A CRITICAL STUDY OF GOMPHUS MODESTUS NEEDHAM, 1942, WITH NOTES ON RELATED SPECIES (ANISOPTERA: GOMPHIDAE)

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Gomhus (Gomphurus) modestus Needham has often been confused with other species of the Gomphurus group. The penis is shown to be a good specific character in this group. The flagella of modestus are short, not long as in G. vastus Walsh with which Needham compared his species. The males of modestus have penes very much like G. dilatatus Rambur, but the subgenital plates of the females are most like G. lineatifrons Calvert. The brownish G. vastus from Texas is here considered the end of a clinal variation in color of this species. Similar clines are suggested for Gomphus (Stylurus) townesi Gloyd, and G. (Stylurus) plagiatus Rambur. G. flavocaudatus Walker is certainly the light end of a clinical variation in color of G. exilis Selys. The need is shown for further study of the relationship between the darker G. brimleyi Muttkowski found from North Carolina to north-western Florida and the yellower G. cavillaris Needham from central and southern Florida.

INTRODUCTION AND GENERAL CONSIDERATIONS

Gomphus modestus was described by NEEDHAM (1942) from a single male collected at Lucedale, Mississippi, April 25, 1929 by Alice L. Dietrich. He compared it with G. vastus Walsh, and NEEDHAM & WESTFALL (1955), in the "Manual of the Dragonflies of North America", keyed it out with vastus in couplet 10. The holotype was dismembered in a vial and for the "Manual" I made photographs of the terminal abdominal appendages and hamules. The two

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males and two females which WILLIAMSON (1914) reported from Black Bayou and Bay City, Texas as G. consanguis Selys were erroneously identified by Needham as "probably modestus" when he visited the museum at Ann Arbor, Michigan, August 7, 1947. He placed the determination on the paper triangle containing the Bay City female. WILLIAMSON (1914) was cited under modestus in the "Manual", and Texas was included in its distribution on this basis. Notations on their triangles indicate that the four Texas specimens were determined by Leonora K. Gloyd in 1936 as vastus and E.J. Kormondy as modestus ? in 1958. Thomas W. Donnelly in 1964 wrote G. externus Hagen on the triangle containing the Black Bayou male. Upon examining the penis of the holotype of modestus I found that the flagella were very short, not long as in vastus and externus. The penis of modestus had not been examined by Needham, and when I compared the penes of modestus and dilatatus Rambur I saw that they were almost identical. It appeared that Needham should have compared these two species, and for several years I thought that modestus might be synonymous with dilatatus.

In 1955 I obtained through the kindness of Septima C. Smith and Robert S. Hodges of Tuscaloosa, Alabama a series of specimens of the *Gomphurus* group which they had reared from larvae collected in Alabama. Among them I found a female reared from the North River, Tuscaloosa County, May 21, 1939 with which

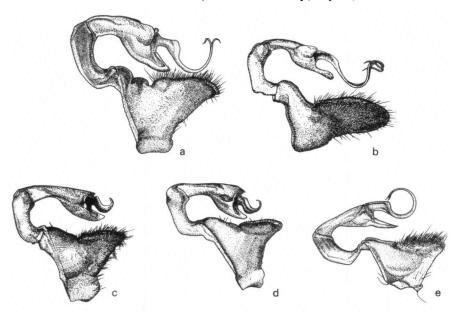


Fig. 1. Penes of males of Gomphus (Gomphurus): (a) lineatifrons Calvert; - (b) externus Hagen; - (c) dilatatus Rambur; - (d) modestus Needham; - (e) vastus Walsh.

was the note, "This, to me, appears to be a small 9 of Gomphus lineatifrons, L.K. Gloyd 1939, July 7." Upon examining the exuviae from which it was said to have emerged I saw that the front margin of the prementum was not at all concave as illustrated by NEEDHAM (1903). It was evident that this was a good specific character for the species. I studied three male and three female exuviae from Cooley Creek, Tuscaloosa County, Alabama, from which Smith and Hodges had reared undoubted specimens of lineatifrons Calvert in May 1938. These, as well as two larvae collected March 24, 1939 had the front margin of the prementum strongly concave. The subgenital plate (vulvar lamina) of the questionable female was very similar to that of lineatifrons, so it was decided there must have been an error in associating the adult and exuviae. Later I found another female reared from the North River, May 14, 1939 with the note, "Small 9 lineatifrons L.K. Gloyd 7/7/39." This agreed in larval and adult characters with the first. Eight males reared from the same lot of apparently identical larvae collected from the North River the same day (April 26, 1939) had been determined by Mrs. Gloyd as apparently dilatatus, but Needham had identified them as modestus, thus accounting for Alabama as a distribution record for the latter species in the Manual. Three additional females were located that had been reared from the same lot of larvae. Their characters matched those of the first.

This started me on a further study of the adults and larvae of modestus, lineatifrons, dilatatus and vastus. This study revealed the fact that males of lineatifrons have the flagella of the penis long, as in vastus, but modestus and dilatatus both have short flagella as mentioned earlier. The subgenital plates of vastus and dilatatus females are narrower and more acutely pointed; those of lineatifrons and modestus are broader and more bluntly tipped. It was possible with closer study of the penes of modestus and dilatatus to see differences which had not been noticed earlier. The same was true of the subgenital plates of modestus and lineatifrons. Thus modestus was seen to be a good species. The female and larva are described later in this paper for the first time.

During my study of *modestus*, Thomas W. Donnelly reared a female of the *Gomphurus* group in Texas on May 8, 1962 which he could not place to species with certainty, and sent it to me. He thought it might be *modestus*. In the subgenital plate it agreed with the Alabama specimens of *modestus*. He later sent me a male and female collected at the same stream, Big Creek, near Shepherd, Texas on June 2 and 9, 1963. The female was like his reared one and the male agreed with the holotype of *modestus* then in my possession, adding further confirmation to the correct association of adults and larvae.

CALVERT (1921) in describing G. lineatifrons compared it in great detail with dilatatus and vastus. He illustrated the subgenital plates of dilatatus and lineatifrons, but not vastus. Drawings of the occiput and vertex of all three females, as well as hamules and penes of the males were published. The flagella of the penis of dilatatus were broken and the supposed missing parts were shown

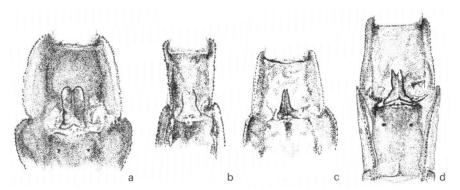


Fig. 2. Subgenital plates (vulvar laminae) of females of Gomphus (Gomphurus): (a) lineatifrons Calvert; - (b) modestus Needham; - (c) vastus Walsh; - (d) dilatatus Rambur.

by dotted lines. Later when he obtained a perfect male he wrote that the dotted lines were too long, and the flagella were really short, not long as in vastus and lineatifrons, as he had previously supposed (CALVERT, 1923). This was apparently overlooked by WALKER (1957) when he stated that all species in the Gomphurus subgenus have the "long" penis. He was not yet aware of my paper of 1956 which gave a drawing of the penis of G. septima Westfall which has very short flagella. In Figure 2 I am presenting camera lucida drawings of subgenital plates of all four species involved for direct comparison.

CALVERT (1921) on p. 230 added a postscript concerning a male and a female labeled Amite River, Louisiana which E.B. Williamson had sent him with the note, "Fragments received in bottle years ago." The parts of the male were carefully glued to a card by Calvert and they are now in the Academy of Natural Sciences, Philadelphia, along with the female. There is one correction to be made to his notes. The inferior appendage of the male is not absent as stated by Calvert. He labeled these specimens dilatatus since in most of his characters they agreed with that species, but he stated that the face was as in lineatifrons, while the rhinarium (anteclypeus) was intermediate. CALVERT (1923) lists these specimens again as dilatatus, and BICK (1957) discusses the record but lists no other Louisiana record of dilatatus. These specimens were the basis of the Louisiana record of dilatatus in the "Manual", but they have been carefully examined by me and relabeled as modestus, thus filling in the distributional gap between Mississippi and Texas. The subgenital plate of the female is missing as stated by Calvert. If he could have seen this he would hardly have labeled it dilatatus.

After carefully relaxing and examining the penis of the Black Bayou, Texas male mentioned earlier, I agree with Mrs. Gloyd in calling it vastus. According to

WILLIAMSON (1914) Calvert had suggested his four specimens might be immaturely colored vastus. This male is teneral and the broken appendages are glued to a piece of paper in the triangle. The penis has the long flagella of vastus, as shown in Figure 1e. In externus the flagella are still longer as shown in Figure 1b. There is a sudden narrowing of the terminal segment of the penis of this specimen, as in other vastus, whereas in externus there is a gradual tapering distally. The projection below the flagella, termed spine of penis by CALVERT (1921) and prepuce by WALKER (1957), is sharply pointed in vastus, blunt or even enlarged at the apex in externus. The apex of the peduncle is uniquely truncate in vastus. The subgenital plate of the female figured by WILLIAMSON (1914) has the two points of the apex divergent, whereas in my specimens of vastus from Alabama and Indiana they are usually subparallel. It is possible that this was because the specimens were teneral, for a teneral specimen of vastus from Alabama collected by Smith and Hodges also has them divergent. The true G. consanguis was described and illustrated by WESTFALL & TROGDON (1962).

Robert B. Cumming has sent me a male collected in Caldwell County, Texas, July 19, 1964 on the San Marcos River at U.S. Hgwy. 90, two miles west of Luling. Dennis R. Paulson has sent me a mated pair and two single females collected in Jim Wells County, Texas on the Nueces River at Texas Hgwy. 359, June 17, 1966. Four males were given me from Brazos County, Texas collected on Cedar Creek at Hgwy. 190, June 23, 1970 by C.D. Bjork. These all agree with the Williamson specimens in structure, size and color, except the apices of the subgenital plates of the females are more parallel, and they are not teneral. When compared with vastus from Alabama, Canada, Indiana, Massachusetts and Virginia they are seen to be on the average larger than the more northern specimens. The light areas on the thorax and abdominal segments do not contrast so markedly with the dark areas as in specimens from Alabama or Indiana, because brown largely replaces black in the paler Texas specimens. A single male from Franklin County, Arkansas is somewhat intermediate between the Texas and Alabama specimens in color and size.

GOMPHUS (GOMPHURUS) MODESTUS NEEDHAM, 1942 DESCRIPTION OF ADULT FEMALE

In general coloration the female is much like the male.

He a d. Face yellowish-green crossed with a narrow brown stripe on the fronto-clypeal suture and another at the base of the labrum. Anteclypeus darker, especially in the maturely colored specimen from Texas. Vertex dark brown to black, this color slightly encroaching on the top of the frons and the base of the occiput. Crest of occiput slightly biconvex, its edge darkened. Rear of head dark except for yellow spot on rear of occiput and one on rear surface of each eye.

Thorax. Prothorax dark brown, the middle lobe with a dorso-median yellow spot and a conspicuous yellow spot laterally on each side. Thorax yellowish-green marked with dark brown. The middorsal brown stripe slightly widened anteriorly to the yellow collar; middorsal carina yellow. The antehumeral brown stripe is about equal in size to the humeral stripe, and may or may not be joined with the middorsal stripe at the collar. Thinner, but complete, brown stripes are present on the first and second lateral sutures, the first joined below with the humeral stripe. Legs entirely black except flexor surface of first femur which is yellowish. Wings entirely hyaline or slightly tinged with yellow in membrane at base.

A b d o m e n. Dark brown (probably more black in fully matured eastern specimens), marked with yellow. Middorsal light stripe wide and full length on segments 1 and 2, narrower and tapered to a point on 3-6, but extending almost full length; 8 with or without a small basal spot; 9-10 brown. Laterally 1 and 2 broadly yellow; 3 with large spot tapering from base toward apex; 4-6 each with a small basal spot continuous with yellow inferior margin; 7-9 with larger basal spots, largest on 9; 10 and appendages dark brown. Subgenital plate extending about three-sevenths of the length of segment 9, constricted about mid-length, the tips slightly divergent and broadly rounded at apex.

Measurements (in millimeters). Total length 55-63; abdomen 43-46; hind wing 34-37.

Material examined. Alabama: Tuscaloosa County, North River, five females reared by Septima C. Smith and Robert S. Hodges in May 1939. Texas: San Jacinto County, Big Creek near Shepherd, two females, one June 2, 1963 (designated allotype, No. 726), and the other reared May 8, 1962 by Thomas W. Donnelly. Louisiana: Amite River, one female, May 28, 1899 collected by Ed. Foster and formerly in the E.B. Williamson collection. All specimens are in the Florida State Collection of Arthropods at Gainesville, Florida, except the Louisiana specimen in the Academy of Natural Sciences of Philadelphia.

In May of 1939 Smith and Hodges collected a number of specimens of both sexes of G. dilatatus on the Black Warrior River above Blue Creek, Tuscaloosa County, Alabama. In May and June of 1937 they collected modestus at Lock 16 on the Black Warrior River, thus establishing the occurrence of both species on the same river, and in the same county.

DESCRIPTION OF LARVA

General color light brown with no conspicuous markings. Abdomen depressed and much wider than the head, abruptly narrowed to the end.

Length 34-36 mm; abdomen 22-23; hind femur 6; width of head 6; width of abdomen 9-10.

Head widest a little behind the middle of the eyes; hind margin only slightly 68

excavated. Hinge of labium extending posteriorly to base of procoxae; prementum contracted in about the proximal 2/5, width by length about as 10:12, widest slightly distal to the contraction. Anterior margin of prementum somewhat convex with a dense brush of about 35-50 pointed scales that are only slightly flattened. Palpal lobes stout, narrowed to form a strong incurved end hook, projecting well beyond the row of 3-4 blunt teeth. Movable hook long and incurved, length about 1.5 times distance from base of palpal lobe to base of movable hook.

The depressed abdomen is widest on segment 6, rather abruptly narrowed to the caudal appendages. Wing pads reach to base of segment 4. Segments 8 and 9 with small dorsal hooks which do not project dorsally above the level of the segments, that of 9 especially quite bluntly and obtusely pointed. Strong lateral spines on 6 to 9, the length of the one on 9 compared to middorsal length of segment 10 about as 17-19 to 10. Lateral margins of 9 strongly serrated with saw-toothed edge; the large sharp teeth numbering about 20-24 and interspersed with fine hairs. Distal margin of 9 also with strong teeth. Lateral margins of 7 and 8 with fewer and smaller serrations. Superior and inferior anal appendages subequal in length, laterals about three-fourths as long. Relative lengths of segments 8, 9, 10, and superior appendages about as 9: 10: 4:6.

The tibial burrowing hooks are large and strong on the first two pairs of legs. Described from two last instar larvae from Texas and exuviae of 14 reared specimens from Alabama and Texas, all in the Florida State Collection of Arthropods at Gainesville. From Texas we also have an antepenultimate larva 27 mm. long that shows all of the distinguishing characteristics.

COMPARISON OF LARVAE OF MODESTUS, LINEATIFRONS, DILATATUS AND VASTUS

CALVERT (1921) compared dilatatus larvae with the descriptions of reared vastus and the description by NEEDHAM (1903) of dilatatus which in reality was lineatifrons. Calvert gave no illustrations of the larvae. Figure 3 shows the entire larva of modestus, an enlarged view of the terminal abdominal segments of the same, and the labia of all four species for comparison.

All of these species have lateral spines on segments 6-9. So far as is known consanguis is the only species of the Gomphurus group with lateral spines only on 7-9. The strong concavity of the front margin of the prementum in lineatifrons sets it apart from all the others. Also its prementum is widest at the front margin, and without the sudden contraction on the lateral margins of the other species. The palpal lobes of modestus, dilatatus and vastus are alike in having the end hook long, projecting far beyond the line of 3-6 large teeth. The lateral spines of 9 do not reach beyond the end of segment 10 in vastus, but far beyond in modestus and dilatatus. The front margin of the prementum is straight in

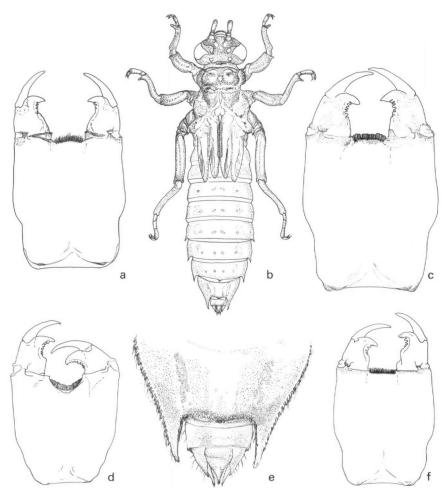


Fig. 3. Larvae of Gomphus (Gomphurus): (a) modestus Needham, labium; – (b) modestus Needham, dorsal view of entire larva; – (c) dilatatus Rambur, labium; – (d) lineatifrons Calvert, labium; – (e) modestus Needham, enlarged view of abdominal segments 9, 10, and appendages; – (f) vastus Rambur, labium.

vastus, slightly convex in modestus and dilatatus. The smallest of these species is vastus, the largest is dilatatus, and the latter also usually has the largest number of teeth on the palpal lobes of the labium. The scales on the front margin of the prementum in modestus are about twice as long as in dilatatus and are less flattened and more sharply pointed. A further good character to separate

modestus from dilatatus seems to be the relative size and number of serrations on the lateral margins of abdominal segment 9. They are much larger and fewer in number on modestus, on each side about 20-24 (usually 20-21) as compared with 24-31 (usually 26-30) on dilatatus. The dorsal hooks on segments 8 and 9 are much larger and more acutely pointed in dilatatus.

DISTRIBUTION AND FLIGHT DATES

G. dilatatus

Listed in "Manual" from Ala., Fla., Ga., La., and S.C. March 6 (Fla.) to June 23 (Ga.). To this we can add N.C. based on a male in the Florida State Collection of Arthropods taken at Fair Bluff, Columbus County by R.D. Cuyler. I have again carefully examined the teneral female which CUYLER (1968) reported from the Haw River, N.C. and it is certainly not this species for the subgenital plate is more than half as long as segment 9 and very differently shaped. We will wait with the final determinations until more mature specimens are found at the Haw River. We must delete La. since Calvert's Amite River specimens are shown to be *modestus*. A new late date may be inserted for Fla. based on a male collected by Michael May on the Ichetucknee River, Columbia County, Florida on August 19, 1971 and now in his collection. It is postulated that the very cold water of this spring-fed river may delay development and emergence.

G. lineatifrons

Listed in "Manual" from Ala., Ill., Ind., Ky., Mich., Minn., N.Y., Ohio, Pa., Tenn. and Va. May 17 (Ky.) to July 4 (Ind.). To this we can add Md. based on larvae reported by ROBACK & WESTFALL (1967) from the Potomac River. W. Va. was added by KORMONDY (1960).

G. modestus

Listed in "Manual" from Ala., Miss., and Tex. April 25 (Miss.) to May 27 (Tex.). While the original Texas record and date were incorrect because based on Williamson's vastus, Donnelly's subsequent records establish it for Texas. A new late date is supplied by a male taken in the Big Biloxi Recreation Area, 10 miles north of Gulfport, Harrison County, Mississippi on June 13, 1971 by R.D. McManaway. The specimen is in the Florida State Collection of Arthropods.

G. vastus

Listed in "Manual" from Canada: Ont., Que.; United States: Ala., Conn., D.C., Ga., Ill., Ind., Iowa, Kans., Ky., Md., Mass., Mich., Minn., Miss., Mo., N.H., N.Y., N.C., Ohio, Pa., S.C., Tenn., Va., W.Va., Wis. April 8 (Miss.) to September 15 (Ohio). To this we can add Tex. based on Williamson's and subsequent

specimens mentioned earlier; Ark. based on a male collected by James Houston in Franklin County July 1, 1966 and now in the Florida State Collection of Arthropods at Gainesville. Okla. may be added based on two males and a female in the same collection contributed by George H. Bick. They were taken in Bryan County, a male and female at Armstrong July 9, 1960 by McDougal, and a male 5 miles south of Bokchito July 21, 1954 by G.H. Bick.

OBSERVED CLINES IN COLOR OF CERTAIN SPECIES OF GOMPHUS

The larger size and browner color of the Texas G. vastus, compared with the more eastern and northern specimens, has caused a number of persons difficulty in recognizing them. More than one suggested to me that the Texas specimens might represent a new species. The fact that the penis was like the northern vastus led me to compare as many as I could get, and it appears there is a cline in the color differences, darker in the more eastern and northern specimens, lighter in southwestern ones.

A similar cline seems to be true of *modestus* for the ground color on the abdomen of two mature males (not reared) from Alabama is considerably darker than on the same areas of the mature male from Texas. A cline has also been noted in G. (Stylurus) plagiatus Selys, but the southwestern specimens, while very pale compared with eastern specimens, are much smaller than Florida specimens. Arizona and southern California individuals were not at first recognized as plagiatus when one had Florida specimens in mind. In this subgenus unfortunately the penes are remarkably uniform from species to species, but the hamules furnish good specific characters. Texas specimens seem to be intermediate between California and eastern specimens in size and color.

The color markings of Mississippi and Florida G. (Stylurus) townesi Gloyd are so different from the South Carolina holotype and North Carolina specimens that they could not be keyed with the color key in the "Manual" and were at first supposed to be a new species. Before he died E.M. Walker said he believed G. (Gomphus) flavocaudatus Walker was just the light end of a color cline from north to south in G. exilis Selys. This sounds a note of caution in describing new species or writing keys based too much on color. This is not to say however that color differences may not constitute an isolating mechanism between sympatric species very similar in structure. Where modestus and dilatatus are sympatric and have penes so similar it would be interesting to know if the bold black face stripes of dilatatus might not serve as an isolating mechanism. It is interesting to speculate on the significance of the marked difference between the female subgenital plates of these two, and why that of modestus resembles that of lineatifrons, whose male has such a different penis.

In North Carolina and northwestern Florida we have found the darkly colored G. (Gomphus) brimleyi Muttkowski, WESTFALL (1953), while from 72

north central to southern Florida occurs the more brownish G. cavillaris Needham. As yet we have found no intermediates in color, but structurally they may be almost identical, and more study of populations in the field is needed. Both species are found in sand-bottomed lakes, and there seems to be a scarcity if not an absence of such lakes for a distance of about a hundred miles between north central Florida in the Gainesville area and the Tallahassee area where brimleyi, as far as known, was first found by W.H. Cross in 1950.

Further study of field populations of a number of species would be helpful in understanding relationships. In several instances in other families of Odonata a study of more specimens is showing that the two ends of a cline have been named different species. This is undoubtedly also true in other parts of the world.

ACKNOWLEDGEMENTS

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