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ANATOMICAL MODIFICATIONS FOR DISPLAYING BRIGHT COLORATION IN MEGAPODAGRIONID AND CHLOROCYPHID DRAGONFLIES (ZYGOPTERA)*

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Males of some species of the Odonata families Megapodagrionidae and Chlorocyphidae flatten brightly colored abdominal segments which thus become more conspicuous from above, and the segments are structurally modified to allow this behavior. In the Chlorocyphidae, species with brightly colored abdomens have the ability to flatten them, and species with extensively colored wings tend to have broader wings than those in which the wings are uncolored.

INTRODUCTION

Although abdominal shape varies greatly among species of Anisoptera, even within some genera of the Libellulidae, the basic zygopteran abdominal shape is that of a cylinder; in fact, ASAHINA (1954: 54) stated "The Zygopterous abdomen is, without exception, cylindrical". That there is some variation on this theme became apparent to me from observations of damselflies of the Megapodagrionidae and Chlorocyphidae in southeast Asia. Furthermore, the variation in wing coloration and wing shape, even within a genus, in the Chlorocyphidae appeared to be a phenomenon worthy of further consideration. This discussion is confined to males, which are brighter and more distinctive among species than are females. They are also better

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represented in my collection, material of which forms the basis for conclusions reached herein. In addition, field observations have allowed me to relate structure to function. Although the conclusions reached can be extended to many groups of Anisoptera, this paper will not deal with that suborder.

MEGAPODAGRIONIDAE

RHINAGRION BORNEENSE (SELYS)

R. borneense is a striking damselfly which may be found at small, slow streams throughout Borneo (LIEFTINCK, 1954). I observed males in western Sarawak in August 1980, where they were perched on the tips of leaves or twigs 1-2 m above streams in patches of sunlight. They seemed quite wary, flying rapidly along the stream to new perches when disturbed. The wings were held in a horizontal position, as previously observed by LIEFTINCK (1954). The thorax was conspicuously patterned with green and black, the abdomen dark reddish brown, brighter beneath. Each male contrasted sharply with the overall green background color of the environment because of the brilliant sky-blue dorsum of the 8th and 9th abdominal segments (Fig. 1), which occasionally were elevated at an angle of as much as 15° from the remainder of the abdomen. What struck me immediately as unusual was the fact that the blue segments were flattened considerably, so that they appeared wider than the more basal segments of the abdomen. At times the flattening was more extreme than shown in the photograph. The most plausible explanation for this flattening is that it is under muscular control. I could easily manipulate the freshly killed specimens to reproduce the effect, as the abdomen tip was rather soft and pliable.

In the dried specimens, which were placed in acetone immediately after death, the 8th and 9th abdominal segments are triangular in cross section, with a pronounced dorsal keel on both segments. The ventrolateral margin of each segment is markedly angulate but not keeled. This modification allows flattening, which would not be possible in a rigid, cylindrical segment.

OTHER MEGAPODAGRIONIDS

I have examined specimens of all other megapodagrionids in my collection to contrast them with *R. borneense*, including 6 species of *Argiolestes* Selys, 1 *Dimeragrion* Calvert, 18 *Heteragrion* Selys, 1 *Heteropodagrion* Selys, 3 *Megapodagrion* Selys, 1 *Oxystigma* Selys, 8 *Paraphlebia* Hagen, 11 *Philogenia* Selys, 1 *Podolestes* Selys and 1 *Thaumatoneura* MacLachlan. None of these species shows the extreme modification exhibited by *R. borneense*, and virtually all of them have simple cylindrically shaped 8th and

9th segments, the 8th in most genera slightly keeled dorsally, the 9th smoothly rounded. Exceptions to this pattern are found in 3 genera: *Heteropodagrion*, in which *H. sanguinipes* Selys has moderately keeled 8th and 9th segments, *Heteragrion* and *Oxystigma*; these 3 genera appear closely related. .

HETERAGRION

Anatomy. — The situation in *Heteragrion* is interesting because the species vary among themselves in the presence and degree of keeling on these segments. All species I have examined have the 8th segment conspicuously keeled, except *H. aurantiacum* Selys, in which the keeling is very weak. Three species, *H. aurantiacum, H. melanurum* Williamson and *H. triangulare* Selys, lack keeling on the 9th segment. *H. ictericum* Williamson and *Oxystigma petiolatum* (Selys) have short keels on the anterior 1/4 of the segment, and 12 other species of *Heteragrion* (*aequatoriale* Selys, *albifrons* Ris, *alienum* Williamson, *chrysops* Hagen, *eboratum* Donnelly, *erythrogastrum* Selys, *majus* Selys, *tricellulare* Calvert and 4 unidentified and/or undescribed species from Ecuador and Peru) have keels extending 1/2 to 3/4 the length of the segment. Finally, *H. angustipenne* Selys, *H. inca* Calvert and *H. speciosum* Sjöstedt have the entire 9th segment keeled.

Functionally, one might expect this keeling to correlate with the ability of these dragonflies to depress (or compress?) their abdomens in the manner of *Rhinagrion borneense*. In many dried specimens of *Heteragrion* the 8th and 9th segments, especially the former, are laterally compressed, appearing quite different from the same segments in *Paraphlebia, Philogenia* and other genera, in which they are approximately cylindrical. Most male *Heteragrion* have dark abdomens with dull to bright yellow tips, which would be even more conspicuous when expanded, but the species with largely yellow abdomens — *alienum, chrysops, speciosum* and *tricellulare* — all have keeled segments, as do the species with largely red abdomens, *albifrons* and *erythrogastrum*. Thus there is no special association of keeled 8th and 9th segments with contrasting abdomen tips as in *R. borneense*.

The complexity of the situation is revealed by photographs in life that show the 8th and 9th segments of the abdomen distinctly expanded in dorsal view in *albifrons, alienum* and *tricellulare* (Fig. 2) but not in the similarly keeled *erythrogastrum*. Nevertheless, even in the more uniformly colored species the abdomen tip is at least a bit brighter than the rest of it. Life photographs of *Megapodagrion, Paraphlebia* and *Philogenia*, all of which have basically dark abdomens with or without pruinosity at the extreme tip, show them with cylindrical abdomens, with no hint of the expansion present in *Heteragrion* and *Rhinagrion*.

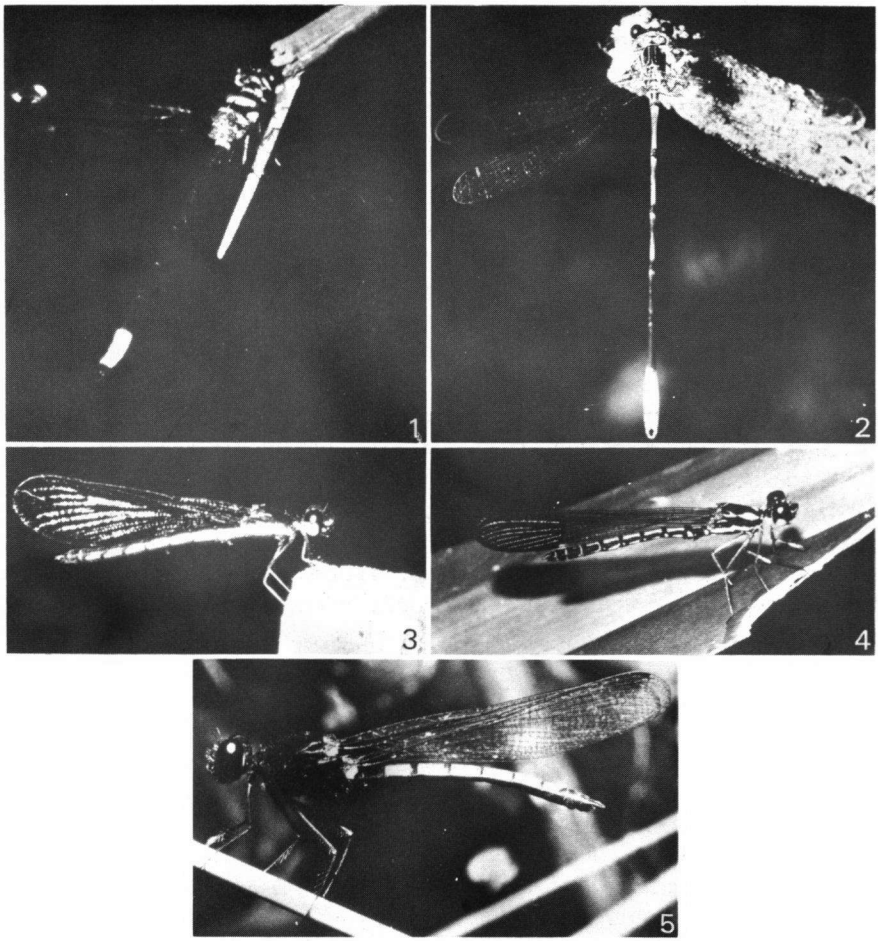
Display. — As in *Rhinagrion borneense*, the expanded abdomen tips in

males of *Heteragrion* should increase their visibility as they perch over forest streams. The yellows and reds of the latter genus may be more conspicuous in the shady situations in which they occur than is the blue of the many zygopterans that perch in sunlight. I have seen what appear to be aggressive displays between males in 2 red species of *Heteragrion, albifrons* and *erythrogastrum*, in Costa Rica. Males hovered in midair about 7 cm apart, facing each other with abdomens inclined 45° below the horizontal, and moved up and down, each male alternately above the other, until one flew away. The shining white face of *albifrons* was vividly conspicuous at that time and probably plays an important part in this display, yet *erythrogastrum*, with dark face, behaves similarly, so the conspicuous face is not a necessity for such a display. Although it is tempting to attribute the different face colors in these 2 sympatric species to selection for species recognition, they rarely occur on the same stream. In both species the brilliant red abdomens seem to glow, even in dense shade, and probably function as agonistic signals. Males of the yellowish *H. tricellulare*, watched at length in Chiapas, Mexico, were not seen to display head to head but instead flew at and displaced each other from perches, the yellow abdomen tips being very conspicuous at that time. But again, to preclude the possibility of generalizations, males of un undescribed species of *Heteragrion* from Limoncocha, Ecuador, with dark, yellow-tipped abdomen and yellow face displayed in the same fashion as the 2 red species.

CHLOROCYPHIDAE

ANATOMY AND DISPLAY

This family is especially interesting from the standpoint of abdominal flattening, as it contains genera the species of which have cylindrical abdomens and genera the species of which have abdominal segments 3 or 4 through 8 or 9 strongly keeled both dorsally and laterally. The abdominal keeling should allow flattening of virtually the entire abdomen, a much more pronounced effect than in the Megapodagrionidae. From the very little information available on displays in males of this family, it appears that the species with cylindrical abdomens display primarily with their wings and the species with keeled, triquetral abdomens display primarily with their abdomens. In addition, the tibiae are modified for display in some species, but this character seems to vary independently of the others. Certain constellations of characters fall into groups that I am designating as units to show the progression from using the wings for display to using the abdomen for display in different chlorocyphids. This discussion is taken largely from species represented in my collection, but I think most or all described species would fall clearly in one of these groups.



Figs. 1-5. (1) *Rhinagrion borneense* (Sel.), Kampong Gayu, 15 mi. N Padawan, Sarawak, 23 August 1980; — (2) *Heteragrion tricellulare* Calv., 20.1 mi. N Ocozocoautla, Chiapas, Mexico, 25 August 1967; — (3) *Rhinocypha colorata* Sel., Los Baños, Luzon, Philippines, 12 August 1980; — (4) *Sundacypha petiolata* (Sel.), Semengo Forest, 20 km S Kuching, Sarawak, 20 August 1980; — (5) *Cyrano unicolor* (Sel.), Los Baños, Luzon, Philippines, 12 August 1980.

Group 1. — *Rhinocypha biseriata* Selys, *R. bisignata* Selys, *R. fenestrella* Rambur, *R. quadrimaculata* Selys, *R. unimaculata* Selys and 2 undetermined species of this genus from Malaysia have cylindrical black abdomens, largely black thoraces and largely black wings with colored translucent markings. Many other species of the genus fall into this group, according to FRASER (1934), who wrote of males hovering in front of females with fore wings

rapidly beating and hind wings stationary, displaying their coloration. Display of the wings must be very important in this group of species, as their wings are as ornately marked as those of any zygopterans. In Sarawak, I saw males of *R. biseriata* displaying by facing one another with fluttering wings, and in Nepal, males of *R. quadrimaculata* circled one another, in both species the wings sparkling in the sun. Some *Rhinocypha* also use the white, flattened flexor surfaces of their hind tibiae in display (FRASER, 1934). During my brief observations I did not notice either dangling tibiae or stationary hind wings, and it is possible these behaviors are used in courtship but not in aggressive displays.

I am placing *Rhinocypha trifasciata* Selys in this group, as it has a similarly black cylindrical abdomen, but the wings are almost entirely iridiscent green in sunlight, with 2-3 narrow dark crossbands. One male I observed in Nepal fluttered in front of 2 different females at the edge of a stream and briefly dangled its showy white tibiae.

Group 2. — Still other *Rhinocypha, R. colorata* Selys and *R. humeralis* Selys (Fig. 3), have cylindrical abdomens black above and conspicuously blue on the sides, and extensive black wing tips with some iridescence but with no translucent spots. I observed *R. colorata* in display flight on Luzon, Philippines. On several occasions, 2 males flew around one another rapidly about 1 m above a stream for 10-30 seconds, their iridescent wings and blue lateral surfaces flashing in the sunlight. Although members of this group also have white tibiae, again I did not see them obviously displayed in interactions between males. *R. tincta* Rambur is like the preceding 2 species but in addition has blue coloration on the dorsum of the abdomen, at least at its base. The amount of black in its wing tips varies geographically.

Group 3. — *Sundacypha petiolata* (Selys) (Fig. 4) is quite different from the species of *Rhinocypha* examined in having only the hind wing tips black, narrower wings and an abdomen largely red above. Its abdomen does not appear to be any more flattened or angulate than in *Rhinocypha*. The tibiae are black with the distal 1/3 to 1/2 white. Rather similar are 2 species of *Libellago, L. stictica* (Selys) with abdomen red above and *L. lineata* (Burmeister) with abdomen yellow above. These species have even smaller black spots on the hind wing tips than does *S. petiolata*. They differ from members of the preceding genera in having the abdominal segments slightly more angulate and the abdomen thus more depressible. *L. lineata* has white tibial surfaces, but those of *L. stictica* are dark. Members of this group are clearly intermediate between the species of *Rhinocypha* on one hand and those of *Chlorocypha* on the other, differing additionally by their small size.

Group 4. — Another series of species includes *Chlorocypha cancellata* (Selys), *C. consueta* (Karsch), *C. cyanifrons* (Selys), *C. hintzi* (Grünberg), *C. jacksoni* Pinhey, *C. molindica* Fraser and *C. rubida* (Selys) and *Cyrano uni-*

color (Hagen) (Fig. 5). This group is characterized by having depressed, angulate, red to orange abdomens and colorless wings. The tibiae of most members of the group are black, but in *C. consueta* they are white internally, much as in *Rhinocypha*, and in *C. molindica* their basal halves are white. Field workers should watch closely for tibial displays in this genus. *Platycypha caligata* (Selys) is similar in having clear wings and a brightly marked, depressed abdomen, but in this species the abdomen is blue (other species of *Platycypha* have red abdomens, and of *Chlorocypha* have blue abdomens (FRASER, 1950)). In addition, it has diverged substantially from *Chlorocypha* in having greatly expanded tibiae, red on their outer and white on their inner surfaces, which are used conspicuously in courtship behavior (PINHEY, 1951). Courtship display is quite different in *Chlorocypha glauca* (Selys) (which I have not examined), in which a male curls the 5th to 10th abdominal segments beneath it to display its bright red coloration as it flies above a female. In addition, males display toward one another in a similar fashion after initially hovering alongside one another (NEVILLE, 1960). Although this is the only species of *Chlorocypha* for which display has been recorded, it may be that all members of this genus use the conspicuous abdomen to display in this manner.

Males of *Cyrano unicolor*, which I observed with *Rhinocypha colorata* on streams in the Philippines, flew at each other, but I saw no lengthy displays between them. Courtship behavior does not seem to be frequently observed in members of this family, although it doubtless occurs in most if not all of them. It is my impression that females of this family, as well as females of species of Calopterygidae, are more frequent at the water than female coenagrionids, for example. This might follow from the use of courtship behavior in the former families, so that a female has the option of refusing a male, while in the Coenagrionidae the male merely lands on the female and attempts tandem, so females of that family are harassed physically and therefore should leave the water if unreceptive to mating.

WING SHAPE

Wing shape in species of the Chlorocyphidae is somewhat variable, and those species that have colored wings tend to have broader wings. The hind wing width (at its widest point)/hind wing length varies from 0.15-0.19 ($\bar{x}$ 0.17) in the 8 species of group 4 with uncolored wings, from 0.16-0.18 ($\bar{x}$ 0.17) in the 3 species of group 3 with black wing tips, and from 0.18-0.29 ($\bar{x}$ 0.22) in the 11 species of groups 1 and 2 with largely colored wings. This difference is readily apparent in Figure 6, where it can be seen that the widest wings are about twice as wide as the narrowest and that relative wing width is not a function of wing length.

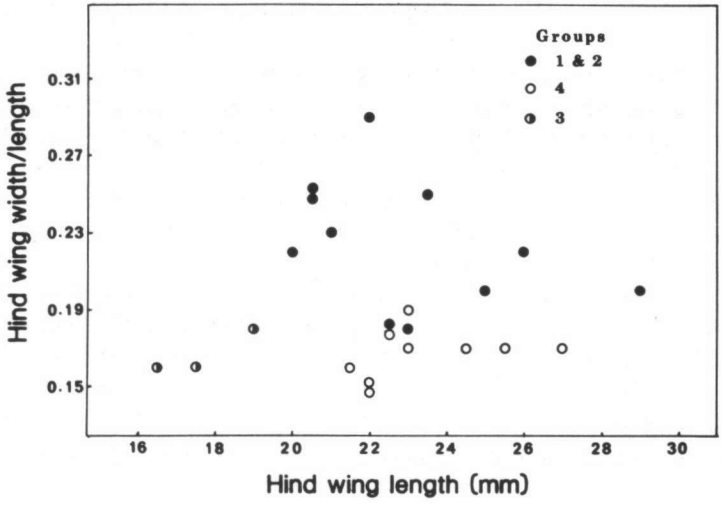


Fig. 6. Relative wing breadth in males of selected species of Chlorocyphidae. Filled-in circles are species with largely colored wings, half-open circles are species with black wing tips, and open circles are species with clear wings. See text for additional details.

Two alternative hypotheses are supported by these data: (1) species with broader wings (for assumed aerodynamic reasons) are more likely to use them for display, developing colored areas for that purpose; or (2) species that use the wings for display are likely to evolve broader wings for that purpose. I favor the second alternative, as variation in wing width (and thus area) should be minimal in ecologically and phylogenetically related species if aerodynamics were the only consideration. In addition, I would have predicted relatively wider wings in larger species for aerodynamic reasons, assuming there is relationship between wing area and support of weight, but there is no such relationship between size (as measured by wing length) and relative wing width.

Thus it is apparent that both the wings and the abdomen are important for display, both courtship and aggressive, in males of this family, but that either one or the other is stressed in different genera. In those genera in which the abdomen is conspicuously brightly colored and the wings largely uncolored, the abdomen is modified to allow its colored surfaces to be better displayed. Those species with colored wings that use the wings in display have those organs relatively larger than those in which they are not used. In addition, some species display their white, expanded tibiae at least during courtship, regardless of whether the wings or abdomen are more important in display.

OTHER FAMILIES

The abdominal keeling in *Rhinagrion borneense* and in *Heteragrion* and closely related genera of the Megapodagrionidae and in *Chlorocypha* and closely related genera of the Chlorocyphidae appears to be unusual in the Zygoptera. I have examined male specimens of several genera each in all other zygopteran families except the monotypic Hemiphlebiidae, and all of them were much like typical megapodagrionids and *Rhinocypha* in having roughly cylindrical 8th and 9th abdominal segments.

The correlation between relative wing width and presence of extensive colored areas in the wings is marked in other zygopteran families: Polythoridae, Euphaeidae, Calopterygidae, Amphipterygidae and Pseudostigmatidae. In some of these families variation in wing width is even greater than in the Chlorocyphidae. The use of wings in display is well documented for calopterygids and doubtless occurs in the other families as well.

CONCLUDING REMARKS

That the anatomical modifications discussed herein are responses to selection for being able to display the bright colors of the abdomen or the wings is clearly indicated by the difference among genera in these families. The lack of similar modificiations in females is also significant. In all megapodagrionid and chlorocyphid species of which female specimens were examined (23 and 14 species respectively), there is no keeling on the 4th to 9th abdominal segments of females, including species in which males exhibit such keeling. On the contrary, the females do share some of the male wing characteristics. Females of many of the species with colored-winged males also have colored wings which are wide like those of the males. An analysis of this phenomenon is planned for Zygoptera in general but is beyond the scope of the present study.

The Chlorocyphidae and Megapodagrionidae lend themselves to further field studies, with the goal of understanding the relationships between structure and function and between coloration and behavior in these animals. Courtship and aggressive displays are easily enough seen and recorded, if enough time is spent observing, and the introduction of cinematography as a field technique would augment such observations greatly, for example in allowing differences in flight between wide-winged and narrow-winged species to be detected. Although behavior can be modified by ecological constraints and opportunities, some aspects of it are conservative enough to provide additional information about systematic and evolutionary relationships among taxa of dragonflies. It is these very diverse tropical forest-stream Zygoptera that we know so little about that would amply repay such comparative ethological studies, and indeed they should be studied

before their habitats disappear forever.

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