

**THE IDENTITY OF SOME WIDESPREAD AND VARIABLE
PHYLLOMACROMIA SPECIES, WITH A REVISED GROUPING
OF THE GENUS
(ANISOPTERA: CORDULIIDAE)**

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Many *Phyllomacromia* spp. appear to be more variable than was hitherto realised. This has led to the description of paler and darker forms as distinct spp. Fortunately, the genus is rich in morphological characters in both sexes. *P. melania* and *P. overlaeti* were described from ♀♀ and both have been allied with non-conspecific ♂♂, leading to great confusion. *P. melania* is the ♀ of the sp. known as *P. funicularia* rather than that of *P. contumax*, while *P. overlaeti* matches *P. subtropicalis* and not *P. schoutedeni*. With the identity of these ♀♀ clarified and the variation considered, many synonyms arise: *P. funicularia*, *P. bredoi* and *P. martorelli* are synonyms of *P. melania*; *P. biflava*, *P. nyanzana*, *P. bifasciata*, *P. reginae*, *P. halei* and *P. leoni* of *P. contumax*; *P. onerata* and *P. clymene* of *P. monoceros*; and *P. subtropicalis*, *P. paludosa* and *P. royi* of *P. overlaeti*. *P. paludis* is not synonymous with *P. contumax* but with *P. paula*. The taxonomy of this large genus is briefly discussed and a new species grouping is proposed.

INTRODUCTION

With the exception of a single Madagascar endemic, all species of *Phyllomacromia* Selys, 1878 are confined to continental Africa. MAY (1997) demonstrated that the genus is distinct from *Macromia* Rambur, 1842, in which most of the African species were originally described. Sixty names have been published (excluding errors and homonyms), although only 36 appear to be valid at present, including changes proposed here (Tab. I). No less than ten names were introduced in the last 25 years (GAMBLES, 1979; GAUTHIER, 1987a; 1987b; LEGRAND, 1980; 1982; 1983; 1991; 1992; 1993; LINDLEY, 1980). This reflects the elusiveness of the species, but also suggests a high degree of variability and taxonomic confusion in the genus. Nonetheless, the morphological diversity of secondary genitalia, S8-10 and appendages in males and of vulvar scales in females is great. Augmented with strong interspecific variation in size and

markings, this makes *Phyllomacromia* one of the most varied genera of African Odonata. DIJKSTRA (2003a; 2003b) pinpointed variability in melanisation (intensity of black pigmentation) and size as an important taxonomic hurdle in African odonatology. It is emphasized below that such variation in *Phyllomacromia* is also strong, but that the morphological diversity provides ample foothold to grasp this problem.

The following acronyms for collections are used: BMNH – Natural History Museum, London; ISNB – Institut Royal des Sciences Naturelles de Belgique, Brussels; MNMS – Museo Nacional de Ciencias Naturales, Madrid; MRAC – Musée Royal de l'Afrique Centrale, Tervuren; NHRS – Naturhistoriska Riksmuseet, Stockholm; NMBZ – Natural History Museum of Zimbabwe, Bulawayo; RMNH – Nationaal Natuurhistorisch Museum Naturalis, Leiden; UMMZ – University of Michigan Museum of Zoology, Ann Arbor; ZFMK – Zoologische Forschungsinstitut und Museum "Alexander König", Bonn; ZMHB – Museum für Naturkunde der Humboldt-Universität, Berlin.

Table I

Grouping and synonymy of *Phyllomacromia* species. Stripes: number of synthoracic pale stripes; – Cones: number of cones on S10 dorsum; – Size: S (Hw 25-35 mm), fS (30-40), M (35-45), fL (40-50) or L (45-55)

Group	Stripes	Cones	Size	Species	Synonyms
Contumax	0	0	fL (M)	<i>contumax</i> Selys, 1879	<i>biflava</i> Martin, 1907 <i>nyanzana</i> (Grünberg, 1911) <i>bifasciata</i> Martin, 1912 <i>reginae</i> (Le Roi, 1915) <i>halei</i> (Fraser, 1928) <i>leoni</i> Fraser, 1928 <i>selysi</i> (Kirby, 1900) <i>lieftincki</i> (Fraser, 1954) <i>camerunica</i> (Pinhey, 1974)
Sophia	0-1 (3)	1	L (fL)	<i>aeneothorax</i> (Nunney, 1895)	<i>aureozona</i> (Pinhey, 1966) <i>caneri</i> (Gauthier, 1987) <i>insignis</i> Kirby, 1889 <i>sophia</i> (Selys, 1871) <i>seydeli</i> (Fraser, 1954) <i>unifasciata</i> (Fraser, 1954)
Unifasciata	1	1	M (fL)	<i>seydeli</i> (Fraser, 1954)	
Trifasciata	3	0	fS (M)	<i>congolica</i> (Fraser, 1955) <i>occidentalis</i> (Fraser, 1954) <i>overlaeti</i> (Schouteden, 1934)	<i>subtropicalis</i> (Fraser, 1954) <i>paludosa</i> (Pinhey, 1976) <i>royi</i> (Legrand, 1982)
Africana	3	0	S	<i>sylvatica</i> (Fraser, 1954) <i>trifasciata</i> Rambur, 1842 <i>africana</i> Selys, 1871 <i>nigeriensis</i> (Gambles, 1971) <i>pseudofrancica</i> (Pinhey, 1961) <i>amicorum</i> (Gambles, 1979) <i>flavimitella</i> (Pinhey, 1966)	
Picta	3	1	S	<i>picta</i> (Hagen in Selys, 1871)	<i>tropicalis</i> (Selys, 1878) <i>flavincta</i> Kirby, 1898 <i>kochi</i> Grünberg, 1911

Table I, continued

					<i>trochi</i> Grünberg, 1912 <i>flavicans</i> (Fraser, 1954) <i>ugandica</i> Fraser, nom.nud.*
Pallidinervis	3	1	fS	<i>pallidinervis</i> (Förster, 1906)	
Maesi	3	1	M (fL)	<i>maesi</i> (Schouteden, 1917)	
Aequatorialis	3	1	fS (S)	<i>aequatorialis</i> Martin, 1907 <i>girardi</i> (Legrand, 1991) <i>hervei</i> (Legrand, 1980) <i>schoutedeni</i> (Fraser, 1954)	
Melania	3	1	M (fS)	<i>funicularioides</i> (Legrand, 1983) <i>gamblesi</i> (Lindley, 1980) <i>legrandi</i> (Gauthier, 1987) <i>melania</i> (Selys, 1871)	<i>funicularia</i> (Martin, 1907) <i>breddoi</i> (Schouteden, 1934) <i>martorelli</i> (Compe Sart, 1964) <i>onerata</i> (Martin, 1907) <i>clymene</i> (Ris, 1921) <i>thetis</i> (Ris, 1921)
				<i>monoceros</i> (Förster, 1906)	
Paula	3	2	fS-M	<i>bicristulata</i> (Legrand, 1975) <i>bispina</i> (Fraser, 1954) <i>kimminsi</i> (Fraser, 1954) <i>lamottei</i> (Legrand, 1993) <i>paula</i> (Karsch, 1892) <i>villiersi</i> (Legrand, 1992)	<i>pinheyi</i> Fraser, nom. nud.** <i>clymene</i> (Fraser, 1954) <i>junior</i> (Pinhey, 1961) <i>paludis</i> (Sjöstedt, 1900) <i>bicornis</i> (Förster, 1906)

* in PINHEY, 1962

** in VICK, 1999

PHYLLOMACROMIA AFRICANA (SELYS, 1871)

Figure 9

Macromia africana SELYS, 1871: 554 (bulletin), 117 (reprint) [type: Nubia, Sudan; ISNB]

A good diagnosis was given by GAMBLES (1971). The male is small, relatively extensively dark in the median groove of the frons, with pale cerci, and S10 with black denticles on apical border but without dorsal cone. Unlike its relatives, vertex and occipital triangle are (partly) pale, while pale markings on S3-6 extend clearly posterior of the jugal sutures. As in all *Phyllomacromia* species, the combination of shapes of hamule and appendages is distinctive. The Selys collection (ISNB) contains one specimen of each sex labelled as type by Martin. The male is from Khartoum, the female from Nubia. These specimens agree with GAMBLES' (1971) diagnosis, being typical examples of the pale insect that occurs widely across the dry North of tropical Africa. As FRASER (1954) remarked "this is a very variable species, dry areas producing

xerophilous forms, whilst forested areas show a much darker melanotic one [...] it is probable that many intermediate forms link up these two, so that it is doubtful if they can be classed as separate races." I have examined several of such dark males, labelled "Nyassaland 1953" (BMNH), "Uvira – Riv. Kalimalenge, 23 ix '52, G. Marlier" and "Baraka, 1-viii-18, R. Mayné" (both MRAC, latter lacks S5-10) and "Tanzania, Mpanda district, Mukuyu 800-900m, ca 5°29'S 29°46'E, xi 69, Kigoma" (RMNH). The latter was published by PINHEY & PINHEY (1984) as *P. africana*. In these males the epiproct, basal third of cerci, S10 and hamule are black, whereas these are (largely) yellow in typical *P. africana*. The pale markings are partly obliterated, but despite this there are traces on occiput, vertex and on the postjugal parts of S3-6. The shape of hamule and appendages (if present) conform with *P. africana*. The denticles on the apical border of S10 are present, but extremely hard to see on the black background. It is peculiar that these specimens all originate from near two large Rift Valley lakes: Uvira and Kigoma lie on the Congolese and Tanzanian shores of Lake Tanganyika respectively, while Baraka probably also refers to a site on the Congolese shore. Most of the former Nyassaland lies along Lake Malawi.

PHYLLOMACROMIA MELANIA (SELYS, 1871)

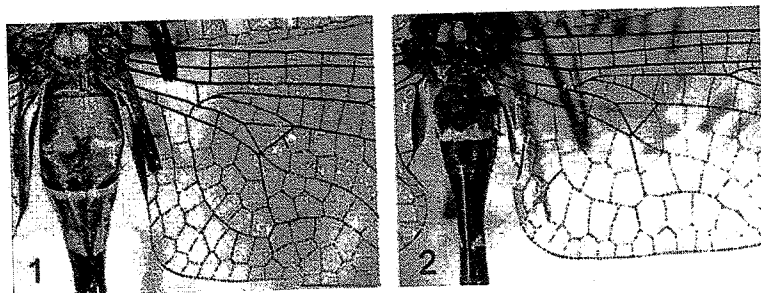
Macromia melania SELYS, 1871: 551 (bulletin), 114 (reprint) [type: Old Calabar, Nigeria; ISNB]

Macromia funicularia MARTIN, 1907a: 75 [type: Cameroon; MNHN]; new synonymy

Macromia bredoi SCHOUTEDEN, 1934: 43 [type: Bambesa, Congo-Kinshasa; MRAC]; new synonymy

Macromia martorelli COMPTE SART, 1964: 13 [type: Mongomo, Equatorial Guinea; MNMS]; new synonymy

GAMBLES (1979) coupled the female holotype of *P. melania* to the male holotype of *P. contumax*, comparing them with *P. nyanzana* and *P. bifasciata*. The *P. contumax* male is so similar to latter two species (see under *P. contumax*) that *P. melania* cannot be its female: The *P. melania* holotype has a sleek build, Hw 41.5 mm, labium and synthorax dark marked boldly with yellow, wings entirely and evenly smoky, and S2 marked



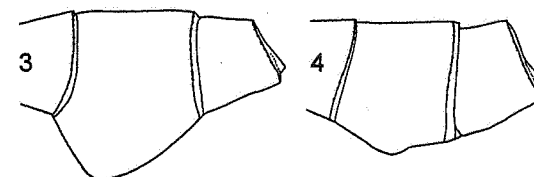
Figs 1-2. *Phyllomacromia overlaeti*, Hw bases: (1) female holotype *P. overlaeti*; – (2) male holotype *P. subtropicalis*.

more extensively with yellow than S3. GAMBLES (1979) showed that the vulvar scale of specimens identified as *P. melania* and *P. nyanzana* are similar, but in the latter it is fringed with hair. The holotype lacks S5-10, so no comparison can be made. Because the *P. melania* holotype is not conspecific, *P. contumax* is the valid name of the taxon it represents (see below), while *P. melania* must return to taxonomic limbo. The problem is matching the name, that outdates most others, to the correct male.

GAMBLES (1979) probably overlooked KARSCH (1891) who described a male from Barombi Station, Cameroon, as *P. melania*. This male in ZMHB pertains to the species known as *P. funicularia*, the male holotype of which is well-illustrated by SCHMIDT (1951). Indeed, by build, size, 19-20 Fw Ax, 2 cells rows at base of Fw discoidal field, smoky wings, dark membranule and markings the *P. melania* holotype is like the *P. funicularia* female. Two males of this species in NHRS labelled "Musana, Fr. Congo, M. Lundgren" were identified as *P. melania* by RIS (in litt.). MNMS has a female labelled "Kamerun, L. Conradt. 1899. Lab. ent. Escalera" and "Macromia funicularia Martin ♀ a décrire" (latter in what is possibly Martin's handwriting) accompanied by a similarly labelled *P. funicularia* male. This may be the specimen MARTIN (1907b) described as "Type ♀ Musée de Madrid [...] Hab. Cameroun." It agrees entirely with the *P. melania* holotype.

P. funicularia has several close relatives (Tab. I), from which it differs by the relatively extensively pale S2 and the absent or strongly reduced antehumeral stripe (GAUTHIER, 1987b; LINDLEY, 1980). The *P. melania* holotype agrees in these features: As SCHMIDT (1951) put it "keine Antehumerallbinden, aber helle Seitenbinden am Thorax", the ventro-lateral corner of the mesepisternum is somewhat pale, but a contrasting antehumeral stripe along its entire length is absent. As shown by GAMBLES' (1979) illustration, the dorsum of S2 is largely pale, in stead of having a narrow band or spots. Although the holotype lacks a vulvar scale, that described by GAMBLES (1979) from other "melania" females agrees with that of *P. funicularia*. The species is common in the general area from where both *P. funicularia* and *P. melania* originate – such as the forests of SW Cameroon and Gabon (LEGRAND, 1975; VICK, 1999) –, but none of the similar species have been reported from either Nigeria or Cameroon. It seems most certain that *P. funicularia* and *P. melania* are conspecific, and I regard them as synonyms. FRASER (1954) previously synonymised *P. bredoi* and LEGRAND (1989) *P. martorelli* with *P. funicularia*. Having seen both holotypes, I concur with their views.

GAMBLES (1979) was probably misled by MARTIN's (1907a) suggestion that *P. biflava* (a true synonym of *P. contumax*) might be the male of *P. melania*, and his subsequent failure to notice the thoracic stripes was the start of the confusion. Note that GAMBLES (1979) made another such mismatch: he described a specimen



Figs 3-4. *Phyllomacromia* male S8-9, lateral view: (3) *P. overlaeti*; – (4) *P. congolica*.

of *P. caneri* as the female of *P. sophia*, despite differences in range and maculation (GAUTHIER, 1987a). The variation of abdominal markings described by GAMBLES (1979) across the range of his "melania" females may indicate the presence of several similar species in his material.

PHYLLOMACROMIA CONTUMAX SELYS, 1879

Figure 5

- Phyllomacromia contumax* SELYS, 1879: 103 [type: Akele, Cameroon; BMNH]
Phyllomacromia bi ava MARTIN, 1907a: 77 [type: Assinie / Grand Bassam, Côte d'Ivoire; MNHN]
Macromia nyanzana GRÜNBERG, 1911: 104 [type: Sesse Islands, Uganda; ZMHB]; new synonymy
Phyllomacromia bifasciata MARTIN, 1912: 96 [type: Dakar, Senegal / Sikasso, Mali; MNHN?]; new synonymy
Macromia reginae LE ROI, 1915: 348 [type: Meshra er Req, Bahr el Ghazal, Sudan; ZFMK]; new synonymy
Macromia halei FRASER, 1928: 137 [type: Entebbe, Uganda; BMNH]; new synonymy
Phyllomacromia leoni FRASER, 1928: 138 [type: Yegi, Ghana; BMNH]; new synonymy
Macromia melania nec SELYS, 1871. — GAMBLES (1979: 399)

GAMBLES (1979) recognised *P. nyanzana* and *P. bifasciata* as close relatives of *P. contumax*. The males of these species are alike in their large size (Hw 39–47 mm), uniformly dark brown labium, unmarked synthorax, white-tipped membranule, restricted pale abdominal markings aside from bold basal rings on S3 and S7, and in the shape of hamule, S10 and appendages (Fig. 5). Females are large and robust, marked similarly to their males, and have yellowish Fw tips and dark basal Hw and often Fw patches, and similar vulvar scales. With the incorrect association of the *P. melania* (which see) female – and thus its apparent distinguishing characters – out of the way, little remains to separate *P. contumax* from *P. nyanzana* and *P. bifasciata* (Tab. II). The way GAMBLES (1979) saw it "[nyanzana] is mainly an East African species, [...] closely related to and replaced in West Africa by *bifasciata* [...], which is slightly smaller, has more yellow on the body, and is a savannah species. [nyanzana] resembles *melania* [= *contumax*] in a number of ways besides the colour-pattern."

Specimens found in open habitats all over Africa (from Senegal to Somalia, Namibia and Natal) are generally identified as *P. bifasciata*, and only dark ones from around Lake Victoria and even darker ones from West African rainforests are named *P. nyanzana* and *P. contumax* respectively. To illustrate the confusion: LE ROI (1915) described a large, pale male from SW Sudan as *P. reginae*, of which RIS (1917) described a dark Lake Victoria form, ignoring GRÜNBERG's (1911) *P. nyanzana* from that area. FRASER (1928) described *P. halei* and *P. leoni* (in separate genera!), the former also being from the shores of the lake. Oblivious of the existing abundance of names, NIELSEN (1935) described a pale specimen as a possible "forma orientale" of the dark *P. bi ava*. LONGFIELD (1936) synonymised *P. halei* with *P. reginae*, although FRASER (1954) considered them forms

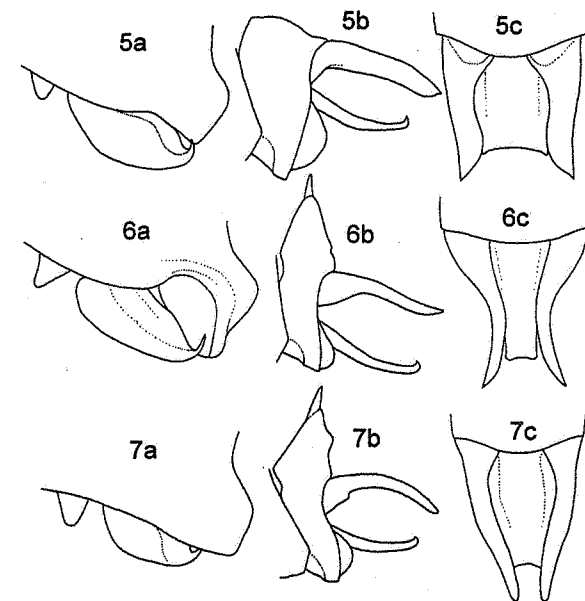
Table II

Characters and synonyms of the three previously recognized species considered as *P. contumax* — [See text for a general diagnosis]

Species	<i>contumax</i>	<i>nyanzana</i>	<i>bifasciata</i>
Synonyms	<i>biflava</i> , <i>melania</i> sensu Gambles	<i>halei</i>	<i>reginae</i> , <i>leoni</i>
Hw length (♂)	41–47 mm	41–46 mm	39–44 mm
Dorsum frons	entirely dark	dark with isolated pale spots	pale base with dark lines on grooves and ridges
Short antehumeral stripe S2 and S4–6	absent	rarely present	sometimes present
Pale ring S3 occupies	less than basal half	basal half or more	basal half or more
Wing markings (♀)	yellow Fw tip deeper, brown base to Ax2 in Fw, to Ax3 in Hw	yellow Fw tip deeper, brown base to Ax2 in Fw, to Ax3 in Hw	yellow Fw tip fainter, brown base vestigial in Fw, to Ax1 in Hw
Habitat and range	rainforest in West Africa	forested shore of Lake Victoria	savannah and woodland throughout tropical Africa

of a single species, and this ultimately lead PINHEY (1962) to synonymise *P. reginae* with *P. nyanzana*. FRASER (1954) was already confused by the variability, remarking that "it is possible that these pale markings [frontal spots, antehumeral stripe] are evanescent and tend to disappear with advancing age." Comparing the wing markings of the female holotype of *P. nyanzana*, PINHEY (1963) stated that he "considers this to be individual variation".

It appears the three species now recognised constitute just a single variable one, as there are no morphological differences in hamule, S8–10 or appendages. Differences in size and maculation vary on continuous and overlapping scales: the largest and darkest individuals corresponding to *contumax*, the smallest and palest to *bifasciata*, while *nyanzana* is intermediate



Figs 5–7. Examples of secondary genitalia in lateral view (a), S10 and appendages in lateral view (b) and appendages in dorsal view (c) of *Phyllomacromia* species groups: (5) *P. contumax* (Contumax); — (6) *P. au-reozona* (Sophia); — (7) *P. unifasciata* (Unifasciata).

(Tab. II). Males assigned to each form by the extent of their markings overlap in size: For instance, two males collected by C. Williams at Uganda's Lake Nabugabo on 1 December 2000 could be assigned to different species based on size (difference only 43 and 44 mm!) and markings of frons and abdomen, but rather suggest that the variation occurs within populations. I have seen both specimens with all-dark ("contumax") and pale-spotted ("nyanzana") frons from the Sese Islands in Lake Victoria. Judging from the wide distribution and habitat range observed, size and darkness are probably environment-related. I believe all this variation can be treated under a single name, which leads to a large number of new synonyms. It may be added that larvae from Cameroon ("contumax"), Uganda ("nyanzana"), Côte d'Ivoire and Namibia ("bifasciata") share the distinctive serration of the labial palps (CORBET, 1957; pers. comm. D. Chelmick and F. Suhling).

Hylaeschna paludis, described by SJÖSTEDT (1900) from Kitta in Cameroon, has been considered a synonym of *P. contumax*, probably because a label reading "=*Macromia melania* Selys" had been attached (by Sjöstedt?) to the holotype (GAMBLES, 1979; PINHEY, 1962). The specimen, examined in NHRS, is indeed large and dark, but the size (Hw 46 mm), uniform labrum, brown wing bases, vulvar scale, and thoracic and abdominal markings show that it is a female of *P. paula*. It perfectly matches GAMBLES's (1979) illustrations of the *P. paula* holotype. I saw *P. bifasciata* from neither Dakar or Sikasso in MNHN, so the type material of that taxon may be lost.

PHYLLOMACROMIA MONOCEROS (FÖRSTER, 1906)

Figure 14

- Macromia monoceros* FÖRSTER, 1906: 319 [type: Nguelo, Tanzania; UMMZ]
Macromia onerata MARTIN, 1907a: 74 [type: German East Africa (= Tanzania); MNHN];
 new synonymy
Macromia thetis RIS, 1921: 379 [type: Chirinda Forest, Zimbabwe; BMNH]
Macromia clymene RIS 1921: 381 [type: Kapiri, Congo-Kinshasa; MRAC]; new synonymy

The holotypes of *monoceros*, *onerata*, *thetis* and *clymene* agree in their fairly large size, simple but diagnostic hamule, high S10 peak with single cone and the slender but blunt cerci (Fig. 14). They differ mainly in the extent of pale markings. *P. clymene* is the palest and *monoceros* the darkest. *P. thetis* and *onerata* are intermediate, the latter being slightly paler. *P. clymene*, for instance, has a broad pale band across the dorsum of the frons, *onerata* and *thetis* merely have a small yellow spot in the frons' groove, and *monoceros* has an all-dark frons. Large and partly fused paired prejugal spots are present on S3-6 in *clymene*. In *onerata* the spots are present on S3-5 and are all separated by a dorsal black line. *P. thetis* is darker with S5 all black and *monoceros* is darker still with the spots on S4 almost indiscernible. PINHEY (1961) already made *thetis* a synonym of *monoceros* and *clymene* of *onerata*, and RIS (1921) admitted that his two species were very similar, although he believed the differences in paleness, especially of the

frons, were significant. The types of *P. monoceros* and *P. onerata* are both from Tanzania. BMNH has a male from the Usambara Mts, the type locality of *monoceros*, which R.M. Gambles (in litt.) compared with the *onerata* holotype and found to be identical, although it is near *clymene* in paleness. Dark and pale forms can thus be found together. RIS (1921) and PINHEY (1961) also mentioned characters of the epiproct length, divergent cerci and the apical spine on S9. The four holotypes do not differ noticeably in these features, although the epiproct varies from being slightly shorter than the cerci (*monoceros*) to distinctly shorter (*clymene*). All characters vary on gradual scales, and I therefore consider the four taxa as a single species, which appears to be the Eastern counterpart of *P. melania*. It occurs from Kenya through Tanzania, Malawi, Mozambique, Katanga, Zambia and Zimbabwe to N South Africa. Note that the female of *P. clymene* described by FRASER (1954) belongs to *P. kimminsi* (PINHEY, 1961).

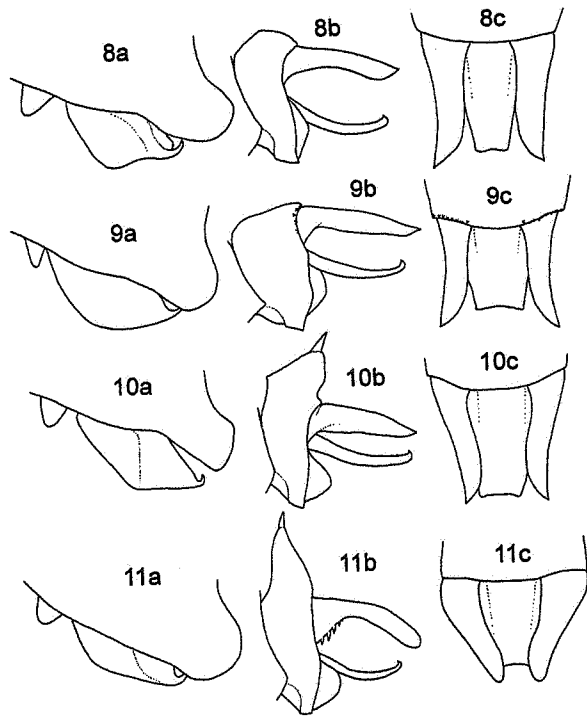
PHYLLOMACROMIA OVERLAETI (SCHOUTEDEN, 1934)

Figures 1-3

- Macromia overlaeti* SCHOUTEDEN, 1934: 44 [type: Kapanga, Congo-Kinshasa; MRAC]
Macromia subtropicalis FRASER, 1954: 60 [type: Bambesa, Congo-Kinshasa; MRAC];
 new synonymy
Macromia paludosa PINHEY, 1976: 565 [type: Shakawe, Botswana; NMBZ]; new synonymy
Macromia royi LEGRAND, 1982: 120 [type: Fumela, Senegal; MNHN]; new synonymy

P. overlaeti was described from a single female. The holotype is unusual in having the base of all wings extensively yellow (up to Ax5-6) and the Hw base expanded. The anal loop is almost twice as long as wide and there are 3 rows of cells between it and the rather square tornus (Fig. 1). Similar sized species have the loop at most as long as wide, with 2 rows between it and a rounded tornus. FRASER (1954) suggested the specimen might be aberrant, but the venation is similar in both wings and not distorted. LONGFIELD (1959) reported a teneral pair from NE Angola presumed to be *P. overlaeti*, of which she selected the male as allotype. The male was identical to *P. schoutedeni*, which would therefore be a synonym. After comparing both females, FRASER (1959) disagreed stating "venational aberration and variation undoubtedly exist but the shape of the wings never differ [with? -] in species" and concluded "the male of *overlaeti* yet remains to be discovered". Nonetheless PINHEY (1984) accepted Longfield's synonymy, although LEGRAND (1991) did not. The allotype female of *P. schoutedeni* (MRAC) matches the male holotype, but the *P. overlaeti* holotype conforms with neither: *P. schoutedeni* cannot be synonymous with *P. overlaeti*.

P. overlaeti kept this obscure status until I was shown a single *Phyllomacromia* male by C. Williams, collected in Uganda's Murchison Falls National Park on 12 September 2001. It proved difficult to identify, although a similar male was found under *P. africana* in BMNH labelled "van Someren, Amua R., Metu, N.W. Madi, W. Nile, Uganda



Figs 8-11. Examples of secondary genitalia in lateral view (a), S10 and appendages in lateral view (b) and appendages in dorsal view (c) of *Phyllomacromia* species groups: (8) *P. sylvatica* (Trifasciata); - (9) *P. africana* (Africana); - (10) *P. picta* (Picta); - (11) *P. pallidinervis* (Pallidinervis).

10 and appendages were dark (dorsally) to pale brown. Despite the difference in extent, the configuration of pale markings in both was identical. They shared several unique characters: The anterior part of the median groove of the frons bore a prominent knob. S8 had broad, triangular foliations with a straight (not notched) posterior border (Fig. 3). No other species have these two features so well developed (Fig. 4). The labium was uniformly pale brown, with at most a fine and indistinct dark central line on the prementum. Similar-sized species have more extensive and contrasting dark labial markings, only much larger species have a plain labium. The hind femur was pale brown with contrasting black apex. In other species the femur is uniformly dark brown to black, at most darkening gradually towards the apex.

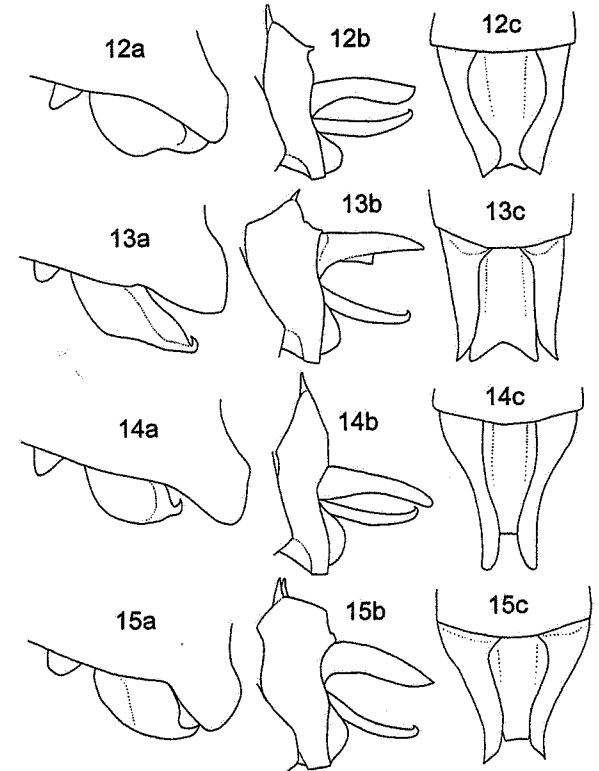
Two other species have been described that share the broad triangular foliations and details of hamule and appendages with *P. subtropicalis*. PINHEY (1976) reported *P. paludosa* from the Okavango Delta. According to his description and illustrations it is larger (Hw 36.5 mm) and paler than *P. subtropicalis*, but not as pale as the Ugandans. For instance, the frons dorsum only has a narrow pale crescent, S5-6 are marked, S8 is

5-6 1954". Comparison of the Murchison Falls male with four males of *P. subtropicalis* from Bambesa in MRAC (including holotype and paratype) revealed they agreed in morphology, including the shape of hamule and appendages. The Murchison Falls male was only smaller (Hw 30 v. 32-34 mm) and much paler. *P. subtropicalis* has the frons all dark metallic, S2-4 and S7 dark with small yellow markings and S5-6, S8-10 and appendages all dark. Dark areas are black, except the lower halves of S7-10 which are dark brown. The Ugandan males were browner overall, with more extensive yellow markings, including a largely yellow base to frons, prejugal markings on S5-6 and small basal spots on S8. S7-

unmarked and the appendages are black. The labium is simply described as "ferruginous" and the hind femora as "ferruginous, black at knees". PINHEY (1976) did not note the frontal knob, but from his drawing the head appears to be crushed. In his discussion he remarked about the frontal crescent that "this fascia is probably variable in such a dark species [*P. subtropicalis*] and might be evanescent". He further mentions two similar males from Maramba River near Victoria Falls, which are "somewhat paler because of their immature condition". Later PINHEY (1984) described *P. subtropicalis* as "a small, pale species, [...], hindwing 33-34 mm. [...] Frons purplish metallic with broad yellow transverse band" while *P. paludosa* is "a larger, darker species, [...], hindwing 35-36 mm. [...] Frons, at maturity, broadly purplish metallic with only traces of yellow transverse band". This contradicts his earlier work and must refer to supposed *P. subtropicalis* specimens from the Middle Zambezi. LEGRAND (1982) compared his *P. royi* with *P. nigeriensis* due to its small size and paleness. The description and direct comparison of

the holotype with the Murchison Falls male show it is slightly smaller (Hw 29-30 mm) and paler than the latter: Vertex and appendages for instance are brownish yellow, instead of brown to black. This results from the overall paleness of the specimen, unlike in species such as *P. africana* and *P. picta* where vertex and cerci are (partly) pale, in contrast with surrounding darker areas (e.g. epiproct, bases of cerci). *P. royi* has all described characters of frons (knob only slightly less prominent), hamule, S8, appendages, and markings of prementum, hind femur and abdomen.

The *P. overlaeti* holotype, matching the *P. royi* holotype in paleness, also has the unique features of frons, labium and hind femur. S8 is not expanded in *Phyllomacromia* females.



Figs 12-15. Examples of secondary genitalia in lateral view (a), S10 and appendages in lateral view (b) and appendages in dorsal view (c) of *Phyllomacromia* species groups: (12) *P. maesi* (Maesi); - (13) *P. schoutedeni* (Aequatorialis); - (14) *P. monoceros* (Melania); - (15) *P. paula* (Paula).

Within species *Phyllomacromia* males and females differ strongly in the coloration and shape of the wings (especially Hw base), therefore it is difficult to compare the *P. overlaeti* venation with that of aforementioned males. Nonetheless the studied males have a narrower anal loop than any other *Phyllomacromia* males seen (Fig. 2) and agree in the number of Ax: 12-12 in *P. overlaeti*, 11-13 in discussed males. Both sexes also agree in the membranule colour, which is dark with approximately the basal half whitish. A more direct match, by a mated pair or syntopic material, cannot be made. Interestingly, PINHEY (1984) reported *P. paludosa*, presumably the two males discussed earlier, from Maramba River on 6 February 1964 and two females of *P. overlaeti* from the same site one day later. He stated that the latter were "compared with holotype in 1964 by Pinhey".

From the above I conclude that discussed taxa constitute a single variable, widespread and scarce species, *P. overlaeti* taking priority. *P. overlaeti* and *P. royi* represent the palest specimens (possibly somewhat immature), *P. subtropicalis* the darkest and *P. paludosa* is intermediate. The single potential obstacle that remains in the puzzle is the *P. subtropicalis* allotype described by FRASER (1957) from Bambesa, which differs from the *P. overlaeti* holotype in numerous respects: It is larger (Hw 38 mm versus 34.5), has 15-17 Fw Ax and 2 rows of cells at base of Fw discoidal field (not 1), the middle third of the prementum, entire hind femur and membranule are dark, the frontal knob is scarcely discernible and the wing bases are almost clear and normally shaped. This female cannot be conspecific with the *P. subtropicalis* holotype. It agrees well with LINDLEY's (1980) description of the *P. gamblesi* female (also by vulvar scale) and a syntopic male of that species in MRAC.

DISCUSSION

Four cases of strong variation in paleness in *Phyllomacromia* are presented in this paper, three of which have led to an overabundance of named taxa. The deceptive power of this variation is illustrated by RIS (1921) and FRASER (1928), who both described a single species under two new names. Three cases are discussed where unrelated males and females have been paired. Recognition of these cases leads to many synonyms, including name-changes of such familiar African dragonflies as *P. bifasciata* and *P. funicularia*. Especially the coloration of frons, abdomen and appendages is variable. In three species, *P. contumax*, *P. monoceros* and *P. overlaeti*, variation ranges from rather black specimens with an all dark metallic frons and largely unmarked abdomen, to those which are brown with the base of the frons pale and all abdominal segments marked. These species are widespread and often scarce, especially *P. overlaeti*, which is only known from a few widely-scattered specimens from N Botswana, the Zambia-Zimbabwe border region, NW Uganda, S and NE Congo-Kinshasa and Senegal. Similar cases may still lie concealed in the genus. For instance, *P. unifasciata* is principally paler than *P. seydeli*, but even the colour of the antealar sinus and membranule differ. *P. congolica* and *P. occidentalis* could also be a pale-dark pair. The quotes by FRAS-

ER (1954), GAMBLES (1979) and PINHEY (1963; 1976) assembled in this paper are testimony of these authors' awareness of the variability of *Phyllomacromia*, although its magnitude as a taxonomic problem was perhaps not fully appreciated. Recognition of the variability of *P. picta*, the genus' most common and widespread species, had already lead to a string of synonyms (Tab. I). Morphology is a better guide for the species classification of this genus. In my experience, coloration of the labium and legs appear to be more stable, and thus more informative, than that of other body parts. In this light re-examination of the forms distinguished by GAMBLES (1979) on the labial markings in *P. aeneothorax* is warranted.

Phyllomacromia is a large, diverse and elusive genus. New species are regularly described: Almost half of the taxa have been added after the review by FRASER (1954), with 3 to 6 described in each of the last four decades of the 20th century. As is usual with such a large genus, numerous groupings of the species have been adopted (e.g. GAMBLES, 1979; LEGRAND, 1992; 1993). Table I presents a revised grouping, based on maculation (principally thoracic stripes and relative colour of cerci), size, and structure of hamule, S8-10, cerci and vulvar scale. The eleven groups recognised strictly serve convenience and (as yet) have no phylogenetic basis, conveying jizz rather than kinship. Three groups are monotypic, the other eight have between 2 and 6 species. Some of the groups are very similar. The Picta-group, for instance, like the Africana-group consists of small and pale open-country species. The latter group only differs by the coneless S10, but similarity in appendages and hamules is remarkable. The Trifasciata-group mainly is larger and darker on average than the Africana-group.

KEY TO SPECIES GROUPS OF PHYLLOMACROMIA

Males of many species have S10 raised to a peak, surmounted by one or two spine- or tuft-like structures. These are coagulations of bristles, called cones. Note that females (and thus vulvar scales) are not known for all species. The number of species is indicated for each group.

- 1 Thorax unstriped or with single pale stripe, either indistinct antehumeral or bold lateral (*aeneothorax* at most with 3 indistinct stripes). Larger, Hw 39-55 mm 2
 - Thorax with 2-3 pale stripes on each side: usually 1 antehumeral and 2 laterals, but one of these may be reduced. Smaller, Hw 27-45 mm 4
- 2 (1) Dorsum S10 flat and bare. Cerci stout and straight. Lobes of vulvar scale fringed with hair. S3 and S7 with conspicuous pale basal ring. Thorax unstriped or with short antehumeral. Membranule with white apex. Fig. 5 **Contumax** (1)
 - Dorsum S10 with peak bearing cone. Cerci slender and sinuous. Lobes of vulvar scale bare. Abdomen marked differently. Thorax unstriped or with single bold stripe through metastigma on each side (*aeneothorax* at most with 3 indistinct stripes). Membranule uniform or paler at base. Figs 6-7 3
- 3 (2) Cerci gradually widened towards base (lateral view), strongly sinuous, apices are sharply pointed and diverge (dorsal view). Epiproct with narrow, slightly notched apex. Hamule with long hook. Border of genital fossa anterior to genital lobe may be hollowed out. Vulvar scale is large bifid structure, at least half as long as S9. Larger, Hw 43-55 mm. Fig. 6 **Sophia** (5)
 - Cerci abruptly widened at base, resulting in subbasal ventral angle or tooth, weakly sinuous, apices blunt and rather parallel. Epiproct with wide, roundly excavated apex. Hamule with short hook. Border of geni-

- tal fossa never hollowed out, running straight into border of genital lobe. Vulvar scale consists of two tiny triangular lobes, much shorter than half of S9. Smaller, Hw 40-42 mm. Fig. 7 **Unifasciata** (2)
- 4 (1) Dorsum S10 flat, at most with rounded hump, without cones 5
 – Dorsum S10 with peak bearing 1-2 cones 6
- 5 (4) Cerci yellow, may be darker at base, usually paler than epiproct. Smaller, Hw 27-32 mm. Fig. 9 **Africana** (3)
 – Cerci brownish yellow to black, often darker than epiproct. Larger, Hw 30-42 mm. Fig. 8 **Trifasciata** (5)
- 6 (4) Peak of S10 bearing 2 cones clearly separated at their base. Fig. 15 **Paula** (6)
 – Peak of S10 bearing 1 cone. Figs 10-14 7
- 7 (6) Cerci yellow, may be darker at base, usually paler than epiproct. Smaller, Hw 29-34 mm. Fig. 10 **Picta** (3)
 – Cerci brown to black, often darker than epiproct. Larger, Hw 32-42 mm. Figs 11-14 8
- 8 (7) Costa largely pale, contrasting with darker Pt. Base of cerci with row of ventral spines, like shark teeth. Cerci short and blunt. Epiproct pale, contrasting with dark cerci. Fig. 11 **Pallidinervis** (1)
 – Costa largely black, not contrasting with Pt. Cerci without basal spines. Cerci if short then pointed, if blunt then elongate. Epiproct and cerci dark. Figs 12-14 9
- 9 (8) S10 with tooth on posterior side of base of peak. Cerci widened before apex, but apex itself pointed, cerci thus appear truncate (dorsal view). Border of hamule strongly sinuous. Vulvar scale long, reaching median processes. Larger, Hw about 42 mm. Fig. 12 **Maesi** (1)
 – S10 without tooth at base of peak. Cerci slender with blunt apex, or taper to fine point. Border of hamule at most weakly sinuous. Vulvar scale short, not reaching median processes. Smaller, Hw 32-42 mm. Figs 13-14 10
- 10 (9) Cerci short and straight, taper to spine-like apex (dorsal view). Hook of hamule large, single-pointed and sharply back-turned, usually well-visible. Smaller, Hw 32-34 mm. Fig. 13 **Aequatorialis** (4)
 – Cerci long and slender, sometimes sinuous, apex blunt. Hook of hamule short, may have 2-3 points, although this is often concealed. Larger, Hw 34-42 mm. Fig. 14 **Melania** (5)

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REFERENCES

- COMPTE SART, A., 1964. Diagnosis preliminaires de nuevos odonatos africanos. *Boln R. Soc. esp. Hist. nat.* (Biol.) 62: 13-24.
- CORBET, P.S., 1957. Larvae of East African Odonata. 9-11. *Entomologist* 90: 111-119.
- DIJKSTRA, K.-D.B., 2003a. Problems in Chlorocypha classification: four cases from West Africa and a discussion of the taxonomic pitfalls (Odonata: Chlorocyphidae). *Int. J. Odonatol.* 6(2): 109-126.
- DIJKSTRA, K.-D.B., 2003b. A review of the taxonomy of African Odonata: finding ways to better identification and biogeographic insight. *Cimbebasia* 18: 191-206.
- FÖRSTER, F., 1906. Libellen. Forschungsreise durch Südschoa, Galla und die Somaliländer von Carlo Freiherr von Erlanger. *Jb. Nassau. Ver. Naturk.* 59: 1-345.
- FRASER, F.C., 1928. Odonata of the African continent. *Trans. R. ent. Soc. Lond.* 76(1): 123-138.
- FRASER, F.C., 1954. New species of Macromia from Tropical Africa. *Revue Zool. Bot. afr.* 49(1/2): 41-76.
- FRASER, F.C., 1957. Some further notes on the Odonata of the Belgian Congo. *Revue Zool. Bot. afr.* 55(3/4): 338-346.
- FRASER, F.C., 1959. A new species of Chlorocypha and some notes on the synonymy of other species of Odonata from the Belgian Congo. *Revue Zool. Bot. afr.* 60(3/4): 307-312.
- GAMBLES, R.M., 1971. A new species of Macromia Rambur 1842 (Odonata, Corduliidae) from Nigeria, and the hitherto undescribed female of *M. pseudaficana* Pinhey 1961. *Entomologist* 104: 177-189.
- GAMBLES, R.M., 1979. West African species of Macromia (Odonata: Corduliidae) belonging to the picta and sophia groups. *Syst. Ent.* 4(4): 389-407.
- GAUTHIER, A., 1987a. Description d'une nouvelle espèce de Macromia Rambur de la forêt camerounaise. *M. caneri* spec. nov. *Bull. Soc. ent. Mulhouse* 1987: 49-52.
- GAUTHIER, A., 1987b. Macromia legrandi n. sp., Odonate nouveau du Togo (Corduliidae). *Annls Limnol.* 23(1): 61-63.
- GRÜNBERG, K., 1911. Zur Kenntnis der Odonatenfauna der Sesse-Inseln im Victoria-Nyanzana. *Ent. Rdsch.* 28: 103-104.
- KARSCH, F., 1891. Uebersicht der von Herrn Dr. Paul Preuss in Deutsch-Westafrika 1890 gesammelten Odonaten. *Ent. Nachr.* 17(5/6): 65-81.
- LE ROI, O., 1915. Odonaten aus Äquatorial-Afrika. *Ergebnisse der zweiten deutschen Zentral-Afrika-Expedition 1910-1911 unter Führung Adolf Friedrichs, Herzog zu Mecklenburg.* Klinkhardt & Biermann, Leipzig.
- LEGRAND, J., 1975. Contribution a la faune du Gabon, odonates: 1er note. *Annls Soc. ent. Fr.* (N.S.) 11(4): 679-696.
- LEGRAND, J., 1980. Macromia hervei n. sp. précédemment confondue avec *M. aequatorialis* (Martin, 1906) (Odonata, Libellulidae). *Revue fr. Ent.* (N.S.) 2(1): 10-14.
- LEGRAND, J., 1982. Une nouvelle corduline du Sénégal, Macromia royi, n. sp. (Odonata, Corduliidae). *Revue fr. Ent.* (N.S.) 4(3): 120-122.
- LEGRAND, J., 1983. Note sur les odonates actuellement connus des Monts Nimba (Afrique Occidentale). *Revue fr. Ent.* (N.S.) 5(4): 152-162.
- LEGRAND, J., 1989. Note synonymique sur trois odonates afrotropicaux. *Revue fr. Ent.* (N.S.) 11(1): 36.
- LEGRAND, J., 1991. Une nouvelle Macromia de Côte d'Ivoire *M. girardi* n.sp. (Odonata, Anisoptera, Corduliidae). *Revue fr. Ent.* (N.S.) 13(4): 163-166.
- LEGRAND, J., 1992. Une nouvelle Macromia du groupe paula Karsch de la République Populaire du Congo (Odonata, Anisoptera, Corduliidae). *Revue fr. Ent.* (N.S.) 14(3): 127-131.
- LEGRAND, J., 1993. Une nouvelle Macromia du groupe paula Karsch des Monts Nimba en Guinée, Afrique occidentale (Odonata: Corduliidae). *Opusc. zool. umin.* 107: 1-6.
- LINDLEY, R.P., 1980. Macromia gamblesi spec. nov. from the Central African Republic (Anisoptera: Corduliidae). *Odonatologica* 9(2): 189-195.
- LONGFIELD, C., 1936. Studies on African Odonata, with synonymy and descriptions of new species and subspecies. *Trans. R. ent. Soc. Lond.* 85: 467-498.
- LONGFIELD, C., 1959. The Odonata of N. Angola. 2. *Publicoens cult. Co. Diam. Angola* 45: 13-42.
- MARTIN, R., 1907a. Cordulines. *Collns zool. Edm. de Selys Longchamps* 17: 1-94.
- MARTIN, R., 1907b. Odonates de la Guinée espagnole. *Mems Soc. esp. Hist. nat.* 1(23): 421-432.
- MARTIN, R., 1912. Les libellules du cercle de Sikasso. *Feuilles jeun. Nat.* 5(42): 92-99.
- MAY, M.L., 1997. Reconsideration of the status of the genera Phyllomacromia and Macromia (Anisoptera: Corduliidae). *Odonatologica* 26(4): 405-414.
- NIELSEN, C., 1935. Spedizione zoologica del Marchese Saverio Patrizi nel Basso Giuba e nell'Oltregubia. Odonati e catalogo odonati del 'Corno orientale dell'Africa. *Annali Mus. civ. Stor. nat. "Giacomo Doria", Genova* 58: 66-78.
- PINHEY, E., 1961. A survey of the dragon ies (order Odonata) of eastern Africa. Br. Mus. (Nat. Hist.), London.
- PINHEY, E., 1962. A descriptive catalogue of the Odonata of the African continent. *Publicoens cult. Co.*

- Diam. Angola* 59: 11-322.
- PINHEY, E., 1963. Some anomalous types of African Odonata and the description of a new species. *J. ent. Soc. sth. Afr.* 26(1): 146-160.
- PINHEY, E., 1976. Dragonflies (Odonata) of Botswana, with ecological notes. *Occ. Pap. natn. Mus. Sth. Rhodesia* (B) 5(10): 524-601.
- PINHEY, E., 1984. A checklist of the Odonata of Zimbabwe and Zambia. *Smithersia* 3: 1-64.
- PINHEY, E. & N. PINHEY, 1984. A preliminary list of the Odonata collected by Dr J. Kielland in Tanzania for Dr M.A. Liefinck. *Odonatologica* 13(1): 129-138.
- RIS, F., 1917. Libellen aus Deutsch-Ostafrika und Uganda. *Revue suisse Zool.* 25(7): 145-151.
- RIS, F., 1921. The Odonata or dragonflies of South Africa. *Ann. S. Afr. Mus.* 18: 245-445.
- SCHMIDT, E., 1951. Libellen aus Portugiesisch Guinea, mit Bemerkungen über andere aethiopische Odonaten. *Arqs Mus. Bocage* 20: 125-200.
- SCHOUTEDEN, H., 1934. Catalogues raisonnés de la faune entomologique du Congo Belge. Pseudonévrop-tères — Odonates. *Annls Mus. r. Congo belge* (Zool.) 3: 1-84.
- SELYS-LONGCHAMPS, E. DE, 1871. Synopsis des cordulines (1), 2me légion. — *Macromia*. *Bull. Acad. r. Belg.* 31:519-565.
- SELYS-LONGCHAMPS, E. DE, 1879. Description of a new species of *Phyllomacromia* (Corduliina) from West Africa. *Ent. mon. Mag.* 16: 103-104.
- SJÖSTEDT, Y., 1900. Odonaten aus Kamerun. *Bih. K. svenska VetenskAkad. Handl.* (IV) 25(2): 1-62.
- VICK, G.S., 1999. A checklist of the Odonata of the South-West province of Cameroon, with the description of *Phyllogomphus corbetiae* spec. nov. (Anisoptera: Gomphidae). *Odonatologica* 28(3): 219-256.