Generic diagnoses within a closely related group of genera: *Brechmorhoga*, *Gynothemis*, *Macrothemis*, and *Scapanea* (Odonata: Libellulidae)

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Abstract—Based on examination of most species of *Brechmorhoga*, *Gynothemis*, *Macrothemis*, and *Scapanea*, these four genera are rediagnosed, resulting in the following taxonomic changes: *Brechmorhoga archboldi* (Donnelly, 1970) **comb. nov.**, *Gynothemis pumila* (Karsch, 1890) **comb. nov.**, *Macrothemis heteronycha* (Calvert, 1909) **comb. nov.**, and *Macrothemis calliste* (Ris, 1913) **comb. nov.** The male of *M. calliste* is described and illustrated for the first time.

Résumé—Après l'examen de la plupart des espèces de *Brechmorhoga*, *Gynothemis*, *Macrothemis* et *Scapanea* nous présentons ici des diagnoses révisées de ces quatre genres. Nous proposons les changements suivants à la taxonomie : *Brechmorhoga archboldi* (Donnelly, 1970) **comb. nov.**, *Gynothemis pumila* (Karsch, 1890) **comb. nov.**, *Macrothemis heteronycha* (Calvert, 1909) **comb. nov.** et *Macrothemis calliste* (Ris, 1913) **comb. nov.** Le mâle de *M. calliste* est décrit et illustré pour la première fois.

Resumen—Se examinó la mayor parte de las especies de *Brechmorhoga*, *Gynothemis*, *Macrothemis*, y *Scapanea*. Estos cuatro géneros son re-diagnosticados y se proponen los siguientes cambios taxonómicos: *Brechmorhoga archboldi* (Donnelly, 1970) **comb. nov.**, *Gynothemis pumila* (Karsch, 1890) **comb. nov.**, *Macrothemis heteronycha* (Calvert, 1909) **comb. nov.** y *Macrothemis calliste* (Ris, 1913) **comb. nov.** El macho de *M. calliste* es descripto e ilustrado por primera vez.

Introduction

With about 393 species and 46 genera, the subfamily Libellulinae comprises the most speciose complex of Odonata in the New World. Its members are commonly observed at almost any aquatic habitat, and many species are familiar to naturalists because of their relatively large size and variously colored bodies. As with any large group, taxonomic problems and disagreements often underpin an understanding of not only generic definitions but phylogenetic considerations as well.

Perhaps no other group of libellulid dragonflies has suffered the vicissitudes of shifting species as much as the genera *Brechmorhoga* Kirby, 1894, *Gynothemis* Calvert *in* Ris, 1909, *Macrothemis* Hagen, 1868, and *Scapanea* Kirby, 1889. These genera comprise an assemblage of over 60 small to moderately sized species with slender bodies, hyaline wings, and often long abdomens. Usually associated with lotic habitats, they are secretive in habits and can be mistaken for gomphids in the field. Species of these genera have been recognized as closely related and have been dealt with by numerous authors. *Macrothemis* was described by Hagen (1868), who included *Libellula celeno* Selys *in* Sagra, 1857, *Libellula pleurosticta* Burmeister, 1839, *Macrothemis marmorata* Hagen, 1868, and *Macrothemis tenuis* Hagen, 1868. He defined the genus by two characters exclusive to males: inferior tooth of the

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pretarsus as long as or longer than superior tooth (*e.g.*, Figs. 26, 27*a*), and short and flattened metafemoral spines curved toward the leg base (*e.g.*, Figs. 17, 18).

Brauer (1868) reiterated Hagen's earlier diagnosis of 1868 and Kirby (1889) keyed *Macrothemis* and his new genus *Scapanea* (type species *Libellula frontalis* Burmeister, 1839), differentiating them by the subequal pretarsal teeth (*Macrothemis*) and the greatly dilated abdominal tip (*Scapanea*). Kirby (1889) also designated *L. celeno* as the type species of *Macrothemis*. Karsch (1890) distinguished *Scapanea* from *Macrothemis* by the well-developed Mspl and provided a key to four new species of *Macrothemis* and listed four others. Calvert (1895) added two species of *Macrothemis* from Baja California and noted that his new species *M. inequiunguis* was characterized "by having the tarsal nails toothed before the apex, not bifid as in typical *Macrothemis*".

Kirby (1894) described *Brechmorhoga* as including a single species, *B. grenadensis*, which he distinguished from *Macrothemis* by its bifid frontal tubercle, distinct Mspl (*e.g.*, Fig. 1), and two cell rows in the parallel trigonal field. He commented that "*Dythemis mendax* and *praecox*, Hagen, probably belong either to this genus or to *Macrothemis*". Calvert (1898), using a table and a tabular key, differentiated among *Brechmorhoga*, *Dythemis* Hagen, 1861, *Macrothemis*, and *Paltothemis* Karsch, 1890. He introduced eight new species — one *Dythemis* sp., two *Brechmorhoga* spp., and five *Macrothemis* spp. — and transferred *Dythemis mendax* Hagen, 1861, *D. praecox* Hagen, 1861, *D. pertinax* Hagen, 1861, and *Libellula nubecula* Rambur, 1842 to *Brechmorhoga*. In his key to the Middle American genera of Libellulidae, Calvert (1906) modified characters differentiating *Brechmorhoga* and *Macrothemis* and commented on the difficulty of separating these two genera.

Gynothemis was first mentioned and diagnosed by Ris (based on a name in a manuscript by Calvert) in his generic key in the first volume of the Libellulinen monograph (1909), before Calvert's description (1909) was published the same year. Reliable generic diagnoses were never provided, and the separation of species of these four genera was based largely on the key by Ris (1909). Borror (1945), in his key to genera of New World Libellulidae, separated the four genera based on several wing and male leg characters; *Brechmorhoga* keyed out three times, *Gynothemis* and *Macrothemis* keyed out twice, and *Scapanea* keyed out once.

Novelo-Gutiérrez and Ramírez (1998) and Ramírez and Novelo-Gutiérrez (1999) attempted to distinguish larvae of *Brechmorhoga* and *Macrothemis* using a suite of about a dozen characters. Generic differences were based on larvae of seven species of *Brechmorhoga* (an eighth, *B. travassosi* Santos, 1946, was described by Santos and Costa (1999)) and six species of *Macrothemis*. In describing the larva of *Macrothemis pumila* Karsch, 1890, Fleck (2004) noted that it differed greatly from the known larvae of *Brechmorhoga* and *Macrothemis* and remarked that *M. pumila* could therefore be placed in its own genus, or that larval characters for *Macrothemis* would need to be modified, or that *Brechmorhoga* could be synonymized with *Macrothemis* to accommodate this species.

More species have since been added to all four genera, so that *Macrothemis* contains about 40 species, *Brechmorhoga* about 14, *Gynothemis* 5, and *Scapanea* 2. Inclusion of yet more recently described species has only made generic definitions increasingly vague, although attempts to more clearly define these genera by adult morphology have been offered by Costa and Santos (1991) and Donnelly (1984).

Our objective here is to more precisely define *Brechmorhoga*, *Gynothemis*, *Macrothemis*, and *Scapanea* based on an examination of adults of most species in these genera. Our analysis has resulted in the following taxonomic changes: *Brechmorhoga archboldi* (Donnelly, 1970) **comb. nov.**, *Gynothemis pumila* (Karsch, 1890) **comb. nov.**, *Macrothemis heteronycha* (Calvert, 1909) **comb. nov.**, and *Macrothemis calliste* (Ris, 1916) **comb. nov.** The male of *M. calliste* is described and illustrated for the first time.

Methods

All specimens were examined to establish variability of characters. Species examined are indicated with an asterisk. Characters were illustrated with the aid of a camera lucida. Acronyms used for collections are as follows:

IRSN Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium

RNHL Nationaal Natuurhistorisch Museum ("Naturalis"), Leiden, the Netherlands
RWG R.W. Garrison personal collection, Sacramento, California, United States of America
USNM National Museum of Natural History, Smithsonian Institution, Washington, D.C., United States of America

Diagnostic characters

Tarsal claw (Figs. 23–29). A smaller inferior tooth typifies most libelluline genera, but most species of *Macrothemis* possess a subequal biramous tarsal claw (inferior tooth as long as or longer than tip of claw, Figs. 26, 27*a*). Two species are dimorphic with respect to inner and outer claws of the same leg (outer tooth longer than claw and inner tooth shorter than claw in meso- and meta-thoracic legs, Figs. 27*a*, 27*b*): *M. heteronycha* and *M. absimilis* Costa, 1991 (the latter species was originally described as *M. absimile*, but since *Macrothemis* is feminine, the specific epithet must be changed to agree with its gender according to Article 34.2 of the *International Code of Zoological Nomenclature* (ICZN 1999)). **Metathoracic femoral armature in males** (Figs. 14–22). Presence (*Brechmorhoga*, *Macrothemis*, *Scapanea*) or absence (*Gynothemis*) of modified proximally directed spines. **Vein Mspl.** Mspl was scored as well defined (*Brechmorhoga*, *Scapanea*, *Macrothemis griseofrons* Calvert, 1909, Figs. 1–3) if at least three cells were delimited ventrally by a continuously smooth arcuate vein (*e.g.*, Fig. 1); otherwise, it was scored as not defined (*Gynothemis*, *Macrothemis*, Figs. 4–10). **Male vesica spermalis** (Figs. 30–39), lateral view. With a long, thin, scimitar-like sclerotization (*Gynothemis*, Figs. 37, 38, except for *G. uniseta* Geijskes, 1972, Fig. 39) or broad and rounded (*Brechmorhoga*, *Macrothemis*, *Scapanea*, Figs. 30–36).

Other characters used by previous workers were also examined but were found to be variable and therefore not diagnostic at the generic level (*e.g.*, bilobed condition of postfrons, undulation of RP_2).

Abbreviations

Wing terminology follows Riek and Kukalová-Peck (1984). Abbreviations are as follows: anx, antenodal crossveins; arc, arculus; thx, pterothorax; fw, forewing; hw, hind wing; fe, femur; cl, claw; ve, vesica spermalis; gf, genital fossa; vu, vulvar lamina; ab, abdomen; s*n*, abdominal segment(s) number(s); and app, caudal appendages (cerci and epiproct).

Taxonomic treatment

Key to *Macrothemis* group of Libellulidae

Males

1. s7–9 not widened 2
1′. s7–9 widened and flattened 3
2(1). Spines of hind fe (CAUTION: check to see that spines are not broken) all short, stout, and directed proximally (*e.g.*, Figs. 17, 18) . . . . . *Macrothemis* (in part)
2′. Spines of hind fe (CAUTION: check to see that spines are not broken) gradually increasing in length distally (Fig. 15) *or* dimorphic; with long and short series (Figs. 14, 16) . . . . . *Gynothemis*
3(1′). Widest point of s7–9 less than twice as wide as base of s7; southwestern United States, Dominica, Grenada, Trinidad, south through northern Argentina 4
3′. Widest point of s7–9 about 3–3.5 times as wide as base of s7 (Fig. 52); Greater Antilles . . *Scapanea*
4(3). Short inner tarsal cl (Figs. 23, 24); relatively wide discoidal field in fw (Figs. 1, 2), with discoidal index (ratio of distance between MA and MP at wing margin divided by distance at proximal portion) approximately 1.4–1.8; longer body (40–62 mm); Mspl usually distinct (Figs. 1, 2) . . . . . *Brechmorhoga*
4′. Long inner tarsal cl (*e.g.*, Figs. 26, 27*a*, except for members of *M. tessellata* group of species); relatively narrow discoidal field in fw (Figs. 4–7), with discoidal index <1.0–1.3; shorter body (21–42 mm); Mspl indistinct (except for *M. griseofrons*) . . . . . *Macrothemis* (in part)

Females

1. Mspl in fw indistinct (*e.g.*, Figs. 4–7) (except for *M. griseofrons*); epiproct shorter than cerci, never polished or greatly enlarged . . . . . *Gynothemis*, *Macrothemis*
1′. Mspl in fw distinct (Figs. 1–3) (except for *B. flavopunctata*, *B. travassosi*, and some *B. nubecula*, in which case the epiproct is as long as or longer than cerci, greatly enlarged, and polished; Fig. 58) . . 2
2(1′). fw discoidal field widening distally (Figs. 1, 2); southwestern United States, Dominica, Grenada, Trinidad, south through northern Argentina . . . . . *Brechmorhoga*
2′. fw discoidal field narrowing distally (Fig. 3); Greater Antilles . . . . . *Scapanea*

Brechmorhoga Kirby, 1894

(Figs. 1–2 (fw, hw), 11–12 (arc), 19–21 (fe), 23–24 (cl), 31 (ve), 44 (gf), 51 (ab), 58 (app), 60–61 (vu))

Brechmorhoga Kirby, 1894

Type species: *Brechmorhoga grenadensis* Kirby, 1894 (by original designation).

Nothemis Navás, 1915: 146.

Type species: *Nothemis apollinaris* Navás, 1915 (by original designation).

Diagnosis

Medium to large libellulines (40–62 mm); elongate, slender, black body with irregular patterns of striping on thorax and white to yellow spots on several abdominal segments. Wings hyaline, with fw discoidal field widening distally and Mspl and Rspl distinct (Fig. 1). Male hind fe (Fig. 19*a*) with short, stout spines directed proximally (shared with *Macrothemis* and *Scapanea*). In most species, male s7–9 widened and flattened, with widest point less than twice as wide as base of s7 (shared with some species of *Macrothemis*); vu less than one third the length of s9 and not projected ventrally (Fig. 60*a*).

Brechmorhoga is similar to *Macrothemis* in stature, shape, and habits. The following characters (those in parentheses applicable to *Macrothemis*) have been used to separate the two genera (Donnelly 1984): shorter inner tarsal cl (longer inner tarsal cl, except for members of *M. tessellata* (Burmeister, 1839) group of species); relatively wider discoidal field in fw (Figs. 1, 2), with discoidal index (ratio of distance between MA and MP at wing margin divided by distance at proximal portion) approximately 1.4–1.8 (narrower, with discoidal index <1.0–1.3, Figs. 4–7); longer body, 40–62 mm (shorter, 21–42 mm). In addition, Mspl is usually distinct in *Brechmorhoga* (Figs. 1, 2), whereas it is usually indistinct in *Macrothemis* (Figs. 4–7) (only known exception being *M. griseofrons*).

Distribution

Southwestern United States south through northern Argentina.

Species

This genus comprises 16 species: *B. archboldi* (Donnelly, 1970)*, *B. diplosema* Ris, 1913, *B. flavoannulata* Lacroix, 1920, *B. flavopunctata* (Martin, 1897), *B. innupta* Rácenis, 1954, *B. latialata* González, 1999*, *B. mendax* (Hagen, 1861)*, *B. neblinae* De Marmels, 1989*, *B. nubecula* (Rambur, 1842)*, *B. pertinax* (Hagen, 1861)*, *B. praecox* (Hagen, 1861)*, *B. praedatrix* Calvert, 1909*, *B. rapax* Calvert, 1898*, *B. tepeaca* Calvert, 1908*, *B. travassosi* Santos, 1946*, and *B. vivax* Calvert, 1906*.

Brechmorhoga archboldi (Donnelly, 1970) comb. nov.

(Figs. 1–2 (fw, hw), 11 (arc), 21 (fe), 23 (cl), 51 (ab), 60 (vu))

Material examined

1 female. **BRITISH WEST INDIES: Dominica,** Freshwater Lake, 16.ix.1964, T. Spilman (1 female, USNM).

Remarks

Through the courtesy of Dr. Oliver S. Flint, Jr., we were able to examine the holotype female and only known specimen of this species. Donnelly (1970) argued that reduction of wing venation characters in *Scapanea archboldi* compared with *Scapanea frontalis* (Burmeister, 1839) would be due to the smaller size of the former. He justified its placement in *Scapanea* based on the position of the arculus opposite to or close to anx 2 (Fig. 11*b*), width of the abdomen ("…conspicuously greater…than in either of the two species [*B. praecox grenadensis* and

B. nubecula] from Trinidad"), and similarity of hind femoral armature ("…femoral spines taper rather gradually in length proximally. In *Brechmorhoga* females the penultimate spines are subequal in length."). However, placement of arc in hw relative to anx 2 is variable among examined females of *Brechmorhoga* (*i.e.*, Figs. 12, 13) and *S. frontalis* (five females from Puerto Rico, six females from Dominican Republic, and one female from Jamaica) and even between both hw in the holotype of *S. archboldi* (Figs. 11*a*, 11*b*). Female hind femoral armature is as variable within species as between species (Figs. 19*b*–22*a*). Although the abdomen in *B. p. grenadensis* is proportionally longer than that in *S. archboldi*, the width of its distal portion in the latter species (we relaxed the flattened posterior abdominal segments and arranged the tergites to their original three-dimensional form, Fig. 60*a*) approximates that in *B. p. grenadensis*. None of the above characters can be used to justify a generic separation between *S. archboldi* and *B. p. grenadensis*. Wing venation characters (especially the widening of the discoidal field at the wing margin, Fig. 2), hind femoral armature (Fig. 21), pretarsal morphology (Fig. 23), and shape of the vulvar lamina (Fig. 60) of the holotype of *S. archboldi* are consistent with those of *B. p. grenadensis* (Figs. 1, 20, 24, 61) and suggest that *S. archboldi* should be placed in *Brechmorhoga* rather than in *Scapanea*. Jerrell J. Daigle (personal communication) recently collected two males and a female of *B. archboldi* in Dominica; his assessment of them in the light of our manuscript and our examination of the photographs of one of the males corroborate our placement of this species in *Brechmorhoga*.

We submerged the pterothorax of the poorly preserved holotype in acetone to reveal the color pattern and found vestiges of an incomplete interpleural stripe not mentioned in the original description (Donnelly 1970). Accordingly, *B. archboldi* will key to the *B. praecox* group in Ris (1913) (with an incomplete narrow light green stripe extending from venter of thorax to metathoracic spiracle, in addition to the two wider lateral pale stripes), but can be separated as follows:

1. Female vu shallowly cleft, mesal margins of lobes divergent, width of each lobe narrower than width of cleft (as in Fig. 59*b*); labrum pale, usually with a dark stripe along free margin; ab (36–40 mm) slightly longer than hw (35–38 mm); Mexico south through northern Argentina . . . . . *B. vivax*

1′. Female vu deeply cleft, mesal margins of lobes parallel or nearly so, width of each lobe wider than width of cleft (Figs. 61*a*, 61*b*); labrum entirely pale; ab (33–39 mm) considerably longer than hw (30–35 mm); Mexico south through Peru and Brazil. . . . . *B. praecox*

1″. Female vu deeply cleft, mesal margins of lobes divergent, width of each lobe about the same as width of cleft (Fig. 60*b*); labrum mostly dark with poorly defined pale area at base; ab (32 mm) slightly longer than hw (31 mm); Dominica . . . . . *B. archboldi*

Gynothemis Calvert *in* Ris, 1909

(Figs. 8–10 (fw, hw), 14–16 (fe), 28–29 (cl), 37–39 (ve), 45–47 (gf), 49–50 (thx), 54 (ab), 56–57 (app), 63–64 (vu))

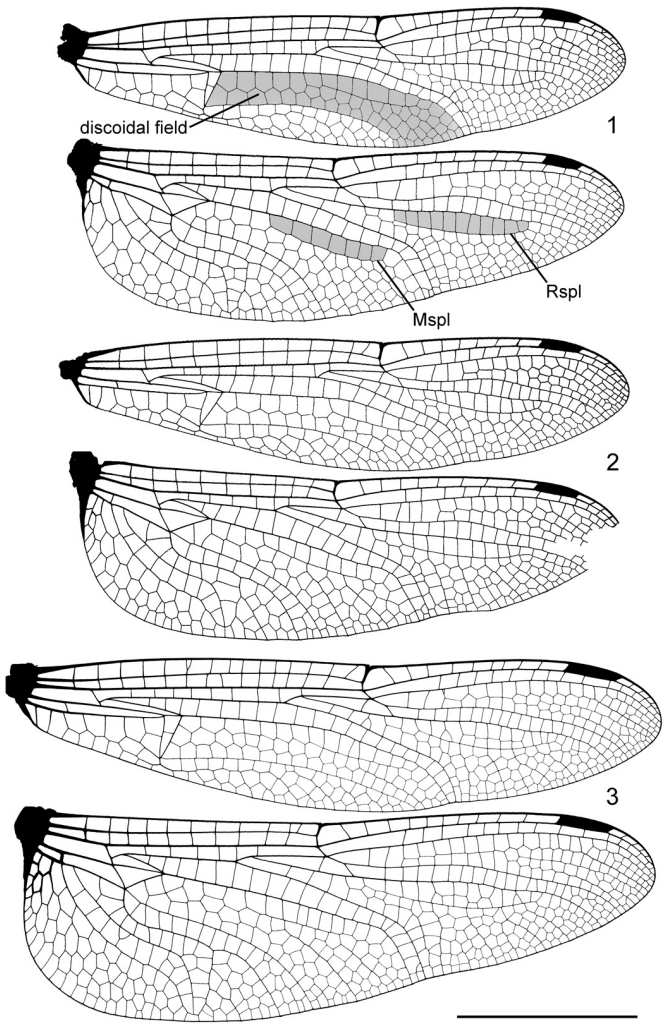
Type species: *Gynothemis venipunctata* Calvert *in* Ris, 1909 (by original designation).

Diagnosis

Moderately small (22–27 mm), delicately built libellulines. Postfrons and vertex brown to metallic blue in mature males; thx relatively small, dark brown with yellow stripes or with yellow lateral sides; ab cylindrical, brown with pale sterna and tergal stripes. Hind femoral armature in males variable: spines gradually increasing in length distally (*G. venipunctata*, Fig. 15), absent except for one distal spine (*G. uniseta*, Fig. 14), or extremely short on basal half and increasing distally on distal half of fe (*G. pumila*, Fig. 16). Tooth of pretarsus shorter than cl (*G. venipunctata* and *G. uniseta*, Fig. 29) or apical in position and as long as cl (*G. pumila*, Fig. 28). Wings hyaline (*G. pumila*, *G. uniseta*, Figs. 8–9) or with golden yellow spot at wing base (*G. venipunctata*, Fig. 10); fw triangle and supratriangle free; Mspl indistinct.

Males of *Gynothemis* can be distinguished from those of *Macrothemis* by the morphology of femoral spines (short, stout, and directed proximally in *Macrothemis*, Figs. 17, 18; not short and stout, and directed distally in *Gynothemis*, Figs. 14–16). Based on examined characters, we have been unable to distinguish females of these

Figs. 1–3. Female wings: 1, *Brechmorhoga praecox grenadensis* (Trinidad); 2, HOLOTYPE *B. archboldi* (Dominica); 3, *Scapanea frontalis* (Dominican Republic). Scale bar = 10 mm.



two genera; thus, assignment of females to genus can be done only by species identification.

The larva of *G. uniseta* is more similar to larvae of the Antillean endemic genus *Scapanea* than to larvae of *Macrothemis*. Fleck (2004) provided a detailed comparison of the larva of *G. pumila* with those of *Macrothemis* and *Brechmorhoga* and showed that it differs from all of them; however, it agrees well with the description of *G. uniseta* (Geijskes 1972).

The status of *G. aurea* Navás, known only from the holotype female of unknown location, is uncertain. According to its original description (Navás 1933), *G. aurea* is larger (hw 30.5 mm) than any of the other known species of *Gynothemis* (hw 19–22 mm) and, with its unequally shaped tarsal claws, could well be placed in the *M. tessellata* group.

Distribution

Trinidad south to São Paulo and Mato Grosso states in Brazil.

Species

This genus comprises 4 species: *Gynothemis aurea* Navás, 1933, *G. venipunctata* Calvert *in* Ris, 1909*, *G. pumila* (Karsch, 1890)*, and *G. uniseta* Geijskes, 1972*.

Gynothemis pumila (Karsch, 1890) comb. nov.

(Figs. 9 (fw, hw), 16 (fe), 28 (cl), 37 (ve), 45 (gf))

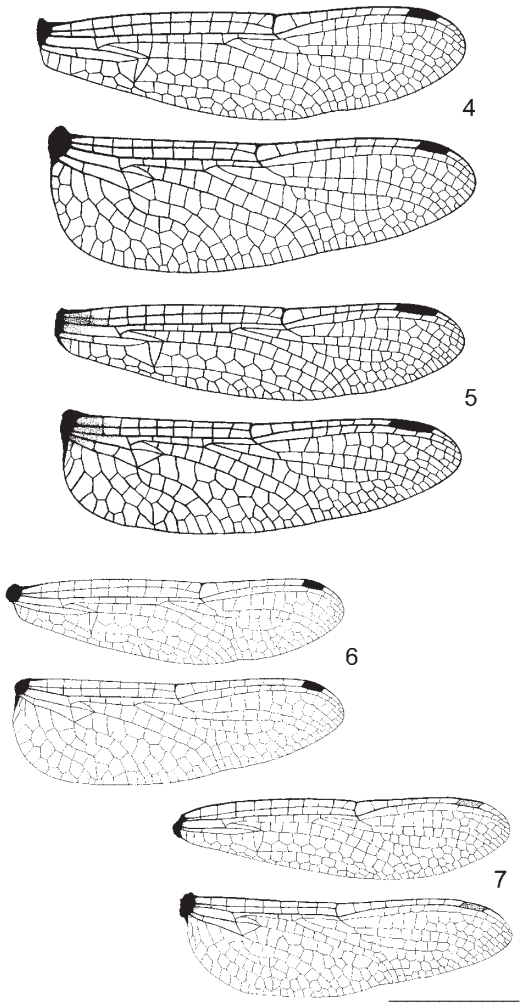
Material examined

8 males, 18 females. **TRINIDAD:** St. George Co., forest and small stream along trail called Indian Walk Ride off Main Road, 1.9 mi. N of Cumato, 11.i.1981, R. Garrison (4 males, 2 females). **FRENCH GUIANA: Departement de la Guyane,** Cacao, 4°35′N, 52°28′W, 31.viii.2001, P. Johnson (2 females). **VENEZUELA: Bolivar State,** Canaima at Río Carrao, palm marsh, 6°30′N, 62°50′W, 700 m, 22–25.xi.1980, R. and J. Garrison (2 females); same data but 12–14.viii.1990, R. Garrison (1 male, 2 females); Río Churun at entrance to Salto Angel, 10–12.viii.1990, R. Garrison (1 female); creek at vicinity of El Pauji, late afternoon, 1000 m, 4.viii.1990, R. Garrison (1 male, 2 females). **BRAZIL: Amazonas State,** Manaus, 3°06′S, 60°00′W, 20.vi.1922, J.H. Williamson and J.W. Strohm (2 males); Reserva Ducke, 26 km E Manaus, 2–4.ii.1979, O. Flint, Jr. (3 females); **Rondônia State,** Fazenda Rancho Grande, 62 km SW of Ariquemes, 10°32′S, 62°48′W, 187 m, 17–24.iii.1989, J. Pasko (1 female); 2–11.xi.1989, R. Garrison (2 females); **São Paulo State,** Represa Beija Flor, Luiz Antonio, 8.ix.2001, F. Lencioni (1 female). All specimens in RWG.

Remarks

The small species *Macrothemis pumila* has long been known to be the sole exception as regards femoral spine morphology in males of *Macrothemis*, and its larva is also strikingly different from remaining known *Macrothemis* larvae (Fleck 2004) and agrees well with that of *G. uniseta*. We transfer this species, as did Costa and Santos (1991), to *Gynothemis* because the condition of the male hind femora (distally directed spines that are extremely short basally and slender distally) is unlike that of any *Macrothemis* species and the morphology of the vesica spermalis (Fig. 37) is the same as that for *G. venipunctata* (Fig. 38) and different from those found in *Macrothemis* (Figs. 32–36). The sole reason for retaining *G. pumila* in *Macrothemis* would seem to be the subequal tarsal teeth, a condition that is found in several *Macrothemis* species. However, this is not a diagnostic character for *Macrothemis*, since several species have unequal tarsal claws (see discussion under *Macrothemis*).

Figs. 4–7. Wings: 4, male *Macrothemis tessellata* (Mexico: Chiapas); 5, male *M. heteronycha* (Brazil: Santa Catarina); 6, male *M. calliste* (Brazil: Brasilia); 7, female HOLOTYPE *M. calliste* (Brazil: Minas Gerais). Scale bar = 10 mm.



Gynothemis uniseta Geijskes, 1972

(Figs. 8 (fw, hw), 14 (fe), 39 (ve), 46 (gf), 50 (thx), 64 (vu))

Remarks

Through the kindness of J. van Tol, we were able to examine a pinned pair of this species from Surinam (Boven Para District, Niskomend, 23.iv.1962 (Jean Belle), 1 male;

Boven Para District, Brokopondo, 5°04′N, 54°58′W, 23.iv.1962 (Jean Belle), 1 female; RNHL). The morphology of the femoral armature indicates that the species is correctly placed in *Gynothemis*. The vesica spermalis (Fig. 39) is similar to that of *G. pumila* and *G. venipunctata* but lacks the lateral scimitar-like sclerotizations present in those species (Figs. 37–38).

Costa and Santos (1991) proposed a redistribution of certain species of *Macrothemis* to *Gynothemis* as follows (translated from the Portuguese):

> "Spines of femur 3 quadrangular; flattened frons; lateral lobes of penis short and median lobe weakly chitinized . . . . . *Macrothemis*.
>
> Spines of femur 3 triangular; bifid frons; lateral lobes of penis apically prolonged and median lobe well chitinized . . . . . *Gynothemis*.
>
> According to this concept, the following species are redistributed: *Gynothemis venipunctata* (Calvert 1909), type by original designation; *Gynothemis heteronycha* (Calvert 1909) Ris 1916; *Gynothemis calliste* (Ris 1916) (only one female described, not examined in the present study); *Gynothemis marmorata* (Hagen 1861); *Gynothemis tenuis* (Hagen 1861); *Gynothemis capitata* (Calvert 1909); *Gynothemis musiva* (Hagen 1861); *Gynothemis pumila* (Karsch 1890); and *Gynothemis hosanai* (Santos 1967). *Macrothemis* and *Brechmorhoga* are closely related, however they can be separated by the characters well-defined by Donnelly (1984)".

Although *G. uniseta* lacks the long lateral sclerotizations of the vesica spermalis present in both *G. pumila* and *G. venipunctata*, it agrees well with these two species in all other characters. We disagree with Costa and Santos's (1991) placement of *M. marmorata*, *M. tenuis*, *M. capitata* Calvert, 1909, *M. musiva* Calvert, 1989, and *M. hosanai* Santos, 1967 in *Gynothemis*, because all of these species have short, stout spines directed proximally on femur 3 (as in Figs. 17, 18), which is characteristic of *Macrothemis*. We examined the frons of three species of *Gynothemis* and 27 of the 40 known *Macrothemis* species (see under *Macrothemis* below), and they all are cleft, from slightly to strongly bifid, without any separation into two groups.

Key to species of *Gynothemis*

1. Sides of thx ochraceous, becoming dark brown ventrally on venter of thx and anteriorly on mesepisternum (Fig. 49), metathoracic tarsal claws with inferior tooth much shorter than attenuate tip of claw (Fig. 29); Venezuela south through Mato Grosso State in Brazil . . . . . *G. venipunctata*

1′. Sides of thx dark with pale thoracic stripes (Fig. 50), metathoracic tarsal claws with inferior tooth slightly shorter than or surpassing claw (Fig. 28); Trinidad south through southeastern Brazil. . . . 2

2(1′) Hind fe lacking spines except for one distal spine (Fig. 14), metathoracic tarsal claws with inferior tooth slightly shorter than tip of claw; Surinam . . . . . *G. uniseta*

2′. Hind fe with outer row of spines extremely short on basal half and increasing in length on distal half of fe (Fig. 16), metathoracic tarsal claws with inferior tooth strongly developed and surpassing tip of claw (Fig. 28); Trinidad south through southeastern Brazil. . . . . *G. pumila*

Macrothemis Hagen, 1868

(Figs. 4–7 (fw, hw), 17–18 (fe), 26–27 (cl), 32–36 (ve), 40–42 (gf), 48 (thx), 53 (ab), 55 (app), 62 (vu))

Macrothemis Hagen, 1868

Type species: *Libellula celeno* Selys *in* Sagra, 1857 (Kirby, 1889 by subsequent designation).

Cendra Navás, 1916: 74.

Type species: *Cendra cearana* Navás, 1916 (by original designation).

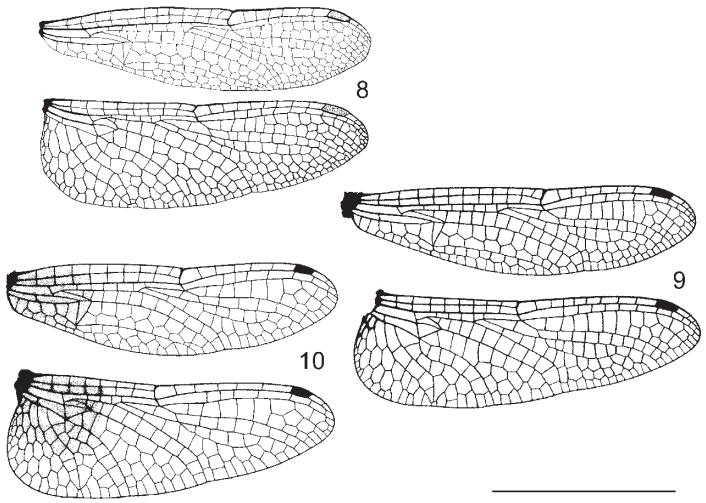
Ophippus Navás, 1916: 76.

Type species: *Ophippus garbei* Navás, 1916 (by original designation).

Diagnosis

Small to large (29–52 mm), delicately built libellulines, with relatively small thorax and spindle-shaped ab that is broadened and flattened on s9 in some species. Antefrons and vertex brown to metallic blue in mature males; thx and ab dark brown to black, often with yellowish green markings. Wings (Figs. 4–7) hyaline

Figs. 8–10. Male wings: 8, *Gynothemis uniseta* (Surinam); 9, *G. pumila* (Trinidad); 10, *G. venipunctata* (Venezuela: Bolivar). Scale bar = 10 mm.

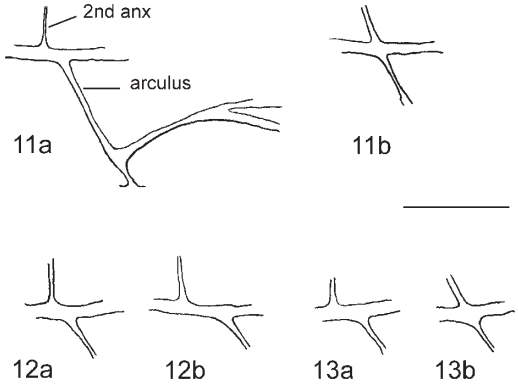


to infumated with brown in some females; fw triangle free (except in *M. griseofrons*); Mspl in fw not developed (except in *M. griseofrons*), often lacking to poorly developed in hw; fw discoidal field narrowing, parallel-sided, or widening slightly toward wing margin; hw not widened at base (except in *M. flavescens* [Kirby]). Metafemora in males (Figs. 17, 18) with short and stout spines directed proximally (shared with *Brechmorhoga* and *Scapanea* species); tooth of pretarsus as long as tip and near middle of cl (Fig. 26), except in *Macrothemis aurimaculata* Donnelly, 1984, *M. brevidens* Belle, 1983, *M. newtoni* Costa, 1990, *M. tessellata*, and *M. valida* Navás, 1916, which have a tooth shorter than cl, and in *M. heteronycha* and *M. absimilis*, which have dimorphic pretarsi with outer tooth longer than cl and inner tooth shorter than cl in meso- and metathoracic legs (Figs. 27*a*, 27*b*).

Males of *Macrothemis* and *Gynothemis* can be diagnosed on the basis of the femoral armature (short, stout, proximally directed spines in *Macrothemis*, Figs. 17, 18; never so in *Gynothemis*, Figs. 14–16), but we have been unable to diagnose the females, and it would not be surprising if future studies proved *Macrothemis* to be paraphyletic, with some species more closely related to *Gynothemis* (*e.g.*, *inequiunguis* group of species shares some aspects of larval morphology with the latter, see Fleck 2004).

This large genus is badly in need of revision; several species are poorly known and inadequately described. Another complicating factor is that females, which are more difficult to identify, are collected more often than males and some species were originally described from this sex. The latest species was described by May (1998), who provided a key to males of all known species.

Figs. 11–13. Second antenodal crossvein (anx) and arculus (*a*, left hind wing; *b*, right hind wing): 11, HOLOTYPE *Brechmorhoga archboldi* (Dominica); 12–13, female *B. praecox grenadensis* (Trinidad). Scale bar = 1 mm.



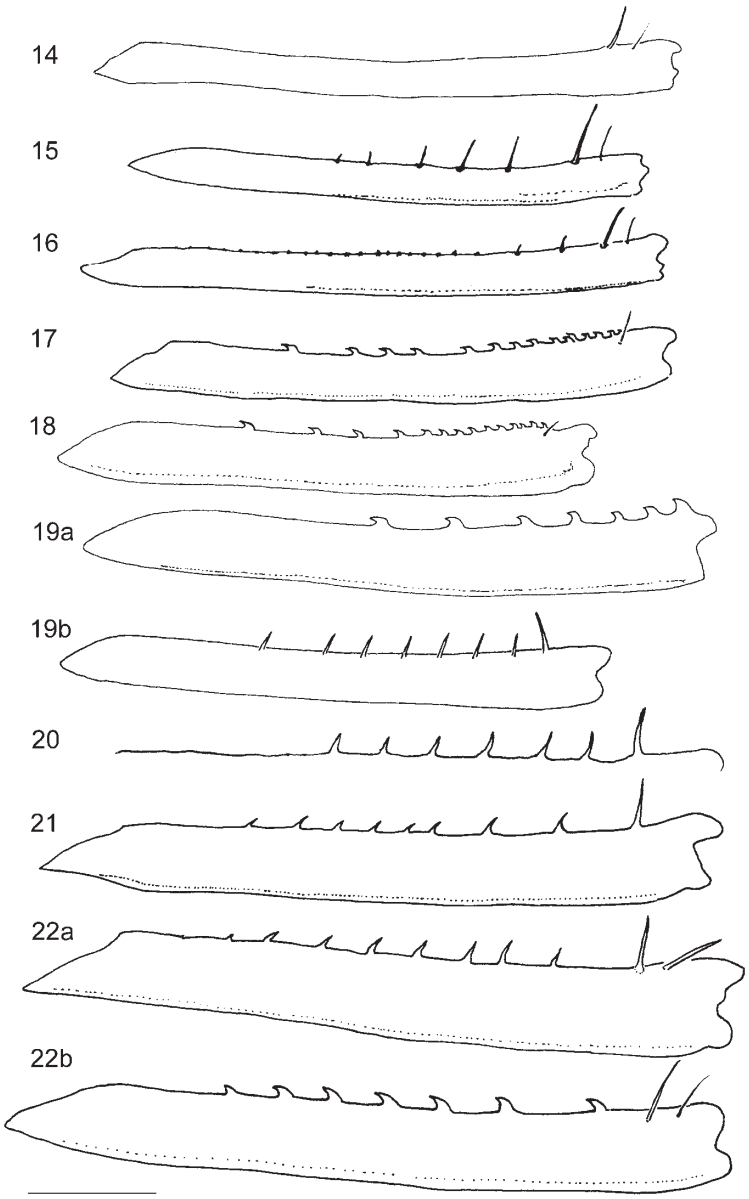
Distribution

Southern Texas and Arizona south through Uruguay and central Argentina.

Species

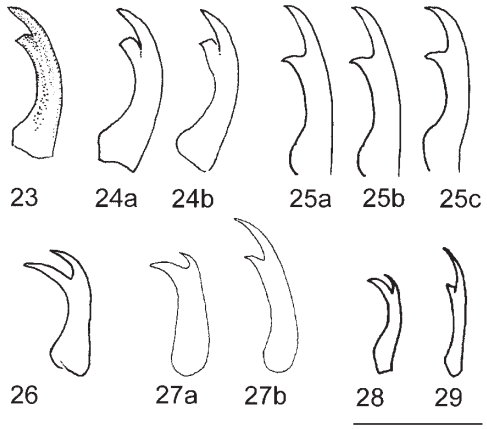
This genus has 40 species: *M. absimilis* Costa, 1991*, *M. aurimaculata* Donnelly, 1984*, *M. belliata* Belle, 1987, *M. brevidens*

Figs. 14–22. Hind femur, lateral view: 14, male *Gynothemis uniseta* (Surinam); 15, male *G. venipunctata* (Venezuela: Bolivar); 16, male *G. pumila* (Brazil: Amazonas); 17, male *Macrothemis calliste* (Brazil: Brasilia); 18, male *M. heteronycha* (Brazil: Santa Catarina); 19*a*, male, 19*b*, female *Brechmorhoga nubecula* (Trinidad); 20, female *B. praecox grenadensis* (Trinidad); 21, female HOLOTYPE *B. archboldi* (Dominica); 22*a*, female (Jamaica), 22*b*, male (Puerto Rico) *Scapanea frontalis*. Scale bar = 1 mm.



Belle, 1983*, *M. calliste* (Ris, 1913)*, *M. capitata* Calvert, 1909, *M. celeno* (Selys *in* Sagra, 1857)*, *M. cynthia* Ris, 1913, *M. declivata* Calvert, 1909*, *M. delia* Ris, 1913*, *M. extensa* Ris, 1913*, *M. fallax* May, 1998*, *M. flavescens* (Kirby, 1897)*, *M. griseofrons* Calvert, 1909*, *M. guarauno* Rácenis, 1957, *M. hahneli* Ris, 1913*, *M. hemichlora* (Burmeister, 1839)*, *M. heteronycha* (Calvert, 1909)*, *M. hosanai* Santos, 1967, *M. idalia* Ris, 1919*, *M. imitans* Karsch, 1890*, *M. inacuta* Calvert, 1898*, *M. lauriana* Ris, 1913, *M. ludia* Belle, 1987, *M. lutea* Calvert, 1909*, *M. marmorata* Hagen, 1868*,

Figs. 23–29. Hind pretarsal claw, lateral view: 23, female HOLOTYPE *Brechmorhoga archboldi* (Dominica); 24*a*, 24*b*, female *B. praecox grenadensis* (Trinidad); 25*a* (Puerto Rico), 25*b* (Dominican Republic), 25*c* (Jamaica), female *Scapanea frontalis*; 26, male *Macrothemis calliste* (Brazil: Brasilia); 27*a*, inner claw, 27*b*, outer claw, male *M. heteronycha* (Brazil: Santa Catarina); 28, male *Gynothemis pumila* (Brazil: Amazonas); 29, male *G. venipunctata* (Venezuela: Bolivar). Scale bar = 0.5 mm.



M. mortoni Ris, 1913*, *M. musiva* Calvert, 1898*, *M. newtoni* Costa, 1990, *M. nobilis* Rácenis, 1957, *M. pleurosticta* (Burmeister, 1839), *M. polyneura* Ris, 1913*, *M. proterva* Belle, 1987, *M. pseudimitans* Calvert, 1898*, *M. rochai* Navás, 1918, *M. rupicola* Rácenis, 1957*, *M. tenuis* Hagen, 1868*, *M. tessellata* (Burmeister, 1839)*, *M. ultima* González-Soriano, 1992*, and *M. valida* Navás, 1916.

Macrothemis heteronycha (Calvert in Ris, 1909) comb. nov.

(Figs. 5 (fw, hw), 18 (fe), 27 (cl), 35 (ve))

Material examined

2 males, 1 female. **BRAZIL: Minas Gerais State,** Caxambu, xi.1978, A. Machado (1 male); Juiz de Fora, iii.1965, A. Machado (1 female); **Santa Catarina State,** Nova Teutonia, 27°11′S, 52°23′W, 300 m, iii.1975, F. Plaumann (1 male). All specimens in RWG.

Remarks

This species was originally described under *Brechmorhoga* and later transferred to *Gynothemis* by Ris (1913: 898; "I do not consider it correct to put *heteronycha* in *Brechmorhoga* as CALVERT did, because of the reasons I provided before under *M. tessellata* [unequal tarsal claws], characters which appear in stronger extent in *heteronycha*."). We have transferred *Gynothemis heteronycha* to *Macrothemis*, as this species has short, stout, proximally directed femoral spines (Fig. 18), and the morphology of the cerci and the distal segment of the vesica spermalis (Fig. 35) are similar to those of the *M. tessellata* group of species. It also shares the presence of two CuA crossveins with *M. absimilis*, *M. tenuis*, and *M. ultima*, and its male dimorphic pretarsal teeth (Fig. 27) are shared only with *M. absimilis*.

Males of *M. heteronycha* key to *M. absimilis* in May (1998) but differ from it (characters for *M. absimilis* in parentheses) by having small dark brown basal wing spots (large golden yellow spots at basal fourth of wings) and by possessing a strongly prominent protuberance laterally on the postfrons (lateral area of postfrons largely flat or slightly prominent).

Macrothemis calliste (Ris, 1913) comb. nov.

(Figs. 6–7 (fw, hw), 17 (fe), 26 (cl), 34 (ve), 40 (gf), 48 (thx), 53 (ab), 55 (app), 62 (vu))

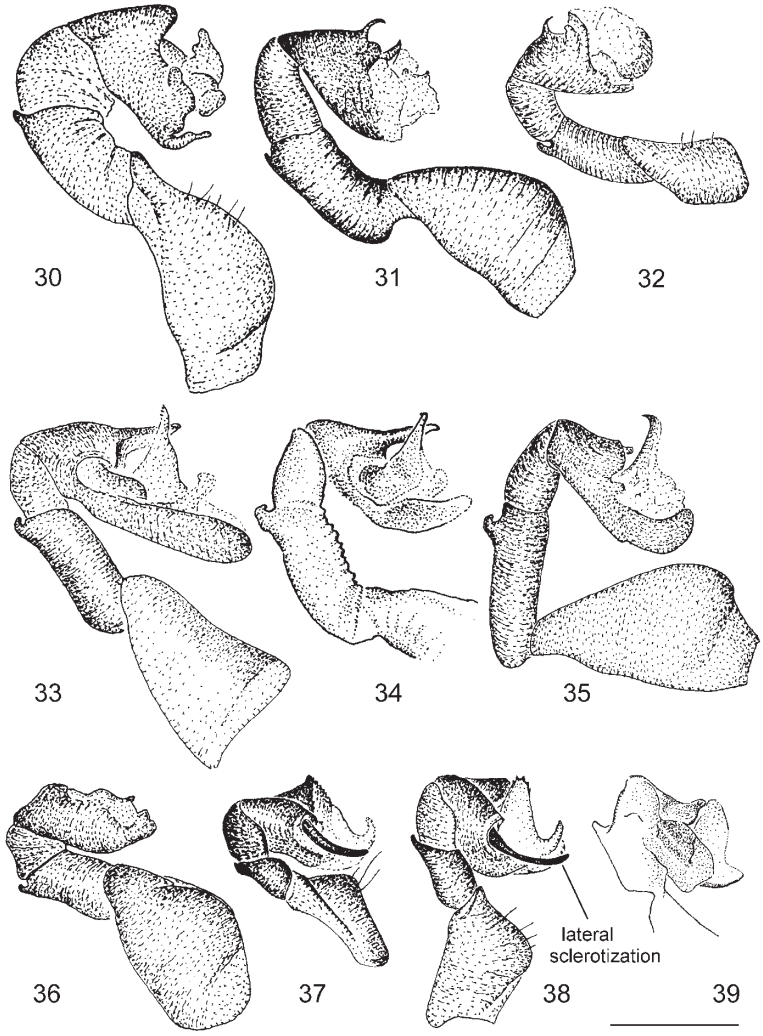
Material examined

1 male, 1 female. **BRAZIL: Brasilia,** Brasilia Lake, small river on north side, 22.x.1978, D.A.L. Davies (1 male, 1 female). All specimens in RWG.

Remarks

This species was originally described under *Gynothemis*, based on a single female from Minas Gerais, Brazil (Ris 1913). Thanks to the courtesy of Jérôme Constant (IRSN), who sent us photographs of the wings, thorax, and abdomen of the holotype female, we were able to identify a pair of specimens from Brasilia as this species. Both specimens agree well with venational characters of the holotype (Figs. 6, 7) and the color pattern, length of abdomen, and overall size (male: hw, 25; ab, 24; pt, 1.5; female: hw, 26; ab, 25; pt[erostigma], 1.7) provided in the original description (Ris 1916: 899), which we translate here:

Figs. 30–39. Male vesica spermalis, lateral view: 30, *Scapanea frontalis* (Puerto Rico); 31, *Brechmorhoga nubecula* (Trinidad); 32, *Macrothemis brevidens* (French Guiana: Montagne-des-chevaux); 33, *M. musiva* (Brazil: São Paulo); 34, *M. calliste* (Brazil: Brasilia); 35, *M. heteronycha* (Brazil: Santa Catarina); 36, *M. celeno* (Puerto Rico); 37, *Gynothemis pumila* (Trinidad); 38, *G. venipunctata* (Venezuela: Bolivar); 39, *G. uniseta* (Surinam). Scale bar = 0.5 mm.

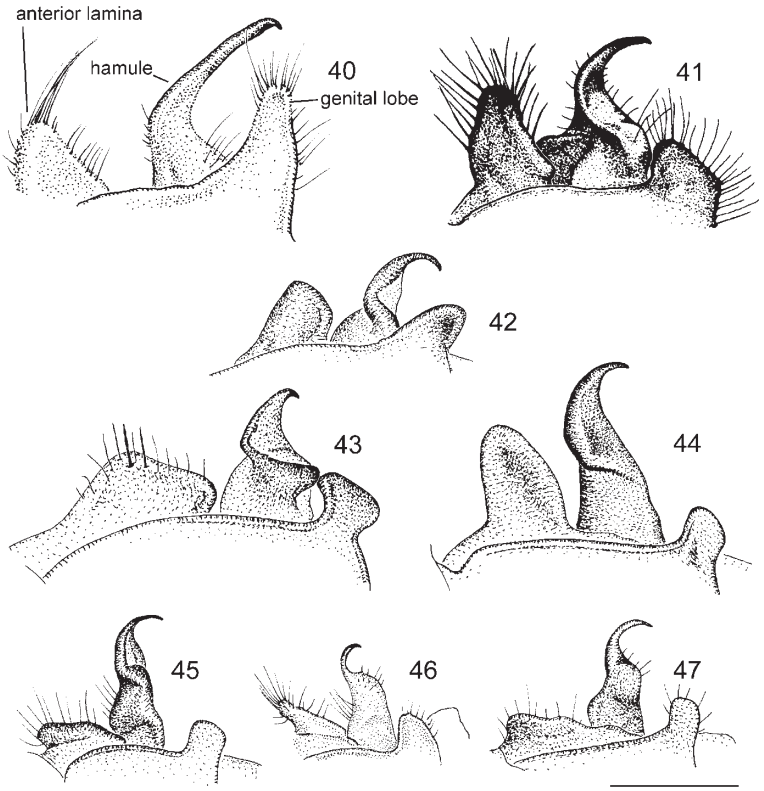


"**G. calliste** (SELYS mss) nov. spec.

Coll. Selys 1 ♀ Minas Geraes

♀. labrum brownish, medial lobe and medial part of lateral lobes darker. Face, frons and vertex brownish yellow. Frons rounded, the cleft flatter and the prominence at the sides lower than in *heteronycha*. Thorax very light reddish brown; at the front above the middle on each side with a quadrangular dark spot, touching the light middle line and reaching to about ⅔ of the height upwards; lateral to its upper end a slightly diffuse small spot. Sides broadly blackish latero-ventrally, and separated by a narrow light intermediate space from an undulated transverse dark band. Abdomen cylindrical, light reddish brown with blackish dorsal carina, blackish articulations and blackish, and from the lateral margin rather widely separated lateral bands on segments 1–9. (Vulvar lamina not clearly visible); the carina of the ventral plate of 9 starts at the proximal third and extends only a little ventrally. Legs light brown with dark spines. Fem. 3 with ca. 9 fine, rather long spines; Fem. 2 similar; tibial spines numerous, relatively

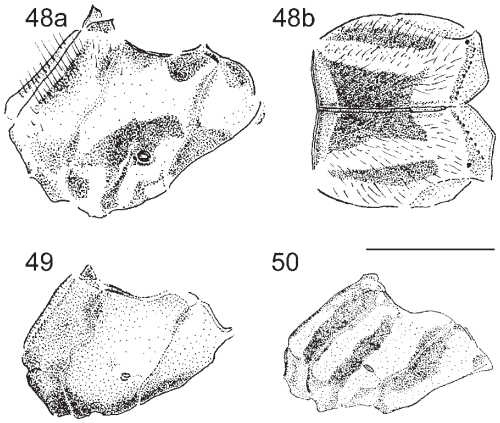
Figs. 40–47. Male genital fossa, lateral view: 40, *Macrothemis calliste* (Brazil: Brasilia); 41, *M. hahneli* (Argentina: Jujuy); 42, *M. celeno* (Puerto Rico); 43, *Scapanea frontalis* (Puerto Rico); 44, *B. nubecula* (Trinidad); 45, *Gynothemis pumila* (Trinidad); 46, *G. uniseta* (Surinam); 47, *G. venipunctata* (Venezuela: Bolivar). Scale bar = 0.5 mm.



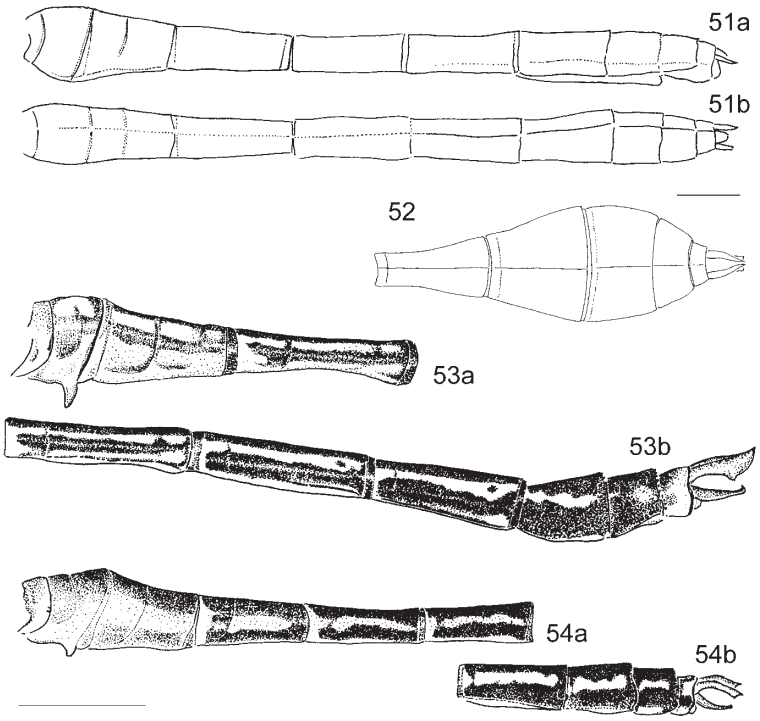
long, fine. Claws long and narrow, the tooth about at the middle. Wings hyaline, a small blackish basal spot narrowly bordered with yellow in hw: in C a trace, in Sc to almost Anx 1, in M and Cu to about half way to Cux. Membranule white; pterostigma light brown. In the anal loop, the cell at the anal corner of t lacking in the left and present in the right wing; ti in fw of 2 cells; in hw 3 × 1 + 2 rows of discoidal cells in the left, 1 + 2 + 1 + 2 rows in the right; 2 rows of cells between A^3 and the margin; bridge crossveins 1.0/1.0; Anx 9 ½. 8 ½. Ab. 23, Hw. 26, Pt. < 2".

The armature of femur 3 (with short, stout spines directed proximally, Fig. 17) and length of pretarsal teeth (longer than tip of claws, Fig. 26) of the male indicate that this species conforms to the diagnosis of *Macrothemis* rather than *Gynothemis*. The morphology of the male vesica spermalis (Fig. 34) shows that it is very likely related to the group of species including *M. heteronycha*, *M. brevidens*, and *M. musiva* (Figs. 32, 33, 35).

Figs. 48–50. Male thorax: 48*a*, lateral view, 48*b*, dorsal view, *Macrothemis calliste* (Brazil: Brasilia); 49, *Gynothemis venipunctata* (Venezuela: Bolivar); 50, *G. uniseta* (Surinam). Scale bar = 2 mm.



Figs. 51–54. Abdomen: 51*a*, lateral view, 51*b*, dorsal view, female HOLOTYPE *Brechmorhoga archboldi* (Dominica); 52, dorsal view, male *Scapanea frontalis* (Dominican Republic); 53, lateral view, male *Macrothemis calliste* (Brazil: Brasilia); 54, lateral view, male *Gynothemis venipunctata* (Venezuela: Bolivar). Scale bars = 2 mm.



The male of *M. calliste* keys to *M. hosanai* (also described from Brasilia) in May (1998), and it is possible that these two species are synonyms. Illustrations of the hamules of the holotype of *M. hosanai* (Santos 1967) agree closely with those of the male described here. The only difference between the description of *M. hosanai* and the male described here as *M. calliste* is in the color of the base of the postfrons; in *M. hosanai*, it is a brilliant metallic blue, whereas it is dark brown in *M. calliste*. Santos (1967) also mentioned a bituberculate condition of the postfrons, which accords with the male of *M. calliste*. We have refrained from formally synonymizing these two names pending examination of the type of *M. hosanai*.

Scapanea Kirby, 1889

(Figs. 3 (fw, hw), 22 (fe), 25 (cl), 30 (ve), 43 (gf), 52, 59*a* (ab), 59*b*–59*c* (vu))

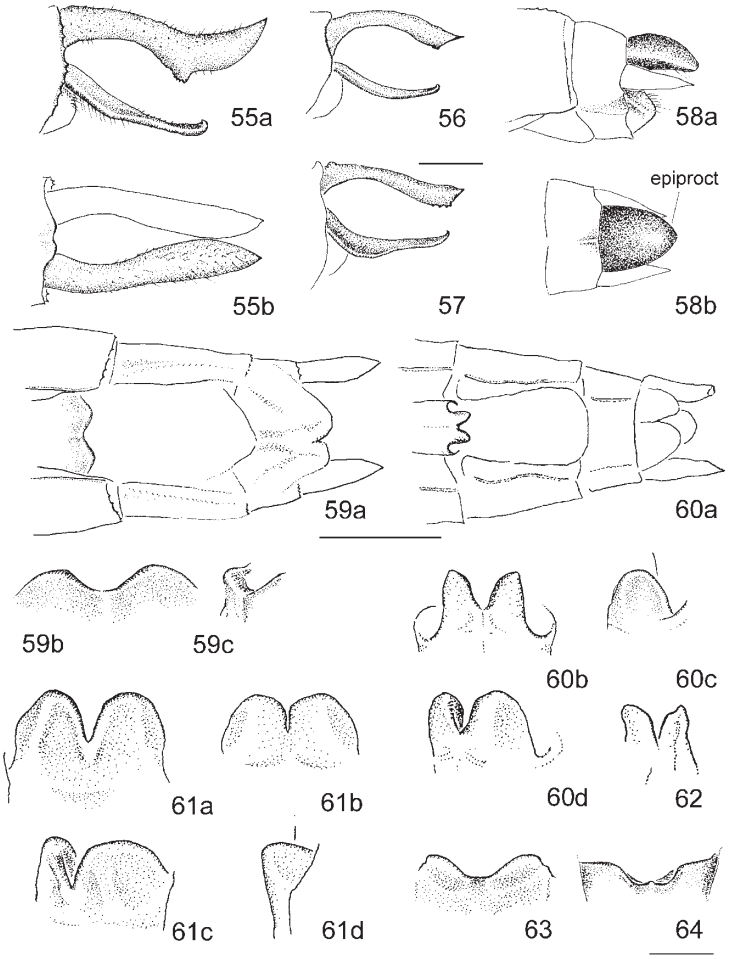
Type species: *Libellula frontalis* Burmeister, 1839 (Kirby, 1889 by original designation).

Diagnosis

Large libellulines (40–47 mm); postfrons and vertex brown to metallic blue in mature males; thx brown with yellow markings; mature males becoming pruinose on thorax and posterior abdominal segments. Wings (Fig. 3) hyaline (with slight opalescent band in populations of *S. frontalis* from Jamaica and Cuba); last antenodal in fw incomplete; fw discoidal field narrowing distally; Mspl distinct; median sector with one row of cells throughout.

Scapanea frontalis is similar to *Brechmorhoga* and *Macrothemis* in the short, stout, posteriorly directed male hind femoral spines (Fig. 22*b*); it differs from *Brechmorhoga* by the distally narrowed discoidal field and from most *Macrothemis* (except *M. griseofrons*) by the well-developed Mspl sector in fw. It differs from all other genera by the extremely wide male s7–9 (with widest point about 3–3.5 times as wide as base of s7; Fig. 52) and the distal segment of ve with a ventral, horizontally flattened lobe at its base (Fig. 30).

Figs. 55–64. Terminalia: 55*a*, lateral view, 55*b*, dorsal view, cerci, male *Macrothemis calliste* (Brazil: Brasilia); 56, lateral view, cerci, male *Gynothemis venipunctata* (Venezuela: Bolivar); 57, lateral view, cerci, male *G. uniseta* (Surinam); 58*a*, lateral view, 58*b*, dorsal view, caudal appendages, female *Brechmorhoga nubecula* (Mexico: Veracruz); 59, female *Scapanea frontalis* (Dominican Republic) (*a*, ventral view, s8–10; *b*, ventral view; *c*, ventrolateral view, vulvar lamina); 60, female HOLOTYPE *B. archboldi* (Dominica) (*a*, ventral view, s8–10; *b,* ventral view; *c*, lateral view; *d*, ventrolateral view, vulvar lamina); 61, female *B. praecox grenadensis* (Trinidad) (*a*, *b*, ventral view; *c*, ventrolateral view; *d*, lateral view, vulvar lamina); 62, ventral view, vulvar lamina, female *M. calliste* (Brazil: Brasilia); 63, ventral view, vulvar lamina, female *G. venipunctata* (Venezuela: Bolivar); 64, ventral view, vulvar lamina, female *G. uniseta* (Surinam). Scale bars = 0.5 mm (Figs. 55, 59*b*–59*c*, 60*b*–60*c*, 61–64) and 2 mm (Figs. 59*a*, 60*a*).



Distribution

Greater Antilles (Cuba, Jamaica, Haiti, Dominican Republic, and Puerto Rico).

Species

Scapanea frontalis (Burmeister, 1839)*.

Acknowledgements

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