

**Inflation by venation and the bankruptcy of traditional genera:
the case of *Neodythemis* and *Micromacromia*, with keys to the
continental African species and the description of two new
Neodythemis species from the Albertine Rift
(Odonata: Libellulidae)**

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Key words: Odonata, dragonfly, Anisoptera, *Allorrhizucha*, *Eothemis*, *Monardithemis*, *Mesumbethemis*, taxonomy, synonyms, Africa.

ABSTRACT

The Afrotropical ‘neodythemistine’ genera are an example of venation-biased classification in Odonata. This example is used to argue the bankruptcy of some traditional classifications in the order, particularly in the Libellulidae, and the need to apply alternative characters to define genera. Two groups of Afrotropical ‘neodythemistines’ are identified by male and female genitalia, supported by colour patterns, and these correspond to the only two genera which we retain: *Micromacromia* and *Neodythemis*. A new classification is proposed on this basis: *Eothemis* and *Monardithemis* are synonyms of *Micromacromia*; *E. zygoptera* and *M. flava* are transferred to *Micromacromia*; *Neodythemis scalarum* is a synonym of *M. zygoptera*. *Allorrhizucha* and *Mesumbethemis* are synonyms of *Neodythemis*; *A. campioni*, *A. klingi*, *A. preussi*, *M. takamandensis* and *Micromacromia afra* are transferred to *Neodythemis*; *N. africana* and *N. gorillae* are synonyms of *N. afra*. A checklist of Afrotropical ‘neodythemistine’ species and a key to the continental species is provided. Two new *Neodythemis* species are described from the Albertine Rift; *N. munyaga* sp. nov. (holotype ♂: Uganda, Bwindi Impenetrable National Park, Buhoma, Munyaga Valley, alt. ca 1,600 m a.s.l., 17 v 2003) and *N. nyungwe* sp. nov. (holotype ♂: Rwanda, Nyungwe National Park, Karamba, alt. ca 1,500 m a.s.l., 28 x 1985).

INTRODUCTION

Vick (2000) gave an overview of the African and Malagasy Tetrathemistinae, a heterogeneous assemblage of superficially similar genera. All species are small and black, marked with yellow or green, and possess a diagnostic combination of venation characters:

- (1) Fw discoidal field of one or two rows of cells at its base;
- (2) Fw discoidal cell (= triangle) quadrangular or an equilateral triangle;
- (3) arculus usually distal of Ax2, but often proximal in *Tetrathemis*;
- (4) distal Ax complete;
- (5) supratrangles with cross-vein, but without in *Malgassophlebia*;
- (6) cubital and bridge spaces often with additional (i.e. more than one) cross-veins.

G. Fleck, M. Brenk and B. Misof (pers. comm.) added two characters:

- (7) Hw arculus well basal of triangle, but sometimes level with triangle's base in *Monardithemis flava*;
- (8) Rspl parallel to IR3 and extending to wing margin.

These characters are considered “primitive” (e.g. Fraser 1957) but a classification founded merely on potential plesiomorphies is unsound (Vick 2000; G. Fleck, M. Brenk, B. Misof pers. comm.). Dijkstra (2003) remarked for Libellulidae in general that the true value of many (small) genera must be established and stated that the lack of clarity had in part been created by an overemphasis on wing venation characters and by a lack of appreciation of their variability by previous authors.

The focus in this paper is on the ‘neodythemistine’ genera, which differ from the remaining ‘tetrathemistines’ by possessing additional bridge cross-veins (Fig. 1). They also have a stronger tendency to double-rowed Fw discoidal fields and addi-

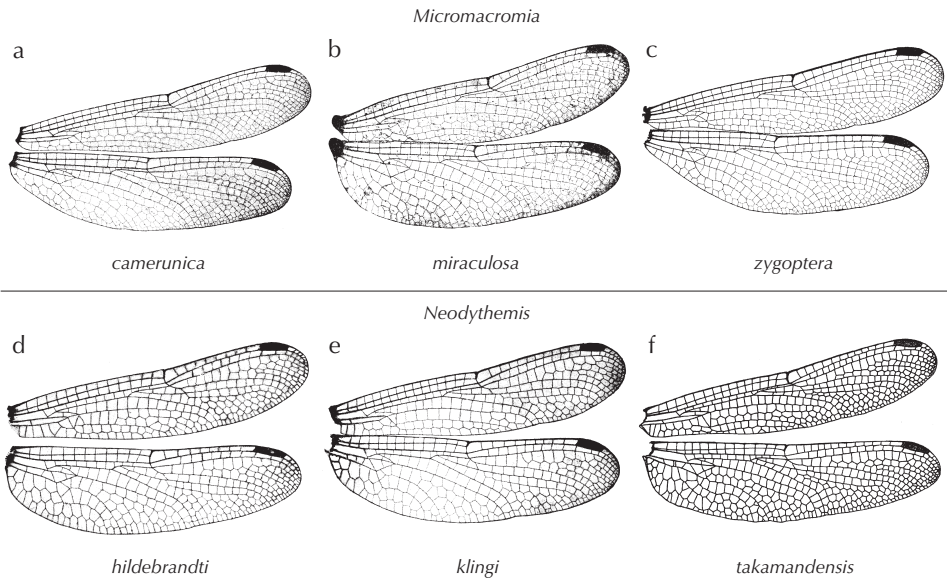


Figure 1: Wings of *Micromacromia* and *Neodythemis* species — (a) *M. camerunica* male; (b) *M. miraculosa* female; (c) *M. zygoptera* male; (d) *N. hildebrandti* male; (e) *N. klingi* male; (f) *N. takamandensis* male. From Ris (1909), except 1b from Ris (1919) and 1f from Vick (2000).

tional cross-veins in the cubital spaces and discoidal cells. More importantly, this group is characterised by its hamular structure: the hook is tilted inwards, lying in a horizontal plain (Fig. 4). There is a longitudinal ridge across the hamule, behind which the hook is often concealed in lateral view (Fig. 3). In the Afrotropics (including Madagascar) six ‘neodythemistine’ genera and 17 species are generally recognised, but we will argue that this must be brought down to two and 14 respectively, while two new species are added (Table 1). When describing *Mesumbethemis takamandensis*, Vick (2000) struggled with genus definitions. His dilemma was either to merge *Neodythemis* and *Micromacromia* so his new species could be incorporated, or to keep them apart and erect a new genus for it. The present paper was instigated by similarities noted between ‘neodythemistine’ species in different genera. This raised the questions of the delimitation of the genera once more. The observations are presented below as separate cases, followed by a general discussion. Where genera are in question and many species may require relocation on the basis of similar arguments, such an approach seems warranted.

The terms ‘tetrathemistines’ and ‘neodythemistines’ for certain Afrotropical libellulids are used here strictly for convenience, following above definitions. Neither can be considered a valid taxon before worldwide phylogenetic analysis of the Libellulidae has been undertaken: ‘tetrathemistines’ are probably polyphyletic although its ‘neodythemistine’ subset may be monophyletic (G. Fleck, M. Brenk, B. Misof pers. comm.), but in neither case are group limits established.

MATERIAL AND METHODS

All relevant specimens in BMNH, ISNB, MRAC, NHRS, NMBZ, NMKE, RMNH, ZMHB and the second author’s collection and many in other collections were examined, including most primary types. Venation characters were quantified based on this material and the literature (Table 2).

Acronyms for collections:

BMNH	Natural History Museum, London
CGVL	Collection Graham Vick, Little London
ISNB	Institut Royal des Sciences Naturelles de Belgique, Brussels
MCSN	Museo Civico di Storia Naturale “Giacomo Doria”, Genova
MNHN	Muséum National d’Histoire Naturelle, Paris
MNMS	Museo Nacional de Ciencias Naturales, Madrid
MRAC	Musee Royal de l’Afrique Centrale, Tervuren
NHRS	Naturhistoriska Riksmuseet, Stockholm
NMBZ	Natural History Museum of Zimbabwe, Bulawayo
NMKE	National Museums of Kenya, Nairobi
RMNH	Nationaal Natuurhistorisch Museum Naturalis, Leiden
UMMZ	University of Michigan Museum of Zoology, Ann Arbor
ZMHB	Museum für Naturkunde der Humboldt-Universität, Berlin
ZMMU	Zoological Museum of Makerere University, Kampala
ZSMC	Zoologische Staatssammlung, Munich.

THE CASES TO BE CONSIDERED

Neodythemis scalarum and *Eothenis zygoptera*

Pinhey (1964) described *N. scalarum* from Sierra Leone as “closest to this genus but ... decidedly more primitive than known members” by its peculiar venation, but he concluded “it seems undesirable to erect a new genus”. Aguesse (1968) added that “un matériel plus abondant serait nécessaire avant créer un nouveau genre pour cette espèce”, but Carfi & D’Andrea (1994) stressed it was “a true *Neodythemis*” that “should not be considered as a case apart”. None of these authors mentioned *Eothenis*, although *E. zygoptera* shares the venational peculiarities of *N. scalarum*: (1) Fw with 3-5 Cux; (2) Fw discoidal field of one row at its base; (3) anal loop indistinct, of only 2-4 cells; (4) Hw triangle uncrossed. Ris (1909) separated *Eothenis* from *Micromacromia* because of these characters and the quadrangular rather than triangular Fw triangle: its fourth side results from a kink (or break) in the anterior vein at about a third of its length from the triangle’s distal corner (Fig. 1c). Pinhey (1964) stated that *N. scalarum* had the Fw “triangle broken on upper edge”, indicating it is not perfectly triangular. By hamular structure, female abdomen shape and colour pattern *N. scalarum* and *E. zygoptera* are almost identical to each other, and also to *M. camerunica* (Figs 2a, 3a, 3d, 6b, 6c).

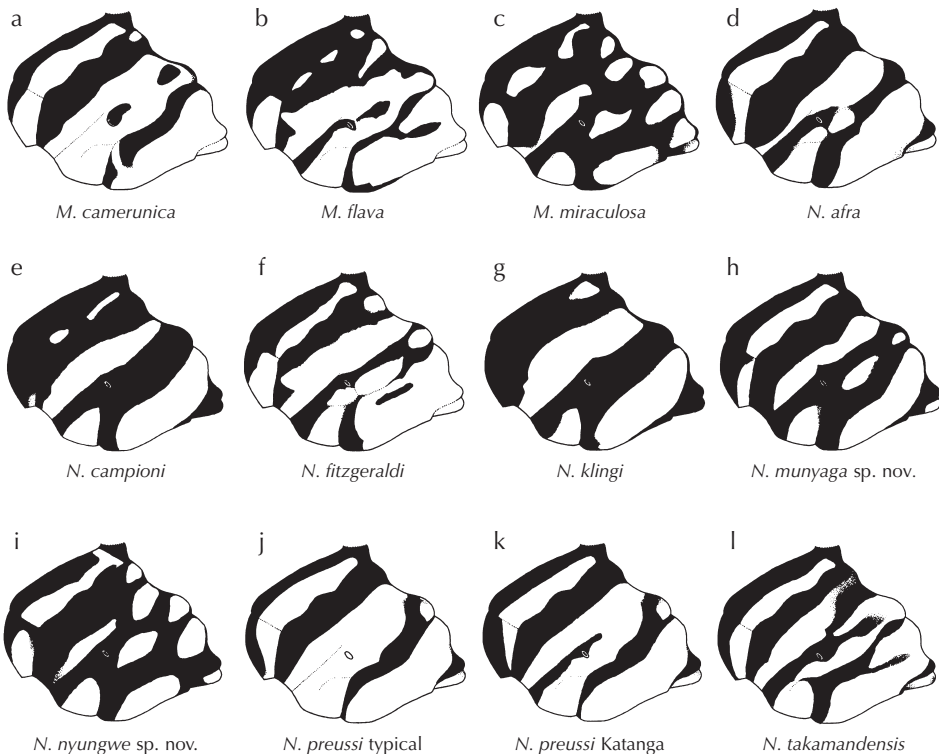


Figure 2: Synthorax of *Micromacromia* and *Neodythemis* species, lateral view.

Some variation, mainly in the intensity and shape of the interpleural and metapleural dark markings, appears to be individual. In *N. scalarum* the posterior corner of the hamule is angular (Fig. 3d), while it is rounded in *M. camerunica* (Fig. 3a). Ris (1909) did not show this feature because it is concealed in the genital fossa of the holotype of *E. zygoptera*, but he described the hamule of a conspecific and topotypical (Cameroon) male to form a fine point towards the rear. Males in NHRS from Cameroon identified by Sjöstedt (1900) as *M. camerunica* and one from that country in MNMS have an angled hamule and typical *Eothenis* venation (see above): the position of the kink in the anterior vein of their Fw triangles is variable, maximally a third from the triangle's distal corner. The shape of the cell is thus unstable and cannot differentiate *E. zygoptera* and *N. scalarum*. The latter is only known from Sierra Leone, while *E. zygoptera* has been reported from Sierra Leone, Guinea, Liberia, Côte d'Ivoire, Ghana, Nigeria, Cameroon, Gabon and possibly further east (Gambles 1980; Ris 1909; 1919; Legrand 1975; 2003; Legrand & Couturier 1985; Lempert 1988; O'Neill & Paulson 2001). Legrand (2003) listed *N. scalarum* from Mt Nimba in Guinea, but his remark "sans bande antéhumérale" suggests he had *Allorrhizucha campioni*, which has this stripe reduced and also has numerous Fw Cux.

Neodythemis africana, *N. gorillae* and *Micromacromia afra*

In his description of *N. africana*, Fraser (1954) noted: "This is the first species of the genus to be reported from the African continent (but only if the genus *Micromacromia* is not synonymous with *Neodythemis*, which I very much doubt). The present species is very similar to *M. afra* Ris from the Cameroons, W. Africa, differing by the narrower discoidal field and lower antenodal index." ISNB possesses the holotype male of the latter from Cameroon and four females from Old Calabar, Nigeria. The series agrees well with the Cameroon specimens reported as *N. africana* by Vick (1999), although the male has the head of another species glued on, possibly of *Orthetrum julia* Kirby. The *N. africana* holotype differs only in being somewhat smaller (Hw 26 mm vs 28 mm) and paler; the black stripe through the metastigma is clearly separated from the metapleural stripe (Fig. 2d), while these are broadly fused in *M. afra*. Venation is similar and Fraser's (1954) remarks probably referred to the *M. afra* females, which are large (Hw 29-31 mm), have 15-17 Fw Ax (holotypes *M. afra* and *N. africana* have 15 and 14-15 respectively) and a tendency to two rows of cells in the Fw discoidal field (only 1-5 cells single). Additional *N. africana* specimens from NE Congo-Kinshasa narrow the gap between the two holotypes: allotype from Bambesa (MRAC; Hw 28.5 mm, 13-15 Fw Ax), another male from Bambesa (ISNB; 27, 13) and a male from PN Garamba (MRAC; 27.5, 14). The allotype has the metathoracic stripes broadly fused, like *M. afra*. Males from Uganda's Semliki NP are smaller (Hw 24.5-25.5 mm) with mostly 4 cells in the anal loop (sometimes 5) instead of 5-6 (sometimes 7) as seen in other material. The previously mentioned specimens are geographically disparate but Pinhey (1962, 1971) reported *N. africana* from Ketta and Mekoum Forests in Congo-Brazzaville and Boukoko in the Central African Republic. Vick (1999) found that a female from Cameroon agreed with one from Ketta Forest in BMNH. The male holotype of *N. gorillae* (NMBZ) is small (Hw 24 mm, 13-14 Fw Ax, 5-5 anal loop cells), but matches all aforementioned specimens in all characters.

Table 1. Revised list of Afrotropical 'neodythemistine' species.

Micromacromia Karsch, 1890	<i>Micromacromia</i> Karsch (1890: 388), type species: <i>M. camerunica</i> . <i>Eothemis</i> Ris (1909: 70), type species: <i>E. zygoptera</i> ; new synonymy. <i>Monardithemis</i> Longfield (1947: 21), type species: <i>M. flava</i> , new synonymy.
<i>M. camerunica</i> Karsch, 1890	<i>Micromacromia camerunica</i> Karsch (1890: 389), type: Cameroon; ZMHB.
<i>M. flava</i> (Longfield, 1947) comb. nov.	<i>Monardithemis flava</i> Longfield (1947: 23), type: Kalukembé, Angola; BMNH.
<i>M. miraculosa</i> (Förster, 1906)	<i>Neodythemis miraculosa</i> Förster (1906: 31), type: E Usambara, Tanzania; lost ¹ . <i>Micromacromia miraculosa</i> (Förster) — Ris (1919: 1052).
<i>M. zygoptera</i> (Ris, 1909) comb. nov.	<i>Eothemis zygoptera</i> Ris (1909: 71), type: Cameroon; MNHN. <i>Neodythemis scalarum</i> Pinhey (1964: 1149), type: Bandakarafaia, Sierra Leone; lost ² ; new synonymy.
Neodythemis Karsch, 1889	<i>Neodythemis</i> Karsch (1889: 252), type species: <i>N. hildebrandti</i> . <i>Allorrhizucha</i> Karsch (1890: 390), type species: <i>A. klingi</i> ; new synonymy. ³ <i>Oreoxenia</i> Förster (1899: 189), type species: <i>O. ouvirandrae</i> . <i>Pseudophlebia</i> Martin (1903: 510), type species: <i>P. trinervulata</i> . <i>Mesumbethemis</i> Vick (2000: 226), type species: <i>M. takamandensis</i> ; new synonymy.
<i>N. afra</i> (Ris, 1909) comb. nov.	<i>Micromacromia afra</i> Ris (1909: 75), type: Cameroon; ISNB. <i>Neodythemis africana</i> Fraser (1954: 257), type: Bambesa, Congo-Kinshasa; MRAC; new synonymy. <i>Neodythemis gorillae</i> Pinhey (1961a: 267), type: Gorilla Mountain, Cameroon; NMBZ; new synonymy.
<i>N. arnaulti</i> Fraser, 1955	<i>Neodythemis arnaulti</i> Fraser (1955: 40), type: Andohahelo, Madagascar; MNHN.
<i>N. campioni</i> (Ris, 1915) comb. nov.	<i>Allorrhizucha campioni</i> Ris (1915: 214), type: Dumballa, Sierra Leone; BMNH.
<i>N. fitzgeraldi</i> Pinhey, 1961	<i>Neodythemis fitzgeraldi</i> Pinhey (1961b: 64), type: Abercorn (= Mbala), Zambia; NMBZ.
<i>N. hildebrandti</i> Karsch, 1889	<i>Neodythemis hildebrandti</i> Karsch (1889: 252), type: Madagascar; ZMHB. <i>Oreoxenia ouvirandrae</i> Förster (1899: 191), type: Montagne d'Ambre, Madagascar; UMMZ. <i>Pseudophlebia minima</i> Kirby — Needham (1903: 763); nomen nudum. <i>Pseudophlebia mimica</i> Selys, in litt. — Martin (1908: 652); nomen nudum.
<i>N. klingi</i> (Karsch, 1890) comb. nov.	<i>Allorrhizucha klingi</i> Karsch (1890: 390), type: Bismarckburg, Togo; ZMHB.
<i>N. munyaga</i> sp. nov.	<i>Pseudophlebia occidentalis</i> Martin (1908: 651), type: Musola, Bioko; MCSN.
<i>N. nyungwe</i> sp. nov.	<i>Neodythemis munyaga</i> sp. nov., type: Munyaga Valley, Uganda; ZMMU.
<i>N. pauliani</i> Fraser, 1952	<i>Neodythemis nyungwe</i> sp. nov., type: Nyungwe Forest, Rwanda; ZSMC.
<i>N. preussi</i> (Karsch, 1891) comb. nov.	<i>Neodythemis pauliani</i> Fraser (1952: 140), type: Anosibe, Madagascar; MNHN.
<i>N. trinervulata</i> (Martin, 1903)	<i>Allorrhizucha preussi</i> Karsch (1891: 30), type: Kribi, Cameroon; ZMHB.
<i>N. takamandensis</i> (Vick, 2000) comb. nov.	<i>Pseudophlebia trinervulata</i> Martin (1903: 510), type: Sakavalana, Madagascar; MNHN. <i>Neodythemis trinervulata</i> (Martin) — Ris (1909: 77).
<i>N. trinervulata</i> (Martin, 1903)	<i>Mesumbethemis takamandensis</i> Vick (2000: 226), type: Takamanda Forest, Cameroon; CGVL.

¹ Not in UMMZ (Garrison et al. 2003); ² Not in MNHN (Legrand 2003); ³ Often misspelt as *Allorrhizucha* (e.g. Vick 2000, Legrand 2003)

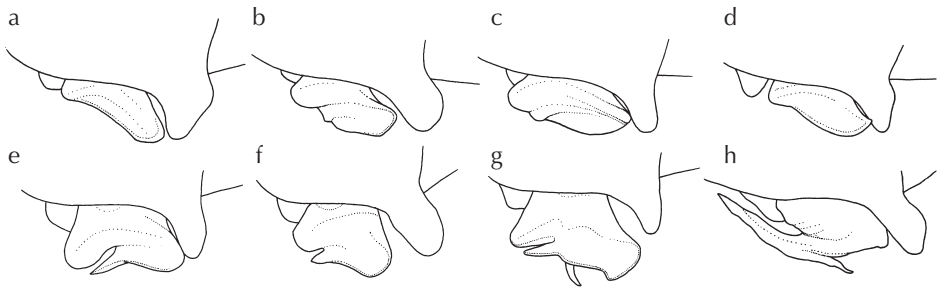


Figure 3: Secondary genitalia of *Micromacromia* and *Neodythemis* species, lateral view (bristles omitted) — (a) *M. camerunica*; (b) *M. flava*; (c) *M. miraculosa*; (d) *M. zygotera*; (e) *N. afra*; (f) *N. klingi*; (g) *N. preussi*; (h) *N. takamandensis*.

Monardithemis flava and *Micromacromia miraculosa*

Longfield (1947) believed her genus *Monardithemis* and its type species *M. flava* were closest to *Micromacromia* and *Neodythemis*. Ris (1919) transferred Förster's (1906) *Neodythemis miraculosa* to *Micromacromia* because of its broad Fw discoidal field and long anal loop, but with this loop and the usually crossed Fw triangle it is more similar to *Monardithemis* than to *M. camerunica*, the type species of *Micromacromia* (Fig. 1b). The fragmented body markings and hamular structure also recall each other (Figs 2b, 2c, 3b, 3c). *Sleuthemis diplacoides* Fraser has been associated with *M. flava* because of its synonym *Monardithemis leonensis* Aguesse (Lieftinck 1969), but *Sleuthemis* is the same as *Aethiothemis* (K.-D.B. Dijkstra unpubl.); thus *Monardithemis* remains monotypic.

Allorrhizucha and *Mesumbethemis*

Allorrhizucha only differs from *Neodythemis* by the narrower Fw discoidal field and smaller anal loop (Vick 2000). Both genera are similar in the ground-plan of markings and share their complex hamular structure (Figs 2d-k, 3e-g). The shape of S8-10 and the vulvar scale are similar in all *Allorrhizucha* and *Neodythemis* females examined (Figs 6d, 7b). *Mesumbethemis takamandensis* is only known from the male holotype (Vick 2000). Although greatly exaggerated, the hamule has the *Neodythemis* structure (Figs 3h, 4c), and the markings also recall that genus (Fig. 2l). The venation differs by the long Fw triangle, many-celled Fw discoidal field and the large anal loop (Fig. 1f).

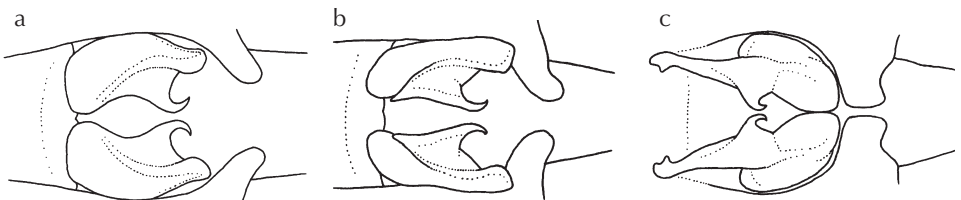


Figure 4: Secondary genitalia of *Micromacromia* and *Neodythemis* species, ventral view (bristles omitted) — (a) *M. flava*; (b) *N. munyaga* sp. nov.; (c) *N. takamandensis*.

Table 2. Venation characters of Afrotropical 'neodythemistine' males — species sorted from 'primitive' to 'advanced' within genera (see Discussion). The Malagasy species (see Table 1) are given as one because of their similarity and limited data. Where samples allowed it the mode and uncommon variations (latter in brackets) are given. — Abbreviations, AL: anal loop (number of cells); Ax: antenodal veins (number); Cux: cubital cross-veins (number); DC: discoidal cell (number of cells); DF: discoidal field – 1: one row at base and at level of node; 2: one row at base, more at node; 3: two rows at base; Fw: forewing; Hw: hindwing. Females may have slightly higher values than males: there is on average a cell more in the anal loop and a stronger tendency to cell-doublings in the Fw discoidal field, leading to occasional values of 2 or 3 where 1 or 2 respectively are the norm, or a few cell-doublings at the base of an otherwise largely single-rowed field.

	Fw DF	Hw AL	Fw Cux	Hw Cux	Fw DC	Hw DC	Fw Ax
Micromacromia							
<i>M. zygoptera</i>	2	2-3 (4)	3-5	3-4	1	1 (2)	13-14 (15)
<i>M. camerunica</i>	3	7-10 (5-12)	1 (2)	3 (2-4)	1 (2)	2	14-16 (13-18)
<i>M. flava</i>	3	10-15	1	2	2	2	9-12
<i>M. miraculosa</i>	3	13-14 (12-15)	1	3 (4)	2 (1)	2	13-14 (12-15)
Neodythemis							
<i>N. campioni</i>	1	4-5	4 (2-5)	3 (4)	1	2 (1)	14 (12-14)
<i>N. klingi</i>	1	4 (3-5)	1 (2)	2 (3)	1	2 (1)	13-14 (12-16)
<i>N. preussi</i>	1	4 (2-4)	1	2 (3)	1	2 (1)	15-16 (13-17)
<i>N. afra</i>	2	4-6 (7)	1	2 (3)	1	2 (1)	14-15 (13-17)
Malagasy <i>Neodythemis</i>	2	4-8	1	2	1	2	11-13
<i>N. munyaga</i> sp. nov.	2	6 (5-8)	1	2 (3)	1	2	13-14
<i>N. nyungwe</i> sp. nov.	2	6-7	1	3	1	2	14
<i>N. fitzgeraldi</i>	2	6-7 (5-8)	1	2 (3)	1	2 (1)	11-12
<i>N. takamandensis</i>	3	13-14	1	3-4	1	2	15

Discussion

As it is demonstrated above, *Micromacromia afra*, *Neodythemis africana* and *N. gorillae* cannot be separated, nor can *Eothenis zygoptera* and *Neodythemis scalarum*. This directly raises the question whether *Eothenis*, *Micromacromia* and *Neodythemis* are distinct. Fraser (1954) and Vick (2000) thought the latter two were likely synonyms, an idea based primarily on venation. The cases show that species placed in different genera because of distinct venation are very similar in other characters. It is therefore necessary to discuss the value of the various characters available.

As mentioned in the introduction, the hamular shape is characteristic of the 'neodythemistines', but it is rather uniform among species. In *Allorrhizucha*, *Mesumbethemis*, *Neodythemis* (except *N. scalarum*) and *Micromacromia afra* the ridge and hook of the hamule are anteriorly separated from its main body by a deep cleft (Figs 3e-h). The anterior cleft is completely absent in *Eothenis*, *Monardithemis*, *Micromacromia* (except *M. afra*) and *N. scalarum* (Figs 3a-d). All the females of the latter group have S8 distinctly expanded, the dilations marked with a conspicuous pale spot (Figs 6a-c). The paired valves of the vulvar scale and the pro-

cesses on the S9 sternite are reduced; the sternite terminates in a hairy swelling that does not surpass the S9 tergite (Fig. 7a). In the former group S8 lacks the spotted dilations (Fig. 6d), and the valves and processes are well-developed; the sternite ends in a hair-fringed plate that in most cases surpasses the tergite (Fig. 7b). The length of the plate and the size and direction of the processes vary among species and may be used to identify them. Although observations for most species are wanting, the dilated abdomen tip appears to be used to place eggs above the waterline (e.g. on stream banks), which otherwise are deposited directly into the water (Clausnitzer & Lempert 1998). Markings are very diverse in the 'neodythemistines' and are the main key to species identification (Fig. 2). It is therefore remarkable that *E. zygoptera* and *N. scalarum* are marked like *Micromacromia camerunica* (Fig. 2a). *Monardithemis flava* and *Micromacromia miraculosa* have more black on the thorax, especially in the interpleural area, and show stronger fragmentation of the pale markings (Figs 2b, 2c). The remaining species share a similar design of the thoracic markings, most notably by the black metastigmal stripe converging with the metapleural stripe dorsally (Figs 2d-l), the former only being absent in most specimens of *A. preussi* (Fig. 2j).

Species with similar sexual characters have been assigned to two, three or even four different genera based solely on venation. The question is how great these differences really are. The states of four venation characters, which largely define the genera, principally reflect the relative width and shape of the wings, and are therefore correlated:

1. — The shape of the Fw triangle (discoidal cell) is determined by the position of its anterior vein and the length of its basal and distal sides. A wider wing can contain a longer triangle, which is more likely to accommodate a cross-vein. In a narrower wing the anterior vein has the tendency to shift up along the posterior sector of the arculus, which leads to a kink in the so-called 'broken' vein. The only species under consideration where the anterior vein is typically kinked and where the Fw triangle is thus actually quadrangular is *E. zygoptera*. This single character has been given so much weight that Pinhey (1964), Aguesse (1968) and Carfi & D'Andrea (1994) successively failed to notice the similarity of *N. scalarum* to *Eothenis*. Nonetheless the shape of the triangle is unstable (see also above): in *A. klingi* the presence and position of the anterior kink varies considerably, even differing in the two Fw of a single individual. Females have slightly longer triangles than males, in which the anterior vein is commonly kinked close to its distal end

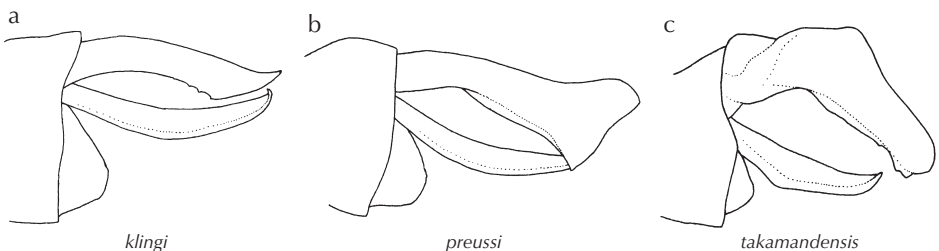


Figure 5: Male appendages of *Neodythemis* species, lateral view.

and occasionally even exactly at midpoint. Similar instability of the Fw triangle occurs in the other ‘tetrathemistines’ (i.e. not ‘neodythemistine’) *Malgassophlebia* (see below) and *Notiothemis*. The previously mentioned Fw quadrangles in some ‘neodythemistines’ cannot be compared with those of *Tetrathemis*, where the cell is part of a more structured configuration of veins: it is supported by the alignment of the distal border of the cubital space with the cross-vein in the supratriangle.

2. — The shape of the Fw discoidal field and the number of rows of cells it contains is determined by the proximity and course of veins MA and CuP, which depend on the distance between the anterior and posterior borders of the wings. The species classified in *Allorrhizucha* have these veins lying closest and most parallel to each other. Thus the Fw discoidal field terminally widens less than in other species, although these display a wide variety of field-shapes including nearly parallel-sided ones (e.g. Fig. 1f).

3. — The shape and sharpness (i.e. differentiation from surrounding venation) of the anal loop and the number of cells it contains is determined by the width of the Hw base. It allows the space for the loop’s development, as Fig. 1 demonstrates. The Hw width is also expressed by the number of undoubled cells at the extreme base of anal field: at most one in *M. camerunica* but three to five in *E. zygoptera* (Figs 1a, 1c).

4. — The relation between wing shape and the number of Fw Cux is not so obvious, but the two species with numerous Cux have narrow wings and corresponding states of characters (1), (2) and (3).

The discussed venation characters appear to be rather independent of other characters. For instance *A. klingi* despite similar venation differs clearly from *A. preussi* in markings and the shape of the male cerci (Figs 2g, 2j, 2k, 5a, 5b), while the nearly identical *A. campioni* differs markedly by its many Fw Cux. The latter character has had ‘generic value’ in the ‘neodythemistine’ complex, i.e. to separate the similar *M. camerunica* and *E. zygoptera*. Table 2 shows that the venation characters are linked: the number of cells in the Fw discoidal field, anal loop and triangles (and their shapes) increase together, while a high number of Fw Cux coincides with low values of the other characters. Females have somewhat broader wings than males, resulting in longer Fw triangles and somewhat higher venation values (see

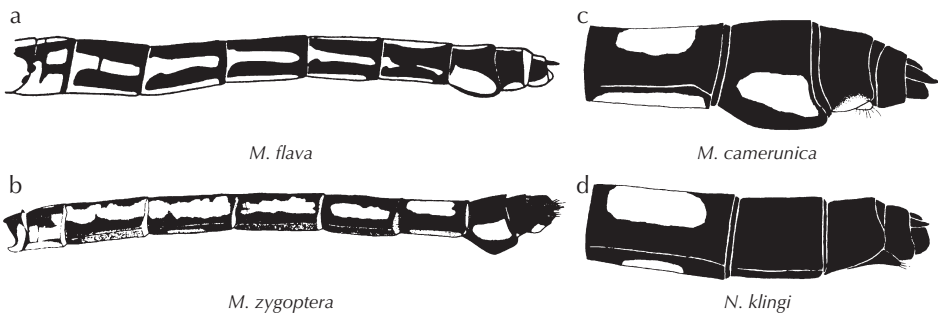


Figure 6: Female abdomen (a-b) or S7-10 (c-d) of *Micromacromia* and *Neodythemis* species, lateral view — (a) *M. flava* from Longfield (1947); (b) *M. zygoptera* from Carfi & D’Andrea (1994; as *N. scalarum*); (c) *M. camerunica*; (d) *N. klingi*.

Table 3. Diagnosis of the Afrotropical 'neodythemistine' genera. Note that characters of the origin of veins relative to the Hw triangle used by Ris (1909) did not prove to be informative. Larval characters are based on *M. camerunica*, *N. afra* and *N. klingi* only (G. Fleck, M. Brenk, B. Misof pers. comm.).

Character	<i>Micromacromia</i>	<i>Neodythemis</i>
Range	Tropical Africa	Tropical Africa and Madagascar
Anterior cleft of hamule	Absent (Figs 3a-d)	Present (Figs 3e-h)
Female S8 dilations	Broad, with black border and large lateral pale spot (Figs 6a-c)	Absent, at most narrow (Fig. 6d). If dilations and/or spot present, border is pale and spot more dorsal, i.e. S8 marked rather like S7.
Valves of vulvar scale and processes on sternite S9	Reduced (Fig. 7a)	Well developed (Fig. 7b)
Apex of sternite S9	With central hairy swelling, falls short of tergite S9 (Fig. 7a)	Hair-fringed plate, usually surpasses tergite S9 (Fig. 7b)
Labrum of continental species	At least with two basal pale spots, only <i>M. miraculosa</i> largely black	Usually all black, only <i>N. fitzgeraldi</i> pale with black border
Larval habitus	Uniformly coloured	Marked strongly with dark spots
Larval wing pads	Parallel	Divergent
Larval abdominal dorsum	Spines present on S4-8	Spines absent

caption of Table 2 for examples), and thus have additional variation within and overlap between species. The definition of taxa on presumed plesiomorphies (i.e. the 'primitive' venation characters of 'tetrathemistines') in itself is questionable as it potentially creates para- and polyphyletic groups. If these characters are correlated and merely reflect a single relative feature (e.g. wing shape) rather than common descent, their strength crumbles further. An example is found in the genus *Thermochoria* that is almost identical to *Hemistigma*. It is separated by the presence of two instead of one Ax between arculus and wing base and numerous cross-veins in the triangles, supratrangles, and bridge and cubital spaces. Traditionally these would be regarded as five distinct 'primitive' characters but more likely they represent a single apomorphy: multiplication of cross-veins. When such characters are also expressed in series of overlapping intermediate stages among morphologically similar taxa, their remaining support collapses. *E. zygotera* → *M. camerunica* → *M. miraculosa* represents such a gradient from 'primitive' to 'advanced' venation. Along it the Fw triangle gradually becomes less quadrangular, and the number of cells in the Fw discoidal field and anal loop increases (Figs 1a-c), but male and female sexual characters and to some degree markings remain uniform (Figs 2a-c,

3a-d, 6a-c, 7a). Note that *M. camerunica* is not uniform in the size of its anal loop: Cameroonian specimens usually have 9-10 (range 7-12) cells in it, Ugandan 7-8 (5-9). *Allorrhizucha* → *Neodythemis* → *Mesumbethemis* also grade from small to large anal loops (2-5 → 4-8 → 13-14) and from narrow to broad Fw discoidal fields (1 row → 1 row becoming 2 at node → 2 rows) (Figs 1d-f). The character overlap in these series excludes clear-cut delimitation of genera within them, e.g. a small anal loop is not unique to *Allorrhizucha*, while *A. klingi* females may have cell-doublings in the Fw discoidal field proximal of the node; a *Neodythemis* character. A parallel is seen in a venationally similar (i.e. also ‘tetrathemistine’) genus: *Malgassophlebia westfalli* Legrand, 1986 possesses the simultaneous expression of a triangular Fw discoidal cell, a Fw discoidal field of two rows (save a few single cells in its middle) and a long anal loop containing 10 cells, while other *Malgassophlebia* have a quadrangular Fw discoidal cell, a Fw discoidal field of one row at its base (and often almost to its end) and an anal loop of 4-5 cells. Legrand (1986) remarked that “certains caractères [including venation] ... m’ont fait penser que nous pourrions être en présence d’un genre nouveau ou au moins d’un sous-genre”, but he refrained from describing a new (sub)genus after examining the similarities in sexual characters of *Malgassophlebia* species. Legrand’s (1986) example can be mirrored in other libellulid groups. Here similar observations will lead to the cancellation of genera: series of intergrading genera, in venation and other characters, are found under *Aethiothemis* and *Congothemis*, which furthermore seem to connect them to *Lokia* and *Trithemis* respectively (K.-D.B. Dijkstra unpubl.).

Throughout Libellulidae a strong, almost blind, emphasis on venation to define genera has led to the description of many superfluous genera and numerous incorrect genus-associations of species. It is illustrative that *Aethiothemis* has three synonyms and that its six recognised species have synonyms in six different genera. Figures for *Congothemis* are identical, although its species have synonyms in ‘only’ five genera (K.-D.B. Dijkstra unpubl.). The overvaluation of a single character-set may likewise have led to the oversight of distinct genera with similar venation. The bankruptcy of traditional classifications is not unique to Afrotropical ‘neodythemistines’. Fleck (2004) in his discussion of the relationships of *Cyanothemis* summarised that “studying wing venation in systematics and phylogeny was till now preponderant, but seems limited in Libellulidae” and put more faith in larval setation, leg armature and genetics. Indeed that author demonstrates that larvae and DNA place *A. klingi*, *M. camerunica* and *N. afra* close to each other and ‘libelluline’ libellulids but not to other ‘tetrathemistines’ (G. Fleck,

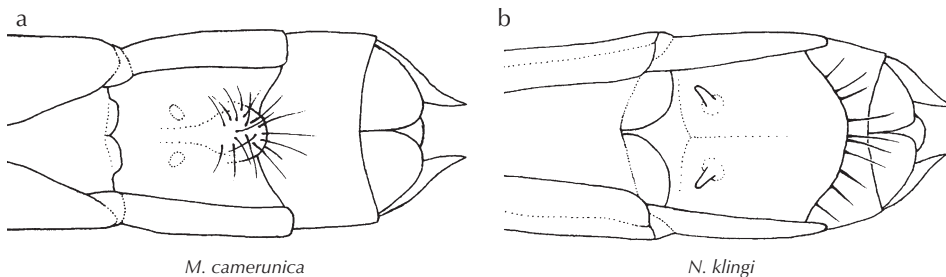


Figure 7: Female S8-10 of *Micromacromia* and *Neodythemis* species, ventral view.

M. Brenk, B. Misof pers. comm.). The fallibility of venation applies at all taxonomic levels. As discussed, 'tetrathemistine' characters (1) and (2) (see Introduction) are related to wing shape, as are (7) and (8): the Hw arcus shifts towards the triangle in wider wings (e.g. if *E. zygoptera*, *M. camerunica* and *M. flava* are compared), while the Rspl develops a tendency to curve towards IR3, thus terminating before the wing margin. Similar cases exist throughout Odonata and the order is probably at the dawn of a major upheaval in its higher classification, e.g. O'Grady & May (2003) showed that in Coenagrionidae venation characters do not even uphold the classifications that they were used to define.

From the above we conclude that within Afrotropical 'neodythemistines' (and more widely in Odonata, especially Libellulidae) there are series of similar species that venationally grade from more 'primitive' to more 'advanced', along which classifications based solely on venation break down. Applied to the presented cases, these taxonomic conclusions at the species level are apt:

- (1) *Eothemis zygoptera* and *Neodythemis scalarum* are conspecific;
- (2) *Eothemis zygoptera* and *Micromacromia camerunica* are congeneric;
- (3) *Micromacromia afra*, *Neodythemis africana* and *N. gorillae* are conspecific;
- (4) *Monardithemis flava* and *Micromacromia miraculosa* are congeneric.

These conclusions must be embedded in a revised classification based on alternative characters. A parsimonious solution that least affects the stability of nomenclature is preferable, in order to minimise the number of direct (and potential future) name-changes. Unifying all species under the single name *Neodythemis* is perhaps the most inclusive option and will result in nine name changes, but ignores the existence of two clear groups defined by sexual characters of both sexes and probably larvae (Table 3). Recognising these two as genera requires seven name changes and is our preference (Table 1). Consequent changes at the genus level are then:

- (1) *Eothemis*, *Micromacromia* and *Monardithemis* are synonyms;
- (2) *Micromacromia afra* belongs in *Neodythemis*;
- (3) *Allorrhizucha*, *Mesumbethemis* and *Neodythemis* are synonyms.

Because of differences in venation, markings and also some in sexual characters *Monardithemis* and *Mesumbethemis* could both be retained and *M. miraculosa* could be transferred to *Monardithemis*. This would imply inconsequent application of the conclusion to reduce the weight of venation and increase that of other characters and yield only one name-change less. *Mesumbethemis* is an example of the practice to separate genera on the basis of exaggerated characters, but such classifications reflect the taxonomist's awe for apomorphies rather than an objectivation of the synapomorphies it shares with relatives.

Micromacromia and *Neodythemis* seem to belong to a libellulid lineage which is especially rich in genera in Australasia. *Hylaeothemis* is extremely close to *Neodythemis* by general appearance and hamule structure. Similar, often more complex, hamular conditions are found in *Amphithemis*, *Hypothemis*, *Lyriothemis* and *Orchithemis*. Other Australasian genera in this lineage seem to be *Agrionoptera*, *Cratilla*, *Nesoxenia* and *Lathrecista*. These in turn recall Afrotropical genera like *Hadrothemis* and *Thermorthemis*. All named genera are either likely or known to belong to the 'libelluline' clade of libellulids identified by G. Fleck, M. Brenk, B. Misof (pers. comm.).

Keys to continental Afrotropical 'neodythemistines'

See Table 3 for the diagnosis of the genera. The keys should work for both sexes, although all values are based on males, and occasional females have higher values than stated, e.g. Hw length greater and Fw discoidal field being of two rows rather than one at base or level of node.

Key to *Micromacromia*

1. Antehumeral stripe reduced to 2-3 spots; black markings present above and below metastigma (Figs 2b-c); labium with central black marking; anal loop of 10-15 cells; Fw triangle and subtriangle of 2 cells, sometimes 1 (Fig. 1b) 2
- 1'. Antehumeral stripe broad and complete; at most small black marking above metastigma (Fig. 2a); labium all pale; anal loop of 2-9 cells, rarely up to 12; Fw triangle and subtriangle of 1 cell, sometimes 2 (Figs 1a, 1c) 3
2. Sides of thorax black with isolated pale spots (Fig. 2c); labrum black, with two pale basal spots; 12-15 Fw Ax; NE Tanzania *miraculosa*
- 2'. Sides of thorax pale, with irregular black lines (Fig. 2b); labrum pale with central black marking; 9-12 Fw Ax; Angola¹ *flava*
3. Fw discoidal field of 2 cell-rows at base; Fw with 1 Cux, rarely 2; Hw triangle of 2 cells; anal loop distinct, of 6-12 cells (Fig. 1a); posterior corner of hamule blunt (Fig. 3a); hind femur with 20-30 denticles in external-anterior row *camerunica*
- 3'. Fw discoidal field of 1 row at base; Fw with 3-5 Cux; Hw triangle of 1 cell, sometimes 2; anal loop indistinct, of 2-4 cells (Fig. 1c); posterior corner of hamule angled (Fig. 3d); hind femur with 10-20 denticles in external-anterior row *zygoptera*

Key to continental *Neodythemis*

1. Fw discoidal field of 1 cell-row at and distal of node, 2-5 cells wide on wing border (Fig. 1e) 2
- 1'. Fw discoidal field of 2-3 rows at and proximal of node, 4-11 cells wide on wing border (Figs 1d, 1f) 4
2. Antehumeral stripe broad and complete; interpleural stripe absent or separated from metapleural stripe (Figs 2j, 2k); labium all yellow, at most with narrow black inner borders; apex of cerci thickened (Fig. 5b) *preussi*
- 2'. Antehumeral stripe absent or reduced to one or two spots; interpleural and metapleural stripes fused to form broad black band (Fig. 2e, 2g); labium broadly black in middle; apex of cerci slender (Fig. 5a) 3

3. Fw with 1 Cux, rarely 2; antehumeral stripe absent or reduced to dorsal spot; mesepimeral pale stripe truncate dorsally (Fig. 2g); hook of hamule lying in horizontal plain, not visible in lateral view (Fig. 3f); widespread *klingi*
- 3'. Fw with 3-5 Cux, rarely 2; antehumeral stripe reduced to short stripe dorsally and spot ventrally; mesepimeral stripe tapered dorsally (Fig. 2e); hook of hamule more erect, visible in lateral view (cf. Fig. 3g); Upper Guinea *campioni*
4. Inner branch of hamule extremely elongated, reaching well over anterior border of hamule base (Figs 3h, 4c); cerci angularly bent at midlength (Fig. 5c); Fw discoidal field starts with 2 rows; anal loop of 13-14 cells (Fig. 1f) ... *takamandensis*
- 4'. Inner branch of hamule shorter, falling short of anterior border of hamule base (Figs 3e, 4b); cerci not bent at midlength (cf. Fig. 5a); Fw discoidal field starts with 1 row; anal loop of 4-8 cells (cf. Fig. 1d) 5
5. Labrum pale with black edge; black markings along metapleural suture interrupted (Fig. 2f); NE Zambia and Katanga² *fitzgeraldi*
- 5'. Labrum black; black markings along metapleural suture continuous (Figs 2d, 2h, 2i); W Uganda to SE Nigeria 6
6. Interpleural stripe ends just dorsal of metastigma (Fig. 2d); black tip of genital lobe separated from black dorsum S2 by broad pale area; latero-basal pale streak S3 aligned with subapical spot (the two separated by transverse carina); ventral pale spots S6-8 only present narrowly along ventral carinae; vertex all black *afra*
- 6'. Interpleural stripe complete, enclosing three pale spots with metapleural stripe (Fig. 2h, 2i); black of genital lobe connected to black dorsum S2; subapical spot S3 shifted ventrally, out of alignment with latero-basal streak; ventral spots S6-8 extend almost to lateral carinae or even onto dorsum; vertex may be yellow anteriorly 7
7. Antehumeral stripe connected dorsally to pale stripe along middorsal carina; pale markings on mesepimeron and metepimeron both broken into two well-separated spots (Fig. 2i); ventral pale spots S3-8 extend across lateral carinae onto dorsum; vertex all black; Hw 30-31 mm *nyungwe* sp. nov.
- 7'. Antehumeral stripe separated from middorsal stripe; pale markings on mesepimeron and metepimeron both forming a single band, sometimes broken narrowly (Fig. 2h); ventral spots S3-8 limited by black on lateral carinae; vertex yellow anteriorly; Hw 26-28 mm *munyaga* sp. nov.

¹ Two females in NMBZ reported from NW Zambia as *M. flava* by Pinhey (1984) pertain to *Aethiothemis basilewskyi* Fraser.

² A rather large female in NMBZ from Lubudi, Katanga, identified as a "new *Micromacromia*" by E. Pinhey, agrees with *N. fitzgeraldi*.

TWO NEW *Neodythemis* SPECIES
FROM THE ALBERTINE RIFT

Specimens studied

N. munyaga sp. nov. — holotype ♂: Uganda, Kanungu District, Bwindi Impenetrable National Park, Buhoma, Munyaga Valley (0°59-1°00'S, 29°36-37'E), tiny streams and seepage in rainforest, alt. ca 1,600 m a.s.l., 17 v 2003, leg. K.-D.B. Dijkstra, J.J. Kisakye & S.G. Kyobe, ZMMU. — 6 paratype ♂: same data, 16-18 v 2003, ZMMU. — 1 ♂: same data, 04 xii 2002, leg. J.J. Kisakye & S.G. Kyobe, ZMMU; — 1 ♂: same data, iv 2002, leg. T.W. Donnelly, coll. Donnelly (reported as *N. fitzgeraldi* by Donnelly (2002)).

N. nyungwe sp. nov. — holotype ♂: Rwanda, Nyungwe National Park, Karamba (2°30'S, 29°10'E), muddy pools and slow-flowing streamlets in rainforest, alt. ca 1,500 m a.s.l., 28 x 1985, leg. H. Mühle, ZSMC).

Neodythemis sp. — 1 ♀: Nigeria, Obudu, 25 iii 1971, leg. R.M. Gambles, BMNH. Identified as *N. gorillae* by Gambles, but is close to the new species, both unknown as females. In markings (the foremost diagnostic feature in the genus) it is most similar to the Uganda species but has narrower pale thoracic stripes and an all black vertex.

Etymology

Both species are named after their type localities as nouns in apposition.

Neodythemis munyaga sp. nov.
(Figs 2h, 4b)

Diagnosis

Dark, fairly robust *Neodythemis* with anteriorly yellow vertex and rather narrow pale thoracic markings composed of complete stripes with the exception of the metepisternal marking broken into three spots (Fig. 2h).

Description of holotype male

Dried in acetone and in good condition.

Head: labium yellow with central third black. Mandibles, genae and labrum all black. Clypeus yellow with lateral anterior borders of postclypeus and extreme lateral corners of anteclypeus black. Frons black with strong blue gloss and narrow yellow anterior border widening laterally. Vertex glossy black with anterior half yellow; demarcation sharp and W-shaped with black narrowly enclosing

lateral ocelli. Antennae black. Occipital triangle black turning brown anteriorly. Back of head all black with round yellow spot on occiput and on eye margin half-way down postgenae. Eyes in life deep blue.

Thorax: prothorax brownish black with central dorsal pale green area covering much of forelobe, narrow area on midlobe and entire hindlobe, the latter with erect fringe of long black hairs. Synthorax black, marked with greenish yellow as follows (Fig. 2h): large central spot on spiracular dorsum; complete narrow stripes flanking middorsal carina; complete fairly broad antehumeral stripe, narrowly separated from aligned large spot on posterior mesokatepisternum; complete mesepimeral stripe tapering ventrally, truncate dorsally and slightly constricted above metastigma; this stripe is about as wide as antehumeral and half of width of black area between it and antehumeral; large elongate metepisternal spot anterior of metapleural suture aligned with small spot on dorsal extreme of metepisternum and large spot on meta-katepisternum; complete broad stripe on metepimeron; large spot on metasternum; central spot covering most of poststernum. Legs all black, save pale posterior areas on fore femora and mid and hind coxae.

Wings: very lightly smoky, slightly tinted yellowish at extreme base; venation and Pt black. In Fw 13-14 Ax, in Hw 11-12, in Fw 10 Px, in Hw 9-10. Three bridge cross-veins in all wings. Cubital space with one cross-vein in Fw, two in Hw. All supratrangles and Hw triangles with one cross-vein, Fw triangles and subtriangles uncrossed. Fw discoidal field of one cell-row for 4-5 cells at base, becoming two at level of Ax10-11. Rspl subtends single row of cells. Anal field fairly small, anal loop about twice as long as wide, of 6 cells in both Hw.

Abdomen: black, tergites marked with pale yellow as follows: S1 with large lateral and dorsal spot. S2 with medio-dorsal stripe, large ventro-lateral spot and small lateral apical spot. S3 with pairs of rectangular sublateral spots at base, roundish lateral spots posterior to it (i.e. more ventral, not aligned with basal spots) and streaks along ventral carinae that are broader at base. S4-6 with rectangular sublateral basal spot pairs diminishing in size posteriorly; very small on S6. S7 with large roundish dorsal spot, somewhat pointed anteriorly and covering subbasal half of segment, narrowly split lengthwise by black on dorsal carina. S8-10 dorsally all black. Ventral part of tergites of S4-9 with pairs of roundish medial spots, which are separated from the lateral carinae by a narrow black border; the spots on S7 are largest, S6 and S8 fairly large, S4-5 small and S9 mere streaks. All sternites are black. Appendages all black, similar to those of *N. klingi* (Fig. 5a) but stouter with obtuse cercal tips. Secondary genitalia very similar to *N. afra* (Figs 3e, 4b), including the dense cluster of strong short bristles on the inner surface of the anterior lobe of the hamule, but the inner profile of the hamule (from the tip of the hook to the mouth of the cleft) is less sigmoidal (Fig. 4b).

Measurements [mm]: entire length 34.2, abdomen length (excl. appendages) 21.2, Fw length 27.8, Hw length 27.7, Pt in Fw 2.4.

Variation

Extent of pale markings varies slightly. See Table 2 for variation in venation. Hw 26-28 mm.

Neodythemis nyungwe sp. nov.
(Fig. 2i)

Diagnosis

Dark, large *Neodythemis* with thoracic pale markings composed of spots, recalling *Micromacromia miraculosa*, but with unique complete antehumeral stripes which are extended dorsally to meet on middorsal carina (Fig. 2i).

Description of holotype male

In fairly good condition but head somewhat crushed and synthorax impressed. Similar to holotype *N. munyaga* sp. nov. but considerably larger with the pale markings configured differently as follows:

Head: vertex all glossy black.

Thorax: antehumeral stripe connected dorsally to stripe along middorsal carina; mesepimeral stripe broken into an elongate ventral streak and a large dorsal spot, with an additional spot anterior to it; metepisternal spots larger; metepimeral stripe broken into two spots of similar size and shape (Fig. 2i); hind coxae with additional spot on anterior side.

Wings: clearer (probably age-related). In Fw 14-14 Ax, in Hw 11-12, in Fw 9-10 Px, in Hw 10. Three bridge cross-veins in all wings. Cubital space with one cross-vein in Fw, three in Hw. All supratrangles and Hw triangles with one cross-vein, Fw triangles and subtriangles uncrossed. Fw discoidal field of one cell-row for 5-6 cells at base, becoming two at level of Ax11-12. Rspl subtends single row of cells. Anal field fairly small, anal loop about twice as long as wide, of 6-7 cells.

Abdomen: ventral spots on S3-9 larger, those on S3-8 extending across lateral carinae onto dorsum, most clearly on S3 where the spots are fused with the subapical lateral spot and the least on S8 where they only reach the lateral carinae. Appendages and secondary genitalia very similar to *N. munyaga* sp. nov.; cerci even thicker.

Measurements [mm]: entire length 38.4, abdomen length (excl. appendages) 24.7, Fw length 30.1, Hw length 30.6, Pt in Fw 2.6.

ACKNOWLEDGEMENTS

Bernhard Misof provided us with important information. John Joseph Kisakye and Gert von Rosen kindly supplied the material of the new species; Nick Donnelly sent scans of his specimen. Raphael Chahwanda, Eliane de Coninck, Jos De Becker, Dave Goodger, Kjell Arne Johanson, Wanja Kinuthia, Marc de Meyer, Shepard Ndlela, Laban Njoroge, Michael Ohl and Rudo Sithole were helpful during visits to BMNH, MRAC, NHRS, NMBZ, NMKE and ZMHB. Natalia von Ellenrieder and Michael Samways kindly reviewed the paper. Work in BMNH, ISNB and NHRS was supported by the SYS-RESOURCE, ABC and HIGH LAT infrastructures of the European Union IHP Programme. The International Dragonfly Fund made additional visits to BMNH and ZMHB possible. This study was further supported by grants from the German Federal Ministry of Science (BMBF, BIOLOG Programme, 01LC0025 and 01LC0404). RMNH provided working facilities.

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