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A NEW GOMPHINE GENUS FROM BRITISH GUIANA
WITH A NOTE ON THE CLASSIFICATION OF THE
SUBFAMILY (ORDER ODONATA)

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Desmogomphus, new genus

Belonging to the legion Gomphoides of the *Monographie des Gomphines* and to the short-legged division of the legion. Separated at once from the "genre Zonophora," as defined in the *Monographie*, by the relatively short uncrossed triangle of the front wing and the simpler venation (anal area of front wing only one cell wide); and from the "genres Progomphus and Gomphoides" by the shorter stigma (in the front wing less than one-third as long as the distance from nodus to stigma), by the proximal angle of the subtriangle in the front wing distal to the arculus, and by the anal crossing in the hind wing proximal to the subtriangle a distance equal to the anterior side of the subtriangle.

Dr. Calvert (*Ent. News*, XIV, June, 1903) describes and figures the venation of a new species of *Diaplebia* giving a careful analysis of the venational characters of *Diaplebia* and *Epigomphus*.

If his *Diaphlebia nexans* is congeneric with the type species, *D. augustipennis*, as there is no reason to doubt, then *Diaphlebia* is the nearest relative of *Desmogomphus*. *Desmogomphus* has a much shorter stigma (about one-eighth the wing length, about one-sixth or slightly longer in *Diaphlebia*); the anal area of the front wing is only one cell wide (two in *Diaphlebia*); and the hind border of the hind wings is normal (not excavated basally as in *Diaphlebia*).

Other venational characters of *Desmogomphus* may be briefly summarized: triangles, supratrangles, and subtriangles all free except the triangle of the hind wing, which is once crossed; triangles of front and hind wings dissimilar, that of front wing nearly equilateral, with the anterior side very slightly the shortest, that of hind wing with the proximal side much the shortest; subtriangles distinct (i.e., A angled at the proximal angle of the subtriangle); M_4 and Cu_1 in front wing more widely separated at the level of the nodus than at the triangle; M_3 in front wing terminating far proximal to the level of the stigma; cross-veins between M_{1-3} and M_4 numerous and unspecialized; two rows of post-trigonal cells in the front wing, three, followed immediately by two, in the hind wing; forking of M_{1-2} and M_3 unsymmetrical; basal antenodal of second series wanting; distal thickened antenodal the fifth; anal area of front wing one cell wide, of hind wing three cells wide, the two anterior postanal cells undivided; anal triangle three-celled, not reaching the anal angle; membranule wanting.

While the affinities of *Desmogomphus* are, I think, with *Progomphus* and *Gomphoides*, there is a striking resemblance between the front wings of *Ischnogomphus* and *Desmogomphus*. *Ischnogomphus* and *Progomphus*, for example, belong, I believe, to two lines of descent. By its characters *Desmogomphus* indicates the common origin of these two lines, and an apparent link between them justifies its name. The relationships will be discussed in the second part of this paper.

Desmogomphus, compared with its allies, is a relatively slender gomphine and the legs are weaker and slightly longer than in related genera (Progomphus and Gomphoides; I do not know Diaphlebia). Type of genus, *Desmogomphus tigrivensis*, new species.

Desmogomphus tigrivensis, new species

Abdomen, male 30.5; hind wing, male 24.

Male.—Rear of head dull brown, darker about the foramen and lighter below, where it is indefinitely patterned with dull yellow; genae, face, and frons above bluish gray or lead-colored, obscurely and indefinitely patterned with brown as follows: labrum with the anterior edge (dark brown, almost black) and a median posterior spot, rhinarium and nasus with more or less diffuse central areas, and frons in front, excepting the angle, and above at the base in the median line. Angle of frons low and rounded. Vertex and occiput dark brown or black; anterior face of vertex relatively flat, in a plane about parallel to the nasus, smooth and bare; dorsal surface with a low median longitudinal sulcus, punctate and bearing hairs equal in length to those on the occipital border, the lateral margins of the middle lobe of the prothorax, and the mesothoracic transverse carina; occipital border broadly concave.

Prothorax brown; anterior lobe largely dull yellow, especially above and in front; middle lobe with a median posterior geminate bluish-gray spot and one or two yellow areas on each side below; hind lobe with yellow shadings on the posterior border.

Thorax rich dark brown marked with olive green. Beneath pale yellowish brown.

Abdomen relatively slender, dark brown basally, progressively darker apically till the apical segments, beginning at the fourth or fifth, are black; marked with yellowish or greenish as follows: segment 1 largely pale, the dorsal apical half or slightly less, brown;

sides below of segment 2, including the auricles and dorsal median longitudinal bar on the apical half of the segment, pale; segment 3 with the sides pale below basally, and with a narrow longitudinal mid-dorsal line, which is widest at the base of the segment, thread-like through most of its length, and does not quite reach the apex; segment 4 apparently entirely brown with the exception of a reduced and frequently interrupted longitudinal mid-dorsal thread-like line extending the full length of the segment except the extreme apex, and a small pale area on either side below basally; segment 5 with a more or less distinct basal median spot, the remnant of the dorsal line, and a small pale area on either side below basally; segment 6 similar to segment 5, but the lateral and median pale areas are slightly larger; in segment 7 these pale spots are joined in a basal band, encircling the segment and occupying about one-fifth its length; segments 8 to 10 black, segments 8 and 9 laterally and segment 10 dorsally and laterally obscurely and indefinitely mottled with dark reddish brown; segment 10 with the apical inferior side obliquely cut; superior appendages yellow, the inferior reddish horn, both tipped with black. The superior appendages are 1.5 mm. long, and segments 8, 9, and 10, measured at mid-height on the side, are respectively 2.4, 1.4, and .8 mm. in length.

Wings hyaline, very slightly tinged yellowish basally, venation dark, stigma brown, covering three to four cells, 2.7 mm. long in the front wing and 3 mm. long in the hind wing; antenodals of front wing 12 or 13 mm., of hind wing 9 or 10 mm.; postnodals of front wing 10 to 13 mm., of hind wing 9 or 10 mm.

Legs weak, of median length, light reddish brown, darker apically beginning on the apices of the femora; apices and angles of the tibiae, and the tarsi black; the first femora darker above through most of their length. Femora circular, tibiae quadrangular in cross-section. First femora with a longitudinal row of very light yellowish-brown inconspicuous bristles on its ventro-

posterior surface; on the postero-ventral surface are scattered small black spines which form a fairly distinct longitudinal row or tract; scattered among these spines are four to six black bristles or long slender spines; on the antero-ventral surface is an inconspicuous row of a few small black spines. Second femora with a row of long almost colorless bristles on the ventro-posterior surface as on the first femora; ventral surface basally with many small black spines which, passing apically, resolve themselves into two rows, the posterior row or tract of uniformly small spines more or less irregularly scattered, the anterior row definitely single-rowed with the spines increasing in size from the base to the apex. Third femora similar to the second, but the row of pale bristles on the ventro-posterior surface confined to the apical half or two-thirds, the black spines on the ventral surface less numerous, the anterior and posterior rows, in the apical half, equally definite and well-defined single rows, and the spines of the posterior row longest at about two-thirds the length of the femur, diminishing in size apically and basally from this point; the anterior row is similar to the anterior row on the second femora. The first femora are 3 mm. long; the second, 3.4 mm.; and the third, 5 mm.; the first tibiae are 2.8 mm.; the second, 3 mm.; and the third, 3.2 mm. (all measurements on the dorsal surface).

Accessory genitalia, including the penis, relatively simple; the first hamule is a flattened plate, convex externally, concave internally, with the anterior edge the heavier and with the apical anterior corner bearing a strong interno-posteriorly directed hook; second hamule thornlike, slightly flattened.

Described from two males, Tiger Creek, near Tumatumari, on the Potaro River, British Guiana, February 5 and 7, 1912, the first the type in Coll. E. B. W., the second in Coll. P. P. C. Both specimens were taken resting on the flat surface of leaves overhanging Tiger Creek. One was taken only a short distance below Washerwoman Falls, the other possibly a mile below.

ON THE CLASSIFICATION OF THE GOMPHINAE¹

The Gomphinae, as used in this paper, is in the restricted sense of modern authors, the latest of whom is Tillyard in the *Biology of Dragonflies*, who states (p. 258): "We still need a thorough study of the Gomphinae, the present division into two tribes being only tentative."² Needham (*A Genealogic Study of Dragon-Fly Wing Venation*, pp. 737-38) says: "Variation from the type is slight considering the large number of genera in the group, and such as there is, it does not lend itself readily to serial arrangement." And after discussing various characters which appear scattered through the subfamily, he adds:

Possibly these features indicate the tips of numerous short developmental twigs. The brief records of the several parts are certainly contradictory, and the parts themselves, which one might use as bases for the first divisions of the group, seem so nearly of equivalent importance that one may hardly choose between them with assurance. Probably the records of other organs will be more easy of interpretation.

This was written sixteen years ago and no attempt has been made by students to employ other organs in elucidating relationships within the subfamily. Since figures of wings are more available

¹ Figures of venation of many gomphines are found in the following papers: James G. Needham, "A Genealogic Study of Dragon-Fly Wing Venation," *Proc. U.S. Nat. Mus.*, 1903; Philip P. Calvert, "On Some American Gomphinae (Odonata)," *Ent. News*, XIV (1903); E. B. Williamson, "The Dragonflies (Odonata) of Burma and Lower Siam. II. Subfamilies Cordulegasterinae, Chlorogomphinae and Gomphinae," *Proc. U.S. Nat. Mus.*, 1907; E. B. Williamson, "A New Cyanogomphus (Odonata)," *Ent. News*, XXVII (1916); E. B. Williamson, "Two Interesting New Colombian Gomphines (Odonata)," *Occ. Papers Museum of Zoology*, University of Michigan, No. 52, 1918; E. B. Williamson, "A New Species of Agriogomphus (Odonata)," *op. cit.*, No. 59, 1918; E. B. Williamson, "Archaeogomphus, A New Genus of Dragonflies (Odonata)," *op. cit.*, No. 63, 1919.

² Tillyard's use of size in defining the two tribes is not justified, as in the Ictinini, "moderate to large-sized Gomphinae," occur many small species, among them the smallest gomphine known, and in the Gomphini are a number of large species. Under his series 1, the Gomphoides series of the Ictinini, he says "Larva with elongated abdomen," but the larva of Hagenius is circular.

and more easily interpreted than figures of any other part it seems worth while to attempt some statement of relationships based on a study of this organ, thus preparing a tentative outline of the classification of the subfamily to be corrected and revised by later studies of other organs.

Since de Selys' *Monographie des Gomphines* was published our definition of Gomphinae has grown by reduction, and it may be noticed that three of the five palaeogenic groups defined by Tillyard, in *The Biology of Dragonflies*, are groups which de Selys included in the Gomphinae. The Gomphinae of recent authors is the "Division Integrilabiées" of de Selys, containing over fifty genera and three hundred and ninety species.

If the wings of the gomphine *Archaeogomphus hamatus* and the libelluline *Hypothemis* are compared certain common characters are obvious: the basal crossing of *ac*, the four-sided triangles, the undifferentiated cross-veins between M_{1-3} and M_4 , and the unsymmetrical forking of M_{1-2} and M_3 . The corduline genus *Cordulephya* has these characters less marked, *ac* is not so basal and M_{1-2} and M_3 are symmetrically forked. If the wings of *Gomphus dilatatus*, for example, are compared with those of *Archaeogomphus* it will be seen that in the former *ac* is very distal, the triangles are typical, the cross-veins between M_{1-3} and M_4 are reduced and specialized, and the forking of M_{1-2} and M_3 is symmetrical. I believe these four characters, in connection with other venational characters, can be employed as valuable criteria in classifying the Gomphinae.

It is assumed that the four characters as found in *Archaeogomphus* are primitive at least for the Gomphinae and that they may be employed as criteria for determining the more primitive members of any particular series. The association of these characters in forms generally recognized as primitive in both Gomphinae and Libellulinae gives weight to this assumption. The four-sided triangle and the unspecialized cross-veins between M_{1-3} and M_4

are certainly primitive gomphine wing characters. When we find a basal position of *ac* and an unsymmetrical forking of M_{1-2} and M_3 associated with these two characters in the same wings it may safely be assumed that the basal position of *ac* and the unsymmetrical forking are relatively primitive characters also.

1. *The Epigomphus series.*—This includes the following genera previously included in the grand genus *Gomphus* of de Selys: *Archaeogomphus*, *Agriogomphus*, *Cyanogomphus*, *Epigomphus*, *Ischnogomphus*, *Leptogomphus*, *Macrogomphus*, and *Microgomphus*. In this series alone, in *Archaeogomphus*, and to a lesser extent in *Microgomphus*, is a four-sided triangle found in the subfamily. (It is indicated also in the hind wing of the single figure I have of the venation of *Neogomphus*.) At the other end of the series from *Archaeogomphus* is the more densely veined *Macrogomphus quadratus* with its strikingly curved sectors. The series is distinguished by free triangles, supratriangles, and subtriangles, and numerous cross-veins between M_{1-3} and M_4 . In the higher members of the series *ac* moves distally, M_{1-2} and M_3 form a symmetrical fork, and there is an increase in density of wing venation. In the next series specialization by addition has been carried still farther. Of the *Epigomphus* series three genera with twenty-two species occur in the Oriental Region and five genera with sixteen species occur in the Neotropical Region.

2. *The Progomphus series.*—This includes the grand genera *Progomphus* and *Gomphoides* of de Selys and *Diaphlebia* and *Desmogomphus*. Genera of this series may be recognized by having the triangles, supratriangles, and subtriangles more or less cross-veined, by dissimilar triangles and subtriangles in fore and hind wings, the triangles of the fore wings being relatively shorter and of the hind wing relatively longer; by the absence of sectors of R_s and M_4 and of strongly developed trigonal supplements, and by the outer side of the triangles not distinctly concave.

In Desmogomphus we have the most primitive genus of the series. The front wing of this genus if considered alone could as well be referred to the Epigomphus series. At the opposite end of the series is the densely veined *Gomphoides stigmata*, for example.

Four genera (if Calvert's views on synonymy, *Biologia Centrali Americana*, are followed) containing about sixty species comprise this series which is Neotropical with a few species which have penetrated into the Nearctic Region.

3. *The Gomphus series*.—This includes the grand genus Gomphus of de Selys less the Epigomphus series. It is the dominant gomphine type in the world at the present time, being represented by more than thirty genera and two hundred and fifty species. It is well represented in all the zoogeographical regions except the Neotropical, where only one genus in the south and one in the north occur. It holds a place in the subfamily similar to the position of the tribe Agrionini in the Agrioninae. Associated with uncrossed triangles, supratrangles, and subtriangles is a reduction and specialization in the cross-veins between M_{1-3} and M_4 (see Davidius under the Hagenius series). This last character is unique in the Anisoptera (see the Hagenius series) and can hardly be associated with greater wing efficiency. The Gomphinae generally, while capable of swift and mobile flight, spend a relatively small portion of their lives on the wing when compared with some of the aeshnines, cordulines, and libellulines, and the genera of this series are no exception to the rule. However the reduction in the venation has been brought about, the fact remains that here we have a different condition from that found in the two preceding series where the higher members are the more densely veined.

The series is very compact and the venational differences between genera are slight.

4. *The Zonophora series*.—Zonophora, the single genus of this series, is characterized by the triangles and subtriangles of fore and hind wings similar, the triangles long and once crossed, the

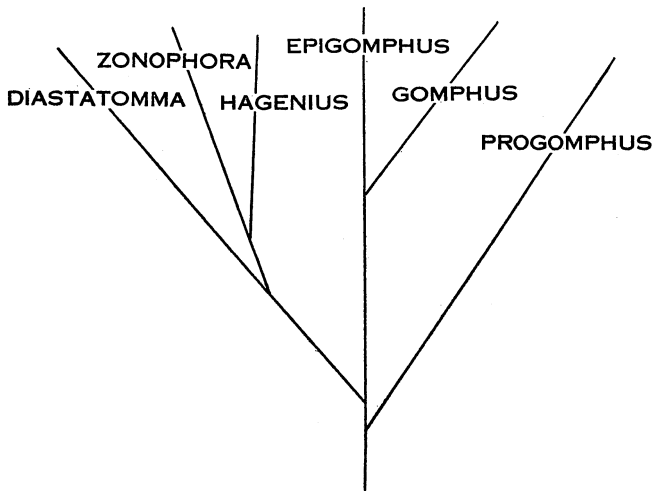
subtriangles and supratriangles all free, absence of trigonal supplements and sectors of R_s and M_4 , and by having the proximal angle at the point of separation of A_1 from $Cu_2 + A_1$, nearly a right angle, and not as obtuse as the distal angle at the same point. Its affinities are with the Hagenius series, and since I regard the latter as a series undergoing reduction and because of the uncrossed supratriangles and subtriangles in the Zonophora series, I believe the latter series has undergone reduction. The genus is represented by three species confined to the Neotropical Region.

5. *The Hagenius series.*—This is another small compact series, characterized by a distinct trigonal supplement in both wings, with the distal side of the triangle posterior to the attachment of the trigonal supplement distinctly concave. In the other characters of the triangles, supratriangles, and subtriangles, this series resembles the Zonophora series. But the Hagenius series is distinct from all others, excepting the Gomphus series, in that a considerable reduction of the cross-veins between M_{1-3} and M_4 has taken place.

Hagenius with a single species (unless a second species, *gigas*, from the Oriental Region should prove to be really congeneric) occurs in the Nearctic Region; and Sieboldius, with three species, occurs in the Palaearctic and Oriental Regions.

The genus Davidius has generally been associated with Hagenius and Sieboldius. I do not know the genus well enough to be certain, but I believe it belongs to the Gomphus series, being probably the most primitive member of that series. If this is correct free triangles is not an infallible character of the Gomphus series any more than crossed triangles is an infallible character of the Progomphus series.

6. *The Diastatomma series.*—I know the venation of the genus Diastatomma only from the figure in the *Monographie des Gomphines*, and the venation of Lindenia and Isomma not at all. Hence, I have to assume that the Legion Lindenia of de Selys is a single series and that the genera I know, Gomphidia, Ictinus, and



ERRATA

On page 11, last paragraph, first line, for *foregoing* read *following* and after *diagram* insert *on page 12*.

On page 2, second line from top, for *angustipennis* read *angustipennis*.

On page 2, third line from bottom, after *and* insert *as*.

On page 4, first line, insert *a* between *and* and *dorsal*.

On page 4, seventh and eighth lines from bottom, eliminate all *mms*.

Cacus, are representative of the series. In the slight concavity of the distal side of the triangles the Hagenius series is suggested; in the dissimilar subtriangles of fore and hind wings and the dense venation the Progomphus series is suggested, but the triangle of the front wing tends to be longer, nearer the shape of the triangle of the hind wings, in the Diastatomma series; it is unique by the presence of a strongly developed sector of Rs and a usually less well-developed sector of M₄. Of the twenty-seven species in the six genera in this series, six belong in the genus Gomphidia and sixteen in Ictinus. Cacus of the Neotropical Region, with one species, alone occurs in the New World; Lindenia with a single species is Palaearctic; the remainder are Ethiopian and Oriental.

Series	Neo-tropical	Nearctic	Palaearctic	Ethiopian	Oriental	Australian
Epigomphus.....	x	x
Progomphus.....	x	x
Diastatomma.....	x	x	x	x
Zonophora.....	x
Hagenius.....	x	x	x
Gomphus.....	x	x	x	x	x	x

The foregoing diagram indicates the relationships of the six series as I understand them. From the vertical line of primitive and simple winged forms the Diastatomma line branched off and became by addition a densely veined type. From some dense-veined member of this line a branch developed which by reduction resulted in the Hagenius and Zonophora series. It is possible these two series should be shown arising independently from the Diastatomma line. The Progomphus series is another lateral branch from the vertical line, developing another type of dense-veined forms. From some dense-veined member of the Epigomphus series a branch appeared which by reduction gave rise to the Gomphus series.

PLATE I

All figures of *Desmogomphus tigrivensis*, n. gen. and n. sp., male type specimen.

Figure 1, wings; 2, diagram of thoracic color pattern; 3, abdominal appendages in profile; 4, superior appendages in dorsal view; 5, inferior appendage in ventral view; 6, hamules fully extended, the first hamule the broader one; 7, seminal vesicle and penis in profile; 8, ventral view of apex of first joint of the penis and of the second and third joints; the larger opening is in the apex of the first joint; in relaxing and expanding the genitalia it was noticed that air and fluids were discharged through this opening; 9, antenna, inner surface; 10, relative position of the ocelli; 11, third tarsal claw.

