elsewhere in East Africa. Sexual activity in *B. lacustris*, *B. leucosticta* and in *T. tillarga* occurred from about 16:00 h until sunset (ca. 18:30 h). Males of all three species patrol the water margin during periods of sexual activity. *B. lacustris* and *B. leucosticta* are territorial, but *T. tillarga* flies incessantly and is not localised. All three copulate on the wing for periods of 14-40 s near to sites which are subsequently used for oviposition. Males guard ovipositing females by hovering close to them without contact. All three species oviposit epiphytically on the wing, *B. lacustris* and *B. leucosticta* females choosing to do so on more or less vertical stems and leaves at or just above the water surface. In contrast female *T. tillarga* oviposit onto horizontal vegetation just below the water surface. The eggs of *Brachythemis* spp. and of *T. tillarga* have trabeculate shells which may carry an air layer and act as a plastron (MILLER, 1987). Trabeculate eggshells have not been described in other libellulids. *P. flavicans* is active during crepuscular periods in Uganda (PINHEY, 1961), but no account of its reproductive behaviour is known.

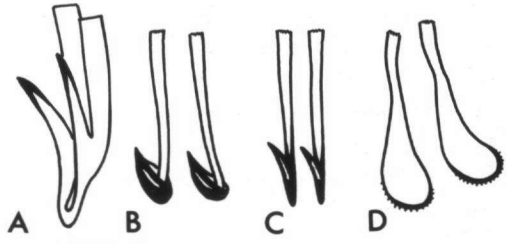


Fig. 3. The armature of the tips of the flagella: (A) *B. lacustris*; — (B) *B. leucosticta*; — (C) *P. flavicans*; — (D) *T. tillarga*. — [Scale bar = 50 μ m].

CONCLUSIONS

Among the Sympetrinae, examinations have shown that the male secondary

genitalia of *Acisoma panorpoides* Rambur, *Bradinopyga cornuta* Ris and *Diplacodes lefebvrei* (Rambur) (P.L. Miller, unpubl.), *Erythemis simplicicollis* (Say) (WAAGE, 1986), *Crocothemis erythraea* (Brullé) (SIVA-JOTHY, 1987), and *Sympetrum* spp. (SIVA-JOTHY, 1984; WAAGE, 1984) are all different from each other and from the four species reported on here. Likewise, among Trameinae, *Tramea basilaris* (P. de Beauv.), *Rhyothemis semihyalina* (Desjardins) and *Pantala flavescens* (Fabr.) are all very different (P.L. Miller, unpubl.).

One feature used to distinguish the Trameinae from some other sub-families is the length of the dorsal confluent zone between left and right compound eyes. In *B. leucosticta* the confluence extends for 9-10 ommatidia, in *B. lacustris* for 13-14, in *P. flavicans* for 22-23, and in *T. tillarga* for 22-25 ommatidia. The crepuscular habits of the last two species perhaps account for with the greater confluence and their relatively larger eyes. Other features used to distinguish the Zyxommatinae from the Sympetrinae include the number of antenodal crossveins and the state of the anal loop in the hindwing (FRASER, 1957; PINHEY, 1961). The number of forewing antenodals in *B. lacustris* and *B. leucosticta* is $7\frac{1}{2}$ - $8\frac{1}{2}$; in *P. flavicans* $8\frac{1}{2}$ - $9\frac{1}{2}$, and in *T. tillarga* $9\frac{1}{2}$ - $11\frac{1}{2}$. Between closely related species the number may perhaps be related to size. Examination of the anal loop shows it to be closed in all 4 species, although the closure in *T. tillarga* occurs at the wing margin. There is however some variation in this between individuals. Thus these features of the wing venation do not provide a reliable guide to the sub-family classification of these species.

In summary, the similarity of several anatomical features including wing

venation and genital structure in *Brachythemis leucosticta*, *B. lacustris* and *Parazyxomma flavicans* suggests that these species are very closely related. *Tholymis tillarga* differs only slightly from the other three in some details of the penis structure, wing venation and wing patterning. It seems unlikely that these similarities which also extend to behaviour could be the result of evolutionary convergence. All four species may therefore be more closely related than previous classifications have suggested and they should probably be placed within the same subfamily of the Libellulidae.

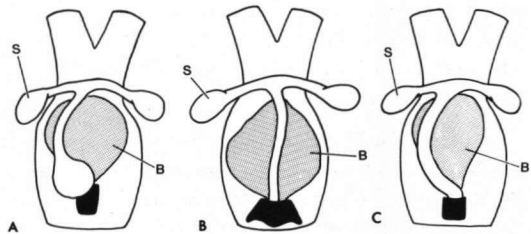


Fig. 4. Dorsal view (anterior upwards) of the female genitalia: (A) *B. lacustris*; — (B) *B. leucosticta*; — (C) *T. tillarga*. — [S: spermatheca; — B: bursa]. — The genitalia of female *P. flavicans* closely resemble those of *B. leucosticta*.

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Note added in proof: A recent opportunity to examine the genital structure and reproductive behaviour of *Brachythemis contaminata* (Fabr.) and *Zyxomma petiolatum* Ramb. has shown that both species have marked similarities with the species described here.