

**A NEW *NEOGOMPHUS* FROM SOUTH AMERICA, WITH EXTENDED
COMMENTS ON THE PHYLOGENY AND BIOGEOGRAPHY OF THE
OCTOGOMPHINI TRIB. NOV.
(ANISOPTERA: GOMPHIDAE)**

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N. edenticulatus sp. n. (♂ holotype, ♀ allotype: Lago Lacar at Estacion Forestal Pucara, Neuquen Prov. Argentina, 30-1-81, O.S. Flint, Jr.) is described and figured. The biology of *Neogomphus* species is discussed and a key to the adults presented along with a summary of their known distributions. The Octogomphini trib. nov. is established comprising *Davidius*, *Fukienogomphus*, *Hemigomphus*, *Lanthus*, *Neogomphus*, *Octogomphus*, *Sinogomphus*, *Stylogomphus*, and *Trigomphus*. Octogomphine phylogeny and biogeography is discussed and the group placed within the Gomphinae.

INTRODUCTION

In 1854 Baron Edmund DE SELYS LONGCHAMPS described *Gomphus* (*Hemigomphus*) *molestus* Selys from male and female specimens collected in Quillota, Chile. Later Selys (SELYS & HAGEN, 1858) established the subgenus *Neogomphus* for his group one of *Hemigomphus* comprising *G. molestus*, *G. elegans* Selys, and *G. specularis* Hagen. *Gomphus elegans* had been described by SELYS (1854) from a single incomplete specimen reportedly collected from the interior of Brazil; it was now placed provisionally with *N. molestus*. SELYS & HAGEN (1858) and SELYS (1859) also corrected the type locality of *G. (Hemigomphus) heteroclytus* Selys from South America to Nouvelle-Hollande (Australia) and referred *Gomphus (Austrogomphus) gouldi* Selys to the

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subgenus *Hemigomphus*. After receiving the male of *G. specularis*, SELYS (1873) removed it from *Neogomphus* and established the monotypic subgenus *Octogomphus* for it. SELYS (1878) then described *G. (Neogomphus) bidens* Selys from specimens collected in Valparaíso Province, Chile.

After obtaining specimens of *Neogomphus* from Chile the present authors independently discovered yet another species of *Neogomphus* described herein which is closely related to *N. molestus*. FRASER (1957a) and BELLE (1978) have reported *N. molestus* from Argentina, and although Fraser's specimens were not studied, examination of Belle's material revealed it to be conspecific with the new species suggesting that *N. molestus* should be removed from the list of Anisoptera known to occur in Argentina. SCHMIDT (1941) and BELLE (1978) both expressed doubt concerning the record of *N. molestus* from Brazil; in addition the present authors question the placement of *G. elegans* in *Neogomphus*.

The taxonomic placement of *Neogomphus* and the related *Hemigomphus* has obscured the close phylogenetic relationship between the two genera. FRASER (1957b), BELLE (1979), and DAVIES (1981) have placed *Hemigomphus* in the Epigomphinae and placed *Neogomphus* in the Gomphinae. Dr T.W. Donnelly (pers. comm.) and FRASER (1957a) have also recognized the close phylogenetic relationship between *Neogomphus* and *Hemigomphus* which parallels petalurine and neopetaline generic relationships between Australia and South America. The closest relatives of this southern generic pair are the octogomphines (cf. CARLE, 1979). These genera, including one other generic pair which again bridges the gap between the Gomphinae and Epigomphinae (*Trigomphus-Fukienogomphus*, placed by CHAO, 1982, near *Macrogomphus*), apparently form a monophyletic group with a world-wide relict distribution paralleled in the Odonata only by the Petaluridae. Some workers might attribute the rank of subfamily to the octogomphines but a conservative approach seems more appropriate in light of the difficulty in determining phylogenetic relationships among gomphines. Therefore, the octogomphines are here considered a tribe of the Gomphinae. However, it is noted that the octogomphines exhibit many similarities with the Hageniinae and Epigomphinae, indicating that they are likely the most ancient group of the Gomphinae.

NEOGOMPHUS EDENTICULATUS SPEC. NOV.

Figure 1

DESCRIPTION

Material examined. — Holotype, male: Argentina: Neuquén Prov., Lago Lacar at Estacion Forestal Pucara, 30-I-1981, O.S. Flint, Jr., deposited U.S. National Museum of Natural History (USNM), Washington, D.C., USA. — Allotype, female: Same as for holotype (captured in copula with holotype), deposited USNM. Paratypes: Argentina: Neuquén Prov.: 13 ♂, same as for holotype; 1 ♂, same locality as holotype, 24-II-1978, O.S. Flint, Jr. Chile: Arauco Prov.: 6 ♂.

Contulmo, 2-I-1966, O.S. Flint, Jr.; Cautín Prov.: 1 ♂, 1 ♀, 30 km NE Villarrica on Cunco Rd., 8-I-1965, Carl Cook; Curicó Prov.: 7 ♂, 2 ♀, El Coigo, 5-I-1963, Carl Cook; 1 ♂, El Coigo, ?-I-1967, L. E. Pena; 1 ♂, El Coigo, 4-I-1968, L. E. Pena; Malleco Prov.: 1 ♀, Adencul W of Victoria, 5-I-1961, Carl Cook; 2 ♂, 7 km N of Victoria, 3-I-1966, O.S. Flint, Jr.; 11 ♂, 1 ♀, Rio Dumo 11 km N of Victoria, 25-I-1978, O.S. Flint Jr.; Ñuble Prov.: 1 ♂, Bulnes, ?-I-1959, L.E. Pena; 1 ♂, Chillan-Las Trancas, ?-I-1967, L.E. Pena; Osorno Prov.: 9 ♂, 1 ♀, Lago Puyehue 5 km W Hosteria Puyehue, 6-II-1978, O.S. Flint, Jr.; Santiago Prov.: 1 ♀, El Peumo, 30-I-1961, Carl Cook; 1 ♀, El Canelo, ?-XI-1977, L.E. Pena; Valdivia Prov.: 1 ♂, 1 ♀, 20 km S of La Union on Osorno Rd., 2-XII-1960, Carl Cook. Representative paratypes deposited at the USNM; Florida State Collection of Arthropods, Gainesville USA; E.B. Williamson Collection, Univ. of Michigan, Ann Arbor, USA; and the Belle, Carle, Cook, Dunkle, and Paulson Collections.

Male. — Total length 42.5-47.5 mm, abdomen including cerci 33.0-35.0 mm, cerci 1.15-1.28 mm, hind femora 5.7-6.8 mm, hind wings 23.5-28.0 mm, pterostigmata 2.1-2.5/2.5-3.0 mm.

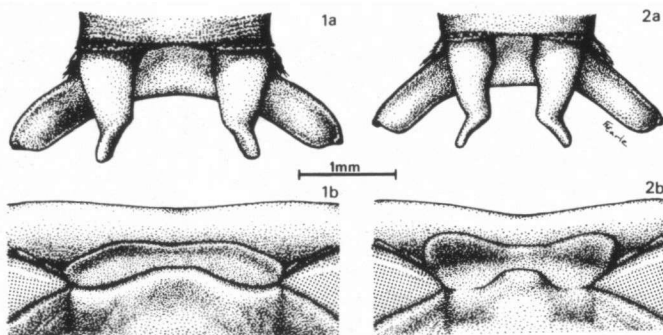
Head. — Labium, maxillae, and mandibles brown, labium yellow laterally; labrum, genae, anteclypeus, and postclypeus brown; anterior surface of antefrons brown on lower half, yellow on upper half; dorsal surface of antefrons brown on proximal half, yellow on distal half, laterally without denticles; antennae and postfrons (vertex) brown, postfrons with small yellowish area posterior to postocellar ridge, laterally postocellar ridge gradually pitched to lateral edges of postfrons; compound eyes separated by ca. 1.5 mm; occiput (dorsal portion) brown with posterior yellow area; posterior surface of head brown, yellowish ventrally.

Thorax. — Prothorax brown with lateral protuberances yellow. Pterothorax yellowish green with brown bands; dorsal mesanepisternal pale stripes wedge-shaped, widened ventrally and extended to just ventral of collar, and separated by parallel-sided brown area about equal in width to width of mesanepisternal pale stripes at 1/3 length; lateral mesanepisternal pale stripes vestigial or absent; mesanepimeral pale stripes broadly confluent with metanepisternal pale stripes above metathoracic spiracles, metanepimera pale laterally, pale area separated from metanepisternal-mesanepimeral pale area by wide brown band along metapleural sulci, brown band widened ventrally to cover lower portion of metanepisternum including metathoracic spiracle; dorsolateral carinae, antealar, katepisterna, and ventral surface of thorax brown.

Legs. — Coxae, trochanters, and femora brown, fore femora yellowish on inner surface, spines and denticles black; tibiae and tarsi black; prothoracic tibial keels pale ca 1/4 length of tibiae.

Wings. — Venation black, costa brown with medial dull yellow line; pterostigmata orange-brown; membrane hyaline, tinted with brown at base. Antenodal crossveins 10-15, 10-15/7-11, 7-11, postnodal crossveins 7-13/7-12; triangles and subtriangles without crossveins, supratrangles 1/1-2-celled; basal subcostal crossvein rarely present; postmedian (intermedian) crossveins 1-3/0-1; gaff 1/4-2/5 length of inner side of triangle; bridge crossveins 3-6/3-5, crossveins under pterostigmata 1-4/2-4; anal loop 1 or 2-celled (rarely 3-celled).

Abdomen. — Brown marked with yellow and green; terga 1 and 2 with medial greenish yellow band, tergum 1 with lateral greenish yellow spots, tergum 2 with greenish yellow auricles and greenish yellow oval spot posterior to each auricle; acrotergite 3 with lateral wedge-shaped yellow spots, tergum 3 with full length middorsal yellow stripe narrowed beyond antecostal suture; terga 4-7 with fine middorsal yellow line; acrotergites 4-6 with middorsal and lateral semicircular basal yellow spots, spots often confluent basally on tergum 5, and almost always confluent on tergum 6; acrotergite 7 yellow dorsal to segmental articulation; lateral margins of terga 2-7 narrowly yellowish brown; tergum 8 with narrow basal yellow band; terga 8 and 9 brownish yellow laterally, tergum 10 yellowish brown with yellow posterolateral areas; intersegmental conjunctiva of segments 1-6 brown and 7-9 yellow; sternum 1 yellowish brown, sterna 3-6 brown, and sterna 8-10 yellow. Terminalia short (Fig. 1a); cerci greenish white with base and ventrobasal spines brown, cerci conical in dorsal view with narrow apical portion directed posterolaterally, cerci separated basally by ca 1/2 length (ca 0.6 mm), maximum outside spread of cerci ca 2.0 mm; epiproct brown and strongly divaricate, each ramus ca 0.5 mm wide in lateral view and with end hook apical, maximum spread of epiproct ca 3.5 mm; paraprocts yellow without ventral ridge, but with dorsolateral extensions which reach dorsal level of epiproct.



Figs 1-2. *Neogomphus edenticulatus* sp. n. (Fig. 1) and *N. molestus* Selys (Fig. 2): (a) dorsal view of male terminalia; (b) posterodorsal view of female head.

Genitalia. — Anterior hamuli light brown with dark brown apices, each with an anterior shoulder (knuckles) and posterior hook (or thumb) arranged to form somewhat handlike appendages; posterior hamuli light brown with brown denticles on anterior surface, shoulder and endhook well developed. Penis brown; segment 1 ca 1.5 mm long, hood basketlike with thin rim and teardrop-shaped apical cleft; segment 2 enlarged distally, ca 1.3 mm long with well developed dorsal spine, segment 3 ca 0.8 mm long excluding prepuce, prepuce sclerotized and directed posteriorly, segment 4 greatly enlarged, ending in two

widely separated upturned filaments, length ca 1.3 mm, width near midlength of filaments ca 1.1 mm.

Female. — Total length 43.5-48.0 mm, abdomen including cerci 31.0-35.0 mm, cerci 0.86-0.93 mm, hind femora 6.3-6.8 mm, hind wings 26.0-30.0 mm, pterostigmata 2.5-3.0/3.0-3.3 mm.

Head. — Colored as in male; dorsal surface of antefrons without denticles; postocellar ridge low (Fig. 1b), lateral portions pitched gradually to form evenly curved ridge; compound eyes separated by ca 2.0 mm; occiput laterally slightly raised above posterior edge of postfrons (vertex) and medially expanded into denticle-covered protuberance, medial portion of occiput more than 1/2 as high as pedicel.

Thorax. — Colored as in male with lateral mesanepisternal pale stripes vestigial or occasionally fully developed but narrow.

Legs. — Colored as in male.

Wings. — Venation, membrane, and pterostigmata colored as in male.

Antenodal crossveins 11-14, 11-14/7-10, 8-11; postnodal crossveins 7-10/8-10; triangles, subtriangles, and fore wing supratrangles 1-celled (one triangle 2-celled), hind wing supratrangles 1 or 2-celled; basal subcostal crossvein absent; postmedian (intermedian) crossveins 1-3/0; gaff 1/4-2/5 length of inner side of triangle; bridge crossveins 3-6/3-4; crossveins under pterostigmata 2-4/3-4; anal loop 1 or 2-celled.

Abdomen. — Colored as in male with dorsal pale areas more extensive; terga 1 and 2 with lateral greenish yellow band, terga 3-7 with yellow spots extended distally to antecostal suture; sternum 9 membranous with lateral circular sclerites; terminalia greenish or yellowish white; outside spread of cerci ca 1.7 mm.

Genitalia. — Vulvar lamina brownish yellow, ca 0.9 length of sternum 9, ca 1.3 mm long and cleft for ca. 1/2 length, ca 1.3 mm wide at base, narrowed in basal 1/4 to ca 2/3 basal width, and apical cleft rounded proximally with apical branches fingerlike and approximate distally.

Larva. — Unknown; it is noted that the larval descriptions by NEEDHAM & BULLOCK (1943) of either *N. molestus* or *N. bidens* may apply to *N. edenticulatus* sp. n.

Remarks. — *Neogomphus edenticulatus* sp. n. is easily distinguished from other *Neogomphus* by its brown face and lateral brown bands of the thorax. These characteristics will also separate it from *G. elegans*. The lyrelike male cerci and hooklike apex of the anterior hamuli are distinctive for *N. bidens*. Female *N. bidens* are distinctive in having the vulvar lamina longer than sternum 9, occiput nearly level, and postocellar ridge ending at about the middle of the lateral ocelli. However, *N. molestus* and *N. edenticulatus* form a closely related species pair.

The following characteristics of *N. molestus* given in the order in which they are described for *N. edenticulatus* will serve to distinguish the two: face yellow, dorsal surface of male antefrons with lateral denticles, female postocellar ridge produced laterally (Fig. 2a), male compound eyes separated by ca 1.3 mm, female compound eyes separated by ca 1.5 mm, female occiput laterally level with posterior edge of postfrons, median portion of female occiput less than 1/2 as high as pedicel, lateral mesanepisternal pale stripes generally well developed (c.f. BELLE, 1978), thorax laterally and ventrally yellow, femora yellow ventrally, costa with bright yellow medial band, pterostigmata orange-tan, cerci yellowish white, male cerci separated basally by ca 1/3 length of cerci, by ca 0.4 mm (Fig. 2b), maximum outside spread of male cerci ca 1.5 mm, maximum outside spread of female cerci ca 1.4 mm, maximum spread of male epiproct ca 3.0 mm with each ramus ca 0.4 mm wide in lateral view, end hook of each ramus subapical.

Etymology. — *N. edenticulatus* [e·den·ti·cu·la'tus] (N.L. pseudoparticiples "edenticulatus" = "lacking small teeth", by analogy to "edentatus" = "lacking teeth", referring to the absence of denticles on the dorsolateral portion of the antefrons).

BIOLOGY

In temperate central Chile dragonflies of the genus *Neogomphus* are quite common, often being the most conspicuous Odonata along streams, rivers, and lakes. Although their showy nature sharply contrasts with the secretive habits of *Lanthus*, it is apparently typical of octogomphines in general. *Neogomphus molestus* and *N. bidens* inhabit lotic habitats, the latter species apparently preferring slower and larger streams. In contrast *N. edenticulatus* is unique in its lacustrine habitat preferences.

The type locality of *N. edenticulatus* is described by Dr O.S. Flint, Jr. (pers. comm.) as "a large glacial lake with clear and cold water, the bottom of cobble and gravel". A large series of *N. edenticulatus* was also collected from the Chilean Lago Puyehue, the description of the site being similar to that of the type locality. At both localities *N. edenticulatus* was the only species of *Neogomphus* taken; most specimens were "found resting on stones along shore". A third large series of *N. edenticulatus* collected by Dr Flint was taken at Rio Dumo, Malleco Province, Chile; here the new species was greatly outnumbered by *N. bidens*. He writes of Rio Dumo "About 5 m wide by about 30 cm deep, water clear. Some flat bedrock, scattered boulders, much of bottom fine sediment. A good flow, but rather low gradient with many rather still reaches. Dragonflies resting on boulders and rock in and marginal to stream; gomphines very abundant".

Neogomphus edenticulatus and the closely related *N. molestus* are generally not collected together, the latter species apparently preferring rapid rivers and

streams. A large series containing only *N. molestus* was collected by Dr Flint from the Rio Pedregoso near Villarrica, Cautín Province, Chile. He describes the Rio Pedregoso as "A braided stream, water about 3-5 m wide by a few cm deep, mostly cobble and gravel bottom". The junior author has collected an extensive series of *N. molestus* from a small stream locally called Rio Luato located near El Vergel, Malleco Province, Chile. Rio Luato originates in the foothills of the Andes and descends swiftly down a rocky canyon until it abruptly changes into a more placid stream 12-15 m wide and 2-6 cm deep where *N. molestus* were very abundant. In contrast to the habit of perching on rocks observed for *N. edenticulatus*, *N. molestus* would perch on the leaves of low bushes extended out over the water, sometimes making a quick flight out over the water and then returning to perch again on the same or a nearby bush. This behavioral difference has a parallel in North American *Lanthus* where the lighter colored *L. vernalis* Carle prefers to perch on leaves, and the darker colored *L. parvulus* (Selys) prefers to perch on rocks. *Progomphus herrerae* Needham & Etcheverry also occurs at Rio Luato, it was typically found perching along the sandbars at the water's edge. The known flight seasons of *Neogomphus* species are as follows: *N. bidens* (26 Dec.-27 Jan.), *N. edenticulatus* (30 Nov.-10 Feb.), *N. molestus* (17 Nov.-15 Jan.).

DISTRIBUTION OF AND KEY TO THE SPECIES OF *NEOGOMPHUS*

DISTRIBUTION

The genus *Neogomphus* is limited in distribution to Chile and western Argentina. The species distributions are highly sympatric. Their known distributions are as follows: *bidens*: Chile: Arauco, Cautín, Concepcion, Malleco, Maule, Nuble, Santiago, and Valparaíso provinces; *edenticulatus*: Argentina: Neuquén and Chubut provinces; Chile: Arauco, Cautín, Curicó, Llanquihue?, Malleco, Nuble, Osorno, Santiago, and Valdivia provinces; *molestus*: Chile: Cautín, Linares, Maule, Malleco, Nuble, Santiago, and Valparaíso provinces.

SPECIES KEY TO THE ADULTS

- 1 Male cerci about twice as long as epiproct, each with two lateral ventrobasal spines; anterior hamuli with recurved apices, each notched for more than 1/3 length; female vulvar lamina longer than sternum 9; ocellar ridge ended behind middle of lateral ocelli *N. bidens* Selys
- Male cerci about as long as epiproct, each with one lateral ventrobasal spine; anterior hamuli without recurved apices, each notched for less than 1/4 length; female vulvar lamina shorter than sternum 9; ocellar ridge ended behind outside edge of lateral ocelli 2
- 2 Face predominantly yellow; pterothorax without brown bands along metapleural sulci; male antefrons with dorsolateral denticles; male cerci separated basally by ca 1/3 length (Fig. 2a),

- female postocellar ridge highest laterally (Fig. 2b), female postfrontal suture ca 1.5 mm long *N. molestus* Selys
- Face predominantly brown; pterothorax with brown bands along metapleural sulci; male antefrons without dorsolateral denticles; male cerci separated basally by ca 1/2 length (Fig. 1a), female postocellar ridge highest medially (Fig. 1b), female postfrontal suture ca 2.0 mm long *N. edenticulatus* sp. n.

OCTOGOMPHINI TRIB. NOV.

DEFINITION

Small to medium-sized gomphines colored dark brown or black with yellow or light green markings; frons inflated, postocellar ridge not biconically elevated (often distinctly bilobate in *Sinogomphus*); occiput without well-developed transverse ridge; legs black, femora occasionally yellow ventrally; distal costal brace of hind wing about midway between proximal costal brace and nodus (except in *Hemigomphus*); basal subcostal vein only rarely present; pterostigmata braced; base of distal pleat generally symmetrical (asymmetrical in *Trigomphus*); postmedian (intermedian) crossveins 2-5/1-3; MA ($1R_3$) without posterior branch; triangles and supratrangles generally 1-celled, occasionally 2-celled; subtriangles 1-celled; trigonal planate generally absent (often developed in *Octogomphus*); CuP and A strongly divergent toward hind wing margin; anal brace present; anal triangle 3-celled, occasionally 4-celled in *Fukienogomphus*, and 5 or 6-celled in *Trigomphus*. Secondary genitalia variable; anterior lamina not strongly elevated except in *Fukienogomphus* and *Trigomphus*; anterior hamuli with anterior portion elongate (*Hemigomphus*, *Stylogomphus*, *Fukienogomphus*, and *Trigomphus*), slightly elongate (*Sinogomphus*, *Octogomphus*, and *Neogomphus*), or not elongate (*Lanthus* and *Davidius*); anterior surface of posterior hamuli with denticles (denticles minute in *Sinogomphus*); penis of *Gomphus* type with prepuce expanded, segment two with dorsal spine (spine absent in *Sinogomphus*); sternum 9 of male membranous posterior to genital valves; sternum 9 of female membranous with laterobasal sclerites. Larval labium with 2-5 ventral teeth along ligula, lateral lobes rounded apically; segment 3 of antennae flattened (only slightly so in *Fukienogomphus* and *Trigomphus*); abdomen with dorsal knobs in only *Fukienogomphus* and *Trigomphus*.

The octogomphines include *Octogomphus* Selys, *Neogomphus* Selys, *Hemigomphus* Selys, *Davidius* Selys, *Lanthus* Needham, *Trigomphus* Bartenef, *Sinogomphus* May, *Stylogomphus* Fraser, and *Fukienogomphus* Chao. They are readily distinguished from other gomphines by the relative position of the distal costal brace, by CuP and A diverging toward the hind wing margin, and by the presence of 2-5 ventral teeth on the larval ligula.

PHYLOGENY

Monophyly for the Octogomphini is hypothesized on the basis of three character states which are practically unique among anisopteroids and therefore considered apomorphic. These are: distal costal brace located about midway between proximal costal brace and nodus, veins CuP and A strongly divergent toward hind wing margins (generally separated by 5 or more cells at wing margins), and larval ligula with 2-5 teeth along ventral edge. *Hemigomphus* is unique among octogomphines in the more proximal relative location of the distal costal brace, and in the less strongly divergent veins CuP and A of the hind wings; both are apparently related to a secondary narrowing of the wings.

Four additional octogomphine character states are shared with the Hageniinae and various Epigomphinae. These are: occiput without well-developed transverse ridge, penile segment 2 with dorsal spine, anterior face of posterior hamuli with scattered denticles, and female sternum 9 membranous with paired lateral sclerites. Basing character state polarity on primitive Anisoptera (i.e. Petaluridae, Neopetaliidae, and Cordulegastridae) indicates that the former two states are plesiomorphic. In contrast, the latter character states are possibly apomorphic indicating that the Hageniinae, Epigomphinae, and Octogomphini may form a monophyletic group. However, sternum 9 of female Zygoptera and primitive Anisoptera is largely membranous, and in other cases where the ovipositor has become reduced (i.e. *Neopetalia*, and primitive Libelluloidea) sternum 9 is largely membranous with the metagonapophyses attached to paired lateral sclerotized areas (metagonocoxae). The denticulate anterior surface of the posterior hamuli suggests contact with female sternum 9. This may represent a plesiomorphic character state within the Gomphidae because gomphines differ from other Anisoptera in that the posterior hamuli engage the female genitalic region during the anterior hamular stroke. It is possible that the anteriorly directed hamular end hooks developed secondarily to better grip female sternum 9 about the metagonocoxae. Considering all four shared character states to be plesiomorphic will avoid substantial modification of the existing classification, for the octogomphines could then be considered the most ancient Gomphinae.

A cladogram illustrating the hypothesized phylogenetic relationships among octogomphines is presented in Figure 3. A technique developed by the senior author is utilized herein to allow easy interpretation of the phylogenetic analysis. Each phylogenetic dichotomy of the cladogram is labeled with a reference number, and each furcation of a dichotomy referred to by the dichotomy number or taxa to which the furcation leads. Apomorphic character states which define each furcation are labeled with a letter code and listed under respective dichotomies. The distribution of character states among Octogomphini and various taxonomic outgroups is presented in Table 1.

Determination of gomphine character state polarities is made difficult by the

Table I
Distribution of character states among Octogomphini and various taxonomic out-groups

Group	Character code																														
	Dichotomy 1							Dichotomy 2							Dichotomy 3							Dichotomy 4									
	a	b	c	d	e	f	g	a	b	c	d	e	f	g	h	i	j	a	b	c	d	e	f	g	a	b	c	d	e	f	g
ZYGOPTERA	—	—	—	—	—	+	—	○	○	—	—	—	—	—	—	—	—	—	—	—	○	○	○	○	—	—	—	○	○	—	○
Epiophlebiidae	—	—	—	—	—	—	—	—	○	—	—	—	—	—	—	+	—	—	—	—	○	○	○	○	—	—	—	○	○	—	○
Petaluridae	—	—	—	—	—	+	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	○	○	—	—	—	—	—	—	—	○
Neopetaliidae	—	—	—	—	—	+	—	—	+	—	—	—	—	—	—	—	—	—	—	—	±	—	○	○	—	—	—	+	—	○	
Cordulegastridae	—	—	—	—	—	+	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	○	○	—	—	—	—	—	—	—	○
Hageniinae	±	±	—	—	—	—	—	—	+	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—
Epigomphinae	—	±	—	—	±	±	—	—	—	±	±	—	—	±	—	+	—	—	—	+	—	—	±	—	—	±	—	—	—	—	—
furcation 2	+	+	+	+	—	—	—	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	—	—	—	—	—	—	—
Stylogomphus	+	+	+	+	—	—	—	+	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
furcation 3	+	+	+	+	—	—	—	—	±	+	+	+	+	+	+	+	+	±	±	±	±	±	±	±	—	—	—	—	—	—	—
Fukienogomphus	+	+	+	+	—	—	—	—	—	+	+	+	+	+	+	+	+	+	+	+	+	+	—	—	—	—	—	—	—	—	—
Trigomphus	+	+	+	+	—	—	—	—	—	+	+	+	+	+	+	+	+	—	+	+	+	+	+	—	—	—	—	—	—	—	—
furcation 4	—	—	—	—	+	+	±	—	±	—	±	—	±	—	—	—	—	—	—	—	—	—	±	—	±	±	±	±	±	±	±
furcation 5	—	—	—	—	+	+	±	—	±	—	±	—	±	—	—	—	—	—	—	—	—	—	—	+	+	—	—	—	—	—	—
Octogomphus	—	—	—	—	+	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	—	—	—	—	—
furcation 6	—	—	—	—	+	+	±	—	±	—	±	—	±	—	—	—	—	—	—	—	—	—	—	—	+	+	—	—	—	—	—
Davidius	—	—	—	—	+	+	±	—	±	—	±	—	±	—	—	—	—	—	—	—	—	—	—	—	+	+	—	—	—	—	—
Lanthus	—	—	—	—	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	—	—	—	—	—
furcation 7	—	—	—	—	+	+	±	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	±	—	—	+	+	+	+	+	+
Sinogomphus	—	—	—	—	+	+	±	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	+	+	+	+
furcation 8	—	—	—	—	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	±	—	—	+	+	+	+	+	+
Hemigomphus	—	—	—	—	+	+	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	+	+	+	+
Neogomphus	—	—	—	—	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	±	—	—	+	+	+	+	+	+

○ Not applicable
— Plesiomorphic
+ Apomorphic

uncertain phylogenetic position of the group. Gomphine morphology is characterized by several modifications achieved through reduction or loss, which include: larval antennae 4-segmented, larval fore and middle tarsi 2-segmented, ovipositor reduced, and labial cleft fused. Although the latter two characteristics suggest an affinity with the higher Libelluloidea, other evidence indicates that these similarities have arisen through convergent losses. Considering the Gomphoidea to be the sister group of remaining Anisoptera (cf. CARLE, 1982a, 1982b) is supported by immobility of the larval mandibular "molar lobe" (cf. GLOYD, 1963) in all nongomphine Anisoptera. Gomphines are also plesiotypic in the wide dorsal separation of the compound eyes, and uniquely apotypic in the development of a postocellar ridge.

The possible sister group position of gomphines coupled with the unique structure of anisopteran secondary genitalia render the plesiotypic condition of male genitalic components difficult to determine. Gomphines are unique in the specialization of the hamuli, a characteristic likely related to the reduction of the ovipositor and subsequent change in hamular function. However, the Aeshnoidea (Neopetaliidae-Aeshnidae) are characterized by a fully developed ovipositor (except *Neopetalia*), but have the male genital fossa uniquely

[illegible]

narrowed and deepened, again suggesting a specialized condition. The relative similarity of petalurine and cordulegastrine secondary genitalia to that of the Zygoptera suggests that this genitalic type represents the anisopteran plesiotypic condition. Unfortunately, epiophlebian secondary genitalia, although in many respects similar to that of gomphines, are apparently too specialized to be of much use in determining this polarity (cf. CARLE, 1982c). It is also noted that among Odonata the mode of petalurine oviposition is most similar to that of archaeanognathan Apterygota.

The secondary genitalia of the Hageniinae appear to be the most similar to the petalurine-cordulegastrine type among gomphines and is herein utilized to establish octogomphine character state polarities. Therefore, the following octogomphine character states are considered apomorphic although each of these characterize the proposed anisopteran plesiotypic condition: (1f) penile receiver not narrow-cleftlike, (2b) penile segment 4 without a terminal filament, (6b and 8d) shoulder of posterior hamuli vestigial or absent, (7c) penile segment 2 J-shaped, and (7i) penile segment 4 wider than stem of segment 3. A reversal to the ancestral condition is also proposed for character 8a in which the wings of *Hemigomphus* are considered to be secondarily elongated. These proposed reversals are readily observed in Table I by the apparent prevalence of apomorphies among out-groups. However, the polarity for character 5g was based on the zygopteran and petalurine condition.

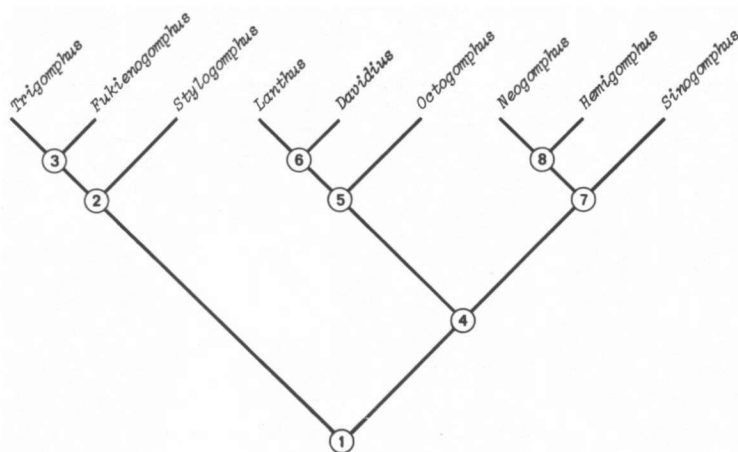


Fig. 3. A cladogram illustrating possible phylogenetic relationships within the Octogomphini.

Dichotomy 1

— Monophyly for furcation 2 is hypothesized on the basis of: (a) anterior lamina laterally swollen, — (b) anterior hamuli elongate and slightly curved with a posterobasal shoulder, — (c) shoulders of posterior hamuli subapical and transverse, and — (d) posterior hamuli with end hooks small and directed mesally. — (The elongate anterior hamuli of *Hemigomphus* are here considered a convergence. However, elongate anterior hamuli may be a plesiomorphic character state for the Octogomphini as this characteristic is shared with most Gomphidae).

— Monophyly for furcation 4 is hypothesized on the basis of: (e) penile hood erect, ventral margin notched posteriorly in lateral view, — (f) penile receiver not narrow-cleftlike, and — (g) epiproct with paired median processes. — (Considering the median epiproctal processes an apomorphic character for furcation 4 requires their independent loss in *Lanthus*, *Hemigomphus*-*Neogomphus*, and some *Davidius* and *Sinogomphus*).

Dichotomy 2

— Monophyly for *Stylogomphus* is hypothesized on the basis of: (a) penile segment 2 L-shaped, — (b) penile segment 4 without a terminal filament, and — (c) larval third antennal segments contiguous along inner margins.

— Monophyly for furcation 3 is hypothesized on the basis of: (d) anterior lamina erect and V-shaped, — (e) female metagonocoxae elongate, — (f) female sternum 10 longer than wide, — (g) larval antennal segment 3 ca 3.5 times as long as wide, — (h) larval ligula with only 2 teeth along ventral margin, — (i) larval abdomen with dorsal knobs, and — (j) larval abdominal segment 10 ca as long as wide, and 5-sided in cross section. — (The numerous apomorphic character states of larval *Fukienogomphus*-*Trigomphus* are apparently related to adaptations for living in lentic habitats).

Dichotomy 3

— Monophyly for *Fukienogomphus* is hypothesized on the basis of: (a) male cerci flat basally with a ventromedial projection, and (b) larval ligula level.

— Monophyly for *Trigomphus* is hypothesized on the basis of: (c) base of distal pleat asymmetrical, — (d) anal triangle 5 or 6-celled, — (e) ventral sclerotized portion of penile segment 4 directed posteriorly, — (f) lateral spine of male cerci vestigial, and — (g) vulvar lamina longer than sternum 9.

Dichotomy 4

— Monophyly for furcation 5 is hypothesized on the basis of: (a) posterior edge of posterior hamuli and end hook thin, and — (b) penile receiver troughlike. — (The apparent paucity of shared apomorphic character states among *Octogomphus*, *Lanthus*, and *Davidius* indicates that the group may be polyphyletic).

— Monophyly for furcation 7 is hypothesized on the basis of: (c) penile receiver dishlike, — (d) neck of penile segment 4 as wide or wider than stem of segment 3, — (e) penile segment 4 with paired apical filaments, — (f) sternum 10 ca 6 times as wide as long in male (ca 4 times in female), and — (g) ventrolateral spine of male cerci located at extreme base.

Dichotomy 5

— Monotypy for *Octogomphus* is hypothesized on the basis of: (a) female postocellar ridge 4-lobed, — (b) female occiput linear, — (c) posterolateral portion of female head with two dorsal pits, — (d) anterior face of pterothorax with a vase-shaped pale area, — (e) lateral spines of male cerci ca 2 times as long as paraprocts, and — (f) epiproctal rami directed laterally.

— Monophyly for furcation 6 is hypothesized on the basis of: (g) postfrontal suture shorter than distance between lateral ocelli in males (about equal in females) and, — (h) anterior hamuli with a narrow apical cleft.

Dichotomy 6

— Monophyly for *Davidius* is hypothesized on the basis of: (a) occiput level with postfrons, — (b) shoulder of posterior hamuli reduced, — (c) penile segment 4 upturned apically and without an apical filament, — (d) ventrobasal spines of male cerci directed mesally, — (e) larval antennal segment 3 ca 2.5 times as long as wide, and — (f) larval wing pads divergent.

— Monophyly for *Lanthus* is hypothesized on the basis of: (g) basal spine of male cerci vestigial.

Dichotomy 7

— Monophyly for *Sinogomphus* is hypothesized on the basis of: (a) anterior hamuli thin-elongate, — (b) posterior hamuli with an inner apical projection, and with denticles reduced, — (c) penile segment 2 J-shaped, and — (d) dorsal spine of penile segment 2 absent.

— Monophyly for furcation 8 is hypothesized on the basis of: (e) postocellar ridge long and narrow, (f) anal triangle more than twice as long as wide, (g) rim of penile hood thin, — (h) penile segment 3 shorter than segment 4, (i) penile segment 4 wider than stem of segment 3, and — (j) ventrobasal cercal spine with apical teeth.

Dichotomy 8

— Monophyly for *Hemigomphus* is hypothesized on the basis of: (a) distal costal brace located closer to proximal costal brace than to nodus, — (b) anterior lamina erect, — (c) anterior hamuli elongate, — (d) posterior hamuli without a shoulder, and — (e) penile segment 4 with a ventral projection. — (The ventral process of penile segment 4 has apparently functionally replaced the sclerotized anterior projection of the prepuce of *Sinogomphus* and *Neogomphus*).

— Monophyly for *Neogomphus* is hypothesized on the basis of: (f) penile segment 4 wider than segment 3 and sigmoid in lateral view, — (g) vulvar lamina with medial cleft rounded basally, and (h) male paraprocts with dorsolateral processes.

BIOGEOGRAPHY

Octogomphine distribution is most similar to that of the Petaluridae among living Odonata, implying a Mesozoic origin of the Octogomphini. The distribution of petalurine and octogomphine genera are as follows: eastern North America- *Tachopteryx*, *Lanthus*, and *Stylogomphus*; western North America- *Tanypteryx* and *Octogomphus*; Japan- *Tanypteryx*, *Davidius*, *Lanthus*, *Sinogomphus*, *Stylogomphus*, and *Trigomphus*; Asia (mainland)- *Davidius*, *Fukienogomphus*, *Sinogomphus*, *Stylogomphus*, and *Trigomphus*; eastern and western Australia- *Petalura* and *Hemigomphus*; New Zealand- *Uropetala*; and western South America- *Phenes* and *Neogomphus*. The distributional similarity of these two groups is striking, with the only exceptions being the absence of the petalurines from the mainland of Asia, and the absence of octogomphines from New Zealand.

The evolutionary center of the Octogomphini has been in Laurasia with the largest diversity of octogomphines in southern Asia. However, the holarctic distributions of the relatively unspecialized *Lanthus* and *Stylogomphus* indicate that the Mesozoic origin of the octogomphines may have been in eastern North America. The current low diversity of octogomphines in North America would then be considered a result of Pleistocene glaciation. A North American origin is also implied by the occurrence of both *Tachopteryx* and *Zoraena* in eastern North America which represent the most archaic living representatives of the Petaluroidea and Libelluloidea*, respectively (cf. CARLE, 1982a, 1983).

Two hypotheses can explain the presence of *Hemigomphus* and *Neogomphus* in Australia and western South America, respectively. One possibility is that the Octogomphini radiated before the complete separation of the Pangaeon supercontinent. This requires a Jurassic age for dichotomies 1, 4, and 7 of the cladogram (Fig. 3), which is at least not yet supported by fossil evidence. Alternatively, the Octogomphini could have radiated in Laurasia during the late

* The First Author does not follow TILLYARD & FRASER (1940) in removing the chlorogomphines and cordulegastrines from the Libelluloidea.

Mesozoic, invading Australia-Antarctica-western South America via the Indonesian Island arc during the late Cretaceous-early Cenozoic. The latter possibility postulates an original north-south orientation of the Indonesian Island arc, the southern end of which contacted northern (now western) Australia. Although such a late Cretaceous connection has apparently not been previously proposed, it would explain the presence of octogomphines in Australia and western South America, and their absence from Africa and New Zealand.

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