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THE CLASSIFICATION, PHYLOGENY AND BIOGEOGRAPHY OF THE GOMPHIDAE (ANISOPTERA). I. CLASSIFICATION*

F.L. CARLE**

Department of Entomology and Economic Zoology, Cook College, New Jersey Agricultural Experiment Station, Rutgers University, New Brunswick, New Jersey 08903, United States

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A brief taxonomic history of the Gomphidae is given, along with an explanation of the methodology used to develop the new classification. The higher classification of the Anisoptera is reviewed and a key to superfamilies presented in which the Gomphoidea and Petaluroidea are formally recognized. Keys to the subfamilies and tribes of Gomphidae are given, followed by detailed tribal descriptions, and verification and classification tables. Gomphine classification is revised as follows (in alphabetical order): GOMPHOIDEA superfam. n.: Gomphidae: Austrogomphinae subfam. n.: (Archaeogomphini trib. n.): *Archaeogomphus, Austroarchaeogomphus* subgen. n. [type *A. infans* Ris]; (Austrogomphini trib. n.): *Antipodogomphus, Austroepigomphus, Austrogomphus;* (Cyanogomphini trib. n.): *Agriogomphus, Cyanogomphus;* (Lestinogomphini trib. n.): *Lestinogomphus;* — Epigomphinae comb. n.: (Epigomphini comb. n.): *Epigomphus, Eugomphus;* (Leptogomphini trib. n.): *Africogomphus, Heliogomphus, Leptogomphus;* (Macrogomphini trib. n.): *Macrogomphus, Eumacrogomphus* subgen. n. [type *M. quadratus* Selys]; (Microgomphini trib. n.): *Microgomphus;* - Gomphinae comb. n.: (Anisogomphini trib. n.): *Anisogomphus, Labrogomphus, Merogomphus, Notogomphus;* (cyclogomphini trib. n.): *Anormogomphus, Burmagomphus, Cyclogomphus, Platygomphus;* (Gomphini trib. n.): *Anatogomphurus* subgen. n. [type *Gomphus personatus* Selys], *Arigomphus, Dromogomphus, Gastrogomphus, Gomphurus, Gomphus, Phanogomphus* subgen. n. [type *Gomphus minutus* Rambur], *Shaogomphus, Stenogomphurus* subgen. n. [type *Gomphus consanguis* Selys], *Stylurus;* (Neurogomphini trib. n.): *Neurogomphus;* — Hageniinae: (Hageniini): *Hagenius, Hagenoides* subgen. n. [type *S. alexanderi* Chao], *Pseudohagenius* subgen. n. [type *H. deflexus* Chao], *Sieboldius;* — Lindeniinae comb. n.: (Gomphoidini comb. n.): *Aphylla, Gomphoides, Peruviogomphus, Phyllocycla, Phyllogomphoides;* (Lindeniini comb.

* Dedicated to Dr M.J. Westfall, Jr, on the occasion of his 70th birthday.

** **Mailing address:** 146 Mountain View Road, Warren, New Jersey 07060, United States

n.): *Africogomphidia* subgen. n. [type *Diastatomma quarrei* Schouteden], *Austrictinogomphus, Cacoides, Cinitogomphus, Diastatomma, Gomphidia, Gomphidictinus, Ictinogomphus, Indictinogomphus, Lindenia, Mitragomphus, Sinictinogomphus, Sinogomphidia* subgen. n. [type *Gomphidia kruegeri* Martin]; (Progomphini trib. n.): *Alloprogomphus* subgen. n. [type *P. complicatus* Selys], *Archaeoprogomphus* subgen. n. [type *P. geijskesi* Needham], *Eoprogomphus* subgen. n. [type *P. tibialis* Belle], *Neaprogomphus* subgen. n. [type *D. obscurum* Rambur], *Progomphus;* (Zonophorini trib. n.): *Desmogomphus, Diaphlebia, Perigomphus, Zonophora;* — Octogomphinae comb. n.: (Hemigomphini trib. n.): *Armagomphus* subgen. n. [type *A. armiger* Tillyard], *Eogomphus, Hemigomphus, Neogomphus, Sinogomphus;* (Octogomphini comb. n.): *Davidius, Dubitogomphus, Lanthus, Paralanthus* subgen. n. [type *Davidius mallorvi* Fraser], *Octogomphus;* (Trigomphini trib. n.): *Fukienogomphus, Stylogomphus, Trigomphus;* — Onychogomphinae comb. n.: (Crenigomphini trib. n.): *Crenigomphus, Paragomphus;* (Onychogomphini comb. n.): *Acrogomphus, Amphigomphus, Cornigomphus, Davidioides, Erpetogomphus, Lamelligomphus, Megalogomphus, Nepogomphoides, Nepogomphus, Nihonogomphus, Nychogomphus* subgen. n. [type *Onychogomphus geometricus* Selys], *Onychogomphus, Ophiogomphus, Ophionuroides* subgen. n. [type *O. anomalus* Harvey], *Ophionurus* subgen. n. [type *O. alleghaniensis* Carle], *Perissogomphus, Phaenandrogomphus, Tragogomphus;* — Phyllogomphinae subfam. n.: (Phyllogomphini trib. n.): *Ceratogomphus, Isomma, Phyllogomphus.*

INTRODUCTION

Gomphines comprise the second largest anisopteran family but remain the least known and most taxonomically confused group among the Odonata. TILLYARD (1917) was the first to propose a formal classification by raising the "Legions" of SELYS (1857) to tribes, but noted that his Gomphini and Ictini were only tentative groupings. WILLIAMSON (1920) divided the gomphines into six series on the basis of venational characteristics, foremost of which were the number of crossveins between "M_{1-3} and M_4" (cf. WILLIAMSON, 1907). Four of Williamson's gomphine series were represented in the Oriental fauna and adopted by LAIDLAW (1930). FRASER (1934) raised three of the Williamson-Laidlaw series to the rank of subfamily, commenting "Owing to the extremely small range of venational differences, upon which systematic writers have almost entirely depended, the classification of this family offers exceptional difficulties". TILLYARD & FRASER (1940), in their treatment of the world fauna, attributed the rank of subfamily to four of the Williamson-Laidlaw series.

Utilization of nonvenational characters in gomphine classification has often not supported the accepted classification. In a study of the gomphine penis FRASER (1940) concluded "In many cases, these characters are merely specific, in others, they are of undoubted generic value, and in still others, they tend to throw doubt on the present position of species within genera and of genera within subfamilies". NEEDHAM (1940) stressed use of the larvae in classifying

Gomphidae, and LIEFTINCK (1941) concluded that "A detailed study of the relationships of the various genera of the Gomphidae will have to be postponed until the larvae of more genera are known". In his study of *Gomphus*, NEEDHAM (1948) employed a variety of characters, although he did not revise his previous classification in accordance with the new evidence. CHAO (1951) introduced several new characters in classifying Chinese gomphines and combined the Epigomphinae and Gomphinae based on the intergradation of venational characters used to separate them. However, FRASER (1957) recognized the Epigomphinae and proposed the Gomphoidinae for a group comprising Williamson's combined *Zonophora* and *Progomphus* series. Fraser remarked that "The family is divided up into five subfamilies by venational differences, but generally the range of these is remarkably small as compared to other Odonata, so that considerable difficulty has been met with in the classification of this family, and it may become necessary to employ other characters for this purpose".

Recent authors have not achieved a consensus concerning gomphine classification. BELLE (1979) concluded that a number of gomphine genera are controversially placed and moved Williamson's *Zonophora* series into the Epigomphinae based on slight venational differences. In a discussion concerning the *Octogomphus*-like genera, CARLE (1980) noted that "recent classifications of the Gomphidae may be artificial, the Gomphinae in particular seemingly polyphyletic". DAVIES (1981) in his synopsis of extant odonate genera did not follow Belle's suggestions, and essentially followed the problematic classification of FRASER (1957). Based on characteristics discovered during his study of Chinese Gomphidae in 1951, CHAO (1984) established the Onychogomphinae. Although nebulously defined, the Onychogomphinae appears to be monophyletic, and with the addition of a few genera is equivalent to the group bearing the manuscript name Ophiogomphinae Carle. CARLE & COOK (1984) confirmed the work of CARLE (1980) and established the tribe Octogomphini for nine genera previously placed in either the Gomphinae or Epigomphinae. Following a phylogenetic analysis of the Anisoptera, CARLE (1982a) concluded that the Gomphidae were the sister group of remaining Anisoptera and accorded the rank of superfamily to the group.

DISCUSSION

CARLE (1982a) and CARLE & COOK (1984) were the first to determine gomphine character state polarity using out-groups. Previously WILLIAMSON (1920) was the only author to base his classification on phylogenetic considerations, but unfortunately he chose the specialized *Archaeogomphus* as exemplifying plesiotypic gomphine venation, and consequently his classification and those to follow were artificial. For example, the number of postmedian

crossveins increases when the distal pleat (cf. CARLE 1982b) recedes apically and becomes asymmetrical basally, as in *Archaeogomphus* and several other gomphines. The resulting increase in crossvein density mimics the apparent plesiotypic condition and has evolved independently in several gomphine and various anisopteran groups.

The classification proposed herein has resulted from phylogenetic and biogeographical research on the Gomphidae which will be published as part two of this study. This classification is based on the determination of character state polarities from out-group comparisons, and the establishment of monophyletic groups from the distribution of derived character states (synapomorphies). Similarities considered likely to have arisen through convergent losses or to be synplesiomorphic are given little or no weight, respectively. Ranking of the various groups is based on branching hierarchy and biogeographical evidence, with little weight placed on perceived degrees of difference. Previous difficulty in classifying gomphines has resulted because of their great geologic age and great diversity coupled with a narrow range of variation between species and genera, variation which in actuality is primarily restricted to sexual characteristics. Gomphine evolutionary history is, therefore, characterized by the preservation of synplesiomorphies and considerable convergent evolution, both of which have resulted in considerable taxonomic confusion following the arbitrary determination of character state polarity or the total misunderstanding of phylogenetic analysis (i.e. FRASER 1954). The present classification is intended to reflect the phylogenetic history of the gomphidae in that it theoretically includes only monophyletic groups which are ranked according to probable geologic age. Such a classification will lead to increased taxonomic stability and improved ecological understanding of the included groups.

Keys to anisopteran superfamilies are provided and the Gomphoidea and Petaluroidea formally established. The Cordulegasteroidea [*sic*] of TILLYARD & FRASER (1940) is paraphyletic and therefore not recognized. Cordulegastridae and Libelluloidea (including Chlorogomphidae) exhibit significant derived differences from each other in both larva and adult, but the Chlorogomphidae has not even been considered separate from the Cordulegastridae until recently (i.e. CARLE, 1984). The recognition of Cordulegastroidea and Libelluloidea (including Chlorogomphidae) is also supported by the apparent great geologic age of the two groups, but establishment of the revised groupings must await the description of a possible annectent species discovered by Dr J.A. Louton. Selected apomorphies which define the anisopteran superfamilies are: larval mesotarsi 2 segmented, larval antennae 4 segmented, adult with postocellar ridge, posterior hamuli engaging female sternum 9 during copulation (Gomphoidea); larval second molar segment fused to first molar segment, proventriculus with less than 8 teeth per lobe (Petaluroidea, Aeschnoidea, Libelluloidea); larval tibiae with apical burrowing hooks, larval prementum abruptly

narrowed basally, larval labial palps quadrate with robust spur at base of endhook (Petaluroidea); adult occiput with dorsal surface triangular, adult compound eyes approximate or contiguous dorsally, medial planate or branch of MA present, male epiproct quadrate or triangular (Aeschnoidea, Libelluloidea); larval epiproct bifurcate apically, posterior hamuli vestigial (Aeschnoidea): larval labium scooplike with long premental and palpal setae, larval labrum concealed by triangular-shaped labial palps, proventriculus with one tooth per lobe, ovipositor reduced (Libelluloidea). The reduction of the ovipositor in Gomphoidea, Aeschnoidea (*Neopetalia*), and Libelluloidea is considered a convergence. In addition to the key to superfamilies the following are provided: key to the subfamilies and tribes of Gomphidae, tribal verification table (Tab. I), tribal descriptions, classification table (Tab. II), and keys to new subgenera.

KEY TO THE SUPERFAMILIES OF ANISOPTERA

ADULTS

1 Compound eyes widely separated dorsally, anterodorsal surface of occiput trapezoidal, male epiproct typically bifurcate 2
Compound eyes contiguous or approximate dorsally, anterodorsal surface of occiput triangular, male epiproct typically quadrate or triangular 3
2 Ligula without medial cleft, pterostigmata convex posteriorly and shorter than distance between costal braces, anterior side of supratriangle convex, ovipositor reduced ..... **Gomphoidea** superfam. n.
Ligula with medial cleft, pterostigmata concave posteriorly and longer than distance between costal braces, anterior side of supratriangle straight, ovipositor complete ..... **Petaluroidea** superfam. n.
3 Anterior lamina with elongate medial cleft, anterior hamuli directed medially, posterior hamuli vestigial, ovipositor typically complete (oviposition typically endophytic) ..... **Aeschnoidea**
Anterior lamina without elongate medial cleft, anterior hamuli directed ventrally or absent, posterior hamuli well developed, ovipositor reduced or absent (oviposition exophytic) ..... **Libelluloidea**

LARVAE

1 Antennae 3 or 4 segmented, third antennal segment longer than first two segments combined, fourth antennal segment vestigial or absent, second mandibular segment movable, mesotarsi 2-segmented ..... **Gomphoidea** superfam. n.
Antennae 6-8 segmented, third antennal segment shorter than first two segments combined, fourth antennal segment well developed, second mandibular segment not movable, mesotarsi 3-segmented 2
2 Prementum scooplike, dorsal surface of labium with long premental and palpal setae, labrum concealed by folded labial palps, proventriculus with 4 teeth ..... **Libelluloidea**
Prementum flat, dorsal surface of labium without long premental and palpal setae, labrum not concealed by folded labial palps, proventriculus with 8 or more teeth 3
3 Tibiae with apical burrowing hooks, prementum abruptly narrowed at base, labial palp with

robust dorsolateral spur at base of endhook, labial endhook distinctly shorter than palp, proventriculus with 8 folds ..... **Petaluroidea** superfam. n.

Tibiae without apical burrowing hooks, prementum gradually narrowed proximally, labial palp without robust dorsolateral spur at base of endhook, labial endhook not distinctly shorter than palp, proventriculus with 4 folds ..... **Aeschnoidea**

KEY TO THE SUBFAMILIES AND TRIBES OF THE GOMPHIDAE

1 Fore wing with trigonal planate, costal margin not curved or widened along pterostigmata, basoventral surface of hind femora with overlapping flat-appressed spines, anterior lamina raised with medial seam ..... **HAGENIINAE — Hageniini**

Fore wing without trigonal planate, costal margin curved and widened along pterostigmata, basoventral surface of hind femora without overlapping flat-appressed spines, anterior lamina not raised with medial seam 2

2 Hind wing with distal costal brace ca midway between proximal costal brace and nodus, and with CuP and A strongly divergent to wing margin.....**OCTOGOMPHINAE — 8**

Hind wing with distal costal brace nearer proximal costal brace than to nodus, and with CuP and A not strongly divergent to wing margin (typically separated by 1-3 cells at wing margin) 3

3 Occipital crest typically not ridgelike 4

Occipital crest typically ridgelike.....5

4 Hind wings typically with 3-5 postmedian crossveins, male cerci well developed without long ventrally directed mediobasal spine, male with lateral margin of abdominal segment 10 not notched ..... **EPIGOMPHINAE — 10**

Hind wings typically with 1 or 2 postmedian crossveins, male cerci either vestigial or well developed with long ventrally directed mediobasal spine, male with lateral margin of abdominal segment 10 notched.....**AUSTROGOMPHINAE — 13**

5 Fore wing with base of distal pleat asymmetrical and closer to posterior end of subnodus than to distal angle of triangle, hind wing with 3-9 postmedian crossveins ..**LINDENIINAE — 16**

Fore wing with base of distal pleat symmetrical and closer to distal angle of triangle than to posterior end of subnodus, hind wing with 1 or 2 postmedian crossveins 6

6 Abdominal segment 9 with dorsomedial carina, anterior hamuli with apices transverse and contiguous medially, female without auricles and with abdominal sternum 9 membranous with paired laterobasal sclerites..... **PHYLLOGOMPHINAE — Phyllogomphini** trib. n.

Abdominal segment 9 without dorsomedial carina, anterior hamuli with apices not transverse or contiguous medially, female with auricles and with at least posterior portion of abdominal sternum 9 sclerotized 7

7 Hind femur shorter than width of head, anal triangle typically 4-celled with small rectangular cell along inner margin, anterior hamuli with shoulder and endhook forming lateral U-shaped notch, female sternum 9 with large U- or V-shaped basal membranous area ..... **ONYCHOGOMPHINAE — 19**

Hind femur typically longer than width of head, anal triangle typically 3-celled without small rectangular cell along inner margin, anterior hamuli rodlike, flattened or elongate with small apical endhook and notch, female sternum 9 typically without large U- or V-shaped basal membranous area ..... **GOMPHINAE** 20

8 Sternum 10 of male 0.7-3.0 times as wide as long, male cerci with small mid-lateral spine, posterior hamuli with transverse shoulder and endhook, penile segment 1 low with cleftlike receiver, female sternum 9 with basal sclerites separated by more than width .....
.....**Trigomphini** trib. n.

Sternum 10 of male 3.0-6.2 times as wide as long, male cerci with basoventral or basomedial spine, posterior hamuli without transverse shoulder and endhook, penile segment 1 raised with troughlike or bowllike receiver, female sternum 9 with basal sclerites separated by more than width 9

9 Fore wing supratriangle typically without acute posterobasal angle, sternum 10 6-8 times in male and 3-4 times in female as wide as long, penis with 2 flagella, male cerci with basal spine ..... **Hemigomphini** trib. n.

Fore wing supratriangle typically with acute posterobasal angle, sternum 10 3-4 times in male and 2-3 times in female as wide as long, penis without or with 1 flagellum, male cerci with suprabasal spine ..... **Octogomphini**

10 Hind wing with 2-3 cubital-anal crossveins, apical planate and RP_1 separated by 2-3 cell rows posterior to distal end of pterostigmata, posterosubapical mandibular tooth present 11

Hind wing with 1 cubital-anal crossvein, apical planate and RP_1 separated by 1 cell row posterior to distal end of pterostigmata, posterosubapical mandibular tooth vestigial or absent 12

11 Abdominal segment 9 shorter than segment 8, without dorsomedial carina, and with sternum largely membranous, anal brace and foretibial laminae absent, anterior surface of posterior hamuli denticulate, penile segment 1 raised with troughlike receiver ..... **Epigomphini**

Abdominal segment 9 longer than segment 8, with dorsomedial carina, and with sternum sclerotized with medial seam, anal brace and foretibial laminae present, anterior surface of posterior hamuli with denticles typically absent, penile segment 1 low with cleftlike receiver ..... **Macrogomphini** trib. n.

12 Pterostigmal brace absent, ventral spine of tarsal claws not subapical, medial ocelli larger than lateral ocelli, antefrons low and rounded, male cerci with ventrolateral spine, male epiproct not triangular ..... **Leptogomphini** trib. n.

Pterostigmal brace present, ventral spine of tarsal claws subapical, medial ocelli smaller than lateral ocelli, antefrons raised and angular, male cerci with ventromedial spine, male epiproct triangular ..... **Microgomphini** trib. n.

13 Middle tooth of posterior maxillary tooth row present, posterosubapical mandibular tooth present, male tibial laminae present, female auricle well developed **Austrogomphini** trib. n.

Middle tooth of posterior maxillary tooth row absent, posterosubapical mandibular tooth absent, male tibial laminae absent, female auricle minute or absent 14

14 Hind wing with base of distal pleat symmetrical, head not tumid posterior to compound eyes, abdominal sternum 10 ca 2 times as long as wide, posterior hamuli with line of denticles at shoulder, anterior hamuli flat with apical hair pencil ..... **Lestinogomphini** trib. n.

Hind wing with base of distal pleat asymmetrical, head tumid posterior to compound eyes, abdominal sternum 10 less than 1/2 as long as wide, posterior hamuli without line of denticles at shoulder, anterior hamuli cupped 15

15 Basal antenodals present, labrum notched along distal margin, male cerci forked, penile segment 1 with thin lateral flanges contiguous posteriorly to form round opening, female sternum 9 sclerotized ..... **Cyanogomphini** trib. n.

Basal antenodals absent, labrum level along distal margin, male cerci not forked, penile segment 1 with two posteroventrally directed lobes separated by wide notch, female sternum 9 membranous ..... **Archeogomphini** trib. n.

16 Middle tooth of posterior maxillary tooth row ca 1/2 length of proximal tooth, tibial laminae at most 1/10 length of tibia, tornus angulate, female sternum 9 membranous ..... **Zonophorini** trib. n.

Middle tooth of posterior maxillary tooth row ca 1/4 length of proximal tooth, tibial laminae more than 1/5 length of tibia, tornus rounded, female sternum 9 sclerotized 17

17 MA with posterior branch originating slightly distal to bridge crossvein, wings with 2-4

Table 1

Verification table for gomphine tribes. — Code: "+" = true or present, "—" = false or absent, "±" = variable, R = reduced, V = vestigial. — Head: (a) length of middle maxillary tooth of posterior tooth row relative to proximal tooth, — (b) posterosubapical mandibular tooth well developed, — (c) labrum width/length, — (d) medial ocelli smaller than lateral ocelli, — (e) occiput ridged. — Wings: (a) basal antenodal present, — (b) distal coastal brace near midway between proximal costal brace and nodus, — (c) pterostigmal brace present, — (d) arculus straight and aslant, — (e) apical planate separated from RP_1 by 1 cell row posterior to distal end of pterostigmata, — (f) number of cells in supratriangle, — (g) number of postmedian crossveins in hind wing, — (h) distal pleat asymmetrical, — (i) MA with posterior branch originating near bridge crossvein, — (j) fore wing with trigonal planate, — (k) number of Cu-A crossveins in hind wing, — (l) CuP and A strongly divergent toward hind wing margin, — (m) anal brace present, — (n) anal triangle extended to tornus. — Legs: (a) male tibial laminae well developed, — (b) female hind femora with two rows of long spines. — Abdomen: (a) female auricles well developed, — (b) shape of anterior hamuli: E = elongate, V = E, F, or N, N = notched, Y = bifurcate, F = short and flat, D = rodlike, C = cupped, — (c) anterior face of posterior hamuli with denticles (L = arranged in a transverse line), — (d) endhook of posterior hamuli present (M = directed medially), — (e) number of penile flagella, — (f) tergum 9 with median carina, — (g) female sternum 9 sclerotized (U = with large U-shaped membranous area), — (h) width/length of sternum 10, — (i) location of male cercal spine: BL = basolateral, BV = basoventral, ML = midlateral, LA = lateral and/or ventroapical, MM = midmedial, BM = basomedial, MV = midlateral and ventromedial. — Notes: (x) rodlike in *Stylurus*, — (y) 1.6 in *Megalogomphus*, — (z) 2 in *Perissogomphus*

	Head					Wings													Legs		Abdomen								
Tribe	a	b	c	d	e	a	b	c	d	e	f	g	h	i	j	k	l	m	n	a	b	a	b	c	d	e	f	g	h	i
Hageniini	ca 0.70	+	ca 3.0	—	—	±	—	+	—	—	1	2-3	—	—	+	1-2	+	+	—	—	—	+	E	+	+	1	—	—	6.0-8.0	BL
Hemigomphini	ca 0.60	+	ca 2.3	—	—	—	+	+	—	—	1	1-2	—	—	—	1	+	+	—	+	—	+	V	±	+	2	—	—	6.0-8.0	BL
Octogomphini	ca 0.70	+	2.4-2.6	—	—	—	+	+	—	±	1	1	—	—	—	1	+	+	—	±	—	+	N	+	+	1	—	—	3.0-5.0	BV
Trigomphini	ca 0.60	+	2.2-2.4	—	—	—	+	+	—	—	1	1-4	±	—	—	1	+	+	—	+	—	+	Y	+	M	1	—	—	1.0-3.0	ML
Anisogomphini	ca 0.65	+	2.1-2.4	—	+	±	—	+	+	—	1	1-2	—	—	—	1	—	+	—	—	+	+	E	V	+	1-2	±	+	2.0-3.0	LA
Cyclogomphini	ca 0.35	R	2.1-2.4	—	+	±	—	+	±	±	1	1	—	—	—	1	—	±	—	V	+	+	F	—	+	1-2	—	+	1.5-2.0	LA
Gomphini	0.20-0.65	+	2.1-2.9	—	+	—	—	+	—	—	1	1	—	—	—	1	—	+	—	+	—	+	Ex	V	+	1-2	—	+	0.7-6.0	LA
Neurogomphini	ca 0.10	+	2.3-2.5	—	+	+	—	+	+	—	1	1	—	—	—	1	—	+	—	+	—	—	D	—	+	1	—	U	ca 0.5	LA
Epigomphini	ca 0.50	+	ca 2.1	—	—	+	—	—	+	—	1	3-4	+	—	—	2-3	—	—	—	—	—	+	E	+	—	1	—	—	ca 2.0	LA
Leptogomphini	ca 0.35	V	ca 2.1	—	—	±	—	—	+	+	1	3-5	+	—	—	1	—	+	—	±	+	+	E	—	+	1-2	—	+	4.0-5.0	ML
Macrogomphini	ca 0.40	+	ca 2.1	—	—	+	—	±	+	—	1	3-4	+	—	—	2-3	—	+	—	+	—	+	E	V	±	1	+	+	1.0-1.5	MM
Microgomphini	ca 0.40	—	ca 2.2	+	—	—	—	+	+	+	1	3	+	—	—	1	—	+	—	—	+	+	E	—	+	2	—	+	5.0-6.0	MM
Archaeogomphini	absent	—	1.8-1.9	—	—	—	—	+	+	±	1	2	+	—	—	1	—	±	—	—	—	V	C	—	+	2	—	—	5.0-6.0	—
Austrogomphini	ca 0.40	+	2.2-2.3	—	—	—	—	+	+	±	1	1-2	—	—	—	1-2	—	+	—	+	—	+	C	—	+	1-2	—	+	2.0-3.0	BM
Cyanogomphini	absent	—	ca 1.8	—	±	+	—	+	+	±	1	2-3	±	—	—	1-2	—	+	—	—	—	—	C	—	+	2	—	+	2.0-3.0	BM
Lestinogomphini	absent	—	ca 2.1	—	+	—	—	+	+	+	1	2	—	—	—	1	—	—	—	—	—	—	F	L	+	2	—	+	ca 0.5	BM
Phyllogomphini	0.00-0.30	V	1.7-2.1	—	+	±	—	+	±	—	1	1-2	—	—	—	1-2	—	+	—	+	—	V	C	—	+	2	+	—	0.5-2.0	MV
Crenigomphini	ca 0.15	V	2.1-2.2	—	+	—	—	+	±	±	1	1	—	—	—	1	—	+	—	—	—	+	Y	—	+	2	—	U	1.0-3.0	LA
Onychogomphini	ca 0.15	R	2.1-2.3y	—	±	—	—	+	±	±	1	1-2	—	—	—	1z	—	+	—	+	—	+	Y	—	+	2	—	+	2.0-5.0	LA
Gomphoidini	ca 0.20	R	1.7-2.0	—	+	+	—	+	+	±	2-4	5-9	+	—	—	1	—	+	+	+	—	—	Y	—	M	1-2	—	+	0.6-2.0	BV
Lindeniini	0.20-0.30	+	1.8-2.0	—	+	±	—	+	+	±	2-4	4-8	+	+	—	2-3	—	+	—	+	±	—	Y	V	M	1-2	±	+	4.0-8.0	BV
Progomphini	ca 0.20	R	1.9-2.5	—	+	±	—	+	±	±	1	3-6	+	—	—	1	—	+	—	+	—	—	Y	L	M	2	—	+	ca 2.5	BV
Zonophorini	ca 0.50	R	1.8-2.0	—	+	±	—	+	+	±	1-2	3-6	+	—	—	1-2	—	+	—	V	—	V	Y	V	+	2	—	—	5.0-6.0	BV

cubital-anal crossveins, male auricles dorsoventrally compressed and produced posteriorly ..... **Lindeniini**

MA without posterior branch originating slightly distal to bridge crossvein, wings with 1 cubital-anal crossvein, male auricles not dorsoventrally compressed and produced posteriorly 18

18 Supratriangles with 2-4 crossveins, anal triangle extended to tornus with cells arranged serially, penile receiver not cuplike, prepuce vestigial, posterior hamuli without transverse row of

denticles ..... **Gomphoidini**

Supratriangles without crossveins, anal triangle not extended to tornus with cells arranged serially, penile receiver cuplike, prepuce well developed, posterior hamuli typically with transverse row of denticles ..... **Progomphini** trib. n.

19 Postgenal suture absent, male tibial laminae absent, penile segment 1 with bilobed cuplike thin-walled hood, female sternum 9 with dome shaped membranous area extended to distal half of sternum ..... **Crenigomphini** trib. n.

Postgenal suture present, male tibial laminae present, penile segment 1 without cuplike thin-walled hood, female sternum 9 with dome shaped membranous area not extended to distal half of sternum ..... **Onychogomphini**

20 Basal half of abdominal segment 9 constricted, middle tooth of posterior maxillary tooth row ca 1/10 length of proximal tooth, male sternum 9 sclerotized with gonocoxae located on posterior half of sternum, female sternum 9 membranous with U-shaped posterior sclerite, female auricles absent ..... **Neurogomphini** trib. n.

Basal half of abdominal segment 9 not constricted, middle tooth of posterior maxillary tooth row 2/10-7/10 length of proximal tooth, male sternum 9 membranous posterior to gonocoxae which are located on anterior half of sternum, female sternum 9 sclerotized over distal half, female auricles present 21

21 Arculus typically angulate with posterior portion nearly perpendicular to midbasal vein stem, male tibial laminae well developed, male sternum 9 with lateral sclerotized areas extended to near posterior margin, female hind femora without 2 rows of long spines ..... **Gomphini**

Arculus straight and aslant, male tibial laminae vestigial or absent, male sternum 9 membranous posterior to gonocoxae, female hind femora with 2 rows of long spines 22

22 Hind femoral length typically less than 1.1 times width of head, posterosubapical mandibular tooth reduced or absent, middle tooth of posterior maxillary tooth row ca 4/10 length of proximal tooth, male tibial laminae present, anterior hamuli short and flat with apical hair pencil, penile segment 4 not elongate-tubular, genital lobe vestigial.. **Cyclogomphini** trib. n.

Hind femoral length typically more than 1.2 times width of head, posterosubapical mandibular tooth well developed, middle tooth of posterior maxillary tooth row ca 6/10 length of proximal tooth, male tibial laminae absent, anterior hamuli elongate with apical hook, penile segment 4 elongate-tubular, genital lobe well developed .... **Anisogomphini** trib. n.

HAGENIINI

Type genus: *Hagenius* Selys, 1854.

The Hageniini include: *Hagenius* and *Sieboldius* Selys, 1854.

Large gomphines generally colored black and yellow.

Head — Mouthparts hypognathous, middle tooth of posterior maxillary tooth row not fused to apical tooth, ca 0.7 length of proximal tooth, and separated from proximal tooth by V-shaped notch, anterosubapical mandibular tooth as robust as apical tooth and not retracted basally, posterosubapical mandibular tooth nearly as robust as apical tooth and not displaced proximally, labrum ca 3 times as wide as long, ligula ca 2 times as wide as long, distance between antennal bases 1.5-1.6 times length of dorsal surface of antefrons, frontal carina present, medial ocelli wider than lateral ocelli, occiput not ridged, head not tumid posterior to compound eyes.

Thorax — Distance between lateral ends of collar carina and antealar carina

ca 1.9 times length of collar carina, lower portion of dorsomedian carina 0.6-0.7 times length of 1/2 collar carina, lateral mesocoxal carina nearly straight and weakly developed, male foretibial lamina absent, hind femur long, female hind femur without elongate spines, spines of male hind tibia not enlarged basally, tarsal spines small and not subapical.

Wings — Basal subcostal crossveins present or absent, distal costal brace of hind wing located closer to proximal costal brace than to nodus, costa not curved or widened along pterostigma, pterostigmal brace present, fore wing arculus angulated with lower portion perpendicular to CuP, sectors of arculus widely separated basally (by ca 1/3 length of arculus in hind wing), base of fore wing distal pleat at ca 0.41 distance between distal ends of triangle and subnodus, base of distal pleat symmetrical, apical planate extended to near halfway between pterostigma and nodus, apical planate divergent from RP_1, MA without posterior branch originating slightly distal to bridge crossvein, supratriangles without crossveins, hind wing with 2 or 3 postmedian crossveins, hind wing subtriangle without crossveins, anal vein not angulated at proximal angle of hind wing subtriangle, CuA brace ca 1/2 length of posterior side of fore wing subtriangle, triangles with crossveins, anterobasal angle of fore wing triangle ca 90°, wings with trigonal planates, CuP and anal vein moderately divergent to hind wing margin (distal pectination of CuP often irregular), anal brace present, anal triangle ca 1.7 times as long as wide, anal triangle not extended posteriorly to tornus, anal triangle 3-6-celled, cells of anal triangle variously arranged (not serially), membranule present and extended to tornus.

Abdomen — Male auricle not dorsoventrally compressed or strongly produced posteriorly, lower portion of auricular ridge well developed and nearly vertical, female auricle present but low, lateral margin of abdominal terga 7-10 not expanded, female sternum 9 membranous with two laterobasal sclerites, male sternum 9 membranous posterolaterally and posterior to gonocoxae, male gonocoxae rounded anteriorly, terga 9 and 10 without medial carina, male with posterolateral margin of segment 10 not notched, female segment 10 with lateral carina well developed, sternum 10 of male 6-8 times as wide as long, male cerci with ventrolateral spines, male epiproct bifurcate with branches parallel sided, male paraproct with lateral ridge lobed and extended dorsally to near base of cerci.

Genitalia — Anterior lamina conically elevated with narrow posteromedial cleft, anterior hamuli elongate with apices contiguous and curved posteriorly, posterior hamulus quadrate with well developed endhook and shoulder, and anterior surface with denticles, penile segment one inflated-elongate with cleft-like penile receiver, second penile segment 3.0-3.5 times as long as wide, penile spine present, third penile segment without ventrobasal transverse indentation and ca 2 times as long as wide, prepuce produced posteriorly and slightly inflated, apex of penis bilobed without flagellum, genital shelf absent.

KEY TO THE SUBGENERA OF HAGENIINI

1 Wings with 1 Cu-A crossvein, without basal antenodal, and with RP_2 extended to distal end of pterostigmata ..... ***Hagenius***
Wings with 2-3 Cu-A crossveins, with basal antenodal, and with RP_2 extended to near middle of pterostigmata ..... ***Sieboldius*** — 2
2 Pterostigmal brace absent, male cerci as long as abdominal segment 10 ..... ***Hagenoides*** subgen. n.
Type species: *Sieboldius alexanderi* Chao
Pterostigmal brace present, male cerci shorter than abdominal segment 10 3
3 Male cerci with acute posteriorly directed apical spine ..... ***Sieboldius***
Male cerci without acute posteriorly directed apical spine ..... ***Pseudohagenius*** subgen. n.
Type species: *Hagenius deflexus* Chao.

HEMIGOMPHINI

Type genus: *Hemigomphus* Selys, 1854.

The Hemigomphini include: *Hemigomphus, Eogomphus* Needham, 1944, *Neogomphus* Selys, 1857 and *Sinogomphus* May, 1935.

Small to medium sized gomphines generally colored black (occasionally dark brown), yellow, and green.

Head — Mouthparts hypognathous, middle tooth of posterior maxillary tooth row not fused to apical tooth, ca 0.6 length of proximal tooth, and separated from proximal tooth by U-shaped notch, anterosubapical mandibular tooth well developed and slightly retracted basally, posterosubapical mandibular tooth slightly less robust than apical tooth and slightly displaced proximally, labrum ca 2.3 times as wide as long, ligula ca 1.25 times as wide as long, distance between antennal bases ca 1.8 times length of dorsal surface of antefrons (ca 2.2 in *Sinogomphus*), frontal carina generally present (vestigial or absent in *Sinogomphus* and *Eogomphus*), medial ocelli wider than lateral ocelli, occiput not ridged, head not tumid posterior to compound eyes.

Thorax — Distance between lateral ends of collar carina and antealar carina 2.0-2.1 times length of collar carina, lower portion of dorsomedian carina 0.8--1.0 length of 1/2 collar carina, lateral mesocoxal carina nearly straight, male foretibial lamina present, hind femur long, female hind femur without elongate spines (spines slightly elongated in *Sinogomphus*), spines of male hind tibia not enlarged basally, tarsal spines small and not subapical.

Wings — Basal subcostal crossveins absent (occasionally present), distal costal brace of hind wing located about midway between proximal costal brace and nodus (located closer to proximal costal brace in *Hemigomphus*), costa curved and widened along pterostigma, pterostigmal brace present, fore wing arculus angulated (angulation occasionally slight in *Hemigomphus*) with lower portion perpendicular to CuP (occasionally not perpendicular in *Hemigomphus*), sectors of arculus separated basally (by 1/6-1/5 length of hind wing

arculus), base of fore wing distal pleat at 0.36-0.43 distance between distal ends of triangle and subnodus (0.32-0.38 in *Sinogomphus*), base of distal pleat symmetrical (asymmetrical in hind wings of *Hemigomphus*), apical planate extended to near middle of pterostigma, apical planate divergent from RP_1 (slightly divergent in *Eogomphus*), MA without posterior branch originating slightly distal to bridge crossvein, supratriangles without crossveins (occasionally with crossvein), hind wing with 1 postmedian crossvein in *Sinogomphus* and *Neogomphus* and with 2 postmedian crossveins in *Hemigomphus* and *Eogomphus,* hind wing subtriangle without crossveins, anal vein slightly angulated at proximal angle of hind wing subtriangle, CuA brace 1/3-2/5 length of posterior side of fore wing subtriangle, triangles without crossveins (occasionally 2-celled in hind wings, and with crossvein in hind wings and occasionally fore wings of *Eogomphus*), anterobasal angle of fore wing triangle slightly acute, wings without trigonal planates, CuP and anal vein strongly divergent, separated at hind wing margin by less than 1/2 width of trigonal space at wing margin, anal brace present, anal triangle 2.1-2.3 times as long as wide (1.3 in *Eogomphus* and 1.4-1.8 in *Sinogomphus*), anal triangle not extended posteriorly to tornus, anal triangle 3-celled, cells of anal triangle arranged to meet at point, membranule present and extended to tornus.

Abdomen — Male auricle not dorsoventrally compressed or strongly produced posteriorly, lower portion of auricular ridge well developed and nearly vertical, female auricle present, lateral margin of abdominal terga not expanded, female sternum 9 membranous with two laterobasal sclerites, male sternum 9 membranous lateral and posterior to gonocoxae, male gonocoxae rounded anteriorly, terga 9 and 10 without medial carina, male with posterolateral margin of segment 10 not notched, female segment 10 with lateral carina well developed, sternum 10 of male 6-8 times as wide as long, male cerci robust with ventrolateral spine directed ventrally and located at extreme base, male epiproct bifurcate with branches divaricate (paired submedial processes present in some *Sinogomphus*), male paraproct with lateral ridge extended dorsally to near base of cerci (ridge with dorsal process in *Neogomphus*).

Genitalia — Anterior lamina low and slightly bilobate with shallow U-shaped posterior margin (raised with V-shaped posterior margin in *Hemigomphus*), anterior hamulus bifurcate with anterior branch longer and with apex directed posteriorly in *Eogomphus* and *Neogomphus,* bladelike in *Sinogomphus,* and tapered-elongate with posterodorsally curved apex in *Hemigomphus* posterior hamulus with anterior denticles and well-developed end hooks (denticles minute in *Sinogomphus* and shoulder well developed in *Sinogomphus* and *Neogomphus*), penile segment one raised with high thin-margined hood, penile receiver dish- or bowllike, second penile segment ca 3.0 times as long as wide, penile spine present, third penile segment without ventrobasal transverse indentation and 1.0-2.0 times as long as wide, prepuce elongate-pointed (only slightly

elongate and rounded posteriorly in *Hemigomphus*), apex of penis with two flagella, genital shelf absent (present in *Neogomphus*).

KEY TO THE SUBGENERA OF *HEMIGOMPHUS*

1 Anterior and lateral mesanepisternal pale stripes not fused to form sinuous stripe, male cerci with clawlike ventrobasal spine, male paraprocts without lateral clawlike process ..... ***Hemigomphus***

Anterior and lateral mesanepisternal pale stripes fused to form sinuous stripe, male cerci with acute subbasal spine, male paraprocts with lateral clawlike process ..... ***Armagomphus*** subgen. n.

Type species *Austrogomphus armiger* Tillyard.

OCTOGOMPHINI

Type genus: *Octogomphus* Selys, 1873.

The Octogomphini include: *Octogomphus, Dubitogomphus* Fraser, 1940, *Lanthus* Needham, 1897, and *Davidius* Selys, 1878.

Small gomphines generally colored black, yellow, and green.

Head — Mouthparts hypognathous, middle tooth of posterior maxillary tooth row not fused to apical tooth, ca 0.7 length of proximal tooth, and separated from proximal tooth by U-shaped notch, anterosubapical mandibular tooth well developed and slightly retracted basally, posterosubapical mandibular tooth slightly less robust than apical tooth and slightly displaced proximally, labrum ca 2.6 times as wide as long (ca 2.4 in *Davidius*), ligula ca 1.4 times as wide as long (1.1-1.3 in *Davidius*), distance between antennal bases ca 2.0-2.1 times length of dorsal surface of antefrons (2.0-2.2 in *Davidius* and 2.5 in female *Octogomphus*), frontal carina present (present or absent in *Davidius*), medial ocelli wider than lateral ocelli, occiput not ridged, head not tumid posterior to compound eyes (tumid in female *Octogomphus*).

Thorax — Distance between lateral ends of collar carina and antealar carina 2.0-2.2 times length of collar carina (2.2-2.7 in *Davidius*), lower portion of dorsomedian carina slightly less than length of 1/2 collar carina (1.1-1.4 in *Davidius*), lateral mesocoxal carina nearly straight, male foretibial lamina present (often absent or vestigial in *Davidius*), hind femur long, female hind femur without elongate spines, spines of male hind tibia not enlarged basally, tarsal spines small and not subapical.

Wings — Basal subcostal crossveins absent (occasionally present), distal costal brace of hind wing located about midway between proximal costal brace and nodus, costa curved and widened along pterostigma, pterostigmal brace present, fore wing arculus angulated with lower portion perpendicular to CuP (posterobasal angle of supratriangle typically acute), sectors of arculus separated basally by 1/5-1/4 length of hind wing arculus (by ca 1/6 length of arculus in some *Davidius*), base of fore wing distal pleat at 0.35-0.40 distance between

distal ends of triangle and subnodus (0.33-0.36 in *Lanthus*), base of distal pleat symmetrical (asymmetrical in hind wings of some *Davidius*), apical planate extended to near middle of pterostigma, apical planate divergent from RP_1 (nearly parallel in *Davidius*), MA without posterior branch originating slightly distal to bridge crossvein, supratriangles without crossveins, hind wing with 1 postmedian crossvein, hind wing subtriangle without crossveins (occasionally 2-celled), anal vein slightly angulated at proximal angle of hind wing subtriangle (curved in *Davidius*), CuA brace ca 1/3-2/5 length of posterior side of fore wing subtriangle, triangles without crossveins, anterobasal angle of fore wing triangle acute (only slightly acute in *Lanthus* and *Octogomphus*), wings without trigonal planates (hind wing often with trigonal planate in *Octogomphus*), CuP and anal vein strongly divergent to hind wing margin (generally separated at hind wing margin by more than 1/2 width of trigonal space at wing margin), anal brace present, anal triangle 1.5-1.7 times as long as wide (0.8-1.1 in *Davidius*), anal triangle not extended posteriorly to tornus, anal triangle 3-celled, cells of anal triangle arranged to meet at point, membranule present (vestigial in *Davidius*).

Abdomen — Male auricle not strongly produced posteriorly, lower portion of auricular ridge well developed and nearly vertical, female auricle present, lateral margin of abdominal terga 7-10 not expanded, female sternum 9 membranous with two laterobasal sclerites which project medially, vulvar lamina with apical lobes fused or contiguous medially, male sternum 9 semimembranous lateral to and membranous posterior to gonocoxae, male gonocoxae rounded anteriorly, terga 9 and 10 without medial carina, male with posterolateral margin of segment 10 not notched, female segment 10 with lateral carina well developed, sternum 10 of male 4-5 times as wide as long, male cerci with basal spine (spines short and directed ventrally in *Lanthus*, long and directed posteromedially in *Octogomphus*, and long, contiguous, and directed medioventrally in *Davidius*), male epiproct bifurcate with branches divaricate (lateral branches vestigial in *Davidius*, paired submedial processes present in *Octogomphus* and *Davidius*), male paraproct with lateral ridge extended dorsally to near base of cerci.

Genitalia — Anterior lamina low and slightly bilobate with shallow U-shaped posterior margin (raised in some *Davidius*), anterior hamulus bifurcate with anterior branch longer and apex directed posteriorly (posterior branch absent in *Octogomphus*), posterior hamulus constricted subbasally with well developed shoulder and endhook, endhook directed posteromedially, and anterior surface with denticles, penile segment one raised with low hood, penile receiver troughlike, second penile segment ca 3.0 times as long as wide, penile spine present, third penile segment without ventrobasal transverse indentation and 1.5-2.5 times as long as wide, prepuce globose, apex of penis without flagellum (pointed in *Lanthus* and *Octogomphus*, and circular-flangelike in *Davidius*), genital shelf present (vestigial or absent in *Davidius*, and well developed in *Lanthus*).

KEY TO THE SUBGENERA OF *DAVIDIUS*

1 Anterior mesanepisternal pale stripes well developed and not fused to medial pale area dorsally, male epiproct triangular with medial cleft, male cerci with elongate medially contiguous ventrobasal spines ..... ***Davidius***

Anterior mesanepisternal pale stripes absent ventrally and fused to medial pale area dorsally, male epiproct divaricate without medial cleft, male cerci with short medially directed ventrobasal spines ..... ***Paralanthus*** subgen. n.

Type species: *Davidius mallory*i Fraser.

TRIGOMPHINI

Type genus: *Trigomphus* Bartenev, 1912.

The Trigomphini include *Trigomphus* (incl. *Xenogomphus* Needham, 1944), *Fukienogomphus* Chao, 1954, and *Stylogomphus* Fraser, 1922.

Small to medium sized gomphines generally colored black, yellow, and green.

Head — Mouthparts hypognathous, middle tooth of posterior maxillary tooth row not fused to apical tooth, ca 0.6 length of proximal tooth, and separated from proximal tooth by V-shaped notch, anterosubapical mandibular tooth well developed and slightly retracted basally, posterosubapical mandibular tooth well developed and slightly displaced proximally, labrum 2.2-2.5 times as wide as long, ligula 1.0-1.2 times as wide as long, distance between antennal bases 2.0-2.1 times length of dorsal surface of antefrons, frontal carina generally present in males and absent in females, medial ocelli wider than lateral ocelli, occiput not ridged, head not tumid posterior to compound eyes.

Thorax — Distance between lateral ends of collar carina and antealar carina 2.2-2.5 times length of collar carina, lower portion of dorsomedian carina slightly less than length of 1/2 collar carina, lateral mesocoxal carina nearly straight, male foretibial lamina present, hind femur long, female hind femur without elongate spines, spines of male hind tibia not enlarged basally, tarsal spines small and not subapical.

Wings — Basal subcostal crossveins absent, distal costal brace of hind wing located about midway between proximal costal brace and nodus, costa curved and widened along pterostigma, pterostigmal brace present, fore wing arculus angulate with lower portion perpendicular to CuP, sectors of arculus separated basally (by 1/5-1/4 length of hind wing arculus), base of fore wing distal pleat at 0.37-0.42 distance between distal ends of triangle and subnodus, base of distal pleat symmetrical (asymmetrical in *Trigomphus*), apical planate extended to near middle of pterostigma, apical planate divergent from RP_1, MA without posterior branch originating slightly distal to bridge crossvein, supratriangles without crossveins, hind wing with 1-4 postmedian crossveins (1 in *Stylogom-*

phus, and 2-4 in *Fukienogomphus* and *Trigomphus*), hind wing subtriangle without crossveins, anal vein slightly angulated at proximal angle of hind wing subtriangle (curved in *Trigomphus*), CuA brace 1/3-2/5 length of posterior side of fore wing subtriangle, triangles without crossveins (occasionally 2-celled), anterobasal angle of fore wing triangle acute (slightly acute in *Stylogomphus*), wings without trigonal planates, CuP and anal vein strongly divergent to hind wing margin (generally separated at hind wing margin by less than 1/2 width of trigonal space at wing margin), anal brace present, anal triangle 1.0-1.5 times as long as wide, anal triangle not extended posteriorly to tornus, anal triangle 3-celled in *Stylogomphus*, 3 or 4-celled in *Fukienogomphus*, and 5 or 6-celled in *Trigomphus*, cells of anal triangle arranged to meet at point in *Stylogomphus* and most *Fukienogomphus*, and with 4 cells along proximal margin in *Trigomphus*, membranule present and extended to tornus.

Abdomen — Male auricle not dorsoventrally compressed or strongly produced posteriorly, lower portion of auricular ridge well developed and nearly vertical, female auricle present, lateral margin of abdominal terga 7-9 not expanded, female sternum 9 membranous with triangular-shaped laterobasal sclerites (sclerites elongate-triangular in *Fukienogomphus* and *Trigomphus*), male sternum 9 membranous posterior to gonocoxae (also semimembranous lateral to gonocoxae in *Stylogomphus*), male gonocoxae rounded anteriorly, abdominal terga 7-10 without medial carina, male with posterolateral margin of segment 10 not notched, female segment 10 with lateral carina well developed, sternum 10 of male 1-3 times as wide as long, male cerci with lateral subbasal spine, male epiproct bifurcate with branches subparallel in *Stylogomphus*, and divaricate in *Fukienogomphus* and *Trigomphus*, male paraproct without lateral ridge extended dorsally to near base of cerci.

Genitalia — Anterior lamina raised-bilobate (with V-shaped raised posterior ridge in *Fukienogomphus* and *Trigomphus*), anterior hamulus elongate with posteriorly directed apex and subbasal shoulder or ramus, posterior hamulus with well developed transverse shoulder and small robust medially directed endhook, anterior surface with denticles, penile segment one low-inflated with anterolateral projections and cleftlike penile receiver, second penile segment ca 3.0 times as long as wide, penile spine present, third penile segment without ventrobasal transverse indentation and 1.5-2.0 times as long as wide, prepuce globose in *Stylogomphus*, and produced posteriorly in *Fukienogomphus* and *Trigomphus*, apex of penis circular-flangelike in *Stylogomphus*, and with short flagellum in *Fukienogomphus* and *Trigomphus*, genital shelf present and flattened.

ANISOGOMPHINI

Type genus: *Anisogomphus* Selys, 1857.

The Anisogomphini include: *Anisogomphus* (incl. *Temnogomphus* Laidlaw, 1922), *Labrogomphus* Needham, 1897, *Merogomphus* Martin, 1904 (incl. *Indogomphus* Fraser, 1922) and *Notogomphus* Selys, 1857 (incl. *Nilogomphus* Fraser, 1928 and *Podogomphus* Karsch, 1890).

Medium sized gomphines generally colored dark brown, yellow, and light green.

Head — Mouthparts hypognathous, middle tooth of posterior maxillary tooth row not fused to apical tooth, ca 0.65 length of proximal tooth, and separated from proximal tooth by U-shaped notch, anterosubapical mandibular tooth well developed and slightly retracted basally, posterosubapical mandibular tooth well developed and slightly displaced proximally, labrum 2.1-2.4 times as wide as long, ligula 1.4-1.8 times as wide as long, distance between antennal bases 2.0-2.4 times length of dorsal surface of antefrons, frontal carina generally absent, medial ocelli wider than lateral ocelli, occiput ridged, head not tumid posterior to compound eyes.

Thorax — Distance between lateral ends of collar carina and antealar carina 2.1-2.3 times length of collar carina, lower portion of dorsomedian carina 1.0--1.2 length of 1/2 collar carina (ca 0.8 in *Merogomphus*), lateral mesocoxal carina nearly straight, male foretibial lamina absent, hind femur very long, female hind femur with two rows of elongate spines (males with at least apical spines lengthened), spines of male hind tibia not enlarged basally, tarsal spines small and not subapical.

Wings — Basal subcostal crossveins generally present, distal costal brace of hind wing located closer to proximal costal brace than to nodus (occasionally closer to nodus in *Notogomphus*), costa curved and widened along pterostigma, pterostigmal brace present, fore wing arculus aslant and either straight or slightly angulate with lower portion not perpendicular to CuP, sectors of arculus separated basally (by 1/6-1/4 length of hind wing arculus), base of fore wing distal pleat at 0.36-0.42 distance between distal ends of triangle and subnodus, base of distal pleat symmetrical, apical planate extended to near middle of pterostigma, apical planate divergent from RP_1, MA without posterior branch originating slightly distal to bridge crossvein, supratriangles without crossveins, hind wing with 1 or occasionally 2 postmedian crossveins, hind wing subtriangle without crossveins, anal vein slightly angulated at proximal angle of hind wing subtriangle, CuA brace 1/3-2/5 length of posterior side of fore wing subtriangle, triangles without crossveins (rarely 2-celled), anterobasal angle of fore wing triangle slightly acute, wings without trigonal planates, CuP and anal vein slightly divergent to hind wing margin, anal brace present, anal triangle 1.2-1.7 times as long as wide, anal triangle not extended posteriorly to tornus, anal triangle 3-celled (occasionally 4-celled), cells of anal triangle arranged to meet at point (when 4-celled with extra rectangular cell along proximal margin),

membranule present and extended narrowly to tornus.

Abdomen — Male auricle not dorsoventrally compressed or strongly produced posteriorly, lower portion of auricular ridge well developed and nearly vertical, female auricle present, lateral margin of abdominal terga 7-9 not expanded (rimlike on 8 and 9), female sternum 9 sclerotized on distal 1/2-2/3 with medial projection and transverse ridges along border of oval laterobasal sclerites, male sternum 9 membranous posterior to gonocoxae (lateral sclerotized areas not approximate posterior to gonocoxae or extended to posterior margin of segment), male gonocoxae rounded anteriorly, abdominal terga 7-10 without medial carina in *Notogomphus* and *Anisogomphus*, 7-8 and base of 9 with carina in *Merogomphus*, and 7-9 with carina in *Labrogomphus*, male with posterolateral margin of segment 10 not notched, female segment 10 with lateral carina well developed, sternum 10 of male 2-3 times as wide as long, male cerci bifurcate with ventral spine or ridge, male epiproct bifurcate with branches widely divergent, male paraproct without lateral ridge extended dorsally to near base of cerci.

Genitalia — Anterior lamina moderately raised with V-shaped posterior margin, anterior hamulus flat-elongate with small posteriorly directed end hook, posterior hamulus robust with small end hook, medially produced shoulder, and anterior surface without denticles (denticles occasionally present), penile segment one moderately raised with shallow trough- or dishlike penile receiver bordered by thick to moderately thin rim, second penile segment 3.0-4.0 times as long as wide, penile spine absent, third penile segment without ventrobasal transverse indentation and 1.5-2.0 times as long as wide, prepuce narrow and extended posteriorly beyond base of segment 4, apex of penis with segment 4 elongate (ca as long as segment 3) and with or without two short flagella, genital shelf well developed and ridgelike with large tuft of hair.

CYCLOGOMPHINI

Type genus: *Cyclogomphus* Selys, 1854.

The Cyclogomphini include: *Cyclogomphus*, *Anormogomphus* Selys, 1854, *Burmagomphus* Williamson, 1907 and *Platygomphus* Selys, 1854.

Small gomphines generally colored brown and yellow.

Head — Mouthparts hypognathous (slightly prognathous in *Platygomphus*), middle tooth of posterior maxillary tooth row not fused to apical tooth, ca 0.35 length of proximal tooth, and separated from proximal tooth by U-shaped notch, anterosubapical mandibular tooth slightly retracted basally, posterosubapical mandibular tooth absent or reduced and displaced proximally (absent or vestigial in *Cyclogomphus* and *Platygomphus*), labrum 2.1-2.4 times as wide as long, ligula 1.3-1.6 times as wide as long, distance between antennal bases 2.2-2.5 times length of dorsal surface of antefrons (ca 4.0 in *Platygom-*

phus), frontal carina present in *Cyclogomphus* and *Anormogomphus*, and absent in *Burmagomphus* and *Platygomphus*, medial ocelli wider than lateral ocelli, occiput ridged, head not tumid posterior to compound eyes.

Thorax — Distance between lateral ends of collar carina and antealar carina 1.9-2.0 times length of collar carina, lower portion of dorsomedian carina 0.7-0.9 length of 1/2 collar carina, lateral mesocoxal carina nearly straight or slightly angulate, male foretibial lamina vestigial ca 1/7 length of foretibia (ca 1/5 in *Burmagomphus*), hind femur long, female hind femur with two rows of moderately elongate spines (spines slightly elongate in males), spines of male hind tibia enlarged basally (not enlarged basally in *Platygomphus*), tarsal spines small and not subapical.

Wings — Basal subcostal crossveins absent (present in *Cyclogomphus*), distal costal brace of hind wing located closer to proximal costal brace than to nodus, costa curved and widened along pterostigma, pterostigmal brace present, fore wing arculus angulate in *Cyclogomphus* and *Platygomphus* with lower portion perpendicular to CuP, and straight in *Anormogomphus* and *Burmagomphus* with lower portion not perpendicular to CuP, sectors of arculus separated basally (by 1/5-1/4 length of hind wing arculus) base of fore wing distal pleat at 0.36-0.45 distance between distal ends of triangle and subnodus, base of distal pleat symmetrical, apical planate extended to near middle of pterostigma, apical planate divergent from RP_1, MA without posterior branch originating slightly distal to bridge crossvein, supratriangles without crossveins, hind wing with 1 postmedian crossvein, hind wing subtriangle without crossveins, anal vein slightly angulated at proximal angle of hind wing subtriangle, CuA brace ca 3/8 length of posterior side of fore wing subtriangle, triangles without crossveins, anterobasal angle of fore wing triangle acute, wings without trigonal planates, CuP and anal vein slightly divergent to hind wing margin, anal brace present in *Burmagomphus* and *Cyclogomphus*, and vestigial in *Anormogomphus* and *Platygomphus*, anal triangle 1.2-1.9 times as long as wide, anal triangle not extended posteriorly to tornus, anal triangle 3-celled (1-celled in *Anormogomphus*), cells of anal triangle arranged to meet at point in *Burmagomphus* and *Cyclogomphus*, and serially in *Platygomphus*, membranule present and extended to tornus.

Abdomen — Male auricle not dorsoventrally compressed or strongly produced posteriorly, lower portion of auricular ridge well developed and nearly vertical, female auricle present, lateral margin of abdominal terga 7-9 not expanded, female sternum 9 sclerotized over distal 7/8 with mediosubbasal ridge (ridge absent or vestigial in *Burmagomphus*), male sternum 9 membranous posterior to gonocoxae, male gonocoxae rounded anteriorly, abdominal terga 7-10 without medial carina, male with posterolateral margin of segment 10 slightly notched (lateral carina and posterolateral margin of segment 10 forming acute angle), female segment 10 with lateral carina weakly developed, sternum

10 of male 1.5-2.0 times as wide as long, male cerci with lateral obtuse spine (cerci often contiguous medially without lateral spine in *Cyclogomphus*, and with accessory medial spine in *Anormogomphus*), male epiproct bifurcate with branches divaricate, male paraproct without lateral ridge extended dorsally to near base of cerci.

Genitalia — Anterior lamina low with lateral swollen areas before anterior hamulus (*Anormogomphus* also with posteromedial swollen area), anterior hamulus short and flat with apical fringe of hairs, posterior hamulus nearly straight without anterior denticles, with small anteriorly directed end hook, and with or without small shoulder, penile segment one moderately raised with cleftlike penile receiver (inflated in *Cyclogomphus*), second penile segment 1.0--4.0 times as long as wide, second penile segment ca as long as wide in *Cyclogomphus, Platygomphus,* and *Anormogomphus,* penile spine absent, third penile segment without ventrobasal transverse indentation and 1.3-1.7 times as long as wide, prepuce moderately expanded and produced posteriorly in *Platygomphus* and *Anormogomphus,* and vestigial in most *Cyclogomphus* and *Burmagomphus,* apex of penis with flagellum short in *Cyclogomphus* and *Anormogomphus,* moderately long and bifurcate in *Platygomphus,* and long and often bifurcate apically in *Burmagomphus*), genital shelf vestigial.

GOMPHINI

Type genus: *Gomphus* Leach, 1815.

The Gomphini include: *Gomphus* (incl. *Hylogomphus* Needham, 1951 and *Shaogomphus* Chao, 1984), *Arigomphus* Needham, 1897, *Dromogomphus* Selys, 1854, *Gastrogomphus* Needham, 1944, *Gomphurus* Needham, 1901 and *Stylurus* Needham, 1897.

Small to medium sized gomphines generally colored black, yellow, and green.

Head — Mouthparts hypognathous (slightly prognathous in *Stylurus*), middle tooth of posterior maxillary tooth row not fused to apical tooth, 0.2-0.6 length of proximal tooth, and separated from proximal tooth by U-shaped notch (by V-shaped notch in *Gastrogomphus, Gomphurus,* and *Dromogomphus*) anterosubapical mandibular tooth well developed and slightly retracted basally, posterosubapical mandibular tooth well developed and slightly displaced proximally (weakly developed in *Stylurus* and *Arigomphus*), labrum 2.1-2.9 times as wide as long, ligula 1.4-2.0 times as wide as long, distance between antennal bases 1.4-2.2 times length of dorsal surface of antefrons (2.3--2.5 in *Stylurus*), frontal carina generally present, medial ocelli wider than lateral ocelli, occiput ridged, head not tumid posterior to compound eyes (slightly tumid in *Arigomphus*).

Thorax — Distance between lateral ends of collar carina and antealar carina 1.8-2.2 times length of collar carina, lower portion of dorsomedian carina 0.7-

-1.0 length of 1/2 collar carina, lateral mesocoxal carina nearly straight, male foretibial lamina present, hind femur long (only moderately long in *Stylurus*), female hind femur without elongate spines (with one row of elongate spines in male and female *Dromogomphus*), spines of male hind tibia not enlarged basally, tarsal spines small and not subapical.

Wings — Basal subcostal crossveins absent (occasionally present in *Gomphurus*), distal costal brace of hind wing located closer to proximal costal brace than to nodus, costa curved and widened along pterostigma, pterostigmal brace present, fore wing arculus angulate with lower portion perpendicular to CuP, sectors of arculus separated basally (by 1/5-1/4 length of hind wing arculus), base of fore wing distal pleat at 0.38-0.52 distance between distal ends of triangle and subnodus, base of distal pleat symmetrical, apical planate extended to near middle of pterostigma, apical planate divergent from RP_1, MA without posterior branch originating slightly distal to bridge crossvein, supratriangles without crossveins, hind wing with 1 postmedian crossvein, hind wing subtriangle without crossvein, anal vein slightly angulated at proximal angle of hind wing subtriangle, CuA brace 3/10-4/9 length of posterior side of fore wing subtriangle, triangles without crossveins, anterobasal angle of fore wing triangle slightly acute, wings without trigonal planates, CuP and anal vein slightly divergent to hind wing margin, anal brace present, anal triangle 1.1-2.2 times as long as wide, anal triangle not extended posteriorly to tornus, anal triangle 3-celled (occasionally 4 or 5-celled in *Gomphus*), cells of anal triangle generally arranged to meet at point, membranule present and extended to tornus.

Abdomen — Male auricle not dorsoventrally compressed or strongly produced posteriorly, lower portion of auricular ridge well developed and nearly vertical, female auricle present, lateral margin of abdominal terga 7-9 expanded (slightly expanded in *Gomphus* and *Gastrogomphus*), female sternum 9 sclerotized with basal 1/5-1/3 membranous, laterobasal sclerites present or absent, male sternum 9 with lateral sclerotized areas approximate posterior to gonocoxae and extended to near posterior margin of segment, male gonocoxae rounded anteriorly, abdominal terga 7-10 without medial carina, male with posterolateral margin of segment 10 not notched, female segment 10 with lateral carina well developed, sternum 10 of male 0.7-6.0 times as wide as long, male cerci divaricate with ventral or lateral ridge or both, male epiproct bifurcate with branches widely divaricate, male paraproct without lateral ridge extended dorsally to near base of cerci.

Genitalia — Anterior lamina raised to form V-shaped ridge, posterior margin V-shaped (U-shaped in *Arigomphus*), anterior hamulus elongate, C-shaped in cross section, and bilobate apically with outer lobe typically spined, (anterior hamulus rodlike in *Stylurus*), posterior hamulus robust with well developed shoulder and endhook, endhook with medial keel and anterior surface of hamulus typically with one or more denticles at shoulder, penile segment one

low-inflated or raised-pyramidal, penile receiver cleft- or troughlike, second penile segment 2.2-3.5 times as long as wide (1.5-2.2 in *Stylurus*), penile spine absent (present in some *Gomphus*), third penile segment without ventrobasal transverse indentation and 1.5-2.5 times as long as wide, prepuce moderately expanded and produced posteriorly, apex of penis generally with short flagellum (bifurcate in *Arigomphus, Gomphurus*, and some *Gomphus*), genital shelf generally low and weakly developed.

KEY TO THE SUBGENERA OF *GOMPHUS*

1 Anterior hamuli with latero-apical edge spinose or hooklike, posterior margin of abdominal sternum 10 level, male cerci with basolateral carina ..... ***Phanogomphus*** subgen. n.
Type species: *Gomphus minutus* Rambur

Anterior hamuli with latero-apical edge denticulate, posterior margin of abdominal sternum 10 V-shaped, male cerci without basolateral carina 2

2 Anterior hamuli with outer edge reduced, with subapical shoulder, and with subapical denticles, raised portion of penile segment 1 laterally compressed, male cerci with ventrosubapical surface convex 3

Anterior hamuli with outer edge well developed, without shoulder, and with apical denticles, raised portion of penile segment 1 not laterally compressed, male cerci with ventrosubapical surface flat or concave 4

3 Face predominantly green or yellow, hind wing triangle with proximal side perpendicular to subcosta and ca 1/2 length of distal side, apices of anterior hamuli notched, male cerci with small ventrosubapical spine ..... ***Stenogomphurus*** subgen. n.
Type species — *Gomphus consanguis* Selys

Face predominantly brown or black, hind wing triangle with proximal side not perpendicular to subcosta and ca 2/3 length of distal side, apices of anterior hamuli rounded, male cerci without ventral spines ..... ***Anatogomphurus*** subgen. n.
Type species — *Gomphus personatus* Selys

4 Male cerci with apical portion curved ventrally and with ventral subapical groove, female with two large processes on posterior surface of head ..... ***Shaogomphus***

Male cerci with apical portion directed posteriorly and with ventrosubapical spine, female without processes on posterior surface of head ..... ***Gomphus***

Comments — CHAO (1984) established *Shaogomphus* on the basis of the five-celled anal triangle, apparently not realizing that the generotype of *Gomphus, Libellula vulgatissima* L., is also characterized by a five-celled anal triangle. Other species of *"Shaogomphus"* have four or occasionally three cells in the anal triangle. It remains to be determined if *"Shaogomphus" lieftincki* is a synonym of *Gomphus postocularis* Selys, *Gomphus chancae* Bartenef, or *Gomphus schmidti* Asahina. Ironically NEEDHAM (1948) considered species of the new subgenus *Phanogomphus* closely related to *Gomphus vulgatissimus* because *Gomphus* (*P.*) *borealis* Needham is also characterized by a five-celled anal triangle. Needham's subgenus *Hylogomphus* is here considered a subjective synonym of *Gomphus*. The name *Phanogomphus* if and when used again is to be credited to CARLE & COOK (1984).

NEUROGOMPHINI

Type genus: *Neurogomphus* Karsch, 1890.

The Neurogomphini include: *Neurogomphus* (incl. *Oxygomphus* Lacroix, 1921 and *Karschiogomphus* Schouteden, 1934).

Medium sized gomphines generally colored brown, yellow, green, and orange.

Head — Mouthparts hypognathous, middle tooth of posterior maxillary tooth row not fused to apical tooth, ca 0.1 length of proximal tooth, and separated from proximal tooth by U-shaped notch, anterosubapical mandibular tooth well developed and not retracted basally, posteroapical mandibular tooth nearly as robust as apical tooth and slightly displaced proximally, labrum 2.3-2.5 times as wide as long, ligula 1.3-1.6 times as wide as long and with lateral margin indented, distance between antennal bases 2.6-2.9 times length of dorsal surface of antefrons, frontal carina absent, medial ocelli wider than lateral ocelli, occiput ridged, head not tumid posterior to compound eyes.

Thorax — Distance between lateral ends of collar carina and antealar carina 1.9-2.1 times length of collar carina, lower portion of dorsomedian carina 0.7--0.8 length of 1/2 collar carina, lateral mesocoxal carina angulate, male foretibial lamina present and slightly displaced proximally, hind femur long, female hind femur without elongate spines, spines of male hind tibia not enlarged basally, tarsal spines small and not subapical.

Wings — Basal subcostal crossveins present, distal costal brace of hind wing located closer to proximal costal brace than to nodus, costa curved and widened along pterostigma, pterostigmal brace present, fore wing arculus straight or slightly angulate with lower portion nearly perpendicular to CuP, sectors of arculus separated basally (by ca 1/5 length of hind wing arculus), base of fore wing distal pleat at 0.34-0.37 distance between distal ends of triangle and subnodus, base of distal pleat symmetrical, apical planate extended to near distal end of pterostigma, apical planate divergent from RP_1, MA without posterior branch originating slightly distal to bridge crossvein, supratriangles without crossvein, hind wing with 1 postmedian crossvein, hind wing subtriangle without crossveins, anal vein angulated at proximal angle of hind wing subtriangle, CuA brace ca 3/8 length of posterior side of fore wing subtriangle, triangles without crossveins, anterobasal angle of fore wing triangle acute, wings without trigonal planates, CuP and anal vein slightly divergent to hind wing margin, anal brace present, anal triangle 1.1-1.3 times as long as wide, anal triangle not extended posteriorly to tornus, anal triangle 3 or 4-celled, cells of anal triangle arranged to meet at point or with small rectangular cell along proximal margin, membranule present and extended narrowly to tornus.

Abdomen — Male auricle not dorsoventrally compressed or strongly produced posteriorly, lower portion of auricular ridge well developed and nearly

vertical, female auricle absent, lateral margin of abdominal tergum 8 widened and with narrow flange, female sternum 9 membranous with narrow apical sclerotized plate with U-shaped anterior margin, male sternum 9 sclerotized with medial seam distal to gonocoxae, male gonocoxae displaced distally and rounded anteriorly, abdominal terga 7-10 without medial carina, abdominal segment 10 elongate with tubular basal constriction, male with posterolateral margin of segment 10 not notched, female segment 10 with lateral carina absent or vestigial, sternum 10 of male ca 0.5 times as wide as long, male cerci divaricate and tapered to obliquely truncate apex with ventral tooth, male epiproct bifurcate with branches divaricate, male paraproct without lateral ridge extended dorsally to near base of cerci.

Genitalia — Anterior lamina low-moundlike, anterior hamulus small-rodlike and directed posteroventrally, posterior hamulus curved-lanceolate and directed anteroventrally, apex pointed with small subapical spine, and anterior surface without denticles, penile segment one raised-triangular with narrow troughlike penile receiver, second penile segment ca 1.3 times as long as wide, penile spine absent, third penile segment without ventrobasal transverse indentation and ca 2 times as long as wide, prepuce moderately expanded and produced posteriorly, apex of penis with one or two short flagella, genital shelf absent.

EPIGOMPHINI

Type genus: *Epigomphus* Selys, 1854.

The Epigomphini include: *Epigomphus* and *Eugomphus* Kennedy, 1947.

Small to medium sized gomphines generally colored brown, yellow, and light green.

Head — Mouthparts slightly prognathous, middle tooth of posterior maxillary tooth row not fused to apical tooth, ca 0.5 length of proximal tooth, and separated from proximal tooth by U-shaped notch, anterosubapical mandibular tooth slightly retracted basally, posterosubapical mandibular tooth well developed and slightly displaced proximally, labrum ca 2.1 times as wide as long, ligula ca 1.1 times as wide as long, distance between antennal bases ca 2.1 times length of dorsal surface of antefrons, frontal carina vestigial, medial ocelli wider than lateral ocelli, occiput not ridged, head not tumid posterior to compound eyes.

Thorax — Distance between lateral ends of collar carina and antealar carina ca 2.4 times length of collar carina, lower portion of dorsomedian carina ca 1.1 length of 1/2 collar carina, lateral mesocoxal carina nearly straight, male foretibial lamina absent, hind femur long, female hind femur with slightly elongate spines, spines of male hind tibia enlarged basally, tarsal spines small and not subapical.

Wings — Basal subcostal crossveins often present, distal costal brace of hind wing located closer to proximal costal brace than to nodus, costa curved and widened along pterostigma, pterostigmal brace absent, fore wing arculus straight and aslant with lower portion not perpendicular to CuP, sectors of arculus contiguous subbasally, base of fore wing distal pleat at ca 0.48 distance between distal ends of triangle and subnodus, base of distal pleat strongly asymmetrical, apical planate extended to near halfway between pterostigma and nodus, apical planate divergent from RP_1, MA without posterior branch originating slightly distal to bridge crossvein, supratriangles without crossveins, hind wing with 3 or 4 postmedian crossveins, hind wing subtriangle without crossveins, anal vein slightly angulated at proximal angle of hind wing subtriangle, CuA brace ca 3/8 length of posterior side of fore wing subtriangle, triangles without crossveins, anterobasal angle of fore wing triangle acute, wings without trigonal planates, CuP and anal vein slightly divergent to hind wing margin, anal brace absent, anal triangle ca 0.7 times as long as wide, anal triangle not extended posteriorly to tornus, anal triangle 2 or 3-celled, cells of anal triangle variously arranged, membranule absent.

Abdomen — Male auricle not dorsoventrally compressed or strongly produced posteriorly, lower portion of auricular ridge well developed and nearly vertical, female auricle present, lateral margin of abdominal terga 7-9 not expanded, female sternum 9 membranous with two laterobasal sclerites, male sternum 9 membranous posterior to gonocoxae (lateral triangular-shaped sclerotized areas well developed), male gonocoxae rounded anteriorly, abdominal terga 7-10 without medial carina, male with posterolateral margin of segment 10 not notched, female segment 10 with lateral carina well developed, sternum 10 of male ca 2 times as wide as long, male cerci not bifurcate (slightly bifurcate apically in *Eugomphus*), male epiproct bifurcate with branches divaricate, male paraproct without lateral ridge extended dorsally to near base of cerci.

Genitalia — Anterior lamina low with inflated transverse ridge and U- or W-shaped posterior margin, anterior hamulus with fingerlike endhook and slight shoulder, posterior hamulus L-shaped, without endhook, and with denticles on anterior surface, penile segment one raised with hoodlike penile receiver, second penile segment 2.5-3.0 times as long as wide, penile spine absent, third penile segment without ventrobasal transverse indentation and 3.0-3.5 times as long as wide, prepuce moderately expanded and produced posteriorly, apex of penis with short flagellum, genital shelf absent.

LEPTOGOMPHINI

Type genus: *Leptogomphus* Selys, 1878.

The Leptogomphini include: *Leptogomphus* (incl. *Malayogomphus* Förster, 1914), *Africogomphus* Fraser, 1936 and *Heliogomphus* Laidlaw, 1922.

Small to medium sized gomphines generally colored black, yellow, and green.

Head — Mouthparts slightly prognathous, middle tooth of posterior maxillary tooth row not fused to apical tooth, ca 0.35 length of proximal tooth, and separated from proximal tooth by wide U-shaped notch, anterosubapical mandibular tooth moderately retracted basally, posterosubapical mandibular tooth vestigial and displaced proximally, labrum ca 2.1 times as wide as long, ligula ca as wide as long, distance between antennal bases 3.0-4.0 times length of dorsal surface of antefrons, frontal carina absent, medial ocelli wider than lateral ocelli, occiput not ridged, head not tumid posterior to compound eyes.

Thorax — Distance between lateral ends of collar carina and antealar carina 2.2-2.4 times length of collar carina, lower portion of dorsomedian carina 1.1-1.3 length of 1/2 collar carina, lateral mesocoxal carina nearly straight, male foretibial lamina present in *Leptogomphus* and absent in *Heliogomphus*, hind femur long, female hind femur with two rows of elongate spines, spines of male hind tibia strongly enlarged basally in *Leptogomphus* and slightly enlarged basally in *Heliogomphus*, tarsal spines small and not subapical.

Wings — Basal subcostal crossveins generally present in *Leptogomphus* and absent in *Heliogomphus*, distal costal brace of hind wing located closer to proximal costal brace than to nodus (often equidistant in *Leptogomphus elegans* and *L. yayeyamensis*), costa curved and widened along pterostigma, pterostigmal brace absent, fore wing arculus straight and aslant with lower portion not perpendicular to CuP, sectors of arculus approximate basally in *Leptogomphus* and nearly contiguous subbasally in *Heliogomphus*, base of fore wing distal pleat at ca 0.48 distance between distal ends of triangle and subnodus, base of distal pleat strongly asymmetrical, apical planate extended to near halfway between pterostigma and nodus, apical planate parallel to RP_1, MA without posterior branch originating slightly distal to bridge crossvein, supratriangles without crossveins, hind wing with 2-4 postmedian crossveins in *Leptogomphus* and 4 or 5 postmedian crossveins in *Heliogomphus*, hind wing subtriangle without crossveins, anal vein angulated at proximal angle of hind wing subtriangle, CuA brace ca 2/5 length of posterior side of fore wing subtriangle, triangles without crossveins (occasionally 2-celled), anterobasal angle of fore wing triangle acute, wings without trigonal planates, CuP and anal vein slightly divergent to hind wing margin, anal brace present but weakly developed, anal triangle 0.7-0.9 times as long as wide, anal triangle not extended posteriorly to tornus, anal triangle 2 or 3-celled, cells of anal triangle arranged to meet at point in *Leptogomphus* and serially in *Heliogomphus*, membranule absent.

Abdomen — Male auricle not dorsoventrally compressed or strongly produced posteriorly, lower portion of auricular ridge well developed and nearly vertical, female auricle present, lateral margin of abdominal terga 7-9 not expanded, female sternum 9 sclerotized with medial triangular membranous area in *Heliogomphus* and membranous with posterior trilobate sclerotized plate in

Leptogomphus, male sternum 9 membranous lateral and posterior to gonocoxae, male gonocoxae rounded anteriorly, abdominal terga 7-10 without medial carina, male with posterolateral margin of segment 10 not notched, female segment 10 with lateral carina weakly developed, sternum 10 of male 4-5 times as wide as long, male cerci with lateral subbasal spine (cerci lyrelike in *Heliogomphus*), male epiproct bifurcate with branches strongly divaricate in *Heliogomphus* and divaricate or parallel in *Leptogomphus,* male paraproct without lateral ridge extended dorsally to near base of cerci.

Genitalia — Anterior lamina bilobate in *Heliogomphus* and raised transverse-platelike in *Leptogomphus,* anterior hamulus robust cuplike (with fingerlike contiguous apices directed posteroventrally in *Leptogomphus* and with slight shoulder and elongate apical portions tapered to recurved endhook in *Heliogomphus*), posterior hamulus without denticles on anterior surface (robust with small endhook and membranous inner portion in *Leptogomphus,* and small and gently curved to acute apex in *Heliogomphus*), penile segment one low-inflated with cleftlike penile receiver, second penile segment 2.5-3.0 times as long as wide, penile spine absent, third penile segment without ventrobasal transverse indentation and 1.5-2.0 times as long as wide, prepuce inflated (without posterior projection in *Leptogomphus*), apex of penis expanded and generally with two flagella in *Leptogomphus,* and minute-spoutlike in *Heliogomphus,* genital shelf absent.

MACROGOMPHINI

Type genus: *Macrogomphus* Selys, 1857.

The Macrogomphini include: *Macrogomphus* (= "*Heterogomphus* group 1" of Selys, 1854).

Medium to large gomphines generally colored black and yellow.

Head — Mouthparts slightly prognathous, middle tooth of posterior maxillary tooth row not fused to apical tooth, ca 0.4 length of proximal tooth, and separated from proximal tooth by V-shaped notch, anterosubapical mandibular tooth slightly retracted basally, posterosubapical mandibular tooth well developed and slightly displaced proximally, labrum ca 2.1 times as wide as long, ligula ca 1.2 times as wide as long, distance between antennal bases 2.2-2.5 times length of dorsal surface of antefrons, frontal carina present, medial ocelli wider than lateral ocelli, occiput slightly or not ridged, head not tumid posterior to compound eyes.

Thorax — Distance between lateral ends of collar carina and antealar carina ca 1.8 times length of collar carina, lower portion of dorsomedian carina ca 0.6 length of 1/2 collar carina, lateral mesocoxal carina nearly straight, male foretibial lamina present, hind femur short, female hind femur without elongate spines, spines of male hind tibia slightly enlarged basally, tarsal spines small and not subapical.

Wings — Basal subcostal crossveins present, distal costal brace of hind wing located closer to proximal costal brace than to nodus, costa curved and widened along pterostigma, pterostigmal brace present or absent, fore wing arculus straight and aslant with lower portion not perpendicular to CuP, sectors of arculus approximate basally, base of fore wing distal pleat at ca 0.46 distance between distal ends of triangle and subnodus, base of distal pleat symmetrical (often asymmetrical in hind wing), apical planate extended to near halfway between pterostigma and nodus, apical planate divergent from RP_1, MA without posterior branch originating slightly distal to bridge crossvein, supratriangles without crossveins, hind wing with 3-5 postmedian crossveins, hind wing subtriangle without crossveins, anal vein angulated at proximal angle of hind wing subtriangle, CuA brace 2/5-1/2 length of posterior side of fore wing subtriangle, triangles without crossveins (occasionally 2-celled), anterobasal angle of fore wing triangle slightly acute, wings without trigonal planates, CuP and anal vein slightly divergent to hind wing margin, anal brace present, anal triangle 1.1-1.4 times as long as wide, anal triangle not extended posteriorly to tornus, anal triangle 3-celled, cells of anal triangle arranged as to meet at point, membranule present and extended narrowly to tornus.

Abdomen — Male auricle not dorsoventrally compressed or strongly produced posteriorly, lower portion of auricular ridge well developed and nearly vertical, female auricle present, lateral margin of abdominal terga 7-9 not expanded, female sternum 9 sclerotized, male sternum 9 sclerotized to beyond middle of segment and with medial membranous seam posterior to gonocoxae, male gonocoxae at anterior margin of sternum 9 and rounded anteriorly, abdominal terga 9 with medial carina, male with posterolateral margin of segment 10 notched, female segment 10 with lateral carina absent, sternum 10 of male 1.0-1.5 times as wide as long, male cerci bifurcate with inner branches directed posteriorly (several species with additional anteroventrally directed spine arising near base of inner spine), male epiproct bifurcate with branches divaricate, male paraproct without lateral ridge extended dorsally to near base of cerci.

Genitalia — Anterior lamina raised- hoodlike, anterior hamulus elongate and slightly sinuous with posteriorly directed apex, posterior hamulus robust L-shaped, anterior surface with or without denticles, and with endhook or lateral ridge, penile segment one low-inflated with cleftlike penile receiver, second penile segment 1.5-2.0 times as long as wide, penile spine absent, third penile segment without ventrobasal transverse indentation and 2.0-2.5 times as long as wide, prepuce moderately expanded and produced posteriorly with apex ventrally curved and sclerotized, apex of penis minute with flared tubelike apex (often with short flagella), genital shelf absent.

KEY TO THE SUBGENERA OF *MACROGOMPHUS*

1 Mesanepisterna black with lower half yellow, CuA meeting wing margin at right angle, 2 cells bordering distal side of hind wing triangle ..... ***Eumacrogomphus*** subgen. n.
Type species: *Macrogomphus quadratus* Selys.
Mesanepisterna black with full length yellow stripes, CuA meeting wing margin at acute angle, 3 cells bordering distal side of hind wing triangle ..... ***Macrogomphus***

MICROGOMPHINI

Type genus: *Microgomphus* Selys, 1857.
The Microgomphini include: *Microgomphus*.

Small gomphines generally colored black and greenish yellow.

Head — Mouthparts slightly prognathous, middle tooth of posterior maxillary tooth row not fused to apical tooth, ca 0.4 length of proximal tooth, and separated from proximal tooth by wide U-shaped notch, anterosubapical mandibular tooth moderately retracted basally, posterosubapical mandibular tooth absent, labrum ca 2.2 times as wide as long, ligula ca as wide as long, distance between antennal bases ca 3.0 times length of dorsal surface of antefrons, frontal carina present, medial ocelli not wider than lateral ocelli, occiput weakly ridged, head not tumid posterior to compound eyes.

Thorax — Distance between lateral ends of collar carina and antealar carina ca 2.2 times length of collar carina, lower portion of dorsomedian carina ca equal to length of 1/2 collar carina, lateral mesocoxal carina nearly straight, male foretibial lamina absent, hind femur long, female hind femur with two rows of elongate spines, spines of male hind tibia slightly enlarged basally, tarsal spines large and subapical.

Wings — Basal subcostal crossveins absent, distal costal brace of hind wing located closer to proximal costal brace than to nodus, costa curved and widened along pterostigma, pterostigmal brace present, fore wing arculus straight and aslant with lower portion not perpendicular to CuP, sectors of arculus nearly contiguous basally, base of fore wing distal pleat at ca 0.46 distance between distal ends of triangle and subnodus, base of distal pleat strongly asymmetrical, apical planate extended to near middle of pterostigma, apical planate nearly parallel to RP_1, MA without posterior branch originating slightly distal to bridge crossvein, supratriangles without crossveins, hind wing with 3-4 postmedian crossveins, hind wing subtriangle without crossveins, anal vein angulated at proximal angle of hind wing subtriangle, CuA brace ca 1/3 length of posterior side of fore wing subtriangle, triangles without crossveins, anterobasal angle of fore wing triangle acute, wings without trigonal planates, CuP and anal vein slightly divergent to hind wing margin, anal brace vestigial, anal triangle ca 0.8 times as long as wide, anal triangle not extended posteriorly to tornus, anal triangle 2 or 3-celled, cells of anal triangle arranged serially, membranule ab-

sent.

Abdomen — Male auricle not dorsoventrally compressed or strongly produced posteriorly, lower portion of auricular ridge well developed and nearly vertical, female auricle present, lateral margin of abdominal terga 7-9 not expanded, female sternum 9 sclerotized with V-shaped membranous area, male sternum 9 membranous posterior to gonocoxae, male gonocoxae rounded anteriorly, abdominal terga 7-10 without medial carina, male with posterolateral margin of segment 10 not notched, female segment 10 with lateral carina weakly developed, sternum 10 of male 5-6 times as wide as long, male cerci bifurcate with inner branches directed posteromedially, male epiproct triangular with bifurcate apex, male paraproct without lateral ridge extended dorsally to near base of cerci.

Genitalia — Anterior lamina low with U-shaped posterior margin, anterior hamulus elongate with shoulder and posteriorly directed endhook, posterior hamulus slightly curved and tapered to apex, and without denticles on anterior surface, penile segment one low-inflated with cleftlike penile receiver, second penile segment ca 3.0 times as long as wide, penile spine absent, third penile segment without ventrobasal transverse indentation and ca 1.5 times as long as wide, prepuce moderately expanded and produced posteriorly, apex of penis with two small flagella, genital shelf absent.

ARCHAEOGOMPHINI

Type genus: *Archaeogomphus* Williamson, 1919.

The Archaeogomphini include: *Archaeogomphus*.

Small gomphines generally colored pale green and brown.

Head — Mouthparts prognathous, middle tooth of posterior maxillary tooth row absent, anterosubapical mandibular tooth strongly retracted basally, posterosubapical mandibular tooth absent, labrum 1.8-1.9 times as wide as long with distal margin level, ligula ca as wide as long, distance between antennal bases 2.0-2.4 times length of dorsal surface of antefrons, frontal carina vestigial, medial ocelli wider than lateral ocelli, occiput not ridged (in female with two large posteriorly directed processes), head tumid posterior to compound eyes.

Thorax — Distance between lateral ends of collar carina and antealar carina ca 2.4 times length of collar carina, lower portion of dorsomedian carina ca equal to length of 1/2 collar carina, lateral mesocoxal carina nearly straight, male foretibial lamina absent, hind femur long, female hind femur without elongate spines, spines of male hind tibia not enlarged basally, tarsal spines small and not subapical.

Wings — Basal subcostal crossveins absent, distal costal brace of hind wing located closer to proximal costal brace than to nodus, costa curved and widened

along pterostigma, pterostigmal brace weakly developed, fore wing arculus straight and aslant with lower portion not perpendicular to CuP, sectors of arculus nearly contiguous subbasally, base of fore wing distal pleat at ca 0.44 distance between distal ends of triangle and subnodus, base of distal pleat strongly asymmetrical, apical planate vestigial, MA without posterior branch originating slightly distal to bridge crossvein, supratriangles without crossveins, hind wing with 2 postmedian crossveins, hind wing subtriangle without crossveins, anal vein strongly angulated at proximal angle of hind wing subtriangle, CuA brace ca 1/4 length of posterior side of fore wing subtriangle, triangles without crossveins (triangles 4-sided), anterobasal angle of fore wing triangle acute, wings without trigonal planates, CuP and anal vein slightly divergent to hind wing margin, anal brace absent, anal triangle ca 0.7 times as long as wide, anal triangle not extended posteriorly to tornus, anal triangle 2-celled, cells of anal triangle arranged serially, membranule absent.

Abdomen — Male auricle not dorsoventrally compressed or strongly produced posteriorly, lower portion of auricular ridge well developed and nearly vertical, female auricle present (minute), lateral margin of abdominal terga 7-9 slightly expanded in male, female sternum 9 largely membranous, male sternum 9 membranous posterolaterally and posterior to gonocoxae, male gonocoxae rounded anteriorly, abdominal terga 7-10 without medial carina, male segment 10 with posterolateral margin notched and with two dorsal processes near base, female segment 10 with lateral carina well developed, sternum 10 of male ca 6 times as wide as long, male cerci vestigial, male epiproct vestigial, male paraproct without lateral ridge extended dorsally to near base of cerci.

Genitalia — Anterior lamina low with medial V-shaped groove, anterior hamulus short-quadrate, posterior hamulus short, with moderate shoulder, with endhook, and anterior surface without denticles, penile segment one raised into two robust divaricate posteroventrally directed lobes separated by U- or V-shaped notch, penile receiver flat, second penile segment ca 2.5 times as long as wide, penile sheath without anteromedial ridge, penile spine absent, third penile segment without ventrobasal transverse indentation and ca as long as wide, prepuce wide, flattened-transverse, and produced posteriorly, apex of penis with two long spiraled flagella, genital shelf present and anterolateral corner of tergum 1 produced medially.

KEY TO THE SUBGENERA OF *ARCHAEOGOMPHUS*

1 Hind wings with CuP and A contiguous at posterior angle of triangle, male with lateral margin of abdominal segment 8 expanded and produced posteriorly, female with submedial spines on dorsal edge of occipital foramen ..... ***Austroarchaeogomphus*** subgen. n. Type species: *Agriogomphus infans* Ris

Hind wings with CuP and A typically not contiguous at posterior angle of triangle, male with lateral margin of abdominal segment 8 not expanded and produced posteriorly, female without submedial spines on dorsal edge of occipital foramen ..... ***Archaeogomphus***

AUSTROGOMPHINI

Type genus: *Austrogomphus* Selys, 1854.

The Austrogomphini include: *Austrogomphus, Antipodogomphus* Fraser, 1951 and *Austroepigomphus* Fraser, 1957.

Small to medium sized gomphines generally colored brown or black, and yellow.

Head — Mouthparts hypognathous, middle tooth of posterior maxillary tooth row not fused to apical tooth, ca 0.4 length of proximal tooth, and separated from proximal tooth by wide U-shaped notch, anterosubapical mandibular tooth slightly retracted basally, posterosubapical mandibular tooth slightly reduced and slightly displaced proximally, labrum 2.2-2.3 times as wide as long, ligula 1.2-1.3 times as wide as long, distance between antennal bases 1.8-2.2 times length of dorsal surface of antefrons, frontal carina present, medial ocelli wider than lateral ocelli, occiput not ridged, head not tumid posterior to compound eyes.

Thorax — Distance between lateral ends of collar carina and antealar carina ca 2.1 times length of collar carina, lower portion of dorsomedian carina ca 0.8 length of 1/2 collar carina, lateral mesocoxal carina nearly straight, male foretibial lamina present, hind femur long, female hind femur without elongate spines, spines of male hind tibia not enlarged basally, tarsal spines small and not subapical.

Wings — Basal subcostal crossveins absent in *Austrogomphus*, occasionally present in *Austroepigomphus*, distal costal brace of hind wing located closer to proximal costal brace than to nodus, costa curved and widened along pterostigma, pterostigmal brace present, fore wing arculus straight and aslant with lower portion not perpendicular to CuP (slightly angulate and nearly perpendicular in *Austroepigomphus*), sectors of arculus approximate basally (separated basally by 1/8-1/6 length of arculus in hind wings), base of fore wing distal pleat at ca 0.41 distance between distal ends of triangle and subnodus, base of distal pleat symmetrical, apical planate extended to near middle of pterostigma, apical planate divergent from RP_1 (divergence slight in *Austroepigomphus*), MA without posterior branch originating slightly distal to bridge crossvein, supratriangles without crossveins, hind wing with 1 or 2 postmedian crossveins, hind wing subtriangle without crossveins, anal vein angulated at proximal angle of hind wing subtriangle, CuA brace ca 1/3 length of posterior side of fore wing subtriangle, triangles without crossveins, anterobasal angle of fore wing triangle acute, wings without trigonal planates, CuP and anal vein slightly divergent to hind wing margin, anal brace present, anal triangle ca 1.2 times as long as wide, anal triangle not extended posteriorly to tornus, anal triangle 3-celled (4 or 5-celled in *Austroepigomphus*), cells of anal triangle arranged serially in *Austrogomphus*, to meet at point in *Antipodogomphus*, and with rectangular cell

along proximal margin in *Austroepigomphus*, membranule present and extended narrowly to tornus.

Abdomen — Male auricle not dorsoventrally compressed or strongly produced posteriorly, lower portion of auricular ridge well developed and nearly vertical, female auricle present, lateral margin of abdominal terga 7-9 not expanded, female sternum 9 sclerotized, male sternum 9 membranous lateral and posterior to gonocoxae, male gonocoxae rounded anteriorly, abdominal terga 7-10 without medial carina, male with posterolateral margin of segment 10 notched, female segment 10 with lateral carina well developed (absent in *Austrogomphus*), sternum 10 of male 2-3 times as wide as long, male cerci bifurcate with inner branches directed ventromedially, male epiproct bifurcate with branches parallel, male paraproct without lateral ridge extended dorsally to near base of cerci.

Genitalia — Anterior lamina low with V-shaped posterior margin, anterior hamulus robust with anterior trough, posterior hamulus flattened S-shaped, with well developed shoulder, and anterior surface without denticles (posterior margin flanged in *Austrogomphus*), penile segment one raised with lateral ventrally directed flanges (flanges directed laterally in *Austrogomphus*), penile receiver dishlike, second penile segment 3.0-4.0 times as long as wide, penile spine absent, third penile segment without ventrobasal transverse indentation and 1.5-2.0 times as long as wide (with indentation in *Austroepigomphus*), prepuce present (low-inflated in *Austroepigomphus*, slightly produced posteriorly in *Antipodogomphus*, and straplike in *Austrogomphus*), apex of penis typically without flagella (with two flagella in *Austrogomphus*), genital shelf absent.

CYANOGOMPHINI

Type genus: *Cyanogomphus* Selys, 1873.

The Cyanogomphini include: *Cyanogomphus* (incl. *Ebegomphus* Needham, 1944 (= *Strumagomphus* Needham, 1944) and *Agriogomphus* Selys, 1869 (= *Ischnogomphus* Williamson, 1918).

Small gomphines generally colored pale green and brown.

Head — Mouthparts prognathous, middle tooth of posterior maxillary tooth row absent, anterosubapical mandibular tooth strongly retracted basally, posterosubapical mandibular tooth absent, labrum ca 1.8 times as wide as long with distal margin notched, ligula 1.1-1.3 times as wide as long, distance between antennal bases ca 2.2 times length of dorsal surface of antefrons, frontal carina present, medial ocelli wider than lateral ocelli, occiput not ridged (ridged in *Cyanogomphus uncatus* Fraser and *C. waltheri* Selys), head tumid posterior to compound eyes.

Thorax — Distance between lateral ends of collar carina and antealar carina ca 2.4 times length of collar carina, lower portion of dorsomedian carina ca equal to length of 1/2 collar carina, lateral mesocoxal carina nearly straight,

male foretibial lamina absent, hind femur long, female hind femur without elongate spines, spines of male hind tibia not enlarged basally (except in *Cyanogomphus uncatus*), tarsal spines small and not subapical.

Wings — Basal subcostal crossveins present or absent, distal costal brace of hind wing located closer to proximal costal brace than to nodus, costa curved and widened along pterostigma, pterostigmal brace present, fore wing arculus straight and aslant with lower portion not perpendicular to CuP, sectors of arculus nearly contiguous subbasally in *Agriogomphus* and separated basally by 1/6-1/5 length of arculus in *Cyanogomphus*, base of fore wing distal pleat at ca 0.44 distance between distal ends of triangle and subnodus, base of distal pleat asymmetrical (slightly asymmetrical in *Cyanogomphus*), apical planate extended to near middle of pterostigma, apical planate slightly divergent from RP_1, MA without posterior branch originating slightly distal to bridge crossvein, supratriangles without crossveins, hind wing with 2 or 3 postmedian crossveins, hind wing subtriangle without crossveins, anal vein strongly angulated at proximal angle of hind wing subtriangle, CuA brace 1/4-1/3 length of posterior side of fore wing subtriangle, triangles without crossveins, anterobasal angle of fore wing triangle acute, wings without trigonal planates, CuP and anal vein slightly divergent to hind wing margin, anal brace vestigial in *Agriogomphus* and well developed in *Cyanogomphus*, anal triangle 0.6-0.8 times as long as wide, anal triangle not extended posteriorly to tornus, anal triangle 2 or 3-celled, cells of anal triangle arranged serially in *Agriogomphus* and to meet at point in *Cyanogomphus*, membranule absent.

Abdomen — Male auricle not dorsoventrally compressed or strongly produced posteriorly, lower portion of auricular ridge well developed and nearly vertical, female auricle absent, lateral margin of abdominal terga 7-9 not expanded, female sternum 9 sclerotized, male sternum 9 membranous lateral and posterior to gonocoxae, male gonocoxae rounded anteriorly, abdominal terga 7-10 without medial carina (posterodorsal margin of tergum 9 often produced posteriorly with apical notch), male with posterolateral margin of segment 10 notched, female segment 10 with lateral carina well developed, sternum 10 of male ca 3.0 times as wide as long, male cerci bifurcate with inner branches directed ventromedially, male epiproct bifurcate with branches parallel, male paraproct without lateral ridge extended dorsally to near base of cerci.

Genitalia — Anterior lamina low with transverse ridge and V- or U-shaped posterior margin, anterior hamulus robust and cupped, posterior hamulus long and slender-goosenecklike, without well developed shoulder, with endhook, and anterior surface without denticles (occasionally with denticles), penile segment one raised with lateral ventrally directed flanges which are contiguous posteriorly to form small round posterior opening, penile receiver wide-troughlike, second penile segment 2.5-3.0 times as long as wide, penile sheath with anteromedial ridge, penile spine absent, third penile segment without ventrobasal trans-

verse indentation and 1.5-2.0 times as long as wide, prepuce small, produced posteriorly, and transverse, apex of penis with two flagella, genital shelf present in *Cyanogomphus* and absent in *Agriogomphus*, anterolateral corner of tergum 1 produced medially.

LESTINOGOMPHINI

Type genus: *Lestinogomphus* Martin, 1914.

The Lestinogomphini include: *Lestinogomphus* (incl. *Echinopterogomphus* Fraser, 1926).

Small gomphines generally colored brown and yellowish green.

Head — Mouthparts slightly prognathous, middle tooth of posterior maxillary tooth row absent, anterosubapical mandibular tooth strongly retracted basally, posterosubapical mandibular tooth absent, labrum ca 2.1 times as wide as long, ligula ca 1.2 times as wide as long, distance between antennal bases ca 2.6 times length of dorsal surface of antefrons, frontal carina present, medial ocelli wider than lateral ocelli, occiput ridged, head not tumid posterior to compound eyes.

Thorax — Distance between lateral ends of collar carina and antealar carina ca 2.2 times length of collar carina, lower portion of dorsomedian carina ca equal to length of 1/2 collar carina, lateral mesocoxal carina nearly straight, male foretibial lamina absent, hind femur long, female hind femur without elongate spines, spines of male hind tibia not enlarged basally, tarsal spines small and not subapical.

Wings — Basal subcostal crossveins absent, distal costal brace of hind wing located closer to proximal costal brace than to nodus, costa curved and widened along pterostigma, pterostigmal brace present, fore wing arculus straight and aslant with lower portion not perpendicular to CuP, sectors of arculus contiguous subbasally, base of fore wing distal pleat at ca 0.41 distance between distal ends of triangle and subnodus, base of distal pleat symmetrical, apical planate extended to near middle of pterostigma, apical planate nearly parallel to RP_1, MA without posterior branch originating slightly distal to bridge crossvein, supratriangles without crossveins, hind wing with 2 postmedian crossveins, hind wing subtriangle without crossveins, anal vein strongly angulated at proximal angle of hind wing subtriangle, CuA brace ca 1/3 length of posterior side of fore wing subtriangle, triangles without crossveins, anterobasal angle of fore wing triangle acute, wings without trigonal planates, CuP and anal vein slightly divergent to hind wing margin, anal brace absent, anal triangle ca 1.5 times as long as wide, anal triangle not extended posteriorly to tornus, anal triangle 2-celled, cells of anal triangle arranged serially, membranule absent.

Abdomen — Male auricle not dorsoventrally compressed or strongly produced posteriorly, lower portion of auricular ridge well developed and nearly vertical, female auricle absent, lateral margin of abdominal terga 7-9 not ex-

panded, female sternum 9 sclerotized, male sternum 9 membranous lateral and posterior to gonocoxae, male gonocoxae rounded anteriorly, abdominal terga 7-10 without medial carina, male with posterolateral margin of segment 10 notched, female segment 10 with lateral carina well developed, sternum 10 of male ca 0.5 times as wide as long, male cerci bifurcate with inner branches directed ventromedially, male epiproct quadrate with apex triangular, male paraproct without lateral ridge extended dorsally to near base of cerci.

Genitalia — Anterior lamina low with U-shaped anterior ridge, anterior hamulus laminate with apical hair pencil, posterior hamulus without endhook, with prominent shoulder, and with transverse line of denticles on anterior surface, penile segment one raised with hoodlike penile receiver, second penile segment ca 2.5 times as long as wide, penile spine absent, third penile segment without ventrobasal transverse indentation and ca 1.5 times as long as wide, prepuce cupped, apex of penis with two flagella, genital shelf absent.

PHYLLOGOMPHINI

Type genus: *Phyllogomphus* Selys, 1854.

The Phyllogomphini include: *Phyllogomphus* (incl. *Guineagomphus* Compte Sart, 1963), *Ceratogomphus* Selys, 1854 and *Isomma* Selys, 1892.

Medium to large gomphines generally colored black or brown, yellow, and pale green.

Head — Mouthparts hypognathous, middle tooth of posterior maxillary tooth row not fused to apical tooth, 0.0-0.3 length of proximal tooth, and separated from proximal tooth by V-shaped notch, anterosubapical mandibular tooth slightly retracted basally, posterosubapical mandibular tooth vestigial and slightly displaced proximally, labrum 1.7-2.1 times as wide as long, ligula 1.1-1.2 times as wide as long, distance between antennal bases 1.6-2.2 times length of dorsal surface of antefrons, frontal carina present and dorsal surface of antefrons with denticles, medial ocelli wider than lateral ocelli, occiput ridged, head tumid posterior to compound eyes.

Thorax — Distance between lateral ends of collar carina and antealar carina 1.7-2.0 times length of collar carina, lower portion of dorsomedian carina 0.5-0.6 length of 1/2 collar carina (ca 0.8 in *Isomma*), lateral mesocoxal carina nearly straight, male foretibial lamina present, hind femur short, female hind femur without elongate spines, spines of male hind tibia not enlarged basally, tarsal spines small and not subapical.

Wings — Basal subcostal crossveins absent in *Phyllogomphus* and *Isomma*, and present in *Ceratogomphus*, distal costal brace of hind wing located closer to proximal costal brace than to nodus, costa curved and widened along pterostigma, pterostigmal brace present, fore wing arculus straight or slightly

angulate and aslant with lower portion not perpendicular to CuP, sectors of arculus separated basally (by 1/5-1/4 length of arculus in hind wings), base of fore wing distal pleat at 0.38-0.43 distance between distal ends of triangle and subnodus, base of distal pleat symmetrical, apical planate extended to near middle of pterostigma (two cell rows between RP_1 and RP_2 for ca 1/3 distance between pterostigma and nodus), apical planate divergent from RP_1, MA without posterior branch originating slightly distal to bridge crossvein, supratriangles without crossveins, hind wing with 1 or 2 postmedian crossveins, hind wing subtriangle without crossveins, anal vein slightly angulated at proximal angle of hind wing subtriangle, CuA brace 1/3-3/8 length of posterior side of fore wing subtriangle, triangles without crossveins (often 2-celled in *Isomma*), anterobasal angle of fore wing triangle acute, wings without trigonal planates, CuP and anal vein slightly divergent to hind wing margin, anal brace present, anal triangle 1.4-2.0 times as long as wide, anal triangle not extended posteriorly to tornus, anal triangle 3-5 celled, cells of anal triangle arranged as to meet at point or with rectangular cell along proximal margin, membranule present and narrowly extended to tornus (vestigial in *Isomma*).

Abdomen — Male auricle not dorsoventrally compressed or strongly produced posteriorly, lower portion of auricular ridge well developed and nearly vertical, female auricle vestigial, lateral margin of abdominal tergum 8 greatly expanded, female sternum 9 membranous, male sternum 9 membranous posterolaterally and posterior to gonocoxae, male gonocoxae with anterolaterally directed points, abdominal terga 9 and 10 with medial carina (male *Ceratogomphus* with carina of tergum 10 produced anteriorly to fit into notch at posterior margin of segment 9), male with posterolateral margin of segment 10 not notched, female segment 10 elongate with lateral carina vestigial in *Ceratogomphus* and *Isomma*, and well developed in *Phyllogomphus*, sternum 10 of male 0.5-2.0 times as wide as long, male cerci bifurcate with inner spine directed anteroventrally in *Phyllogomphus*, ventrally in *Ceratogomphus*, and posteriorly in *Isomma* (outer branch vestigial and directed ventrally beyond base in *Ceratogomphus*), male epiproct bifurcate with branches divaricate (parallel in *Ceratogomphus*), male paraproct without lateral ridge extended dorsally to near base of cerci.

Genitalia — Anterior lamina raised and moundlike in *Ceratogomphus* and *Isomma*, and transverse ridgelike in *Phyllogomphus*, anterior hamulus robust and cuplike anteriorly with apical transverse ridges contiguous medially, posterior hamulus short and robust (elongate in *Phyllogomphus*), with anteroventrally directed endhook, and anterior surface without denticles, penile segment one raised with lateral ventrally directed flanges which form troughlike penile receiver with open apex, second penile segment 4.0-4.5 times as long as wide, penile spine vestigial, third penile segment without ventrobasal transverse indentation and 2.0-8.0 times as long as wide, prepuce located distally on segment 3

(without apical projection in *Ceratogomphus*), apex of penis with two parallel ventrally spiraled flagella, genital shelf absent.

CRENIGOMPHINI

Type genus: *Crenigomphus* Selys, 1892.

The Crenigomphini include: *Crenigomphus* (incl. *Dentigomphus* Martin, 1912 and *Bursigomphus* Martin, 1912) and *Paragomphus* Cowley, 1934 (= *Mesogomphus* Förster, 1906).

Small to medium sized gomphines generally colored brown or black, yellow, and light green.

Head — Mouthparts hypognathous, middle tooth of posterior maxillary tooth row fused to apical tooth, ca 0.15 length of proximal tooth, and separated from proximal tooth by U-shaped notch, anterosubapical mandibular tooth moderately retracted basally, posterosubapical mandibular tooth vestigial and displaced proximally, labrum 2.1-2.2 times as wide as long, ligula 1.2-1.5 times as wide as long, distance between antennal bases 1.6-2.0 times length of dorsal surface of antefrons, frontal carina present, medial ocelli wider than lateral ocelli, occiput ridged, head slightly tumid posterior to compound eyes.

Thorax — Distance between lateral ends of collar carina and antealar carina 1.8-2.0 times length of collar carina, lower portion of dorsomedian carina 0.6-0.7 length of 1/2 collar carina, lateral mesocoxal carina nearly straight, male foretibial lamina absent, hind femur short, female hind femur without elongate spines, spines of male hind tibia not enlarged basally, tarsal spines small and not subapical.

Wings — Basal subcostal crossvein absent (occasionally present), distal costal brace of hind wing located closer to proximal costal brace than to nodus, costa curved and widened along pterostigma, pterostigmal brace present, fore wing arculus straight or angulate with lower portion perpendicular or not perpendicular to CuP, sectors of arculus separated basally (by 1/6-1/5 length of arculus in hind wing), base of fore wing distal pleat at 0.35-0.41 distance between distal ends of triangle and subnodus, base of distal pleat symmetrical, apical planate extended to near middle of pterostigma, apical planate divergent from RP_1, MA without posterior branch originating slightly distal to bridge crossvein, supratriangles without crossveins, hind wing with 1 postmedian crossvein, hind wing subtriangle without crossveins, anal vein angulated at proximal angle of hind wing subtriangle, CuA brace ca 1/3-3/8 length of posterior side of fore wing subtriangle, triangles without crossveins (occasionally 2-celled), anterobasal angle of fore wing triangle acute in *Paragomphus* and slightly acute in *Crenigomphus*, wings without trigonal planates, CuP and anal vein slightly divergent to hind wing margin, anal brace present, anal triangle 1.6-2.1 times as long as wide, anal triangle not extended posteriorly to tornus, anal triangle 4-celled (occasionally 5 or 6-celled), cells of anal triangle arranged to border

rectangular cell along proximal margin, membranule present and extended to tornus.

Abdomen — Male auricle not dorsoventrally compressed or strongly produced posteriorly, lower portion of auricular ridge well developed and nearly vertical, female auricle present, lateral margin of abdominal terga 8 and 9 expanded in male *Paragomphus* and some female *Crenigomphus,* female sternum 9 sclerotized apically to surround large dome-shaped membranous area, male sternum 9 membranous posterior to gonocoxae (lateral triangular--shaped sclerotized areas well developed), male gonocoxae rounded anteriorly, abdominal terga 7-10 without medial carina, male with posterolateral margin of segment 10 not notched, female segment 10 with lateral carina well developed, sternum 10 of male 1-3 times as wide as long, male cerci elongate with ventral ridge and ventrally directed apex, male epiproct bifurcate with branches contiguous and directed posterodorsally (base of epiproct directed ventrally), male paraproct with lateral ridge extended dorsally to near base of cerci.

Genitalia — Anterior lamina slightly raised and bilobate with posterior margin wide U-shaped, anterior hamulus hooklike with well developed shoulder, posterior hamulus L-shaped with distal exposed portions short, with small endhook, and anterior surface without denticles, penile segment one raised into bilobate thin-walled hood with posterior margin indented, penile receiver bilobed and bowllike, second penile segment ca 2.5 times as long as wide, penile spine absent, third penile segment with ventrobasal transverse indentation and ca 1.0 times as long as wide, prepuce slightly to moderately inflated without posteriorly directed process, apex of penis with two ventrally curved flagella and ventral transverse hyaline frill, genital shelf absent.

ONYCHOGOMPHINI

Type genus: *Onychogomphus* Selys, 1854.

The Onychogomphini include: *Onychogomphus* (= *Paradigma* Buchecker, 1876), *Acrogomphus* Laidlaw, 1925, *Amphigomphus* Chao, 1954, *Cornigomphus* Martin, 1907, *Davidioides* Fraser, 1924, *Erpetogomphus* Selys, 1857, *Lamelligomphus* Fraser, 1922 (= *Lamellogomphus* Fraser, 1924), *Megalogomphus* Campion, 1903 (= *Heterogomphus* Selys, 1854 and incl. *Allogomphus* Needham, 1930), *Nepogomphoides* Fraser, 1952, *Nepogomphus* Fraser, 1934, *Nihonogomphus* Oguma, 1926 (incl. *Altaigomphus* Bartenef, 1930), *Ophiogomphus* Selys, 1854, *Perissogomphus* Laidlaw, 1922, *Phaenandrogomphus* Lieftinck, 1964 and *Tragogomphus* Sjöstedt, 1899 (incl. *Libyogomphus* Fraser, 1926).

Small to large gomphines generally colored brown or black, green, and yellow.

Head — Mouthparts hypognathous (slightly prognathous in *Phaenandrogomphus*), middle tooth of posterior maxillary tooth row fused to apical tooth, ca 0.15 length of proximal tooth, and separated from proximal tooth by U--shaped notch, anterosubapical mandibular tooth moderately retracted basally,

posterosubapical mandibular tooth reduced and slightly displaced proximally (tooth well developed in *Ophiogomphus*, and vestigial in *Megalogomphus* and *Erpetogomphus*), labrum 2.1-2.3 times as wide as long (ca 1.6 in *Megalogomphus*), ligula 1.0-1.5 times as wide as long, distance between antennal bases 1.3-2.5 times length of dorsal surface of antefrons (ca 4.0 in *Phaenandrogomphus*), frontal carina present or absent, medial ocelli wider than lateral ocelli, occiput ridged (occiput inflated and crest rounded in *Nihonogomphus*, *Ophiogomphus*, and *Megalogomphus*), head not tumid posterior to compound eyes.

Thorax — Distance between lateral ends of collar carina and antealar carina 1.9-2.0 times length of collar carina (ca 1.7 in *Megalogomphus*, 2.1 in *Nepogomphus*, and 2.2 in *Phaenandrogomphus*), lower portion of dorsomedian carina 0.7-0.9 length of 1/2 collar carina (0.5-0.6 in *Megalogomphus*), lateral mesocoxal carina nearly straight or curved, male foretibial lamina present, hind femur short, female hind femur without elongate spines, spines of male hind tibia not enlarged basally, tarsal spines small and not subapical.

Wings — Basal subcostal crossveins absent (occasionally present in *Megalogomphus* and *Ophiogomphus*), distal costal brace of hind wing located closer to proximal costal brace than to nodus, costa curved and widened along pterostigma, pterostigmal brace present, fore wing arculus straight or slightly angulate with lower portion not perpendicular to CuP (strongly angulate and perpendicular in *Ophiogomphus*), sectors of arculus separated basally by 1/5-1/4 length of arculus in hind wing (by ca 1/6 in *Nepogomphus*, *Nepogomphoides*, *Phaenandrogomphus*, *Perissogomphus*, and many *Onychogomphus*), base of fore wing distal pleat at 0.36-0.44 distance between distal ends of triangle and subnodus, base of distal pleat symmetrical (asymmetrical in hind wings of *Phaenandrogomphus*, *Acrogomphus*, and *Perissogomphus*), apical planate extended to near middle of pterostigma, apical planate divergent from RP_1, MA without posterior branch originating slightly distal to bridge crossvein, supratriangles without crossveins (occasionally 2-celled), hind wing with 1 or 2 postmedian crossveins (2 or 3 in *Perissogomphus* and *Phaenandrogomphus*), hind wing subtriangle without crossveins, anal vein slightly or strongly angulated at proximal angle of hind wing subtriangle, CuA brace 1/3-2/5 length of posterior side of fore wing subtriangle (ca 1/4 in *Nepogomphus* and *Phaenandrogomphus*), triangles without crossveins (2-celled in *Perissogomphus*, and occasionally in *Onychogomphus* and *Ophiogomphus*), anterobasal angle of fore wing triangle acute (nearly 90° in *Ophiogomphus*, *Megalogomphus*, and *Nihonogomphus*), wings without trigonal planates, CuP and anal vein slightly divergent to hind wing margin, anal brace present, anal triangle 1.3-2.0 times as long as wide (shortest in *Nepogomphus*, *Phaenandrogomphus*, and *Nepogomphoides*; and longest in *Ophiogomphus*), anal triangle not extended posteriorly to tornus, anal triangle generally 4-celled (3-celled in *Nepogomphus* and many *Erpetogomphus* and some *Onychogomphus*, 4-7-celled in *Ophiogomphus*), cells

of anal triangle arranged to meet at point when 3-celled, with rectangular cell along proximal margin when 4-celled, and in two rows when 5-7-celled, membranule present and extended to tornus.

Abdomen — Male auricle not dorsoventrally compressed or strongly produced posteriorly, lower portion of auricular ridge well developed and nearly vertical, female auricle present, lateral margin of abdominal terga 7-9 not expanded (8 and 9 expanded in male *Cornigomphus*, female sternum 9 sclerotized with basal oval or subtriangular membranous area, sclerotized portion with raised medial area and lateral ridges posterior to membranous portion (raised medial area and lateral ridges absent in *Ophiogomphus*), male sternum 9 membranous posterior to gonocoxae (lateral triangular-shaped sclerotized areas well developed), male gonocoxae rounded anteriorly, abdominal terga 7-10 without medial carina, male with posterolateral margin of segment 10 not notched, female segment 10 with lateral carina well developed, sternum 10 of male 2-5 times as wide as long, male cerci elongate with apex directed medially or ventrally (short and directed posteriorly in *Perissogomphus* and in many *Ophiogomphus*), male epiproct bifurcate with branches elongate and contiguous (branches divaricate in *Acrogomphus, Amphigomphus, Perissogomphus, Megalogomphus, Nihonogomphus, and some Ophiogomphus*), male paraproct with lateral ridge extended dorsally to near base of cerci.

Genitalia — Anterior lamina raised and inflated with U- or shallow V-shaped posterior margin, anterior hamulus bifurcate with apical branch hooklike and directed posteriorly (subbasal branch shoulderlike in *Nepogomphus, Nepogomphoides, Nihonogomphus,* and many *Onychogomphus*), posterior hamulus elongate-conical, with small medially or anteriorly directed endhook and small shoulder, and anterior surface without denticles (endhook and shoulder often well developed in *Ophiogomphus* and often absent in *Erpetogomphus*), penile segment one raised with thin lateral anteroventrally directed flanges (flanges reduced in *Lamelligomphus* and *Onychogomphus,* and absent in *Nepogomphus*), penile receiver dishlike (with medial cleft in *Nepogomphus, Lamelligomphus,* and many *Onychogomphus*), second segment 3.0-5.0 times as long as wide, penile spine generally absent (present in *Ophiogomphus, Megalogomphus, Nepogomphoides, Nihonogomphus,* and *Acrogomphus*), third penile segment with ventrobasal transverse indentation and 1.0-3.0 times as long as wide, prepuce generally present and elongate (absent in *Perissogomphus, Tragogomphus, Amphigomphus, Cornigomphus,* in most *Onychogomphus* and *Nihonogomphus,* and in some *Erpetogomphus*), third penile segment short with ventral transverse indentation (indentation absent in *Onychogomphus* and *Lamelligomphus*), apex of penis with two ventrally curved flagella and ventromedian process (flagella curved dorsally and median process absent in *Nepogomphus, Lamelligomphus,* and most *Onychogomphus*; and median process also absent in *Nihonogomphus,* and *Amphigomphus*), genital shelf absent.

KEY TO THE SUBGENERA OF *ONYCHOGOMPHUS*

1 Male cerci with apical third directed medially, prepuce spinelike and directed anterodorsally, anterior hamuli with elongate shoulder, anterior lamina raised-hoodlike.. ***Onychogomphus***
Male cerci with apical third directed posteroventrally, prepuce absent, anterior hamuli without shoulder, anterior lamina low and not hoodlike ..... ***Nychogomphus*** subgen. n.
Type species: *Onychogomphus geometricus* Selys.

KEY TO THE SUBGENERA OF *OPHIOGOMPHUS*

1 Male epiproct ca. 6/10 length of cerci and with rami widely separated and directed dorsally, female sternum 10 ca. 4 times as wide as long ..... ***Ophionuroides*** subgen. n.
Type species: *Ophiogomphus anomalus* Harvey
Male epiproct more than 6/10 length of cerci and without rami widely separated and directed dorsally, female sternum 10 ca. 3 times as wide as long 2
2 Posterior hamulus with elongate hooklike apex, male epiproct with well developed dorsolateral spine, female postocellar ridge well developed medially ..... ***Ophionurus*** subgen. n.
Type species: *Ophiogomphus alleghaniensis* Carle
Posterior hamulus without elongate hooklike apex, male epiproct without well developed dorsolateral spine, female postocellar ridge typically vestigial medially ..... ***Ophiogomphus***

Comments — The Asiatic species of Onychogomphini have been divided into several genera, many of which may eventually be considered subgenera. NEEDHAM (1930) considered *Nihonogomphus* a synonym of *Ophiogomphus,* and FRASER (1934) included a species of *Nihonogomphus* in *Onychogomphus* along with two other species which appear close to *Amphigomphus* Chao. *Lamelligomphus* is primarily distinguished by its larva (FRASER, 1934), which is actually the larva of *Heliogomphus.* As presently defined, the subgenus *Onychogomphus* does not occur in China or India, the *Onychogomphus* of CHAO (1954) being *Lamelligomphus* and the remaining *Onychogomphus* of FRASER (1934) being placed in the new subgenus *Nychogomphus.* It is also noted that the *"Onychogomphus"* of Africa are very likely *Cornigomphus.*

Ophiogomphus alleghaniensis is herein considered a distinct species and designated the type species of *Ophionurus.* All eastern North American *Ophiogomphus,* with the exceptions of *O. anomalus, O. howei* Bromley and *O. colubrinus* Selys, are placed in *Ophionurus.*

GOMPHOIDINI

Type genus: *Gomphoides* Selys, 1850.

The Gomphoidini include: *Gomphoides* (= *Negomphoides* Muttkowski, 1910 and incl. *Ammogomphus* Förster, 1914), *Aphylla* Selys, 1854, *Peruviogomphus* Klots, 1944, *Phyllocycla* Calvert, 1948 (= *Cyclophylla* Selys, 1854) and *Phyllogomphoides* Belle, 1970.

Medium sized gomphines generally colored brown and yellow.

Head — Mouthparts slightly prognathous, middle tooth of posterior maxillary tooth row not fused to apical tooth, ca 0.2 length of proximal tooth, and

separated from proximal tooth by U-shaped notch, anterosubapical mandibular tooth absent or strongly retracted basally and vestigial, posterosubapical mandibular tooth slightly reduced and displaced proximally, labrum 2.0-2.8 times as wide as long with central portion inflated, ligula typically 1.0-1.5 times as wide as long (up to two times in *Aphylla*), distance between antennal bases 2.0-2.8 times length of dorsal surface of antefrons, frontal carina present, medial ocelli wider than lateral ocelli, occiput ridged, head not tumid posterior to compound eyes.

Thorax — Distance between lateral ends of collar carina and antealar carina 1.7-2.2 times length of collar carina, lower portion of dorsomedian carina 0.5--0.9 length of 1/2 collar carina, lateral mesocoxal carina curved, male foretibial lamina present, hind femur short, female hind femur without elongate spines, spines of male hind tibia not enlarged basally (slightly enlarged basally in *Peruviogomphus*), tarsal spines small and not subapical (large and displaced apically in *Peruviogomphus*).

Wings — Basal subcostal crossveins present, distal costal brace of hind wing located closer to proximal costal brace than to nodus, costa curved and widened along pterostigma, pterostigmal brace present, fore wing arculus straight and aslant with lower portion not perpendicular to CuP, sectors of arculus contiguous or nearly contiguous basally, base of fore wing distal pleat at 0.54-0.65 distance between distal ends of triangle and subnodus, base of distal pleat strongly asymmetrical, apical planate extended to near middle of pterostigma, apical planate slightly divergent from RP_1, MA without posterior branch originating slightly distal to bridge crossvein, supratriangles with crossveins, hind wing with 5-9 postmedian crossveins, hind wing subtriangle generally with crossveins in *Gomphoides* and *Phyllogomphoides*, and generally without crossveins in *Peruviogomphus*, *Phyllocycla*, and *Aphylla*, anal vein angulated at proximal angle of hind wing subtriangle, CuA brace 1/5-1/4 length of posterior side fore wing subtriangle (ca 1/3 in *Peruviogomphus*), triangles with crossveins (often 1-celled in *Peruviogomphus*), anterobasal angle of fore wing triangle acute, wings without trigonal planates, CuP and anal vein slightly divergent to hind wing margin, anal brace present, anal triangle 1.8-2.4 times as long as wide (1.1-1.5 in *Peruviogomphus*), anal triangle extended posteriorly to tornus, anal triangle 4-celled, cells of anal triangle arranged serially, membranule present and narrowly extended to tornus (absent in *Peruviogomphus*).

Abdomen — Male auricle dorsoventrally compressed and produced posteriorly, lower portion of auricular ridge weakly developed, female auricle absent, lateral margin of abdominal terga 8 and 9 at least slightly extended, female sternum 9 sclerotized with basal ridge and accessory genital valves, male sternum 9 sclerotized with transverse semimembranous articulation just posterior to gonocoxae, male gonocoxae rounded anteriorly (produced anteriorly in *Peruviogomphus*), abdominal terga 7-10 without medial carina, male with pos-

terolateral margin of segment 10 not notched, female segment 10 with lateral carina vestigial or absent, sternum 10 of male 0.6-2.0 times as wide as long, male cerci elongate with apex curved medially, male epiproct bifurcate or valvelike (vestigial and bifurcate in *Phyllogomphoides,* and valvelike in *Aphylla* and *Phyllocycla*), male paraproct with lateral ridge extended dorsally to near base of cerci.

Genitalia — Anterior lamina raised transverse-ridgelike (slightly raised and bilobate with posterior margin U-shaped in *Peruviogomphus*), anterior hamulus bifurcate with proximal lobe often shouderlike (half shell-like with apical hook in *Gomphoides,* and with anterior inflated area and apical notch in *Phyllogomphoides*), posterior hamulus short and robust, with incurvate endhook, and anterior surface with well developed setae and without denticles (endhook vestigial or absent in *Phyllogomphoides,* and shoulder well developed only in *Peruviogomphus* and *Gomphoides*), penile segment one raised with paired elongate posteroventrally directed flanges and troughlike penile receiver (flanges short in *Gomphoides* and ridgelike in *Aphylla,* penile receiver flat in *Aphylla*), second penile segment 1.5-3.0 times as long as wide, penile spine present, third penile segment with weak ventrobasal transverse indentation and 0.5-1.0 times as long as wide, prepuce absent, apex of penis with two flagella (with short-triangular flagellum in *Aphylla*), genital shelf present.

LINDENIINI

Type genus: *Lindenia* de Haan, 1826.

The Lindeniini include: *Lindenia* (= *Vanderia* Kirby, 1890), *Austrictinogomphus* Fraser, 1940, *Cacoides* Cowley, 1934 (= *Cacus* Selys, 1854), *Cinitogomphus* Pinhey, 1964, *Diastatomma* Burmeister, 1839 (= *Longchampia* Kirby, 1890), *Gomphidia* Selys, 1854, *Gomphidictinus* Fraser, 1942, *Ictinogomphus* Cowley, 1934 (= *Ictinus* Rambur, 1842), *Indictinogomphus* Fraser, 1939, *Mitragomphus* Needham, 1944 and *Sinictinogomphus* Fraser, 1939.

Large gomphines generally colored brown or black, and yellow.

Head — Mouthparts slightly prognathous, middle tooth of posterior maxillary tooth row not fused to apical tooth (fused in *Indictinogomphus*), ca 0.3 length of proximal tooth, and separated from proximal tooth by U-shaped notch, anterosubapical mandibular tooth slightly retracted basally, posterosubapical mandibular tooth well developed and slightly displaced proximally, labrum 1.8-2.0 times as wide as long, ligula 1.3-1.6 times as wide as long, distance between antennal bases 1.4-1.7 times length of dorsal surface of antefrons, frontal carina present, medial ocelli wider than lateral ocelli, occiput ridged, head not tumid posterior to compound eyes.

Thorax — Distance between lateral ends of collar carina and antealar carina 1.5-1.9 times length of collar carina, lower portion of dorsomedian carina 0.3-0.5 length of 1/2 collar carina, lateral mesocoxal carina curved, male foretibial lamina present, hind femur short, female hind femur with or without elongate

spines, spines of male hind tibia not enlarged basally, tarsal spines small and not subapical.

Wings — Basal subcostal crossveins absent (present in *Cacoides*), distal costal brace of hind wing located closer to proximal costal brace than to nodus, costa curved and widened along pterostigma, pterostigmal brace present (weakly developed in *Diastatomma*, and absent in *Mitragomphus* and *Gomphidictinus*), fore wing arculus straight and aslant with lower portion not perpendicular to CuP, sectors of arculus approximate basally (well separated basally in *Sinictinogomphus*, and contiguous basally in *Gomphidictinus*, and many *Indictinogomphus* and *Gomphidia*), base of fore wing distal pleat at 0.56-0.61 (0.51 in *Gomphidia quarrei*) distance between distal ends of triangle and subnodus, base of distal pleat asymmetrical (nearly symmetrical in *Lindenia*), apical planate extended to near proximal end of pterostigma, apical planate divergent from RP_1 (nearly parallel in *Diastatomma*), MA with posterior branch originating slightly distal to bridge crossvein, supratriangles with crossveins, hind wing with 5-8 postmedian crossveins (occasionally 4 in *Cinitogomphus*), hind wing subtriangle with crossveins, anal vein slightly angulated at proximal angle of hind wing subtriangle, CuA brace 1/3-2/5 length of posterior side of fore wing subtriangle, triangles with crossveins, anterobasal angle of fore wing triangle acute, wings without trigonal planates, CuP and anal vein slightly divergent to hind wing margin, anal brace present, anal triangle 1.7-2.3 times as long as wide, anal triangle not extended posteriorly to tornus, anal triangle 3-9-celled, cells of anal triangle arranged in two rows, membranule widened basally and extended to tornus.

Abdomen — Male auricle strongly dorsoventrally compressed and produced posteriorly, lower portion of auricular ridge absent, female auricle absent, lateral margin of abdominal terga 7-9 not expanded in *Distatomma*, *Gomphidia*, *Mitragomphus*, and *Gomphidictinus*, and expanded on tergum 8 of *Sinictinogomphus*, *Ictinogomphus*, *Indictinogomphus*, *Cacoides*, *Cinitogomphus*, *Austrictinogomphus*, and *Lindenia*, (also expanded on tergum 7 in *Lindenia*), female sternum 9 sclerotized, male sternum 9 sclerotized with transverse membranous articulation just posterior to gonocoxae, male gonocoxae rounded anteriorly, abdominal tergum 8 with acute medial ridge (ridge vestigial in *Lindenia*), tergum 9 with acute medial ridge in *Gomphidia* and *Mitragomphus*, segment 10 swollen dorsally in male *Diastatomma* and *Austrictinogomphus*, male with posterolateral margin of segment 10 not notched, female segment 10 with lateral carina well developed, sternum 10 of male 4-8 times as wide as long, male cerci elongate and tapered to apex (with small lateral spine in *Austrictinogomphus* and with large subapical medially directed spine in *Diastatomma*), male epiproct short and bifurcate (vestigial and quadrate in *Diastatomma*, *Cacoides*, *Austrictinogomphus*, and some *Gomphidia*), male paraproct with lateral ridge extended dorsally toward base of cerci.

Genitalia — Anterior lamina low-bilobate with U-shaped posterior margin (shallow U-shaped in *Diastatomma, Indictinogomphus, Austrictinogomphus, Mitragomphus, Gomphidictinus,* and *Gomphidia;* and inflated in *Sinictinogomphus*), sternum one variously produced posteriorly (sternal process absent in *Cacoides* and weakly developed in *Gomphidia, Ictinogomphus, Lindenia,* and *Austrictinogomphus*), anterior hamulus elongate and directed posteriorly with dorsally directed endhook and shoulder (shoulder weakly developed in *Cinitogomphus* and some *Gomphidia*), posterior hamulus robust L-shaped, with membranous posteromedial area, and anterior surface without denticles (with shoulder in *Diastatomma,* with endhook in *Lindenia* and *Ictinogomphus,* and with anteroventral denticles in *Cinitogomphus* and *Sinictinogomphus*), penile segment one raised into thin-walled hoodlike shield, penile receiver dish- or bowllike (reduced in *Sinictinogomphus*), second penile segment 3.0-8.0 times as long as wide, penile spine absent, third penile segment with weak ventrobasal transverse indentation and reduced to ventral straplike sclerite 1.5-3.0 times as long as wide (third segment typically elongated and often fused to fourth segment), prepuce absent (present in *Mitragomphus, Gomphidictinus,* and *Gomphidia*), apex of penis with two spiraled flagella in *Mitragomphus, Gomphidictinus,* and *Gomphidia,* and two narrow short flagella in *Austrictinogomphus* and *Indictinogomphus,* with two short stout flagella in *Sinictinogomphus,* and without flagella in *Ictinogomphus, Diastatomma, Lindenia, Cacoides,* and *Cinitogomphus,* genital shelf vestigial or absent.

KEY TO THE SUBGENERA OF *GOMPHIDIA*

1 Male cerci laterally compressed without ventral carina, male epiproct dorsoventrally flattened, forked, and ca. 1/3 length of cerci, metanepisternal pale stripe typically vestigial or absent ..... ***Gomphidia***

Male cerci conical with ventromedial carina, male epiproct less than 1/4 length of cerci, metanepisternal pale stripe well developed 2

2 Male cerci with basal ventromedial spine, male epiproct not apparent, prepuce fused to penile segment 4, penile flagella contiguous basally, lateral mesanepisternal pale stripe vestigial ..... ***Sinogomphidia*** subgen. n.
Type species: *Gomphidia kruegeri* Martin

Male cerci without basal spine, male epiproct apparent, prepuce elongate, penile flagella not contiguous basally, lateral mesanepisternal pale stripe well developed ..... ***Africogomphidia*** subgen. n.
Type species: *Diastatomma quarrei* Schouteden.

Comments — The large size and distinctiveness of lindeniines have resulted in the relative inflation of taxonomic rank within and of this group. For example, the following genera should possibly be considered subgenera of *Ictinogomphus: Austrictinogomphus, Cinitogomphus, Indictinogomphus,* and *Sinictinogomphus.*

PROGOMPHINI

Type genus: *Progomphus* Selys, 1854.
The Progomphini include: *Progomphus*.

Small to medium sized gomphines generally colored brown and yellow or pale green.

Head — Mouthparts slightly prognathous, middle tooth of posterior maxillary tooth row not fused to apical tooth, ca 0.2 length of proximal tooth, and separated from proximal tooth by U-shaped notch, anterosubapical mandibular tooth slightly to moderately retracted basally, posterosubapical mandibular tooth vestigial or occasionally well developed and slightly displaced proximally, labrum 1.9-2.5 times as wide as long, ligula 1.0-1.5 times as wide as long, distance between antennal bases 1.7-3.0 times length of dorsal surface of antefrons, frontal carina present or occasionally absent, medial ocelli wider than lateral ocelli, occiput ridged, head not tumid posterior to compound eyes.

Thorax — Distance between lateral ends of collar carina and antealar carina 1.7-2.3 times length of collar carina, lower portion of dorsomedian carina 0.4--1.0 length of 1/2 collar carina, lateral mesocoxal carina curved, male foretibial lamina present, hind femur short, female hind femur without elongate spines, spines of male hind tibia not enlarged basally, tarsal spines small and not subapical.

Wings — Basal subcostal crossveins present or absent, distal costal brace of hind wing located closer to proximal costal brace than to nodus, costa curved and widened along pterostigma, pterostigmal brace present, fore wing arculus straight and aslant or angulated with lower portion generally not perpendicular to CuP, sectors of arculus approximate basally (separated by 1/6-1/5 length of hind wing arculus), base of fore wing distal pleat at 0.44-0.50 distance between distal ends of triangle and subnodus, base of distal pleat asymmetrical (asymmetry moderate in fore wing with distal pleat subbasally constricted), apical planate extended to near middle of pterostigma, apical planate divergent from RP_1, MA without posterior branch originating slightly distal to bridge crossvein, supratriangles without crossveins (occasionally 2-celled), hind wing with 3-5 postmedian crossveins (occasionally 6), hind wing subtriangle with crossveins (occasionally 1-celled), anal vein angulated at proximal angle of hind wing subtriangle, CuA brace 1/4-1/3 length of posterior side of fore wing subtriangle, triangles with crossveins, anterobasal angle of fore wing triangle acute or slightly acute, wings without trigonal planates, CuP and anal vein slightly divergent to hind wing margin, anal brace present, anal triangle 1.3-1.8 times as long as wide, anal triangle not extended posteriorly to tornus, anal triangle generally 3-celled (occasionally 2 or 4-celled), cells of anal triangle arranged to meet at point at or near proximal wing margin, membranule present and extended to tornus.

Abdomen — Male auricle dorsoventrally compressed and slightly produced posteriorly, lower portion of auricular ridge present and often nearly horizontal, female auricle absent, lateral margin of abdominal terga 7-9 not expanded, female sternum 9 sclerotized, male sternum 9 membranous lateral and posterior to gonocoxae, male gonocoxae rounded anteriorly, abdominal terga 7-10 without medial carina, male with posterolateral margin of segment 10 not notched, female segment 10 with lateral carina weakly developed or absent, sternum 10 of male ca 2.5 times as wide as long, male cerci typically dorsoventrally compressed with basal ventrolateral ridge, male epiproct bifurcate with branches parallel and individually movable, male paraproct with lateral ridge extended dorsally to near base of cerci.

Genitalia — Anterior lamina low-bilobate with V-shaped posterior margin, anterior hamulus small and bifurcate with apex directed posteriorly, posterior hamulus robust and L-shaped, with endhook directed medially, anterior surface with well developed setae and typically with transverse denticulate ridge at shoulder, penile segment one hoodlike, hood slightly bilobate with thin walls and wide ventral notch, penile receiver bowllike, second penile segment 2.0-3.0 times as long as wide, penile spine present, third penile segment with weak ventrobasal transverse indentation and 0.7-1.0 times as long as wide, prepuce subbasal and typically elongate, apex of penis with two ventrally spiraled flagella, genital shelf well developed.

KEY TO THE SUBGENERA OF *PROGOMPHUS*

1 Abdominal segment 1 typically with midventral process 2
Abdominal segment 1 typically without midventral process 3

2 Hind tibial length 6/10-7/10 width of head, male cerci not dorsoventrally compressed and without ventrobasal carina or denticles, male epiproctal rami angled upward and separated by ca. width of a ramus ..... ***Archaeoprogomphus*** subgen. n.
Type species: *Progomphus geijskesi* Needham

Hind tibial length 4/10-5/10 width of head, male cerci dorsoventrally compressed and with ventrobasal carina and denticles, male epiproctal rami level and separated by at least 2 times width of a ramus ..... ***Neaprogomphus*** subgen. n.
Type species: *Diastatomma obscurum* Rambur

3 Basal subcostal crossvein absent, male cerci with lateral margin evenly rounded to a typically blunt apex, posterodorsal margin of segment 10 typically without denticles .... ***Progomphus***

Basal subcostal crossvein present in at least one wing, male cerci with lateral margin not evenly rounded to blunt apex, posterodorsal margin of segment 10 with denticles 4

4 Hind tibial length ca. 6/10 width of head, anterior hamulus with apical cleft directed medially, posterior margin of penile hood quadrangular ..... ***Eoprogomphus*** subgen. n.
Type species: *Progomphus tibialis* Belle

Hind tibial length 4 10-5 10 width of head, anterior hamuli with apical cleft directed posterolaterally, posterior margin of penile hood U- or V-shaped ..... ***Alloprogomphus*** subgen. n.
Type species: *Progomphus complicatus* Selys.

Comments — The first couplet of the subgeneric key apparently does not divide *Progomphus* into monophyletic groups, it is employed here for convenience. It is noted that *P.P. elegans* is characterized by a low ventromedial tubercle on abdominal segment one, and that *P. (Archaeoprogomphus) geijskesi* is characterized by a hair-covered transverse fold on abdominal segment one.

ZONOPHORINI

Type genus: *Zonophora* Selys, 1854.

The Zonophorini include: *Zonophora, Desmogomphus* Williamson, 1920, *Diaphlebia* Selys, 1854 and *Perigomphus* Belle, 1972.

Small to large gomphines generally colored dark brown, and yellow or pale green.

Head — Mouthparts slightly prognathous, middle tooth of posterior maxillary tooth row not fused to apical tooth, ca 0.5 length of proximal tooth (ca 0.7 in *Perigomphus*), and separated from proximal tooth by U-shaped notch, anterosubapical mandibular tooth slightly retracted basally, posterosubapical mandibular tooth vestigial and displaced proximally in *Diaphlebia* and *Desmogomphus,* well developed and slightly displaced proximally in *Zonophora* and *Perigomphus,* labrum 1.8-2.0 times as wide as long, ligula 1.1-1.2 times as wide as long, distance between antennal bases 1.8-2.5 times length of dorsal surface of antefrons, frontal carina present (vestigial in *Desmogomphus* and *Perigomphus*), medial ocelli wider than lateral ocelli, occiput ridged (not ridged in *Perigomphus*), head not tumid posterior to compound eyes.

Thorax — Distance between lateral ends of collar carina and antealar carina 1.9-2.0 times length of collar carina, lower portion of dorsomedian carina 0.6-0.9 length of 1/2 collar carina, lateral mesocoxal carina slightly curved, male foretibial lamina vestigial (absent in *Perigomphus*), hind femur short, female hind femur without elongate spines, spines of male hind tibia not enlarged basally, tarsal spines small and not subapical (displaced apically in *Desmogomphus*).

Wings — Basal subcostal crossveins present or absent, distal costal brace of hind wing located closer to proximal costal brace than to nodus, costa curved and widened along pterostigma, pterostigmal brace present (occasionally displaced proximally and weakly developed), fore wing arculus straight and aslant with lower portion not perpendicular to CuP, sectors of arculus approximate or nearly contiguous basally (separated by 1/8-1/6 length of hind wing arculus), base of fore wing distal pleat at 0.48-0.55 distance between distal ends of triangle and subnodus, base of distal pleat asymmetrical, apical planate extended to slightly proximal of pterostigma, apical planate divergent from RP_1, MA without posterior branch originating slightly distal to bridge crossvein, supratriangles with or without crossveins, hind wing with 3-6 postmedian crossveins

Table II
Classification of the Gomphidae

Division ***HAGENIUS***

Hageniinae
Hageniini: *Hagenius, Sieboldius*

Division ***GOMPHUS***

Octogomphinae
Hemigomphini: *Eogomphus, Hemigomphus, Neogomphus, Sinogomphus*
Octogomphini: *Davidius, Dubitogomphus, Lanthus, Octogomphus*
Trigomphini: *Fukienogomphus, Stylogomphus, Trigomphus*

Gomphinae
Anisogomphini: *Anisogomphus, Labrogomphus, Merogomphus, Notogomphus*
Cyclogomphini: *Anormogomphus, Burmagomphus, Cyclogomphus, Platygomphus*
Gomphini: *Arigomphus, Dromogomphus, Gastrogomphus, Gomphurus, Gomphus, Stylurus*
Neurogomphini: *Neurogomphus*

Division ***EPIGOMPHUS***

Epigomphinae
Epigomphini: *Epigomphus, Eugomphus*
Leptogomphini: *Africogomphus, Heliogomphus, Leptogomphus*
Macrogomphini: *Macrogomphus*
Microgomphini: *Microgomphus*

Austrogomphinae
Archaeogomphini: *Archaeogomphus*
Austrogomphini: *Antipodogomphus, Austroepigomphus, Austrogomphus*
Cyanogomphini: *Agriogomphus, Cyanogomphus*
Lestinogomphini: *Lestinogomphus*

Division ***LINDENIA***

Phyllogomphinae
Phyllogomphini: *Ceratogomphus, Isomma, Phyllogomphus*

Onychogomphinae
Crenigomphini: *Crenigomphus, Paragomphus*
Onychogomphini: *Acrogomphus, Amphigomphus, Cornigomphus, Davidioides, Erpetogomphus, Lamelligomphus, Megalogomphus, Nepogomphoides, Nepogomphus, Nihonogomphus, Onychogomphus, Ophiogomphus, Perissogomphus, Phaenandrogomphus, Tragogomphus*

Lindeniinae
Gomphoidini: *Aphylla, Gomphoides, Peruviogomphus, Phyllocycla, Phyllogomphoides*
Lindeniini: *Austrictinogomphus, Cacoides, Ciniogomphus, Diastatomma, Gomphidia, Gomphidictinus, Ictinogomphus, Indictinogomphus, Lindenia, Mitragomphus, Sinictinogomphus*
Progomphini: *Progomphus*
Zonophorini: *Desmogomphus, Diaphlebia, Perigomphus, Zonophora*

(2 in *Perigomphus*), hind wing subtriangle without crossveins, anal vein angulated at proximal angle of hind wing subtriangle (slightly angulated in *Zonophora*), CuA brace 1/3-1/2 length of posterior side of fore wing subtriangle, triangles with crossveins (1-celled in *Perigomphus* and in fore wings of *Desmogomphus*), anterobasal angle of fore wing triangle acute, wings without trigonal planates, CuP and anal vein slightly divergent to hind wing margin, anal brace present, anal triangle 1.0-3.0 times as long as wide, anal triangle not extended posteriorly to tornus, anal triangle 3 or 4-celled, cells of anal triangle arranged to meet at point (with isolated cell at posterior angle in *Zonophora*), membranule present and extended to tornus (2-celled in *Perigomphus*), in *Zonophora* and *Perigomphus*.

Abdomen — Male auricle not dorsoventrally compressed or strongly produced posteriorly (slightly compressed in *Diaphlebia*), lower portion of auricular ridge present and nearly vertical (vestigial and nearly horizontal in *Diaphlebia*), female auricle absent or vestigial, lateral margin of abdominal terga 7-9 not expanded, female sternum 9 membranous over distal half in *Zonophora, Perigomphus* and *Desmogomphus,* and semimembranous in *Diaphlebia,* male sternum 9 membranous lateral and posterior to gonocoxae, male gonocoxae rounded anteriorly, abdominal terga 7-10 without medial carina, male with posterolateral margin of segment 10 not notched, female segment 10 with lateral carina weakly developed or absent, sternum 10 of male 5-6 times as wide as long, male cerci elongate with apex incurvate, male epiproct bifurcate with branches parallel or divaricate, male paraproct with dorsolateral process (absent in *Desmogomphus*), male paraproct with lateral ridge extended dorsally to near base of cerci (ridge absent in *Desmogomphus*).

Genitalia — Anterior lamina slightly raised bilobate with posterior margin ridgelike and shallow U- or V-shaped, anterior hamulus bifurcate (with inner branch shoulderlike in *Diaphlebia*), posterior hamulus lanceolate (L-shaped in *Perigomphus*) with slight shoulder and incurvate apex, and anterior surface with denticles and well developed setae, penile segment one raised with high thin-margined hood, penile receiver dish- or bowllike, second penile segment 3.0-5.0 times as long as wide, penile spine present or absent, third penile segment with weak ventrobasal transverse indentation and 1.0-1.5 times as long as wide, prepuce absent or vestigial (well developed in *Perigomphus*), apex of penis with two flagella (absent in *Diaphlebia*), genital shelf lobelike (absent in *Diaphlebia*).

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REFERENCES

BELLE, J., 1979. An attempt at the subfamily classification of the Gomphidae, based on some new interpretations of wing venation (Anisoptera). *Odonatologica* 8: 43-46.

CARLE, F.L., 1979. A new Lanthus (Odonata: Gomphidae) from eastern North America with adult and nymphal keys to American octogomphines. *Ann. ent. Soc. Am.* 73: 172-179.

CARLE, F.L., 1982a. *A contribution to the knowledge of the Odonata.* Ph. D. thesis, Virginia Polytech. Inst. & St. Univ., Blacksburg.

CARLE, F.L., 1982b. The wing vein homologies and phylogeny of the Odonata: A continuing debate. *Soc. int. odonatol. rapid. Comm.* 4: X + 66 pp.

CARLE, F.L. & C. COOK, 1984. A new Neogomphus from South America, with extended comments on the phylogeny and biogeography of the Octogomphini trib. nov. (Anisoptera: Gomphidae). *Odonatologica* 13: 55-70.

CHAO, H.-f., 1951. *Classification of the Chinese dragonflies of the family Gomphidae (Odonata).* Ph. D. thesis, Univ. Massachusetts, Amherst.

CHAO, H.-f., 1984. Reclassification of Chinese gomphid dragonflies, with the establishment of a new subfamily and the descriptions of a new genus and species (Anisoptera: Gomphidae). *Odonatologica* 13: 71-80.

DAVIES, D.A.L., 1981. A synopsis of the extant genera of the Odonata. *Soc. int. odonatol. rapid Comm.* 3: XIV + 60 pp.

FRASER, F.C., 1934. *Fauna of British India, Odonata,* Vol. 2. Taylor & Francis, London.

FRASER, F.C., 1940. A comparative study of the penes of the family Gomphidae (order Odonata). *Trans. R. ent. Soc. Lond.* 90: 541-550, pls 1-6 excl.

FRASER, F.C., 1954. The origin and descent of the order Odonata based on the evidence of persistent archaic characters. *Trans. R. ent. Soc. Lond.* (B) 23: 89-94.

FRASER, F.C., 1957. *A reclassification of the order Odonata.* Roy. Zool. Soc. N.S.W., Sydney.

LAIDLAW, F.F., 1930. A synonymic list of dragonflies of the family Gomphidae (Odonata, Anisoptera) found in the Oriental Region. *Trans. R. ent. Soc. Lond.* 78: 171-197.

LIEFTINCK, M.A., 1941. Studies on oriental Gomphidae (Odonata) with descriptions of new or interesting larvae. *Treubia* 18: 233-253.

NEEDHAM, J.G., 1940. Studies on neotropical gomphine dragonflies (Odonata). *Trans. Am. ent. Soc.* 65: 363-394.

NEEDHAM, J.G., 1948. Studies on the North American species of the genus Gomphus (Odonata). *Trans. Am. ent. Soc.* 73: 307-347.

SELYS LONGCHAMPS, E. de, 1857. Monographie des Gomphines. *Mém. Soc. roy. Sci. Liège* 11: 1-460.

TILLYARD, R.J., 1917. *The biology of dragonflies.* Cambridge Univ. Press, Cambridge.

TILLYARD, R.J. & F.C. FRASER, 1940. A reclassification of the order Odonata, based on some new interpretations of the venation of the dragonfly wing. *Aust. Zool.* 9: 359-396.

WILLIAMSON, E.B., 1907. Dragonflies of Burma and Lower Siam. II. Subfamilies Cordulegasterinae, Chlorogomphinae and Gomphinae. *Proc. U.S. Natn. Mus.* 33: 267-317.

WILLIAMSON, E.B., 1920. A new gomphine genus from British Guiana with a note on the classification of the subfamily (order Odonata). *Occ. Pap. Mus. Zool. Univ. Mich.* 80: 1-12.