A REVIEW OF THE GENUS ARCHAEOGOMPHUS WILLIAMSON (ODONATA, GOMPHIDAE)  

by  
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Abstract  

The genus Archaeogomphus Williamson is reviewed. Both sexes of A. densus sp. n. (male holotype: Santa Catarina, Brazil) and the hitherto unknown male of A. infans (Ris) are described and illustrated. The female from Misiones, Argentina referred to A. infans by Ris is conspecific with the new species A. densus. New distributional records of Archaeogomphus species are given and a key to the five known species is constructed. Generic characters, structures of specific value, mutual mating adaptations, immature stages, habitats, behaviour in the field, and distribution are discussed. The manner of grasping of the female by the male during copulation is indicated. A historical survey of the genus is provided as well as a full bibliography on the subject. 

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“T named a Gomphine genus Archaeogomphus and Tillyard took one look and said it was the most highly specialized Gomphine he ever saw. Had it turned up as a fossil what would it have been? God only knows — but I think it would have been whatever they needed to fit in with something else. At the present time when systematists are nearly extinct, I think some good generic monographs dealing with what is observable would be a fine thing.”  
E. B. Williamson in a letter to J. G. Needham  
Dated February 18, 1928 (Entomological News, 62)  

Introduction  

The incentive to start this study was the receipt of a new species of Archaeogomphus Williamson, 1919, from the collection of Mr. Carl Cook (Center, USA) in December, 1977 and the discovery of a (hitherto undescribed) male of A. infans (Ris, 1913) in the collection of René Martin, Paris, in the same month. Later on, specimens of the new species were received from Prof. Dr. Gerhard Jurzitza (Karlsruhe, BRD), Prof. Dr. Angelo B. M. Machado (Belo Horizonte, Brazil), and Prof. Dr. Minter J. Westfall, Jr. (Gainesville, USA). Besides, the Argentine specimen of Archaeogomphus referred to A. infans by Ris (1913) proved to be identical with the new species as well.  

Earlier I had obtained specimens of A. hamatus (Williamson, 1918) and A. nanus Needham, 1944, from the Rijksmuseum van Natuurlijke Historie at Leyden (the Netherlands), specimens of A. furcatus Williamson, 1923, and A. nanus from the Museo de Biologia at Caracas (Venezuela), and a specimen of A. hamatus collected in Surinam by my eldest son. Paratypes of A. hamatus in the Smithsonian Institution at Washington, D.C. (USA), one of the Kartabo males of A. hamatus in the Academy of Natural Sciences of Philadelphia (USA), and some of the paratypes of A. hamatus and A. furcatus as well as a specimen of A. nanus in the Museum of Zoology at Ann Arbor (USA) were available for study. Additionally the material of A. nanus previously assembled in Surinam (see Belle, 1970, 1972, and 1977) was re-examined. Finally, Mr. and Mrs. George H. Beatty (Lemont, USA), Dr. Oliver S. Flint, Jr. (Washington, D.C., USA) and Dr. Dennis R. Paulson (Seattle,
USA) provided me with material of *A. furcatus* collected during their explorations in Central-America.

The present opportunity is used to review the genus *Archaeogomphus* and publish a key to the five known species.

All figures of structural details illustrating this paper are reproductions of original camera lucida drawings (the details were completed by free hand), except for fig. 21, which is a reproduction of an illustration published by Williamson (1923), while the figures representing thoracic colour patterns are diagrammatic, all drawn over the same outline.

**Acknowledgements**

The following lists the names of the institutions and individuals from whom material was received on loan or as a gift; the names are preceded by the abbreviations used in the text. I wish to express my gratitude to all those who have assisted me whole-heartedly.

AC — Author’s collection.

ANSP — Academy of Natural Sciences of Philadelphia; Dr. Daniel Otte.

CC — Collection Cook, Center; Mr. Carl Cook.

CJ — Collection Jurzitza, Karlsruhe; Prof. Dr. Gerhard Jurzitza.

CM — Collection Machado, Belo Horizonte; Prof. Dr. Angelo B. M. Machado.

CP — Collection Paulson, Seattle; Dr. Dennis R. Paulson.

CUI — Cornell University, Ithaca; Prof. Dr. L. L. Pechuman.

FEM — Frost Entomological Museum, Lemont; Mr. and Mrs. George H. Beatty.

FSC — Florida State Collection of Arthropods, Gainesville; Prof. Dr. Minter J. Westfall, Jr.

MBC — Museo de Biologia, Caracas; Dr. Janis Ráčenis (†).

ML — Rijksmuseum van Natuurlijke Historie, Leyden; Dr. P. H. van Doesburg.

MNP — Muséum National d’Histoire Naturelle, Paris; Dr. Jean Legrand.

MNHW — National Museum of Natural History, Washington, D.C.; Dr. Oliver S. Flint, Jr.

MZM — Museum of Zoology, Ann Arbor; Dr. Irving J. Cantrall.

SMF — Natur-Museum und Forschungs-

Institut Senckenberg, Frankfurt am Main; Dr. Heinz Schröder.

ZMH — Zoologisches Staatsinstitut und Zoologisches Museum, Hamburg; Prof. Dr. H. Strümpel.

**Historical survey**

1903. Needham published a figure of the right pair of wings of a shrivelled tenerial male of *Archaeogomphus* from São Paulo, Brazil, under *Agriogomphus* sp.

1909. Ris published a figure of the (transposed) right pair of wings of a female of *Archaeogomphus* from Espirito Santo, Brazil, under *Agriogomphus* sp.

1913. Ris described *Archaeogomphus insanus* under the generic name *Agriogomphus* on the basis of two females. The holotype is the Brazilian female of which he had published a figure of the right pair of wings in 1909. The description was illustrated with a diagram of the colour design of the female holotype. The other female, referred to the same species, is from Misiones, Argentina.

1918. Williamson gave a description of *Archaeogomphus hamatus* under the generic name *Agriogomphus* on the basis of 13 males and 9 females from Colombia. Important details of generic and specific value were elucidated by figures, and photographs of the left pair of wings of the male and the female were published. In the same paper he included a description with an illustration of a Colombian female of *Archaeogomphus* under *Agriogomphus* species but refrained from naming it since the corresponding male was unknown.

1919. Williamson created the new genus *Archaeogomphus* with *Agriogomphus hamatus* as the type-species to contain his two *Agriogomphus* species of 1918 and those of Needham (1903) and Ris (1913). He placed *Archaeogomphus* in the group of genera of the legion *Gomphus* of Selys having numerous intermedian cross-veins in the wings.

1920. Williamson placed *Archaeogomphus* in the *Epigomphus* series of his classification of the family Gomphidae.

1923. Williamson described and illustrated *Archaeogomphus furcatus* on the basis of a male and a female from Venezuela, and the female from Colombia which he had
described under Agriogomphus species in 1918.

1940. Needham described and illustrated the larva of an Archaeogomphus species on the basis of a single male exuviae from Santa Catarina, Brazil. In the same paper he also gave 13 features of Archaeogomphus in his Verification Table for the Neotropical Gomphidae.

1940. Fraser compared the penile organ of Archaeogomphus hamatus with that of the gomphids pertaining to other genera.

1940. Tillyard and Fraser placed Archaeogomphus in the subfamily Gomphinae.

1944. Needham described and illustrated Archaeogomphus nanus on the basis of two males and a female from Surinam. He referred the male of his supposed Agriogomphus sp. of 1903 to Archaeogomphus hamatus.

1948. Calvert recorded Archaeogomphus hamatus from Guyana.

1970. Belle described and illustrated the larva of Archaeogomphus nanus on the basis of two exuviae, one of which belonging to a reared male, and also published photographs of the exuviae and of the right pair of wings of the male and female of Archaeogomphus nanus.


The genus Archaeogomphus


The type-species of Archaeogomphus is Agriogomphus hamatus Williamson, 1918, as explicitly stated by Williamson (1919a) when he established the genus.

Characters of the genus

An amended definition of the genus Archaeogomphus was given by Williamson (1923) after the description of A. furcatus.

In the venation of the wings Archaeogomphus is at once recognizable from the other Neotre-
the occipital foramen of the corresponding females enable me to answer the question of the manner of the grasping of the female by the male during copulation. The males of *A. infans* and *A. densus* spec. nov. exhibit an inferior groove at either lateral side of the base of the snout-like projection of the tenth abdominal segment, an adaptation that is in perfect conformity with the following method of grasping during copulation. In seizing the female the apex of the snout-like projection is pushed against the superior margin of the occipital foramen; the denticles along the inferior margin of the apex of the snout-like projection prevent a slip backward. The spines at the superior margin of the occipital foramen rest in the inferior grooves at the base of the snout-like projection. The superior caudal appendages are pressed against the rear of the head. The dorsum of the tenth abdominal segment is placed on the prothorax of the female with the dorsal hooks snapped behind the posterior margin of the prothorax.

The male of *A. infans* possesses minute denticles at the inner side of the tip of the dorsal hooks in order to prevent slip on the posterior margin of the prothorax, and the rear of the head of the paratype female of *A. furcatus* exhibits two distinct mating marks against which the apices of the male superior appendages may be applied during pairing. Both characters are in agreement with the copulatory position of the male tenth abdominal segment and superior caudal appendages.

The postero-lateral projections (horns) on the occiput of the female of some species are not of essential value in this method of grasping, but serve only as lateral guards to give the male tenth abdominal segment additional support.

Mr. Kiyoski Inoue, Osaka, who studied a male of *A. nanus*, wrote in a letter (dated 6.XII.1975) to me: “I think these hooks fit the structures on female prothorax in tandem, if it is true, a transition phenomenon from Zygoptera holding prothorax to Anisoptera holding head is observed here”.

When Williamson (1919a) established the genus *Archaeogomphus* he only knew the male of one species and the female of two species of this genus. After describing *A. furcatus* in 1923 he gave an amended definition of the genus but neglected the generically important penile organ. All species of *Archaeogomphus* possess a penis of the same complicated structure that is typical of the genus and that emphasizes the isolated position of *Archaeogomphus*. A detailed description and a figure of the penile organ were published by Williamson (1919a), Fraser (1940), and Needham (1944).

The femoral hair and armature are typical of the genus. The second and third femora have a conspicuous row of arranged bristles along the outer and inner sides, and between these rows, on the ventral side, are scattered small spines, which are twice to three times longer in the females than in the males. The first femora have an arrangement of bristles only along the inner side, while in both sexes the spines are equal in length.

Also the shape of the vulvar lamina is typical of *Archaeogomphus*. The vulvar lamina consists of a broad short base and two long, slender, hardly diverging and acutely pointed branches.

The colour pattern of the pterothorax is very similar in the two sexes of each species but the pale colours are clearer in the male than in the corresponding female.

The wings are often slightly amber-coloured on the basal half but for the rest they are clear.

### The species of Archaeogomphus

**General remarks**

With the description of *A. densus* spec. nov. in the present paper the total number of species belonging to the genus is brought up to five. These species, together with their type locality, sex of the holotype and type location are chronologically listed in Table 1.

Distinct differences of specific value exist in the venation of the wings, the position and relative length of the pterostigma, the colour design of the body, the hood of the penial peduncle, the vulvar lamina, the occiput of the female, and the conformation of the superior margin of the occipital foramen of the female.

Table 2 shows the features of the wings of the diverse species listed in order of the date of description. The reticulation of the wings of *A. furcatus* exhibits the slightest density, that of *A. densus* the greatest (hence the specific name *densus*). Although *A. nanus* is the smallest representative of the genus its wings are more densely veined than those of *A. hamatus* and *A. furcatus*. The number of antenodal crossveins in the wings of the male of *A. infans* is remarkably low, possibly due to individual variation (only one male available).

In all species, except in *A. densus*, the triangles are normally four-sided. In *A. densus*, the
Table 1. Chronologic list of the species of Archaeogomphus, with type locality, sex of the holotype, and type location

<table>
<thead>
<tr>
<th>Species</th>
<th>Type locality</th>
<th>Holotype</th>
<th>Type location</th>
</tr>
</thead>
<tbody>
<tr>
<td>infans (Ris, 1913)</td>
<td>Brazil (Espirito Santo)</td>
<td>♂</td>
<td>ZMH</td>
</tr>
<tr>
<td>hamatus (Williamson, 1918)</td>
<td>Colombia (Fundación)</td>
<td>♂</td>
<td>MZM</td>
</tr>
<tr>
<td>furcatus Williamson, 1923</td>
<td>Venezuela (Bejuma)</td>
<td>♂</td>
<td>MZM</td>
</tr>
<tr>
<td>nanus Needham, 1944</td>
<td>Surinam (Litani River)</td>
<td>♂</td>
<td>CUI</td>
</tr>
<tr>
<td>densus spec. nov.</td>
<td>Brazil (Nova Teutonia)</td>
<td>♂</td>
<td>MZM</td>
</tr>
</tbody>
</table>

Table 2. Features in the wings of Archaeogomphus species

<table>
<thead>
<tr>
<th>Species</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M1 M2</td>
<td>in fw</td>
<td>in hw</td>
<td>in fw</td>
<td>in hw</td>
<td>Cu1 fw</td>
<td>Cu1 hw</td>
<td>Cu2 hw</td>
<td>n-p fw</td>
<td></td>
</tr>
<tr>
<td>infans ♂</td>
<td>2</td>
<td>10</td>
<td>8</td>
<td>5—7</td>
<td>5—6</td>
<td>1—2</td>
<td>2—3</td>
<td>3—4</td>
<td>3</td>
<td>19.5</td>
</tr>
<tr>
<td>hamatus ♂</td>
<td>2</td>
<td>10—11</td>
<td>8—9</td>
<td>4—6</td>
<td>4—6</td>
<td>1—2</td>
<td>1—2</td>
<td>0—2</td>
<td>3</td>
<td>16—17.5</td>
</tr>
<tr>
<td>furcatus ♂</td>
<td>2</td>
<td>10—12</td>
<td>9</td>
<td>4—6</td>
<td>5—6</td>
<td>1</td>
<td>1—2</td>
<td>0—3</td>
<td>3</td>
<td>18—18.5</td>
</tr>
<tr>
<td>nanus ♂</td>
<td>2</td>
<td>10—12</td>
<td>9</td>
<td>5—7</td>
<td>4—6</td>
<td>1—2</td>
<td>1—3</td>
<td>1—2</td>
<td>3</td>
<td>13.7—16</td>
</tr>
<tr>
<td>densus ♂</td>
<td>3</td>
<td>10—11</td>
<td>8—9</td>
<td>5—6</td>
<td>5—7</td>
<td>3—6</td>
<td>3—5</td>
<td>3—5</td>
<td>2.5</td>
<td>17—19</td>
</tr>
<tr>
<td>infans ♀</td>
<td>2</td>
<td>11</td>
<td>9</td>
<td>7</td>
<td>7</td>
<td>3</td>
<td>4—5</td>
<td>6</td>
<td>3</td>
<td>21.5</td>
</tr>
<tr>
<td>hamatus ♀</td>
<td>2</td>
<td>11</td>
<td>9</td>
<td>5—7</td>
<td>6—7</td>
<td>1—2</td>
<td>2—3</td>
<td>1—3</td>
<td>3—3.5</td>
<td>18—20</td>
</tr>
<tr>
<td>furcatus ♀</td>
<td>2</td>
<td>10—12</td>
<td>9—10</td>
<td>5—8</td>
<td>5—8</td>
<td>1—2</td>
<td>1—5</td>
<td>2—6</td>
<td>2.7—3.3</td>
<td>19—21.5</td>
</tr>
<tr>
<td>nanus ♀</td>
<td>2</td>
<td>10—12</td>
<td>9</td>
<td>7—8</td>
<td>6—8</td>
<td>1—2</td>
<td>2—4</td>
<td>3—5</td>
<td>3</td>
<td>16—18</td>
</tr>
<tr>
<td>densus ♀</td>
<td>3</td>
<td>11—13</td>
<td>9—11</td>
<td>6—7</td>
<td>6—8</td>
<td>6—9</td>
<td>4—9</td>
<td>6—7</td>
<td>2.3—2.5</td>
<td>20—21</td>
</tr>
</tbody>
</table>

For ease of reference the abbreviated multiple column-headings are to be taken as follows:
1. Cell-rows near marginal row of cells, between M1 and M2.
3. Antenodal cross-veins of first series in hind wing.
4. Postnodal cross-veins in fore wing.
5. Postnodal cross-veins in hind wing.
6. Cells on anterior side of Cu1 which do not reach M4, in fore wing.
7. Cells on anterior side of Cu1 which do not reach M4, in hind wing.
8. Cells posterior to Cu2 and distal to postanal cells which do not reach the posterior wing margin, in hind wing.
9. Relative length of distance between nodus and pterostigma in fore wing, the costal edge of the pterostigma being taken as the standard for comparison.
10. Length of hind wing in millimeters.

All numbers in the table are approximate and sometimes derived from a single specimen.

triangle is always three-sided in the hind wings and sometimes four-sided in the fore wings.
The lateral dilatations of the eighth abdominal segment of the male of A. infans and A. densus are well-developed and widen broadly backwards, those of A. hamatus, A. furcatus and A. nanus are very slightly developed and a little prolonged in posterior direction.
The posterior margin of the tenth abdominal segment of the male of A. infans and A. densus is denticulated at the level of the base of the superior caudal appendages and along the ventral side of the segment, that of A. hamatus, A. furcatus and A. nanus is entirely denticulated (excluding the snout-like projection).

In A. infans and A. densus, the superior margin of the opisthosomal foramen of the female bears a pair of submedian spines, and in correlation with these spines the snout-like projection of the tenth abdominal segment of the corresponding males has a pair of inferior grooves in which the spines fit during copulation. The superior margin of the opisthosomal foramen of the female of A. hamatus has a pair of submedian lobes, whereas that of the female of A. furcatus and A. nanus has no prominences. The snout-like projection of the tenth abdominal segment of the male of these three species exhibits no mating adaptation in the shape of a pair of grooves.
The rear of the opisthosoma of the female of
A. furcatus has a pair of long, posteriorly directed horns, that of the female of A. hamatus a small prominence at either lateral end, whereas in the females of other species it is smooth, lacking any projecting angles whatever. The rear of the occiput of the male of A. furcatus has a small knob at either lateral end, that of the male of other species has no prominences of any kind.

Classification
The species of the genus Archaeogomphus can be conveniently divided into two well-defined groups, viz.:

(1) The infans group, comprising the two species A. infans and A. densus spec. nov. The species of this group have the five veins coalesced at the posterior angle of the triangle in the hind wings. The lateral dilatations of the eighth abdominal segment of the males are well-developed and widen broadly in posterior direction. The posterior margin of the tenth abdominal segment of the males is denticulated at the level of the base of the superior caudal appendages and along the ventral side of the segment. The females have a pair of submedian spines at the superior margin of the occipital foramen.

(2) The hamatus group, comprising the three species A. hamatus, A. furcatus and A. nanus. The species of this group have the five veins normally not coalesced at the posterior angle of the triangle in the hind wings but separated into two groups, three anterior and two posterior. The lateral dilatations of the eighth abdominal segment of the males are narrow. The posterior margin of the tenth abdominal segment of the males is entirely denticulated (excluding the snout-like projection). The superior margin of the occipital foramen of the females lacks spines.

Key to the species of Archaeogomphus

1. Males ........................................ 2
   — Females ................................... 6
2. Posterior margin of base of hind wings hardly angulate ........ nanus
   — Posterior margin of base of hind wings strongly angulate .......... 3
3. Lateral dilatations of eighth abdominal segment well-developed, strongly widened posterad and extending to nearly half the length of segment ........................................ 4
   — Lateral dilatations of eighth abdominal segment narrow ........ 5
4. Wings with three rows of cells near margin-al row, between M1 and M2 .......... densus
   — Wings with two rows of cells near marginal row, between M1 and M2 .......... infans
5. Ventral margin of penial peduncle, in posterior view, broad, concave and with a shallow median notch .......... hamatus
   — Ventral margin of penial peduncle, in posterior view, deeply excised V-shaped .......... furcatus
6. Rear of occiput with a pair of long, posteriorly directed spines (see fig. 8) .......... furcatus
   — Rear of occiput with small prominences or without any prominences .......... 7
7. Rear of occiput with a small prominence at either lateral end (see fig. 7) .......... hamatus
   — Rear of occiput smooth, lacking any projecting angles whatever ........... 8
8. Wings with three rows of cells near marginal row, between M1 and M2 .......... densus
   — Wings with two rows of cells near marginal row, between M1 and M2 .......... infans
9. Superior margin of occipital foramen with a pair of submedian spines .......... infans
   — Superior margin of occipital foramen without spines .......... nanus

Treatment of the species
The species are treated chronologically. For each species are given a list of synonyms, the material studied (in addition to those mentioned in my former papers of 1970, 1972 and 1977), and a description or descriptive notes.

Archaeogomphus infans (Ris, 1913) (figs. 3, 10, 15, 19, 23—26, 31)
Agriogomphus spec., Needham, 1903: 738, fig. 27. Ris, 1909: 11, fig. 1. Agriogomphus infans Ris, 1913, 72—73, fig. 11 (?). Williamson, 1918b: 15—17; 1919a: 5; 1923: 1.

Material. — Brazil: Espirito Santo, 20.v.1898, 1 ♀ (holotype), J. Michaelis leg. (ZMH); Espirito Santo, 1 ♂ (MNP).

This species was described in a paper dealing with Argentine Odonata. As explicitly stated by Ris (1913) the type is the female from Espirito Santo. However, the locality data of the type as given by Ris prove to be incomplete. The label attached to the pin of the type indicates that the female has been taken in Espirito Santo, Brazil, on 20.v.1898 by J. Michaelis. Since the female
from Misiones, Argentina, referred to the same species by Ris, is conspecific with my new species A. densus described hereafter, and since the distance from Espirito Santo to Argentina is about 1000 miles, the occurrence of A. infans in Argentina is subject to doubt.

The female holotype of A. infans has a sub-oval depression in the swelling behind each compound eye. The distance between the two depressions, however, is much too great for a possible correlation with the grasping organs of the corresponding male. In my opinion the depressions are injuries owing to the fact that the head was turned one-fourth around with its rear surface to the side when the specimen was originally stored in an envelope (the pterothorax of the type is partly and the abdomen largely flattened).

The color pattern of the present male resembles greatly that of the female holotype, but the dark interpleural and metapleural stripes are not connected with each other. These stripes are largely confluent above the spiracle in the holotype female. The wings of the male are somewhat less densely veined than those of the female holotype, a character likewise found in the two sexes of other congeners. The number of antenodal cross-veins in the present male is only 10 in each fore wing and only 8 in each hind wing; in Archaeogomphus normally 11 in the fore wing and normally 9 in the hind wing.

The male of Archaeogomphus of which Needham (1903) published the right pair of wings may be A. infans as already suggested by Williamson (1923). The venation agrees in having the five veins at the posterior angle of the triangle practically coalesced in the hind wing, and in having this wing with four cells posterior to Cu2 which do not reach the posterior wing margin (in the male of A. hamatus, at the most two cells posterior to Cu2 which do not reach the posterior margin, cf. table 2). Also the anal margin of the hind wing is more resembling that of A. infans than that of A. hamatus. It is not to be forgotten that Needham's figure of the wings is a drawing made after boiled and unrolled wings of a very teneral male (cf. Williamson, 1918b: 1, footnote 5; Needham, 1944: 175) and that due to these conditions certain deviations in the form of the wings and the position of the veins are probable. Finally, the place of capture (São Paulo, Brazil) is in conformity with the type locality of A. infans (Espirito Santo, Brazil). On the distribution map (fig. 31) the symbol referring to the locality of the male from São Paulo is marked by a question mark.

Description of male (hitherto undescribed; pterothorax partly crushed). — Total length, 35 mm; abdomen, 27 mm; hind wing, 19.5 mm; costal edge of pterostigma in fore wing, 2.0 mm.

Face pale grey-green, the frons somewhat darker. Lateral sides of labrum and margin of facial lobes pale yellow. Free border of labrum fringed with brown-yellow hairs. Frons rounded on edge, its superior surface grey-green in front, becoming darker at base. Vertex as in holotype female, dark brown, the transverse ridge becoming bulbous behind each lateral ocellus. Occiput dark brown, rounded on edge, without crest line but with hairs. Swollen area of head behind each compound eye dark brown, sparsely covered with long brown hairs. Tempora yellow. Spines at superior margin of occipital foramen closer to each other and smaller than in female holotype. Labium and adjacent mouth parts pale green.

Prothorax largely brown. Front margin of anterior lobe brownish yellow. Swollen rear margin of middle lobe green. Posterior lobe pale yellow but brown in middle.

Pterothorax dark brown with pale green markings; its colour pattern shaped as shown in fig. 3.

Wings clear but subcostal and cubito-anal interspaces very slightly brownish yellow tinged. Venation of wings dark brown, including frontal margin of costa. Pterostigma dark brown, surmounting 2½ cells. Intermedian cross-veins 4—5/3—3 in fore and hind wings, respectively. Base of hind wings strongly angled. Other venational features given in table 2.

Femora brown, the outer side with a yellowish brown band along anterior row of spines. Tibiae brown, the outer side yellow. First tibiae without lamina tibialis. Tarsi and claws brown, but second joint of tarsi yellow.

Abdomen predominantly yellow-brown on segments 1 to 7, dark brown on segments 8 and 9, and brown on segment 10, including caudal appendages. Segment 1 brown above. Segment 2 grey-green along dorsal anterior margin and on auricles. Segments 3 to 6 becoming dark brown backwards, being dark brown ringed, respectively on half, two-fifths, one-third, and one-fourth the way along each segment. Segment 7 without such a ring. Lateral dilatations of segment 8 broadly widening in posterior direction
and extending to a point about half the way along segment 9. Lateral dilatations of about segment 9 much narrower than those of segment 8, equal in width, more or less inflexed against sternum, and prolonged backwards. Dorsal side of segment 10 convex except for dorsal side of snout-like projection which is concave.

**Archaeogomphus hamatus** (Williamson, 1918) *(figs. 7, 11, 16, 20, 31)*


Williamson (1918b) gave a figure of the vulvar lamina with the parallel slender divisions. The females recorded here have the tips of these divisions divergent (fig. 11). The female from Surinam is somewhat larger and stouter than the other two females; its measurements are: total length, 33 mm; abdomen, 25 mm; hind wing, 19 mm. Those of the other females are: total length, 30 mm; abdomen, 22.5 mm; hind wing, 18 mm (paratype) and 18.5 mm (Rio Paraim). The distance between the nodus and the pterostigma in the fore wing of the female from Surinam, however, is three and a half times the length of the costal edge of the pterostigma; it is only three times in the other females. The female from Rio Paraim is somewhat paler than the other females and it has better developed first pale antehumeral stripes.

The female of *A. hamatus* is readily recognizable from that of the other congeners by the conformation of the occipit the rear margin of which possesses a small prominence at either lateral side.

The tenth abdominal segment (including the snout-like projection) of the male of *A. hamatus* is concave on the dorsal side.

The numerals for the number of cross-veins and cells as stated by Williamson, 1918b: 9) are not correct in all respects. Some of the misstatements were already corrected by him (Williamson, 1923: 4). The photograph of the left pair of wings of the male of *A. hamatus* (Williamson, 1918b: fig. 14) shows only 10 and 8 antenodal cross-veins in the fore and hind wings, respectively. These numerals are 11 and 9, respectively, in the original description. Further, in the wings figured, there are only 4 postnodal cross-veins in the fore wing as well as in the hind wing; according to the original description 5 or 6.

**Archaeogomphus furcatus** Williamson, 1923 *(figs. 1, 4, 8—9, 12, 21, 31)*

*Agriogomphus* sp. Williamson, 1918b: 17—18, pl. 1 fig. 13 (♀).


The occiput of the female of *A. furcatus* is peculiar by the two long, posteriorly directed
spines. On the contrary, the occiput of the corresponding male has at the most a very small knob at either lateral end.

The rear of the head of the female paratype mentioned above exhibits two distinct postgenal cicatrices on which apparently the tips of the male superior caudal appendages were applied during copulation. The other females here recorded (as well as the females of the other congeners) have no, or no distinct copulation marks.

The single (reared) female from Mexico resembles those from continental South America but the females from Costa Rica are different in some respects. Most striking is the development of the occipital spines which in the females from Costa Rica are much stouter and longer. The wings of the females from Costa Rica have also a denser reticulation. They have generally one extra cell or two extra cells (near the marginal row) for a third row, between M1 and M2. For the Costa Rican females the numbers in the columns of table 2 are 2—3, 11—12, 9—10, 7—8, 6—8, 1—2, 3—5, 3—6, 3.1—3.3, 20—21.5, respectively; for the Mexican female Fraser and the South American females these numbers are 2, 10—11, 9, 5—6, 5—6, 1, 1—2, 2—3, 2.7—3, 19—20, respectively. However, no difference of any importance was found between the single (reared) male from Costa Rica and the males from Mexico and South America. The conformation of the hind lobe of the accessory genitalia is very similar and the wings have no denser reticulation. Also no differences were found between the larvae from Costa Rica and Mexico.

Dr. Alice F. Beatty informed me (letter dated 25.vi.1979) that the Mexican male from Tuxtepec is one of a series of 13 δ and 1 η collected on 27 and 29.v.1962 at the same locality. Another male was taken west of Cosamaloapan de Carpio in Veracruz by Harold White. Many larvae were also assembled from three localities in the Pacific coastal region of Chiapas on 18—23.i.1963, and some of these larvae were reared (see immature stages). A detailed study of the Mexican material of A. furcatus by Mr. and Mrs. Beatty is in progress.

Archaeogomphus nanus Needham, 1944 (figs. 5, 13, 17, 22, 31)


Material. — Surinam: Upper Litani River, 18.vi.1939, 1 δ (FSC); Marowijne District, La- wa River, Benzordorp, 18.ix.1960, 1 δ, 1 η, J. Belle leg. (ML). — Venezuela: Bolivar, Caicara, 3.i.1957, 1 η, J. Rácenis leg. (MBC); Bolivar, El Dorado-Brasil (km 67), 27.vii.1966, 1 η, Camp-o sis leg. (AC). — Brazil: Mato Grosso, Rio Tapi-rápê, Pórto Velho, 23.i.1963, 1 η, Celia Pinheiras leg. (ML); Território do Roraima, Surumu (NW. of Depósito, 4° 14' N., 60° 55' W.), ix.1966, 1 δ, Moacir Alvarenga leg. (MZM).

The male from the Upper Litani River belonged to the gomphid material sent to Needham (1944) for description by Dr. D. C. Geijskes. The cellophane envelope in which the specimen has been stored contains a label “Archaeogomphus nanus Paratype Det. by J. G. Needham” but the male has no official standing since it has not been cited in the original description. The male has the five veins coalesced at the posterior angle of the triangle in the hind wings. A. nanus has these veins normally separated into two groups, three anterior and two posterior.

The Brazilian male from Surumu differs in size and coloration with my males from Surinam. It is a smaller specimen with the measurements: total length, 27 mm; abdomen, 20.9 mm; hind wing, 13.7 mm. The males from Surinam have the (average) measurements: total length, 29 mm; abdomen, 22.5 mm; hind wing, 15.5 mm. The light colours of the pterothorax are light grey; they are tawny yellow in the males from Surinam.

The Venezuelan female from El Dorado-Bra- sil has the basal half of the hind wings strikingly brown-tinged. The trigonal interspace in the hind wings of this female starts with an extra initial cell at the posterior angle of the triangle.

The vulvar lamina of A. nanus has not been figured before. Needham’s (1944) depiction of the vulvar lamina (his fig. 1c, pl. 14) fits that of Cyanogomphus demerarae Selys (his Ebetegom- phus strumens) whereas that of fig. 4d (pl. 14) fits that of Agriogomphus sylvicola Selys.

Archaeogomphus densus spec. nov. (figs. 2, 6, 14, 18, 27—31)

Agriogomphus infans Ris, 1913: 72—73 (δ from Ar- gentina).

Archaeogomphus infans; Fraser, 1947: 432. Paulson, 1977: 175.
Material. — Argentina: Misiones, 14.iv.1909, 1 ♀ (paratype), Joergensen leg. (SMF, no. 15232). — Brazil: Minas Gerais, Lagoa Santa, Campinho, 21.iii.1979, 3 ♂, G. Jurzitza leg. (CJ); same locality data, 2 ♂ (AC); same locality, 21.iii.1979, 1 ♂ and 21.iv.1979, 1 ♀, both C. Mascarenhas leg. (CM); Minas Gerais, Serra do Cipó, Santana do Rio Acho, Soberbo stream (19° 20' S., 43° 38' W.), 14.i.1975 (6 p. m.), 1 ♀ (paratype), Angelo B. M. Machado leg. (CM); same locality, 29.iii.1975 (1 p. m.), 1 ♀ (paratype), Paulo A. R. Machado leg. (AC); Santa Catarina, Nova Teutonia, 3.ii.1941, 1 ♂ (holotype) (MZM); same locality, 4.ii.1941, 1 ♀ (paratype) (MZM); same locality, ii.1949, 1 ♀ (allo-type) (CC), F. Plaumann leg.

In the venation of the wings this species differs markedly from all other congeneres by the following two characters: (1) there are three rows of cells near the marginal row, between M1 and M2; two in other congeneres; (2) the distal portion of the wings beyond the pterostigma is more prominent and, correlated with this character, the pterostigma is nearer to the nodus than in other congeneres; the distance from nodus to pterostigma is 2.3 to 2.5 times the length of the costal edge of the pterostigma, 3 to 3.5 times in other congeneres.

In the colour pattern of the pterothorax it differs from all other congeneres in having the first pale antehumeral stripes isolated.

The nearest relative of the new species is *A. infans*. It agrees with *A. infans* in the coalescence of the five veins at the posterior angle of the triangle in the hind wings. The female agrees with *A. infans* in having the superior margin of the occipital foramen armed with a pair of submedian spines but the male differs from this species by the lack of these spines.

Male (holotype; colours of thorax and abdomen obscured; abdomen broken between segments 5 and 6). — Total length, 33 mm; abdomen, 25 mm; hind wing, 19 mm; greatest width of hind wing, 5.5 mm; costal edge of pterostigma in fore wing, 2.0 mm.

Face grey-green, the frons darker but the frontal ridge paler. Lateral margins of labrum and facial lobes pale yellow. Free border of labrum fringed with brown-yellow hairs. Vertex dark brown, with well-developed transverse ridge behind lateral ocelli. Occiput brown, rounded on edge, without crest line but with hairs. Anterior part of occiput slightly elevated at either lateral end. Swollen area of head behind each compound eye dark brown and sparsely covered with brown hairs. Tempora yellow. Labium and adjacent mouth parts pale green.

Prothorax dark brown but anterior border of first lobe brown-yellow.

Pterothorax dark brown with pale yellowish brown markings; its colour pattern shaped as shown in fig. 28.

Legs brown but outer side of tibiae and outer side of second joint of tarsi yellow. First tibiae without lamina tibialis.

Wings slightly brown tinged on basal half. Venation of wings dark brown but frontal margin of costa yellow. Pterostigma brown, surnooring 2½—3½ cells. Intermedian cross-veins 4—4/2—3 in fore and hind wings, respectively. Base of hind wings strongly angled. Other venational features as shown in verification table 2.

Abdomen brown, the segments 3 to 6 darker at apex. Lateral dilatations of eighth abdominal segment well-developed, broadly widening backward and extending to about one-third the length of segment 9. Dorsal side of segment 10 basally convex but concave on snout-like projection. Inner side of tip of dorsal hooks of segment 10 without minute denticles.

Female (allo-type; broken in several pieces but complete). — Total length, 31 mm; abdomen, 23 mm; hind wing, 20 mm; greatest width of hind wing, 6 mm; costal edge of pterostigma in fore wing, 2.4 mm.

Head similar to that of male holotype, but superior margin of occipital foramen with a pair of submedian spines diverging downward. Pale markings of pterothorax less extended than in holotype. Colour pattern of pterothorax shaped as shown in fig. 6. Legs as in holotype, but spines of femora longer and less in number. Abdomen dark brown. Vulvar lamina extending to a point about one-third of the way along venter of segment 10. Apical segments 7, 8, 9, and 10 approximately in ratio 35:28:16:10, with the caudal appendages 6 on the same scale.

Wings slightly brown tinged, especially on basal half. Venation in right pair of wings shaped as shown in fig. 2. Pterostigma surnooring 3—3½ cells. Intermedian cross-veins 4—4/2—3 in fore and hind wings, respectively.

The males from Lagoa Santa are smaller than the type; the measurements of the smallest one are: total length, 30 mm; abdomen, 22 mm;
hind wing, 17 mm. Further, the dark colours are darker and pale colours are paler than in the holotype (the males were put in aceton, whereas the colour design of the type is obscured due to post mortem changes). As a result the abdomen of the males from Lagoa Santa is distinctly annulated on the middle segments (broad black rings covering joinings of segments and a narrower black ring just before middle of each). The face, the first pale antehumeral stripes, and the pale colours of the abdominal segments 3 to 7 of these males are greenish white. The abdominal segments 8, 9 and 10, however, are yellow except for the nodules which are black. The lateral dilatations of the abdominal segments 8 and 9 of some males from Lagoa Santa are inflexed against the sternum of these segments.

The body coloration of the Argentine female is largely obliterated due to post mortem changes. The slender divisions of the vulvar lamina of this female are more bent from each other than in the other females.

The variation in the number of antennal cross-veins in *A. densus* is as follows: antennal cross-veins in fore wing, male 11 (81%) or 10 (19%), female 11 (80%), 12 (10%) or 13 (10%); antennal cross-veins in hind wing, male 9 (75%) or 8 (25%), female 9 (90%) or 11 (10%).

Remarks: (1) The allotype female of *A. densus*, while in my possession as a loan, had a fall that broke off the tip of the right fore wing and left hind wing, after drawings had been made of the right pair of wings. The wing tips, inclosed in a cellophane triangular envelope, have been added to the otherwise complete specimen. (2) Mr. Carl Cook wrote me (in a letter dated 13.iii.1978), that the allotype of *A. densus* in his collection at present, will, together with the whole of his collection, be deposited in the National Museum of Natural History, Washington, D.C.

A NOTE ON THE IMMATURE STAGES

The larva of *Archaeogomphus* is peculiar by the libelluline-like appearance owing to its thin skin, its slender legs, its very large compound eyes, and its broad lateral labial lobes which are concave. The tarsi are 2—2—2 jointed, they are 2—2—3 jointed in the larvae of other Neotropical Gomphidae.

Needham (1940) described the exuviae of *Archaeogomphus* from Nova Teutonia, Santa Catarina, Brazil. The cast-off skin possibly belongs to *A. densus* since this species is known from the same locality.

Schmidt (1951) studied the sclerotizations in the lateral body wall of the abdomen of an *Archaeogomphus* larva from Nova Teutonia, Santa Catarina. This larva may also belong to *A. densus*.

Belle (1970) described comparatively the exuviae of *A. nanus*. The cast-off skin belongs to a reared individual collected in Surinam by Dr. D. C. Geijskes.

During their explorations in Central-America, Mr. and Mrs. Beatty as well as Dr. Paulson collected many larvae of *A. furcatus* and succeeded in rearing some imagines from them. A description of the larva of *A. furcatus* will be given by Mr. and Mrs. Beatty.

HABITAT AND BEHAVIOUR IN THE FIELD

There is some environmental and behavioural information available on *Archaeogomphus* species. Williamson (1918a, 1918b, 1923) described the localities and circumstances in which he had collected his *Archaeogomphus* species in Colombia and Venezuela. As regards the behaviour in the field of *A. hamatus*, Williamson (1918b) cited the following: “The gomphines were usually resting on twig tips or similar perches from six inches to two and one-half feet high, lower locations being preferred. No difference was detected in the actions of the sexes. They were not wary, but flushed, the flight was followed with difficulty and the individual was usually lost”.

Dr. Geijskes provided the triangular envelope in which the unofficial paratype of *A. nanus* has been stored with the field note that the specimen was taken “in bushes”. This is in agreement with my experiences in the field with regard to this species. The favourable environment of *A. nanus* is obviously the tropical rain forest. I found the species in numbers during my collecting trips in the interior of Surinam, but nearly always along the banks of the rivers and larger streams and only by way of exception along the banks of the small creeks. Its behaviour in the field is not typical of gomphids in general. When searching for specimens of *A. nanus* I approached carefully the overhanging bushes and smaller trees along the banks of the streams in a small wooden boat masterly navigated on the swiftly flowing water by a Red Indian. The males were generally found hidden in these overhanging bushes and trees, and when dis-
turbed they flew between the branches over short distances from one branch to another or took refuge into the bushes. This circumstance made it difficult, if not impossible, to net them and will explain that, although many of these males were seen, only a relatively small number of them could be captured. Females were also often taken by me on the river banks along the footpaths immediately behind the overhanging small trees and bushes. Larval cast-off skins can be found close to the water edge, attached against the roots or twigs of the bank vegetation. Dr. Geijskes told me, that, when exploring the shores of an island of the Marowijne River in Surinam, he saw a number of specimens (males?) of A. nanus perching together on a bare twig "like a row of birds". This was a most curious sight.

Dr. Paulson, in a letter (dated 30.ix.1980) to me, wrote about A. furcatus in Costa Rica: "They are devilishly hard to find, and I have never seen a male on territory. One adult female was collected near, but not at, a fair-sized rocky river (Río Santa Rosa) with wooded banks; actually she was on a twig in dry forest 30' from the river and 8' above the ground. The other adult (Taboga) was taken about 100' from a rather slow, muddy river through moist forest, also 8' above the ground on a flat leaf. It was sunny, time 11:00. Her eyes were dull red over gray, which seemed an unusual eye color for a gomphid. Other rivers at which I have taken them (larvae) include the Corobici, which is fairly wide and quite rocky, and the Puerto Viejo, which is also large but entirely sandy. The larvae live in pools with sand and detritus, along with Phyllogomphoides, Phyllocycla and other gomphids." And about the Archaeogomphus in South Mexico he said in the same letter: "I have not taken larvae in small streams, although I believe one or more of the rivers in Chiapas was no more than 5 m in width".

Apparently A. furcatus prefers the more open rivers and larger streams, as A. nanus does in Surinam. However, this behaviour is not typical of Archaeogomphus species in general as clearly appears from the experiences with A. densus. In a letter (dated 10.iv.1978) to me, Prof. Machado wrote about the females of A. densus collected by himself and his son Paulo: "My specimen was found perching on a dead branch about 2 meters high, inside the small stream called "Soberbo" close to the point where it ends in the Cipó River. Paulo's specimen was found in the bushes about 10 meters from this stream. My specimen was collected late in the afternoon (about 6 p.m.) and Paulo's at 1 p.m. Although the place is called "Serra do Cipó" (Cipó mountain) actually it is not on the "Serra" but on the Cipó River Valley close to the "Serra" at the municipality of Santana do Rio Acho, a poor village which you will probably not find on the map. The exact position of the area is 19° 20' Lat. and 43° 38' Long. at about 70 kilometers North of Belo Horizonte". Concerning the males of A. densus collected by himself and Prof. Jurzitza he wrote in a letter (dated 16.x.1979): "The first males were discovered by Gerhard Jurzitza about 70 kilometers from the place where the females were collected. They were perched in the grass at the banks of a stream 1—2 meters wide, tributary of the Río das Velhas close to the village of Campinho, 10 kilometers from the town of Lagoa Santa. The vegetation of the region has been described in detail by the Danish botanist Eugenio Warming (Warming, J. E. B. — 1892 — Lagoa Santa: Et bildrag til den biologiske plantgeografi. Det. Kongel. Danske Videnske. Selskabs. Skrifter. R. 6B: 153—488). It is a kind of savanna known as "cerrado" with gallery forests along the streams. However, most forest has been destroyed and no vestige of it exists nowadays along the stream where the Archaeogomphus were collected."

Geographical distribution

The genus Archaeogomphus is primarily a South American group but occur also in Central-America (fig. 31). The species belonging to this genus are relatively rare, and due to the scantiness of the material available a prediction cannot or can hardly be made as to the occurrence of a certain species in a given region.

I. The infans group. A. infans was described from Espírito Santo, Brazil. Its range apparently covers a part of the south-eastern coastal border of Brazil. São Paulo lies in this region and this circumstance corroborates my supposition that Needham's (1903) male of Archaeogomphus belongs really to this species. A. densus, described from Nova Teutonia (Santa Catarina), Brazil, but also known from Lagoa Santa and the nearby Serra do Cipó (Minas Gerais), Brazil, and Misiones, Argentina, apparently occurs in the south-eastern part of Brazil and the north-eastern part of Argentina.

II. The hamatus group. A. hamatus was described from Fundación, Colombia. Calvert (1948) recorded the species from Kartabo,
Guyana. The discovery of *A. hamatus* in Albinia, Surinam, and at the Rio Paraíba (Goiás), Brazil, extends the range of this species further eastwards and considerably more southwards. Although no record is known from Venezuela the occurrence of *A. hamatus* along the entire northern coastal region of continental South America is probable and even its occurrence in the southern part of Central-America can be expected. *A. furcatus* was described from Bejuma, Venezuela, and Cristalina, Colombia. The new locality Táchira in Venezuela is situated about half-way between Bejuma and Cristalina. The surprising discovery of the species in Costa Rica (Guanacaste and Heredia) and South Mexico (Veracruz, west of Cosamaloapan de Carpio; Oaxaca, south of Tuxtepec; and Chiapas, coastal region of the Sierra Madre) extends its range considerably towards the north. A prediction can be made as to the occurrence of the species in the other Central-American countries. *A. nasus* was described from the upper part of the Litaní River, Surinam. The present records from Bolivar, Venezuela, and the Rio Tapirapé, Brazil, extends its range considerably to the West and South. Obviously the species occurs not alone in the Amazon basin but also along a large part of the northern coastal region of South America.

Using the zoogeographical division of South America after Scudder & Scudder, 1899 (cf. Rapoport, 1968: 68) we can say that the members of the *infans* group occur in the Sud-brasileiro region whereas the members of the *hamatus* group occur in the Colombiana and Amazonica regions.

**References**


Tillyard, R. J. & F. C. Fraser, 1938—1940. A reclassification of the order Odonata. Based on some new interpretations of the venation of the dragonfly


Figs. 1—2. Right pair of wings of female (cells mentioned in table 2 shaded): 1, *A. furcatus* Williamson (para-type), Colombia; 2, *A. densus* spec. nov. (allotype), Brazil.
Figs. 3—6. Diagram of pterothorax: 3, *A. infans* (Ris) ♂, Brazil; 4, *A. furcatus* Williamson ♀ (paratype), Colombia; 5, *A. nanus* Needham ♂, Surinam; 6, *A. densus* spec. nov. ♀ (allotype), Brazil. Figs. 7—8. Occiput of female, dorsal view: 7, *A. hamatus* (Williamson), Surinam; 8, *A. furcatus* Williamson (paratype), Colombia. Fig. 9. *Archaeogomphus furcatus* Williamson ♀ (paratype), Colombia. Superior part of rear of head, showing postgenal cicatrices (pgc).
Figs. 23—26. *Archaeogomphus infans* (Ris) ♀, Brazil: 23, apical segments of abdomen, left lateral view; 24, ninth and tenth abdominal segments, dorsal view; 25, accessory genitalia, right lateral view; 26, right pair of wings (cells mentioned in table 2 shaded).
Figs. 27–30. Archaeogomphus densus n. sp., holotype ♂, Brazil: 27, apical segments of abdomen, left lateral view; 28, diagram of pterothorax; 29, accessory genitalia, right lateral view; 30, right pair of wings (cells mentioned in table 2, shaded).
Fig. 31. Distribution of the species of *Archaeogomphus* Williamson.