

# **Higher classification of the South-American Gomphidae (Odonata)**

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The adults and larvae of the South-American Gomphidae are classified. Keys to the subfamilies and tribes are constructed followed by tribal descriptions and descriptive notes. The existing classification is revised as follows: - Octogomphinae comb. nov.: Hemigomphini (*Neogomphus*, *Praeviogomphus*), Anomalophlebiini trib. nov. (*Anomalophlebia*); - Onychogomphinae: Onychogomphini (*Erpetogomphus*); - Epigomphinae: Archaeogomphini (*Archaeogomphus*), Agriogomphini trib. nov. (*Agriogomphus*, *Brasiliogomphus*, *Ebegomphus*), Cyanogomphini comb. nov. (*Cyanogomphus*, *Tibiagomphus*), Epigomphini (*Epigomphus*); - Ictinogomphinae comb. nov.: Ictinogomphini comb. nov. (*Cacoides*, *Melanocacus*); - Zonophorinae: Zonophorini (*Mitragomphus*, *Zonophora*); - Gomphoidinae comb. nov.: Aphyllini trib. nov. (*Aphylla*, *Phyllocycla*), Diaphlebiini trib. nov. (*Desmogomphus*, *Diaphlebia*), Gomphoidini comb. nov. (*Gomphoides*, *Idiogomphoides*, *Phyllogomphoides*), Peruviogomphini trib. nov. (*Peruviogomphus*), Progomphini (*Progomphus*).

## **Introduction**

The incentive to classify the South-American Gomphidae is the discovery of three genera of primitive little gomphids from this continent. The present subfamilial classification is based on diagnostic characters found in the South-American Gomphidae. In some respects this classification agrees with that of the Gomphidae in general as proposed by Carle (1986) but a number of alterations are made to lodge the South-American gomphids in six subfamilies. Three tribes in his classification, viz. the Lindeniiini, the Gomphoidini and the Zonophorini merit, in my opinion, subfamilial rank while the name Lindeniiinae should be discarded in favor of Ictinogomphinae. The definition of the Octogomphinae is simplified in order to accept the genus *Anomalophlebia* Belle.

The division in subfamilies is based not alone on foremost venational characteristics. Most interesting is the following hitherto neglected nonvenational character, namely the occurrence of coloured (brown or brown-yellow) areas in the wings. These can be basal spots, nodal spots, costal bands or other coloured parts of the wings. All gomphids with a conspicuous maculation in their wings are referable to the subfamily Gomphoidinae irrespective of the venational characteristics. The wings of gomphids belonging to other subfamilies are hyaline and uncoloured with at the most a brownish patch or wash at their extreme base. The small gomphid *Progomphus perithemoides* Belle, for example, has open supratriangles, subtriangles and triangles (= discoidal triangles) but its wings have large brown-yellow areas. Due to this colour feature it is linked with the other species of the subfamily Gomphoidinae which have these triangular spaces generally crossed.

The division in tribes is based on venational as well as on morphological cha-

racteristics. Of each tribe the main larval characters are also given. However, sometimes the larva of a genus pertaining to a certain tribe is unknown so improvements are probable by further collecting. In my paper of 1992 dealing with the ultimate instar larvae of the South-American Gomphidae I drew attention to the so-called *Cyanogomphus* problem. At that time I have ascertained that the exuviae originating from the Brazilian State of Santa Catarina and by supposition referred to *Cyanogomphus* Selys by Needham (1940) have a quite different dorsal outline if compared with those of the congeners occurring in the northern regions of continental South America. A restudy of the species referred to *Cyanogomphus* has revealed that they all, except for two, have controversially been placed in this genus; the adults of the southern species *Cyanogomphus waltheri* Selys and its near ally *Cyanogomphus comparabilis* Belle have a distinct occipital plate with a well-developed posterior ridge whereas the adults of the northern regions have the top of the head rounded off posteriorly and without a transverse ridge. I consider this structural character of generic value. Therefore, I have reinstated Needham's genus *Ebegomphus* for the northern species. *Ebegomphus* is placed in the new tribe Agriogomphini together with *Agriogomphus* Selys and *Brasiliogomphus* Belle. The adults of *Agriogomphus* have also the top of head rounded off posteriorly and the only specimen (a female) of *Brasiliogomphus* has the occiput rounded off posteriorly in the middle part. It is not improbable that the exuviae from Santa Catarina studied by Needham belong to *Brasiliogomphus*, the latter genus being reported from the nearby State of São Paulo. This would be in agreement with the *Agriogomphus*-like appearance of these exuviae. The genus *Cyanogomphus* is placed in the new tribe Cyanogomphini together with *Tibiagomphus* Belle the larva of which is structurally different from that of the Agriogomphini. Other new tribes introduced in the present classification are the Aphyllini, including *Aphylla* Selys and *Phyllocycla* Calvert, the Diaphlebiini, including *Diaphlebia* Selys and *Desmogomphus* Williamson, and the Peruviogomphini, including *Peruviogomphus* Klots only. All these tribes have larvae with morphological characteristics which are typical of the tribe.

I think that, to achieve a satisfied gomphid classification on world basis, it is necessary to acquire not alone an intimate knowledge of the larvae in general but also of the interrelationships between the larvae of the New World and those of the Old World.

The Comstock-Needham notation (1899) for the wing veins is used throughout this paper. Carle, in his classification of 1986, used a notation that is based on new interpretations of the veins (Carle, 1982); these interpretations may be correct but on factual reasons it seems advisable to preserve the Comstock-Needham notation which is used almost a century long in the taxonomic literature of insects.

The depictions of the wings presented at the end of this paper are based on actual photographs made by myself. They are not on scale because of the great difference in size but at each figure the length of the hind wing (hw) is given (in mm). Through the kindness of Dr Oliver S. Flint, Jr., Curator of Insects at the Smithsonian Institution, Washington D.C., U.S.A., I am also able to publish here the important wing characteristics of the male holotypes of *Perigomphus pallidistylus* (Belle) and *Mitragomphus ganzanus* Needham.

### Key to the subfamilies and tribes of the South-American Gomphidae

The term "usually" as here employed in regard of the wing venation means "to be expected"; that the venational feature designated occasionally deviates from the rule, thus that it is present in at least one of the wings (cf. Byers, 1939: footnote on page 25).

1. Hind wing with second primary antenodal cross-vein midway between first primary antenodal cross-vein and nodus or slightly nearer to nodus ..... **OCTOGOMPHINAE** comb. nov. - 6
- Hind wing with second primary antenodal cross-vein nearer to first primary antenodal cross-vein than to nodus ..... 2
- 2(1). Hind wing with one intermedian cross-vein ..... **ONYCHOGOMPHINAE** - **Onychogomphini**
- Hind wing with two or more intermedian cross-veins ..... 3
- 3(2). Hind wing triangle usually uncrossed and wings clear ..... **PIGOMPHINAE** - 7
- Hind wing triangle crossed and wings clear or hind wing triangle uncrossed and wings with coloured areas ..... 4
- 4(3). Rsa strongly developed ..... **ICTINOGOMPHINAE** - **Ictinogomphini**
- Rsa not or weakly developed ..... 5
- 5(4). Hind wing with open anal loop (open on proximal side due to a weak development of A2) and metaparapteron (= subalar carina just before base of hind wing) with a strong posterior spine ..... **ZONOPHORINAE** - **Zonophorini**
- Hind wing with or without anal loop; metaparapteron bluntly pointed at posterior end ..... **GOMPHOIDINAE** - 10
- 6(1). Hind wing with Cu1 and Cu2 strongly divergent to wing margin; top of head without occipital plate but with a transverse ridge that is thickened in middle ..... **Hemigomphini**
- Hind wing with Cu1 and Cu2 parallel; occipital plate present ..... **Anomalophlebiini** trib. nov.
- 7(3). Occipital plate present and posteriorly ridged .... **Cyanogomphini** comb. nov.
- Top of head rounded off posteriorly, its surface often strongly deformed (especially in females by mating adaptations), the transverse ridge entirely or medially undeviated ..... 8
- 8(7). Basal subcostal cross-vein absent ..... **Archaeogomphini**
- Basal subcostal cross-vein present ..... 9
- 9(8). Wings with one cubito-anal cross-vein ..... **Agriogomphini** trib. nov.
- Wings usually with two or more cubito-anal cross-veins (fig. 9) .... **Epigomphini**
- 10(5). Supratriangles crossed; male anal triangle in hind wing extending posteriorly to anal angle of wing ..... 11
- Supratriangles uncrossed or usually uncrossed; male anal triangle in hind wing not extending posteriorly to anal angle of wing ..... 13
- 11(10). Abdominal segment 10 with a dorso-apical rim ..... **Aphyllini**
- Abdominal segment 10 without a dorso-apical rim ..... 12
- 12(11). Subtriangle in fore and hind wings uncrossed; triangle in fore wing uncrossed, in hind wing once crossed; pterostigma in fore wing one-third as long as

- distance between nodus and stigma or shorter .... **Peruviogomphini** trib. nov.
- Subtriangles and triangles usually crossed but subtriangle in hind wing crossed or uncrossed; pterostigma in fore wing longer than one-third the distance between nodus and stigma ..... **Gomphoidini**
- 13(10). Posterior genital hamule of male broadly expanded at base, this part with an anterior row of denticles or with a chitin ridge; vulvar lamina of female short and not extending to halfway the ninth sternum ..... **Progomphini**
- Posterior genital hamule of male not as above; vulvar lamina of female extending to beyond halfway the ninth sternum ..... **Diaphlebiini** trib. nov.

**Key to the larva of the tribes of the South-American Gomphidae**

(Larva of the Anomalophlebiini unknown)

Caution should be taken in the use of this key since the larvae of some genera are unknown or known only by supposition.

1. Abdomen without dorsal hooks ..... 2
- Abdomen with dorsal hooks ..... 4
- 2(1). Lateral margins of abdominal segments 8 and 9 posteriorly with a strong upcurving spine ..... **Zonophorini**
- Lateral margins of abdominal segments 8 and 9 posteriorly with a short triangular spine or ending in an angulation ..... 3
- 3(2). Ligula with two or three minute brown denticles in middle of front border .....
- ..... **Hemigomphini**
- Ligula with 6 to 12 minute black denticles in middle of front border .....
- ..... **Epigomphini**
- 4(1). Wing-cases broadly divergent on the back ..... 5
- Wing-cases parallel on the back ..... 6
- 5(4). Mesocoxae generally indrawn; caudal appendages short to very long with the cerci notably shorter than the paraprocts ..... **Progomphini**
- Meso- and procoxae about equally distant at their bases; caudal appendages short with the cerci a little shorter than the paraprocts ..... **Onychogomphini**
- 6(4). Hind tarsi two-jointed ..... 7
- Hind tarsi three-jointed ..... 8
- 7(6). Larva stocky, broadly depressed and limpet- or tent-shaped; tenth abdominal segment dovetailed into preceding segment ..... **Ictinogomphini**
- Larva delicate and libelluline-like in appearance; tenth abdominal segment not dovetailed into preceding segment ..... **Archaeogomphini**
- 8(6). Abdominal segment 10 tubular and of exceptional length being in length more than one-fourth the total length of abdomen ..... **Aphyllini**
- Abdominal segment 10 much shorter ..... 9
- 9(8). Larva broadly depressed ..... 10
- Larva not broadly depressed but more or less of the ordinary gomphid form .....
- ..... 11
- 10(9). Middorsal 'hook' on abdominal segment 9 straight, pointed rearward in an

- oblique direction and about three times as long as the middorsal hook on preceding segment ..... **Cyanogomphini**
- Middorsal hook of abdominal segment 9 similar to the one on preceding segment, high, erect and with the tip curved rearward or about twice as long as dorsal hook on preceding segment and tilted rearward ..... **Agriogomphini**
- 11(9). Inner margin of palpal lobe with a row of spaced slender teeth ..... **Peruviogomphini**
- Inner margin of palpal lobe toothless or with minute, low, rounded or truncated teeth ..... 12
- 12(11). Dorsal hooks on abdominal segments 8 and 9 sharp-tipped ..... **Gomphoidini**
- Dorsal hooks on abdominal segments 8 and 9 blunt-tipped ..... **Diaphlebiini**

#### Annotated list of the subfamilies and their tribes

##### Subfamily Octogomphinae comb. nov.

From the key constructed by Carle (1986: 280) it may be apparent that the definition of his Octogomphinae is based on the following four venational characters: 1, fore wing without trigonal planate; 2, costal margin curved and widened along pterostigma; 3, hind wing with second primary antenodal cross-vein situated midway or almost midway between first primary antenodal cross-vein and nodus; 4, hind wing with the veins Cu1 and Cu2 strongly divergent to wing margin. The genus *Anomalophlebia* Belle, however, agrees with the first three characters but not with the fourth one. Since there is no other subfamily with the first three characters combined, I have decided to drop the fourth character for the Octogomphinae in order to admit *Anomalophlebia* into this subfamily.

##### Tribe Hemigomphini Carle, 1986

Type genus: *Hemigomphus* Selys, 1854; additional genera: *Neogomphus* Selys in Selys & Hagen, 1858, and *Praeviogomphus* Belle, 1995.

Adult.— Basal subcostal cross-vein usually absent; second primary antenodal cross-vein in hind wing midway between first primary antenodal cross-vein and nodus; pterostigmal brace vein present; hind wing with one or two intermediate cross-veins; middle fork almost symmetrical or slightly askew forward; usually no extra cubito-anal cross-veins; supratriangles usually uncrossed, other triangular spaces uncrossed; trigonal interspace with two rows of cells near triangle; Cu1 and Cu2 of hind wing divergent to wing margin; anal loop in hind wing absent (distal paranal cell occasionally crossed suggesting an anal loop); male anal triangle in hind wing not extending to anal angle of wing and three-celled. Head without occipital plate but only with a transverse occipital ridge which is thickened in middle. Female auricle absent.

Larva.— Abdomen depressed, more or less oval in outline, widest on segment 5 and without middorsal hooks; lateral margins of abdominal segments 6-9 posteriorly without sharp spines but at the most with short triangular projections; wing-cases parallel on the back; hind tarsi three-segmented; prementum a third longer than

wide; ligula a little produced and with three minute brown denticles in middle of front border; palpal lobe with scarcely hooked tip and with a finely denticulated inner margin; movable hook about a third longer than palpal lobe to base of hook.

Notes.—In the original diagnosis of the genus *Praeviogomphus* there appears the erroneous statement that the second primary antenodal cross-vein in the hind wing is much nearer to the first primary antenodal cross-vein than to the nodus. In fact the second primary antenodal in the hind wing is midway between the first primary antenodal cross-vein and the nodus as may be seen from the accompanying figures of the wings (Belle, 1995: figs 3-4). The subtriangle in the right hind wing of the only specimen of *Praeviogomphus* is two-celled but from the local irregular course of the venation I conclude that this deviation is due to a damage during the immature stage of the specimen and that normally the hind wing subtriangle in this species is one-celled.

*Praeviogomphus* is easily recognizable from *Neogomphus* by the relatively longer pterostigma and in having the hind wing with five to six paranal cells with the distal two ones not or not markedly enlarged. The hind wing of *Neogomphus* has four paranal cells with the third and fourth ones greatly enlarged (fig. 1); the fourth paranal cell is the first postanal cell and it is occasionally crossed suggesting an anal loop.

The larval characters enumerated above are derived from the larva of *Neogomphus*. The larva of *Praeviogomphus* is unknown; it may have the same general body form that is typical of the Hemigomphini.

In 1854 Selys described *Hemigomphus elegans* from an incomplete male collected in the interior of Brazil. The correctness of the afterwards placement of this gomphid in the genus *Neogomphus* is a question to doubt as already suggested by Carle & Cook (1984). Unfortunately, the specimen in question is lost but assuming that the locality data are correctly given, it cannot be conspecific with *Praeviogomphus proprius* for two reasons. Firstly *Praeviogomphus proprius* is a much larger species with an abdomen of 36 mm and a hind wing of 33 mm against an abdomen of 28 mm and a hind wing of 23 mm in the male of Selys' *Hemigomphus elegans*. And secondly the hind wing of *Praeviogomphus proprius* (and in *Neogomphus* species) is not narrowed at the base as it is the case in Selys' specimen. In the Monographie des Gomphines of 1858 (page 446 (186 sep.)) Selys even compared the hind wing of his *Hemigomphus elegans* with that of *Diaphlebia angustipennis* (figs 2-3). Since the Hemigomphini are found in the eastern as well as in the western costal regions of the South-American continent it is not improbable that a species belonging to a third genus pertaining to this tribe occurs in the interior of Brazil.

Carle (1986) in his key to the subfamilies and tribes of the Gomphidae states in rubric 9 that the fore wing subtriangle is typically without acute postero-basal angle. In several specimens of *Neogomphus* I found this angle 90° or somewhat smaller than 90°.

*Perigomphus* Belle, 1972, known from Costa Rica and Panama, possibly occurs in Colombia and Ecuador. Its wing venation (fig. 5) complies with the characters of the Octogomphinae as defined by Carle (1986) in rubric 2 of his key to the subfamilies. Further *Perigomphus* fits well the definition of Carle's (1986) Hemigomphini having the posterobasal angle of the fore wing subtriangle obtuse, the tenth abdominal sternum five times as wide as long, the end segment of the penis with two flagellae and

the male cerci with an inferior basal projection. Also the configuration of the male epiproct (inferior appendage) and the larva of *Perigomphus* exhibit a certain likeness with that of other members of the *Hemigomphini*. The larva of *Perigomphus* has the same general body form and no dorsal hooks and lateral spines. Peculiar in the larva of the only species of *Perigomphus* is the strongly aberrant conformation of the antennae; the third antennal segments are extremely broad and have straight inner margins where they meet (Westfall, 1989: fig. 2).

#### Tribe Anomalophlebiini trib. nov.

Type genus: *Anomalophlebia* Belle, 1995; this new tribe includes only the type genus.

Adult (female only).— Basal subcostal cross-vein absent; second primary antenodal cross-vein in hind wing slightly nearer to nodus than to first primary antenodal cross-vein; pterostigmal brace vein absent; hind wing with two intermedian cross-veins; middle fork very strongly askew forward; no extra cubito anal cross-veins; hind wing triangle once crossed, other triangular spaces uncrossed; trigonal interspace with two rows of cells near triangle; Cu1 and Cu2 of hind wing parallel; anal loop in hind wing absent. Occipital plate present and posteriorly ridged. Female auricle absent.

Notes.— The male and the larva are unknown.

#### Subfamily Onychogomphinae Chao, 1984

##### Tribe Onychogomphini Chao, 1984

Type genus: *Onychogomphus* Selys, 1854; additional genus: *Erpetogomphus* Hagen in Selys, 1858.

Adult.— Basal subcostal cross-vein absent; second primary antenodal cross-vein in hind wing nearer to first primary antenodal cross-vein than to nodus; pterostigmal brace vein present; hind wing with one intermedian cross-vein; middle fork symmetrical; no or one extra cubito-anal cross-veins; triangular spaces uncrossed; trigonal interspace with two rows of cells near triangle; Cu1 and Cu2 of hind wing slightly divergent to wing margin; anal loop in hind wing absent; male anal triangle in hind wing three-celled. Male occipital plate present and ridged posteriorly; female occiput very much reduced and with a strongly convex posterior margin. Female auricle vestigial.

Larva.— Abdomen depressed and about twice as long as wide; wing-cases broadly divergent on the back; meso- and procoxae about equally distant at their bases; abdominal segments 2 to 9 with middorsal hooks which increase in size to rearward; abdominal segments 3 to 9 with lateral spines which increase in size to rearward; caudal appendages short, the cerci a trifle shorter than the paraprocts; hind tarsi three-segmented; prementum somewhat longer than wide; ligula moderately produced and almost evenly convex; palpal lobe with broadly rounded tip and serrulate inner margin; movable hook about four-fifths length of palpal lobe to base of hook.

Notes.— In South America the genus *Erpetogomphus* is only represented by *Erpetogomphus sabaeticus* Williamson, 1918. The characters enumerated here are derived from that species.

Subfamily Epigomphinae Fraser, 1934

Tribe Archaeogomphini Carle, 1986

Type genus: *Archaeogomphus* Williamson, 1919; this tribe includes only the type genus.

Adult.— Basal subcostal cross-vein absent; second primary antenodal cross-vein in hind wing nearer to first primary antenodal cross-vein than to nodus; pterostigmal brace vein absent; hind wing with two or three intermedian cross-veins; middle fork strongly askew forward; no extra cubito-anal cross-veins; triangular spaces uncrossed; trigonal interspace with one row of cells near triangle; Cu1 and Cu2 of hind wing convergent to wing margin; anal loop absent; male anal triangle absent. Top of head rounded off posteriorly. Female auricle absent.

Larva.— Body delicate and libelluline-like in appearance; abdomen moderately depressed and almost parallel sided on segments 4 to 7; wing-cases parallel along middorsal-line; abdominal segments 4 to 9 with middorsal hooks which increase in size to rearward; lateral margins of abdominal segments 3 and 4 serrate with minute teeth, these teeth on segment 3 smaller than on segment 4; abdomen with strong lateral spines on segments 7 to 9; caudal appendages short; hind tarsi two-segmented; prementum spoon-shaped when palpal lobes are retracted; ligula almost not produced; palpal lobe with blunt tip and toothless inner margin; movable hook somewhat longer than palpal lobe to base of hook.

Notes.— In the wings of *Archaeogomphus* there are often a cross-vein immediately under the proximal posterior angle of the stigma. It could lead to confusion to name such a vein a 'weakly developed' brace vein as Carle (1986) did. Because a true brace vein is a prolongation of the proximal side of the stigma, and it is usually also distinguished in being thicker than and not parallel with the adjacent cross-veins. The proximal end of the bridge has no supporting cross-vein to M3 in *Archaeogomphus* (fig. 10) contrary to the other gomphids.

The hind tarsi of the neotropical gomphid larvae are three-segmented except for the larvae pertaining to the Archaeogomphini and the Ictinogomphini (*vide postea*); these have two-segmented hind tarsi.

Tribe Agriogomphini trib. nov.

Type genus: *Agriogomphus* Selys, 1869; additional genera: *Brasiliogomphus* Belle, 1995, and *Ebegomphus* Needham, 1944.

Adult.— Basal subcostal cross-vein present; second primary antenodal cross-vein in hind wing nearer to first primary antenodal cross-vein than to nodus; pterostigmal brace vein present; hind wing with two or three intermedian cross-veins; middle fork askew forward; no extra cubito-anal cross-veins; triangular spaces uncrossed; trigonal interspace with one row or two rows of cells; Cu1 and Cu2 of hind wing

divergent to wing margin; anal loop in hind wing absent; male anal triangle in hind wing absent or present and if present than not extending posteriorly to anal angle of wing and three-celled. Top of head rounded off posteriorly. Female auricle absent.

Larva.—Abdomen short, broadly depressed and widest on middle segments; abdominal segments 2-5 to 9 with middorsal hooks, these hooks often conspicuous on segments 6 to 9 and curved rearward at tip; abdomen with lateral spines on segments 3 to 9; wing-cases parallel along middorsal-line; caudal appendages short, thick and blunt; prementum short, wide and about as short as wide; ligula moderately produced and evenly convex; lateral labial lobe very short and stout, its tip sharply pointed and longer than half the movable hook; inner margin of lateral labial lobe toothless; movable hook somewhat longer than twice the palpal lobe to base of hook.

Notes.—In the only specimen (a female) of *Brasiliogomphus* the occipital ridge is medially undeveloped; this character and correlated with it the single row of cells in the trigonal interspaces may justify a placement in this tribe.

The male of *Agriogomphus* differs from *Cyanogomphus* by the absence of a male anal triangle in the hind wing, and the female differs in having the superior margin of the occipital foramen with a pair of dorsal spines; there is not such a pair of spines in the female of *Ebegomphus* and *Brasiliogomphus*. In the venation of the wings *Brasiliogomphus* is easily distinguished from the other two members of the tribe by the following combination of characters: The trigonal interspace of the fore wing has a single row of cells and, the hind wing has three rows of cells behind Cu2.

The larval characters enumerated here are derived from the larvae of *Agriogomphus* and *Ebegomphus*. The larva of *Brasiliogomphus* is unknown. The larva of *Ebegomphus* have the middorsal hooks on abdominal segments 6 to 9 conspicuously large, subequal and strongly erect with the tip curved rearward, those of *Agriogomphus* are not so high and more or less inclined rearward with the dorsal hook on segment 9 often larger and strongly tilted rearward.

#### Tribe Cyanogomphini comb. nov.

Type genus: *Cyanogomphus* Selys, 1873; additional genus: *Tibiagomphus* Belle, 1992.

Adult.—Basal subcostal cross-vein usually present; second primary antenodal cross-vein in hind wing nearer to first primary antenodal cross-vein than to nodus; pterostigmal brace vein present; hind wing with two or three intermedian cross-veins; middle fork askew forward; no extra cubito-anal cross-veins; hind wing triangle usually uncrossed, the other triangular spaces uncrossed; trigonal interspace with two rows of cells near triangle; Cu1 and Cu2 slightly divergent to wing margin; anal loop in hind wing absent; male anal triangle in hind wing not extending posteriorly to anal angle of hind wing and three-celled (fig. 8). Occipital plate present and ridged posteriorly. Female auricle absent.

Larva.—Abdomen short, broadly depressed and widest on middle segments; abdominal segments 3 to 9 with middorsal hooks, the ones on 5 to 9 large with the one on 9 straight, greatly elongated and about three times as long as the hook on preceding segments; abdominal segments 3 to 9 with lateral spines which are large on segments 3 to 8 but very small on segment 9; wing-cases parallel along middorsal-

line; caudal appendages short; prementum short and wide; ligula well produced and evenly convex; palpal lobe very short and stout, the inner margin toothless, the acute tip longer than half the length of palpal lobe and the movable hook about twice as long as palpal lobe to base of hook.

Notes.— The male of *Tibiagomphus* is easily distinguished from *Cyanogomphus* by the modified spination of the hind tibia; the spines of the outer anterior row are very short and thickened at base; in *Cyanogomphus*, long and not markedly thickened at base. The female of *Tibiagomphus* has a vulvar lamina that extends posteriorly to a point beyond the basal half of the ninth sternum; in *Cyanogomphus*, extending posteriorly to a point not beyond the basal half of the ninth sternum. The larval characters here enumerated are derived from the larva of *Tibiagomphus*. The larva of *Cyanogomphus* is known only by supposition (*vide antea* in the Introduction).

#### Tribe Epigomphini Fraser, 1934

Type genus - *Epigomphus* Selys, 1854; this tribe includes only the type genus.

Adult.— Basal subcostal cross-vein usually present; second primary antenodal cross-vein in hind wing nearer to first antenodal cross-vein than to nodus; pterostigmal brace vein absent; hind wing with three or four intermedian cross-veins; middle fork strongly askew forward; wings usually with extra cubito-anal cross-veins (fig. 9); triangular spaces usually uncrossed; trigonal interspace usually with two rows of cells near triangle; Cu1 and Cu2 of hind wing divergent to wing margin; anal loop in hind wing absent; male anal triangle in hind wing absent. Top of head rounded off posteriorly. Female auricle present; female lamina supra-analis markedly enlarged.

Larva.— Abdomen stout, flat, blunt-tipped, widest on middle segments and without middorsal hooks; lateral margins of abdominal segments 7 to 9 posteriorly ending in an angulation; wings-cases parallel along middorsal-line; tibial burrowing hooks present; prementum widened forward and as long as wide anteriorly; ligula slightly produced, the middle part of front border with six to twelve black denticles; palpal lobe with blunt tip and finely denticulated inner margin; movable hook a half to a quarter longer than palpal lobe to base of hook.

Notes.— The lamina supra-analis of the female has often such vast proportions that it suggests to be a rudimentary eleventh abdominal segment (cf. Calvert, 1903: 189).

#### Subfamily Ictinogomphinae comb. nov.

Several authors, including I myself, have used the name Lindeniinae for this subfamily following Lieftinck (1954) but in my present opinion its introduction is founded on an incorrect interpretation of the international code rules. The subfamily name Ictinogomphinae is proposed by Fraser in 1940 (in Tillyard & Fraser, 1940: 372). In 1957 Fraser defines this subfamily on two venational characters: 1, triangular spaces all traversed by cross-veins; 2, wings with extra cubito-anal cross-veins. But the genera which he includes in this subfamily have for the most part species with an uncrossed hind wing subtriangle.

The Ictinogomphinae are characterized in having the triangular spaces crossed

except for the hind wing subtriangle which is crossed or uncrossed, in having a strongly developed sector R<sub>sa</sub>, in having the fore wing with extra cubito-anal cross-veins but the hind wing with or without extra cubito-anal cross-veins, and in having the metaparapteron distally pointed but not spine-like as in the Zonophorinae.

#### Tribe Ictinogomphini comb. nov.

Type genus: *Ictinogomphus* Cowley, 1934 (= *Ictinus* Rambur, 1842); additional genus: *Melanocacus* Belle, 1986.

Adult.—Basal subcostal cross-vein present; second primary antenodal cross-vein in hind wing much nearer to first primary antenodal cross-vein than to nodus; pterostigma exceptionally long; pterostigmal brace vein present; hind wing with five to ten intermedian cross-veins; middle fork slightly askew forward; R<sub>sa</sub> strongly developed; wings with extra cubito-anal cross-veins; hind wing subtriangle uncrossed, other triangular spaces crossed; trigonal interspaces with two rows of cells near triangle and with a weak development of the trigonal planate; Cu<sub>1</sub> and Cu<sub>2</sub> in hind wing parallel or very slightly divergent to wing margin; anal loop in hind wing present and consisting of four or five often weakly bordered cells; male anal triangle in hind wing not extending posteriorly to anal angle of wing and usually four celled. Occipital plate present and ridged posteriorly. Female auricle absent.

Larva.—Abdomen broadly depressed, stocky of form and widest on segments 6 or 7; abdominal segment 10 dovetailed into apex of segment 9; abdomen with hooks or high ridges on middorsal-line; abdomen with lateral spines on segments 3-7 to 8; wing-cases parallel along middorsal-line; tibial burrowing hooks absent; hind tarsi two-jointed; prementum somewhat longer than wide; ligula well produced and evenly convex; palpal lobe with blunt tip and crenate inner margin; movable hook about as long as palpal lobe to base of hook.

Notes.—*Cacoides* is easily recognizable in having M<sub>2</sub> suddenly curved to M<sub>1</sub> at the level of a point situated between the nodus and the stigma and in having the spines on the outer anterior margin of the hind femur widely spaced and large, the longest spines being about three-fourths of the diameter of the femur; in *Melanocacus*, M<sub>2</sub> and M<sub>1</sub> are parallel at the level between the nodus and the stigma and the spines of the outer anterior row of the hind femur are not widely spaced and in length about one-third of the diameter of the femur. The larva of *Cacoides* is limpet-shaped, that of *Melanocacus* tent-shaped. The larvae of both genera have the hind tarsi two-segmented, a condition also found in the Archaeogomphini (*vide ante*).

#### Subfamily Zonophorinae Belle, 1983

##### Tribe Zonophorini Belle, 1983

Type genus: *Zonophora* Selys, 1854; additional genus: *Mitragomphus* Needham, 1944.

Adult.—Basal subcostal cross-vein present or absent; second primary antenodal cross-vein in hind wing nearer to first primary antenodal cross-vein than to nodus; pterostigmal brace vein present or absent; hind wing with three to seven intermedian

cross-veins; middle fork askew forward; cubito-anal cross-veins absent or usually absent; supratriangles uncrossed or usually crossed, subtriangles uncrossed and triangles once crossed; trigonal interspace with two rows of cells near triangle; Cu1 and Cu2 in hind wing slightly divergent to wing margin; anal loop of hind wing open on proximal side due to a weak development of A2; male anal triangle in hind wing not extending posteriorly to anal angle of wing and four-celled. Occipital plate present and ridged posteriorly. Female auricle absent.

Larva.—Abdomen stout, elongate-oval in outline, widest on segment 6 and with long caudal appendages; abdomen without middorsal hooks; abdominal segments 8 and 9 with strong upcurving lateral spines; wing-cases parallel along middorsal-line; tibial burrowing hooks present; prementum one-third longer than wide; ligula not or slightly produced, the front border with two black submedian denticles; palpal lobe abruptly wider at base, its end hook strong, its inner margin with a row of incurving teeth which diminish in size proximally; movable hook about twice as long as palpal lobe to base of hook.

Notes.—The adults of this tribe are unique in having the metaparapteron armed with a strong posterior spine and in having the hind wing with an open anal loop (-Schmidt, 1941a). Carle (1986) put *Diaphlebia* Selys, 1854, *Desmogomphus* Williamson, 1920 and *Perigomphus* Belle, 1972 in the Zonophorini but they lack these two characters which are typical of the tribe. In the present classification *Perigomphus* is placed in the Hemigomphini and *Desmogomphus* and *Diaphlebia* in the Diaphlebiini.

*Mitragomphus* has a denser wing reticulation than *Zonophora*. In the only specimen of *Mitragomphus* the supratriangle is three-celled in each fore wing and two-celled in each hind wing (fig. 6); in *Zonophora*, only two species (*Zonophora supratriangularis* Schmidt, 1941 and *Zonophora nobilis* Belle, 1983) have the supratriangle regularly traversed by a vein, the other species have uncrossed supratriangles. The fore wing of *Mitragomphus* has a three-celled subtriangle and triangle; the triangle is somewhat longer in the axis of the wing. The fore wing of *Zonophora* has the subtriangle uncrossed and the triangle once crossed; the triangle is elongated in the axis of the wing and about of equal size and form as the triangle in the hind wing. *Mitragomphus* has also no pterostigmal brace vein.

The larval characters enumerated above for the tribe are derived from the larvae of *Zonophora*. The larva of *Mitragomphus* is still unknown but it may be comparable with that of *Zonophora*. The exuviae referred to *Mitragomphus* by supposition (Belle, 1977: 298) undoubtedly belongs to another genus since its abdomen has well-developed middorsal hooks (cf. Belle, 1992: 19).

#### Subfamily Gomphoidinae comb. nov.

Tillyard & Fraser (1940) used the spelling Gomphoidiinae but since this name is derived from a genus name with the ending -des (namely *Gomphoides*) Fraser's (1957) emended spelling Gomphoidinae should be followed. His definition of this subfamily in 1957 is based on the following two venational characters: 1, triangular spaces all crossed; 2, only one cross-vein in the cubito-anal interspace. But some genera here included in the subfamily have specimens with one or more open triangular spaces or have sometimes an extra cubito-anal cross-vein. The present definition of this sub-

family is based on the following combination of characters: 1, wings clear and hind wing triangle crossed (other triangular spaces crossed or uncrossed) or wings with coloured areas; 2, R<sub>sa</sub> not or weakly developed; 3, metaparapteron bluntly pointed at posterior end.

#### Tribe Aphyllini trib. nov.

Type genus: *Aphylla* Selys, 1854; additional genus: *Phyllocycla* Calvert, 1948.

Adult.— Basal subcostal cross-vein usually present; second primary antenodal cross-vein in hind wing nearer to first primary antenodal cross-vein than to nodus; pterostigmal brace vein present; hind wing with five to nine intermedian cross-veins; middle fork askew forward; no extra cubito-anal cross-veins; subtriangle in fore wing usually crossed, in hind wing usually uncrossed, other triangular spaces crossed; trigonal interspace with two rows of cells near triangle; Cu<sub>1</sub> and Cu<sub>2</sub> in hind wing divergent to wing margin; anal loop in hind wing absent or consisting of one to three weakly bordered cells; male anal triangle in hind wing extending posteriorly to anal angle of wing and made up of four to five cells. Occipital plate present and ridged posteriorly. Female auricle absent.

Larva.— Abdomen sub-cylindric, the tenth segment tubular and in length more than one-fourth of the total length of abdomen, the caudal appendages very short; middorsum of abdominal segments 2-3 to 9 with small hooks or low humps; lateral spines of abdomen absent or very small and thorn-like on segments 3-7 to 9; tibial burrowing hooks present; prementum one-third to half longer than wide anteriorly; ligula well produced and evenly convex or semi-elliptical; palpal lobe with a strong end hook which is sometimes large and undulate, the inner margin of the base of the end hook being sometimes serrate; inner margin of palpal lobe toothless or with strong teeth; movable hook one-fifth to one-third longer than palpal lobe to base of hook.

Notes.— I have never seen a specimen of *Phyllocycla* with an uncrossed subtriangle in the fore wing or with a crossed subtriangle in the hind wing; these deviations I have only found in examples of *Aphylla*. The spines on the anterior side of the hind femur are about a quarter of the diameter of the femur in *Phyllocycla*, one-sixth of the diameter of the femur or shorter in *Aphylla*. In the living individuals the venter of the end segments of the abdomen is reddish in *Aphylla*, brown in *Phyllocycla*. The larvae of this tribe is unique for the South-American gomphid fauna in having the tenth abdominal segment greatly elongated and tubular. The larva of *Aphylla* differs from *Phyllocycla* in having the abdomen without lateral spines and in having the inner margin of the palpal lobe with large sharp-pointed recurved teeth. The larva of *Phyllocycla* has short thorn-like lateral spines on the segments 3-7 to 9 while the inner margin of the palpal lobe is toothless or serrate only in the notch at the base of the end hook.

#### Tribe Diaphlebiini trib. nov.

Type genus: *Diaphlebia* Selys, 1854; additional genus: *Desmogomphus* Williamson, 1920.

**Adult.**— Basal subcostal cross-vein usually absent; second primary antenodal cross-vein nearer to first primary antenodal cross-vein than nodus; pterostigmal brace vein weakly developed or present; hind wing with 3 to 5 intermedian cross-veins; middle fork askew forward; usually no extra cubito-anal cross-veins; supra- and subtriangles uncrossed, fore wing triangle usually uncrossed, hind wing triangle usually crossed; trigonal interspace with two rows of cells near triangle; Cu1 and Cu2 in hind wing parallel or slightly to strongly divergent to wing margin; anal loop in hind wing absent; male anal triangle in hind wing not extending posteriorly to anal angle of wing and three-celled. Occipital plate present and ridged posteriorly. Female auricle absent.

**Larva.**— Short and stout of body, and widest on segment 6; abdomen with dorsal hooks on segments 4 to 9; abdominal segments 3-6 to 9 with lateral spines; tibial burrowing hooks present; wing cases parallel along middorsal line; prementum slightly longer than wide anteriorly to nearly twice as long as wide anteriorly; ligula slightly produced and with two submedian black denticles in middle of front border; palpal lobe with blunt tip, the inner margin distally with sharp teeth, the movable hook about as long as palpal lobe to base of hook.

**Notes.**— *Diaphlebia* is easily recognizable from *Desmogomphus* by the following three characters in the wing venation: Cu1 and Cu2 of the hind wing are strongly divergent to the wing margin; in *Desmogomphus*, parallel or slightly divergent (fig. 4). There are two or three rows of cells behind Cu2 of the fore wing; in *Desmogomphus*, only one row of cells. At the base and distal to the tornus the posterior margin of the male hind wing is slightly concave or straight (fig. 2); in *Desmogomphus*, evenly convex.

The larval characters here enumerated are derived from the larva of two named *Desmogomphus* species. The larva of *Diaphlebia* is still unknown. The most striking difference between the larvae of the two *Desmogomphus* species is found in the position of some dorsal hooks. *Desmogomphus paucinervis* has a single row of dorsal hooks on the midline of the abdomen. *Desmogomphus tigrivensis* has two rows of submedian hooks on the segments 4 to 7, the ones on segments 4 and 5 being vestigial but the ones on segments 6 and 7 are well developed and about as large as the middorsal hook on the segments 8 and 9.

#### Tribe Gomphoidini comb. nov

Type genus: *Gomphoides* Selys, 1854; additional genera: *Idiogomphoides* Belle, 1984, and *Phyllogomphoides* Belle, 1970.

**Adults.**— Basal subcostal cross-vein present; second primary antenodal cross-vein nearer to first primary antenodal cross-vein than to nodus; pterostigmal brace vein present; hind wing with 7 to 11 intermedian cross-veins; middle fork askew forward; no extra cubito-anal cross-veins; hind wing subtriangle crossed or uncrossed, other triangular spaces crossed; trigonal interspace two rows wide near triangle, and sometimes and especially in the hind wing, with a weakly developed trigonal plate springing from the angle of the triangle side; Cu1 and Cu2 of hind wing parallel to strongly divergent to wing margin; anal loop in hind wing two- to four-celled; male anal triangle in hind wing extending posteriorly to anal angle of wing and

made up of four to seven cells. Occipital plate present and ridged posteriorly. Female auricle absent.

Larva.— Body of the usual gomphid form; abdomen with middorsal hooks on segments 2-3 to 9 (often obsolete or very low on segment 2 and middle segments); abdomen with lateral spines on segments 6-7 to 9; tibial burrowing hooks present; prementum distinctly longer than wide and sometimes a half longer than wide; palpal lobe with a short and stocky to a large and undulate end hook, the inner margin smooth or armed with low and truncated teeth; movable hook about one-fourth longer than palpal lobe to base of hook.

Notes.— *Gomphoides* is distinguished from the other two genera of the tribe by the unusually stout tenth abdominal segment, and which is longer than the preceding one. Its male has also a very robust, deeply cleft epiproct and strong, more or less conical cerci. *Idiogomphoides* differs from *Phyllogomphoides* in having the male posterior genital hamule with two subapical internal teeth; it ends in a single tooth in *Phyllogomphoides*. The male anal triangle in the hind wing is made up of 6 to 8 cells; in *Phyllogomphoides*, made up of 4 cells. The female of *Idiogomphoides* is unique by its outstanding vulvar lamina which is large and deeply cleft for nearly the entire length with the slender divisions reaching to the apex of the penultimate segment.

A distinct and interesting species-group within the genus *Phyllogomphoides* is the *fuliginosus* group. The adults belonging to this group are unique in the venation of their wings in having the narrow fore wing triangle unusually elongated perpendicularly to the axis of the wing and in having vein A2 in the hind wing strongly forked. The subtriangle and triangle are mostly four-celled in the fore wing, mostly three-celled in the hind wing and the anal loop in the hind wing is mostly two-celled. The eighth abdominal segment has broad leaf-like lateral dilatations in both sexes and the anterior genital hamules of the male are of very complicated form (cf. Needham, 1944: 196). The larva, although of the usual gomphid form, is peculiar by the conformation of the prementum. The ligula is well produced, slightly convex at the sides and almost straight in the middle three-fifths of the front border and the palpal lobe has a pronouncedly undulate end hook that is set off from the toothless produced distal half of the inner side by a deep notch.

#### Tribe Peruviogomphini trib. nov.

Type genus: *Peruviogomphus* Klots, 1944; this tribe includes only the type genus.

Adults.— Basal subcostal cross-vein present; second primary antenodal cross-vein nearer to first primary antenodal cross-vein than to nodus; pterostigmal brace vein present; with six intermedian cross-veins cross-veins; middle fork askew forward; no extra cubito-anal cross-veins; supratriangles and hind wing triangle once crossed, other triangular spaces uncrossed; trigonal interspace with a single row of cells near triangle; Cu1 and Cu2 divergent to wing margin; anal loop in hind wing absent; male anal triangle in hind wing extending posteriorly to anal angle of wing and four-celled. Occipital plate present and posteriorly ridged. Female auricle absent.

Larva.— Abdomen of the usual gomphid form but segment 10 elongated and longer than segment 9; abdomen with middorsal hooks on segments 3 to 9; abdomen

with lateral spines on segments 7 to 9; tibial burrowing hooks absent; prementum widened forward, its anterior width about three-fourths the length of prementum; ligula well produced wide and evenly convex; palpal lobe with long slender end hook, the inner margin with spaced slender teeth; movable hook slightly shorter than palpal lobe to base of hook.

#### Tribe Progomphini Carle, 1986

Type genus: *Progomphus* Selys, 1854; this tribe includes only the type genus.

**Adult.**— Basal subcostal cross-vein absent or present; second primary antenodal cross-vein nearer to first primary antenodal cross-vein than to nodus; pterostigmal brace vein present; intermedian cross-veins in hind wing two to six; middle fork askew forward; cubito-anal cross-veins absent or present; supratriangles uncrossed or usually uncrossed, other triangular spaces uncrossed or crossed; trigonal interspace with one row or two rows of cells near triangle, the larger species with a weak development of the trigonal plate springing from the angle of the triangle side; Cu1 and Cu2 in hind wing slightly divergent to wing margin; anal loop in hind wing absent; male anal triangle in hind wing not extending posteriorly to hind angle of wing and two- or three-celled. Occipital plate present and posteriorly ridged. Female auricle absent.

**Larva.**— Abdomen short and stout to long and torpedo-shaped; fourth antennal segment obsolete or well-developed and recurved on upper side of third antennal segment; wing cases widely divergent to rearward; mesocoxae generally much closer together at bases than procoxae but in some species meso- and procoxae about equally distant at their bases; tibial burrowing hooks absent or present; abdomen with dorsal hooks on segments 1-2 to 9 and lateral spines on segments 4-6 to 9; caudal appendages short to very long, the cerci notably shorter than paraprocts; hind tarsi three-segmented; prementum a quarter to twice as long as wide; ligula well produced and evenly convex or subtriangular; palpal lobe rather long, the tip blunt, the inner margin smooth or serrate; movable hook slightly shorter to one and a half longer than palpal lobe to base of hook.

**Notes.**— The genus *Progomphus* has several species with a maculation in their wings. Most striking are the costal bands in *Progomphus costalis* Hagen in Selys, 1854 and *Progomphus aberrans* Belle, 1973, the basal spots in *Progomphus basistictus* Ris, 1911 and *Progomphus basalis* Belle, 1994, the basal and nodal spots in *Progomphus joergenseni* Ris, 1908 and the large coloured areas in *Progomphus maculatus* Belle, 1984, *Progomphus superbus* Belle, 1973 and *Progomphus perithemoides* Belle, 1980.

All species have no extra cubito-anal cross-veins except for *Progomphus phyllochromus* Ris, 1918 and its near ally *Progomphus occidentalis* Belle, 1983 which have often an extra cubito-anal cross-vein in the wings.

The most outstanding species-group the *Progomphus geijskesi* group. It is formed by the border line species *Progomphus geijskesi* Needham, 1944, *Progomphus pipersi* Belle, 1966 and *Progomphus flinti* Belle, 1975. The male cerci of these species are more or less round in cross-section (blade-shaped in other species) and lack the usual inferior ridge with the denticles. Only the larva of *Progomphus geijskesi* is known but that of the other members may have the same aspect. The larva is peculiar in having a

short thickset abdomen (generally torpedo-shaped in other species) and in having the middorsal hook on the abdominal segments 4 to 6 vestigial and that of the other segments small and sharp-tipped. Also of the *Progomphus tibialis* group only the larva of *Progomphus tibialis* Belle, 1973 is known. It resembles that of *Progomphus geijskesi* but the middorsal hooks on the abdominal segments 2 to 9 are stout and blunt-tipped. Carle (1986), who separates *Progomphus* into subgenera, elevating these species-groups to subgeneric rank, but without necessity.

#### Summary of the proposed classification

##### **Octogomphinae**

Hemigomphini: *Neogomphus*, *Praeviogomphus*

Anomalophlebiini: *Anomalophlebia*

##### **Onychogomphinae**

Onychogomphini: *Erpetogomphus*

##### **Epigomphinae**

Archaeogomphini: *Archaeogomphus*

Agriogomphini: *Agriogomphus*, *Brasiliogomphus*, *Ebegomphus*

Cyanogomphini: *Cyanogomphus*, *Tibiagomphus*

Epigomphini: *Epigomphus*

##### **Ictinogomphinae**

Ictinogomphini: *Cacoides*, *Melanocacus*

##### **Zonophorinae**

Zonophorini: *Mitragomphus*, *Zonophora*

##### **Gomphoidinae**

Aphyllini: *Aphylla*, *Phyllocycla*

Diaphlebiini: *Desmogomphus*, *Diaphlebia*

Gomphoidini: *Gomphoides*, *Idiogomphoides*, *Phyllogomphoides*

Peruviogomphini: *Peruviogomphus*

Progomphini: *Progomphus*

#### **Depictions of wings or parts of wings of South-American Gomphidae**

In the course of my efforts to classify the South-American Gomphidae by means of the venation it has been necessary for me to give close heed to the likeness and differences in their wings. In this connection I have compiled for my own use a list of references to the many illustrations of wings or parts of wings. In the belief that it may be of use to others I offer this list below. Formerly published wing illustrations copied by Belyshev & Haritonov (1977) and by Bridges (1994) are also cited. Since there is a possibility that the Panamanian species *Perigomphus pallidistylus* Belle, *Phyllocycla volsella* (Calvert) and *Progomphus longistigma* Ris occur in Colombia and/or Ecuador, their names are also included in the list.

- Agriogomphus ericae* (Belle, 1966). Right pair of wings of male holotype and female allotype. Belle, 1966b: pls 6a-b (under *Ischnogomphus ericae*).
- Agriogomphus jessei* (Williamson, 1918). Right pair of wings of male holotype. Williamson, 1918a: pl. 1, fig. 1 (under *Ischnogomphus jessei*). Belyshev & Haritonov, 1977: 102, fig. 2. Bridges, 1994: part 13, fig. 563.
- Agriogomphus* spec. Right pair of wings of male (may be *Agriogomphus sylvicola* Selys, 1869). Needham, 1903: 730, fig. 27.
- Agriogomphus sylvicola* Selys, 1869. Left pair of wings in female lectotype. Williamson, 1919: pl. 1, fig. 1; right pair of wings of first described male. Fraser, 1943: 162, fig. 1; base of left fore wing of first described male. Fraser, 1943: 164, fig. 2; right pair of wings of male and female. Belle, 1966b.
- Anomalophlebia nitida* Belle, 1995. Left pair of wings and right hind wing of female holotype. Belle, 1995: 33, figs 1-2.
- Aphylla alia* Calvert, 1948. Anal field in right hind wing of male holotype. Calvert, 1948: pl. 1, fig. 18.
- Aphylla dentata* Selys, 1859. Right pair of wings of male holotype and female allotype of *Aphylla simula-ta* Belle, 1964. Belle, 1964: 29, figs 9-10.
- Aphylla brevipes* Selys, 1854. Right pair of wings of male lectotype. Belle, 1970: pl. 7a; right pair of wings of male holotype and female allotype of *Aphylla albinensis* Belle, 1970). Belle, 1970: pls 8a-b.
- Aphylla janirae* Belle, 1994. Anal triangle in right hind wing of male holotype. Belle, 1994a: 142, fig. 12.
- Aphylla producta* Selys, 1854. Right pair of wings of male. Needham, 1903: pl. 33, fig. 3; right pair of wings of male. Belle, 1970: pl. 9a.
- Aphylla robusta* Belle, 1976. Apex of left fore wing (transposed) of male holotype. Belle, 1976: 373, fig. 2.
- Aphylla tenuis* Selys, 1859. Right pair of wings of female holotype of *Cyclophyllea obscura* Kirby, 1899. Kirby, 1899: pl. 5, fig. 4.
- Aphylla theodorina* (Navás, 1933). Anal triangle in right hind wing of male. Belle, 1994a: 142, fig. 13.
- Archaeogomphus densus* Belle, 1982. Right pair of wings of female allotype. Belle, 1982: 51, fig. 2; right pair of wings of male holotype. Belle, 1982: 55, fig. 30.
- Archaeogomphus furcatus* Williamson, 1923. Right pair of wings of paratype female. Belle, 1982: 51, fig. 1; base of right hind wing of male. Belle & Quintero Arias, 1992: 95, fig. 13.
- Archaeogomphus hamatus* (Williamson, 1918). Left pair of wings of male and female. Williamson, 1918b: pl. 2, figs 14-15 (under *Agriogomphus hamatus*). Belyshev & Haritonov, 1977: 85, fig. 11 (under *Agriogomphus namatus*). Bridges, 1994: part 13, fig. 557.
- Archaeogomphus infans* (Ris, 1913). Right pair of wings of male. Belle, 1982: 54, fig. 26.
- Archaeogomphus nanus* Needham, 1944. Right pair of wings of male and female. Belle, 1970: pls 1a-b.
- Brasiliogomphus uniseries* Belle, 1995. Left pair of wings of female holotype. Belle, 1995: 34, fig. 5.
- Cacoides latro* (Erichson, 1848). Right pair of wings of male. Belle, 1970: pl. 6a; right pair of wings of male. Belle, 1986a: 99, fig. 1. Bridges, 1994: part 13, fig. 588.
- Cyanogomphus waltheri* Selys, 1873. Left pair of wings of male. Williamson, 1916: pl. 8, fig. 2; right pair of wings of male holotype. Belle, 1970: pl. 3a.
- Desmogomphus paucinervis* (Selys, 1873). Right pair of wings of female holotype. Belle, 1970: pl. 5b
- Desmogomphus tigrivensis* Williamson, 1920. Right pair of wings of male holotype. Williamson, 1920b: pl. 1, fig. 1. Belyshev & Haritonov, 1977: 100, fig. 2. Bridges, 1994: part 13, fig. 597.
- Diaphlebia nexans* Calvert, 1903. Left and right pair of wings of male lectotype. Calvert, 1903: pl. 8, fig. 5.
- Diaphlebia* spec. Right pair of wings of female. Klots, 1944: 11, fig. 18. Bridges, 1994: part 13, fig. 598.
- Ebegomphus conchinus* (Williamson, 1916). Right pair of wings of male and female. Williamson, 1916: pl. 8, fig. 1 (under *Cyanogomphus conchinus*); right pair of wings of male and female. Belle, 1966b: pls 8a-b.
- Ebegomphus demerarae* (Selys, 1894). Base of right hind wing of male. Needham, 1944: pl. 16, fig. 4e (under *Ebegomphus strumens*). Bridges, 1994: part 13, fig. 564; right pair of wings of male and female. Belle, 1966b: pls 7a-b.
- Ebegomphus minutus* (Belle, 1970). Right pair of wings of male holotype and female allotype. Belle, 1970: pls 3b, 4a (under *Cyanogomphus minutus*).

- Ebegenomphus pumilus* (Belle, 1986). Right pair of wings of male paratype. Belle, 1986: 111, fig. 1 (under *Cyanogomphus minutus*).
- Epigomphus hylaeus* Ris, 1918. Right pair of wings of male. Belle, 1970: pl. 2a.
- Epigomphus obtusus* Selys, 1869. Left pair of wings of male. Ris, 1918: tab. 2, fig. 82 (numbers 82 and 98 interchanged); right pair of wings of female. Fraser, 1947: 673: fig. 1e.
- Epigomphus paludosus* Hagen in Selys, 1854. Right pair of wings of male. Needham, 1903: 715, fig. 8.
- Erpetogomphus sabaeticus* Williamson, 1918. Right pair of wings of male holotype. Williamson, 1918a: pl. 1, fig. 3.
- Gomphoides infumata* (Rambur, 1842). Right pair of wings of male holotype. Belle, 1970: pl. 17a (under *Negomphoides infumatus*); left pair of wings of male. Ris, 1911: 105, fig. 3.
- Idiogomphoides ictinia* (Selys, 1878). Triangular spaces in right fore wing of female holotype. St Quentin, 1967: 134, fig. 1b (under *Gomphoides ictinia*).
- Idiogomphoides demoulini* (St. Quentin, 1967). Triangular spaces in right fore wing of male holotype. St. Quentin, 1967: 139, fig. 4a (under *Gomphoides demoulini*); anal field in left hind wing of male holotype. Belle, 1984a: 108, fig. 2. Bridges, 1994: part 13, fig. 551.
- Melanocacus interioris* Belle, 1986. Right pair of wings of male holotype and female paratype. Belle, 1986a: 99, figs 2-3. Bridges, 1994: part 13, figs 601-602.
- Melanocacus mungo* (Needham, 1940). Right pair of wings of male lectotype. Needham, 1940: pl. 22, figs 37-38 (under *Cacus mungo*). Belyshev & Haritonov, 1977: 102, fig. 1 (under *Cacus mungo*). Bridges, 1994: part 13, fig. 600.
- Neogomphus bidens* Selys, 1878. Right pair of wings of male. Schmidt, 1941b: 236, fig. 3. Belyshev & Haritonov, 1977: 90, fig. 1. Bridges, 1994: part 13, fig. 517.
- Perigomphus pallidistylus* (Belle, 1972). Anal field in left hind wing (transposed) of male holotype. Belle, 1972: 70, fig. 17; base of right fore wing. Belle & Quintero Arias, 1992: 95, fig. 11.
- Peruviogomphus moyobambus* Klots, 1944. Right pair of wings of male holotype. Klots, 1944: 11, fig. 16. Bridges, 1994: part 13, fig. 585.
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- Phyllocycla bartica* Calvert, 1948. Anal field in right hind wing of female and male holotype. Calvert, 1948: pl. 1, figs 12-13.
- Phyllocycla brasilia* Belle, 1988. Right pair of wings of male paratype. Belle, 1988: 85, fig. 43.
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- Phyllocycla modesta* Belle, 1970. Right pair of wings of male and female. Belle, 1970: pls 10b-11a.
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- Phyllocycla volsella* (Calvert, 1905). Right pair of wings and detail of right fore wing base of male holotype. Calvert, 1905: tab. 7, figs 10-10a; base of right hind wing of male and female. Needham, 1940: pl. 22, figs 40-41.
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- Phyllogomphoides audax* (Hagen in Selys, 1854). Right hind wing of female holotype. Belle, 1984c: 96, fig. 2.
- Phyllogomphoides brunneus* Belle, 1981. Right pair of wings of male holotype. Belle, 1981: 174, fig. 4; right hind wing of male. Belle & Quintero Arias, 1992: 96, fig. 17.
- Phyllogomphoides cristatus* (Needham, 1944). Right pair of wings of male and female. Belle, 1970: pls 17b-18a (under *Negomphoides cristatus*).
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- Phyllogomphoides major* Belle, 1984. Right pair of wings of male. Belle, 1970: pl. 15a (under *Phyllogomphoides fuliginosus*); right hind wing of female allotype. Belle, 1984c: 96, fig. 3.
- Phyllogomphoides pedunculus* Belle, 1984. Right pair of wings of male holotype. Belle, 1984c: 100, fig. 34.
- Phyllogomphoides selysi* (Navás, 1924). Left hind wing of female. Belle, 1984c: 96, fig. 4.
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- Praeviogomphus proprius* Belle, 1995. Right hind wing and left pair of wings of female holotype. Belle, 1995: 33-34, figs 3-4.
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- Progomphus auropictus* Ris, 1911. Left pair of wings of male holotype. Ris, 1911: 110, fig. 6.
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- Progomphus conjectus* Belle, 1966. Right pair of wings of female holotype. Belle, 1966a: pl. 4.
- Progomphus costalis* Hagen in Selys, 1854. Left pair of wings of male. Ris, 1911: 117, fig. 17.
- Progomphus fassli* Belle, 1973. Anal field in left hind wing of female holotype. Belle, 1973: 287, fig. 285
- Progomphus geijskesi* Needham, 1944. Right pair of wings of female holotype and first described male. Belle, 1966a: pls 2a-b.
- Progomphus guyanensis* Belle, 1966. Right pair of wings of male holotype and female allotype. Belle, 1966a: pls 3a-b.
- Progomphus joergensenii* Ris, 1908. Left pair of wings (transposed) of female allotype. Ris, 1908: 522, fig. 3b.
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- Progomphus pygmaeus* Selys, 1873. Right pair of wings of male. Williamson, 1920a: pl. 2, fig. 5.
- Progomphus recurvatus* Ris, 1911. Right pair of wings (transposed) of male lectotype. Ris, 1911: 115, fig. 15.
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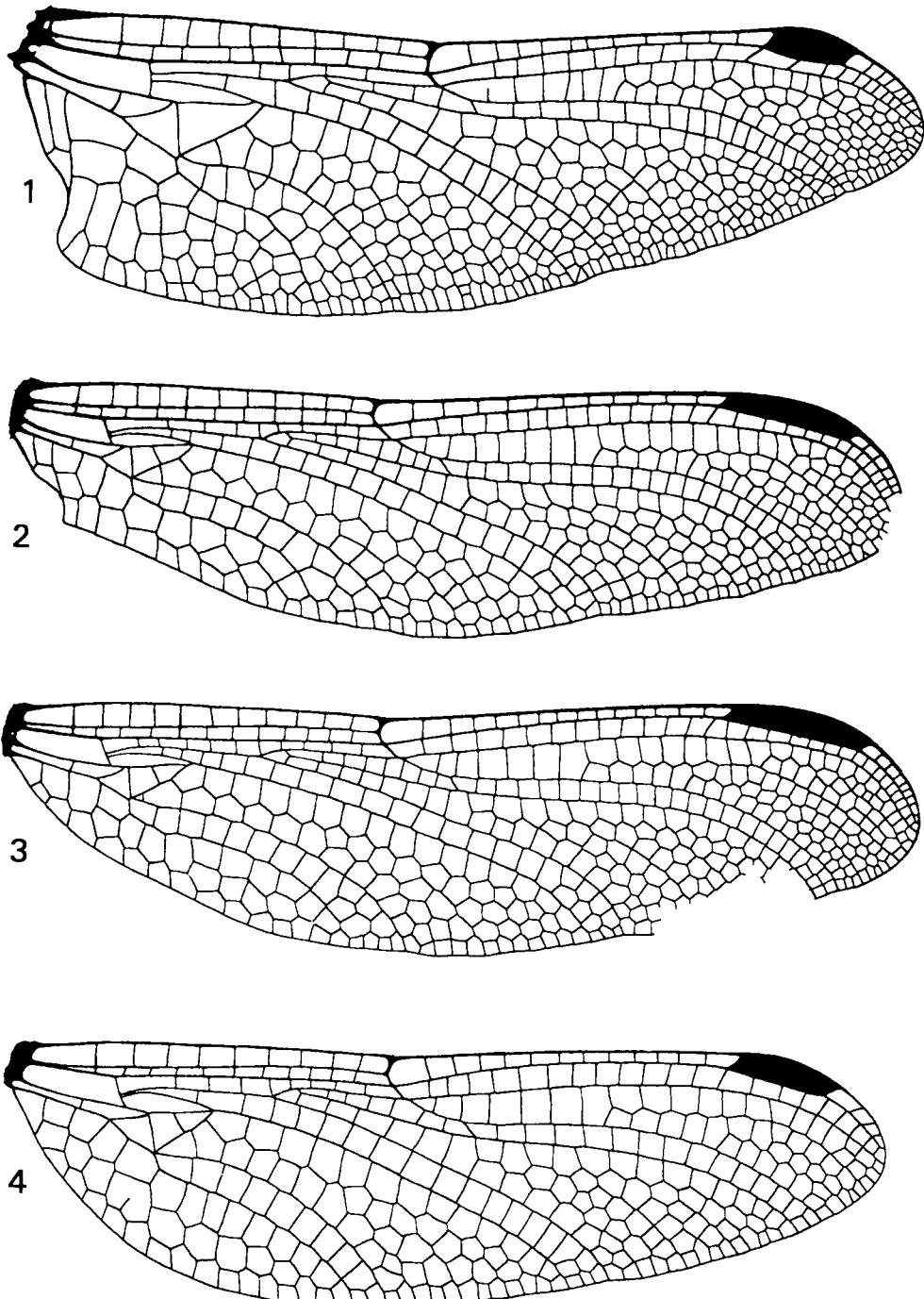
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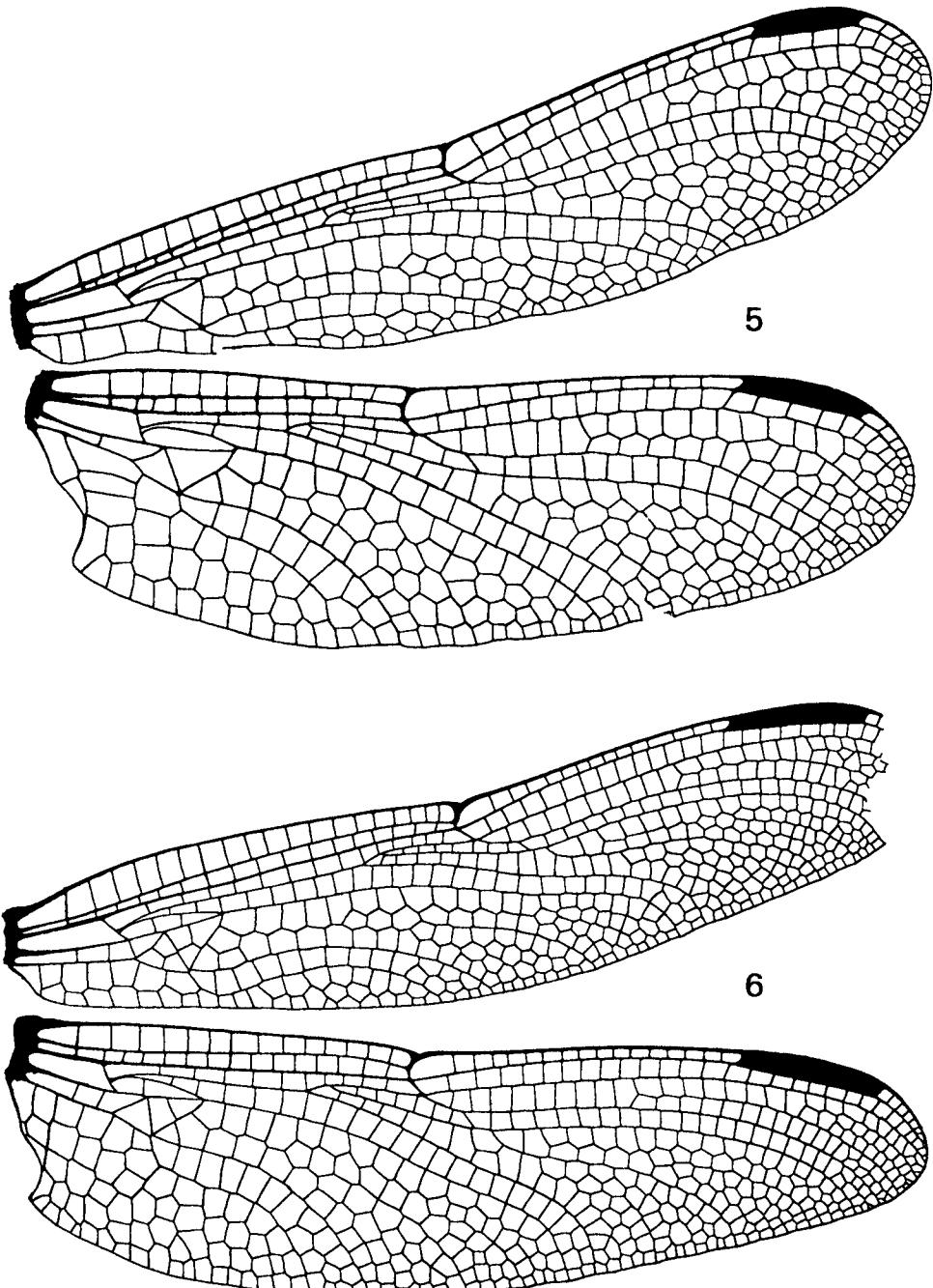
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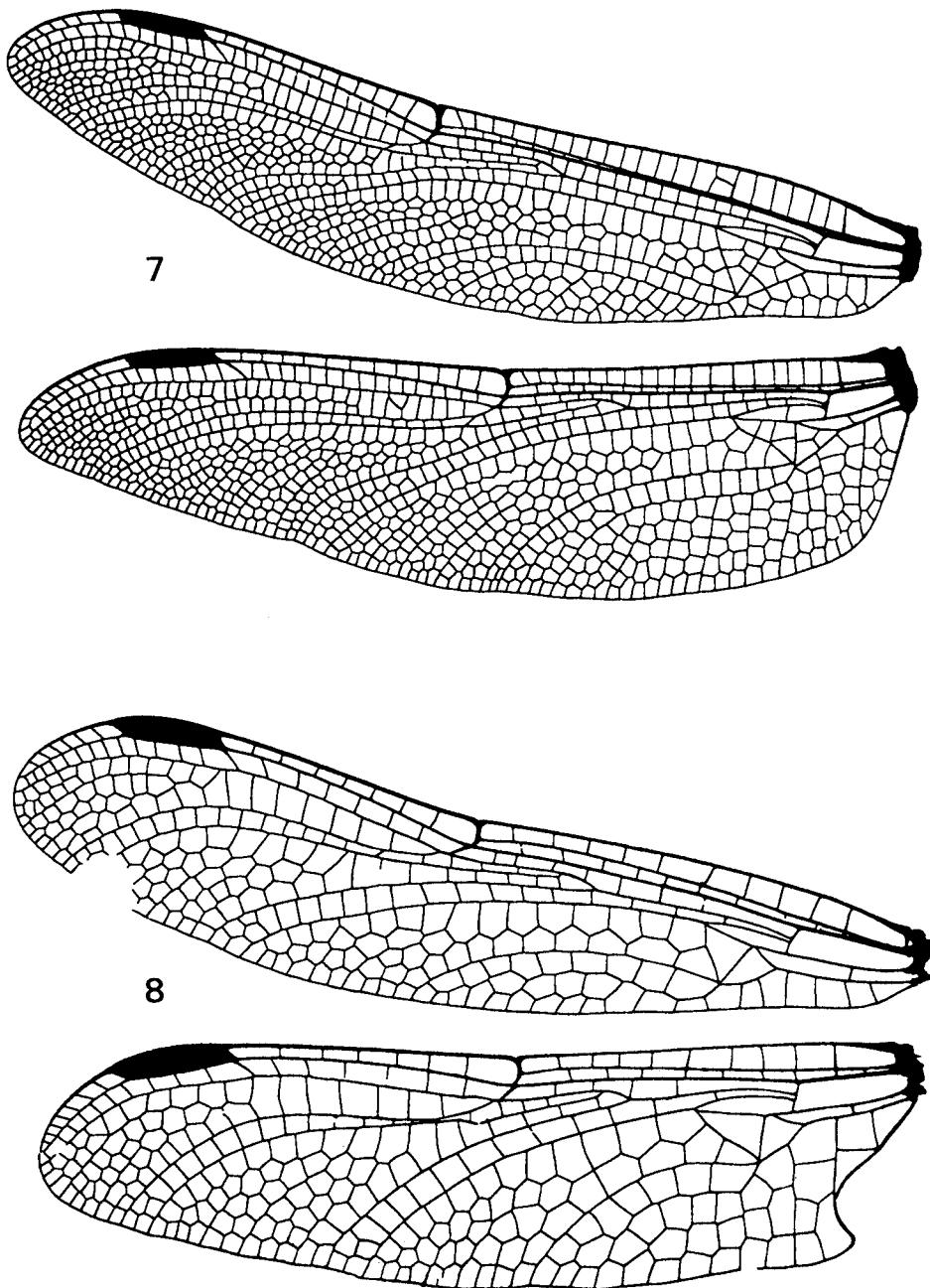
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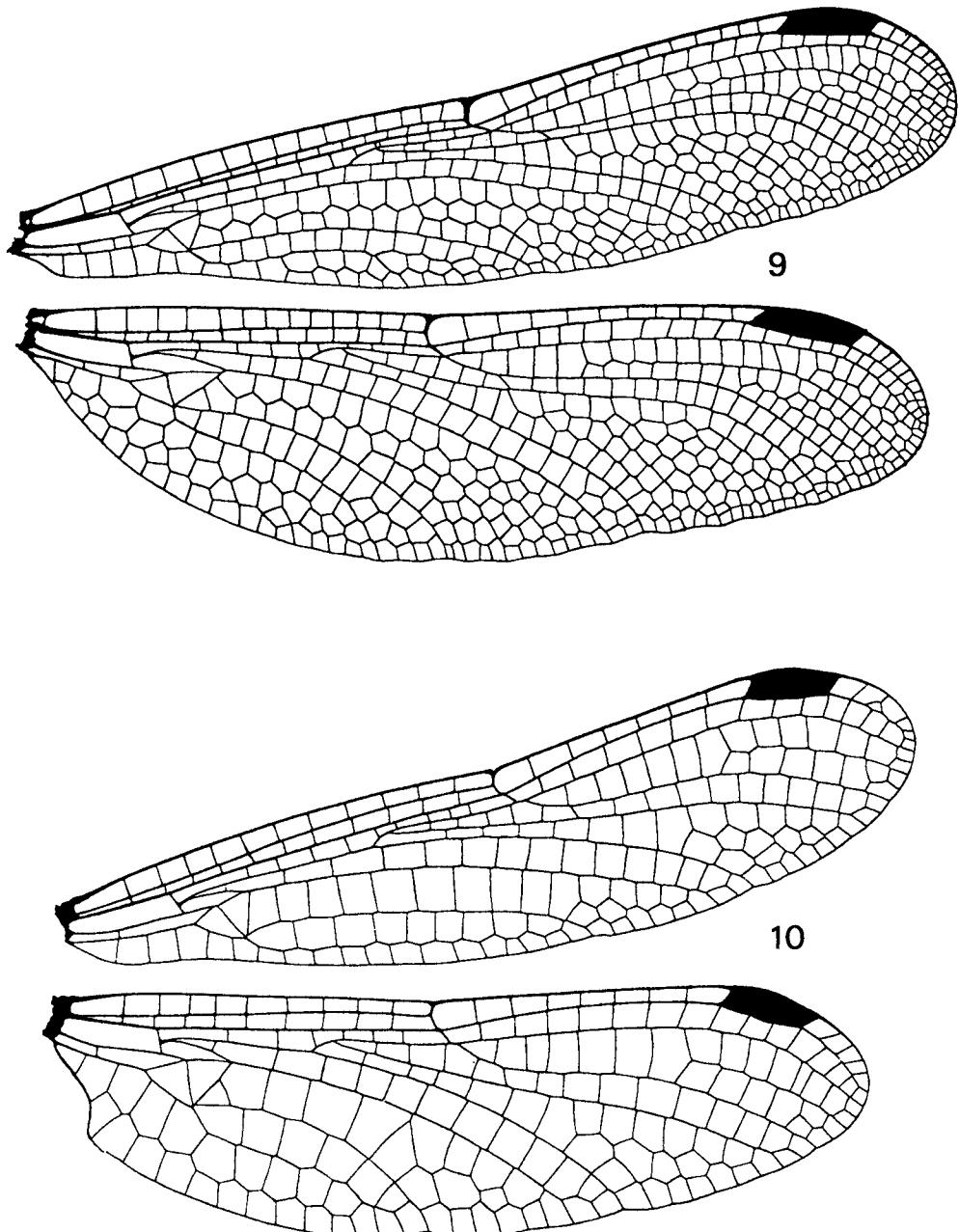
Figs 1-4. Fig. 1, *Neogomphus edenticulatus* Carle & Cook, ♂, paratype; 2-3, *Diaphlebia angustipennis* Selys; 4, *Desmogomphus tigrivensis* Williamson. 1, right hind wing (27 mm). Argentina; 2, right hind wing (32.5 mm) of ♂. Brazil, Amazon region; 3, right hind wing (34 mm) of ♀. Brazil, State of Pará; 4, right hind wing (28 mm) of ♀. Brazil, State of Amapá.



Figs 5-6. Fig. 5. *Perigomphus pallidistylus* (Belle), ♂, holotype; 6, *Mitragomphus ganzanus* Needham, ♂, holotype. 5, right pair of wings (hw 26 mm). Panama; 6, right pair of wings (hw 38 mm). Brazil, State of Pará.



Figs 7-8. Fig. 7. *Idiogomphoides demoulini* (St. Quentin); 8, *Tibiagomphus uncatus* (Fraser). 7, left pair of wings (hw 45 mm) of ♀. Brazil, State of Paraná; 8, left pair of wings (hw 22.5 mm) of ♂. Uruguay.



Figs 9-10. Fig. 9. *Epigomphus paludosus* Hagen in Selys; 10, *Archaeogomphus globulus* Belle, ♂, paratype. 9, right pair of wings (hw 34.5 mm) of ♀. Argentina; 10, right pair of wings (hw 21 mm). Brazil, State of Santa Catarina.