

African *Diplacodes*: the status of the small species and the genus *Philonomon* (Odonata: Libellulidae)

Klaas-Douwe B. Dijkstra

National Museum of Natural History Naturalis, PO Box 9517, 2300 RA,
Leiden, The Netherlands. <dijkstra@nmm.nl>

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ABSTRACT

The small African species of *Diplacodes* have been confused for a long time, in part because the black mature males are difficult to separate. The holotype of *D. deminuta* belongs to the species commonly known as *D. okavangoensis*, the former name taking priority, while its paratypes belong to that known erroneously as *D. deminuta*, which is described as the new species *D. pumila*. *Philonomon* is considered a junior synonym of *Diplacodes* and the sole species, *P. luminans*, is transferred accordingly. Species identification relative to sex and developmental state is clarified: some specimens, either very old or young, will be difficult to separate without reference material.

INTRODUCTION

The genus *Diplacodes* Kirby, 1889 occurs throughout the warm regions of the Old World. Of species currently recognised, four are principally African, including one Madagascan endemic, two range from India to tropical Australia and two from Australia across the Pacific; one is endemic to E Australia. All are excellent dispersers that breed in standing, often temporary, waters. Five of the nine species occur on oceanic islands. The Australian *D. bipunctata* (Brauer, 1865) is the only libellulid besides *Pantala flavescens* (Fabricius, 1798) to have reached New Zealand. The Asian *D. trivialis* (Rambur, 1842) ranges from the Seychelles to Fiji, and the African *D. lefebvrii* (Rambur, 1842) extends into Europe, Asia and across the Indian Ocean.

The African species are difficult to separate, differing mainly in size and coloration, but only slightly in morphology. As they mature, males and some females become black, obliterating diagnostic markings (Plates I, II). The existence of a small species occurring locally alongside the ubiquitous *D. lefebvrii* in continental Africa had been recognised since Grünberg (1903) reported the Madagascan *D. exul* (Selys, 1883) from the north end of Lake Malawi. Such diminutive specimens continued to be mistaken for that species (renamed *D. exilis* Ris, 1911) until Lieftinck (1969) described *D. deminuta*, following an initial investigation of the penes by Pinhey (1967). Pinhey (1976) added *D. okavangoensis*, but remarked that “the naming of this taxon ... is just a further stage but this does not necessarily account for all the African taxa of this genus.” After examining numerous specimens, I reached the conclusion that his concerns were correct: small *Diplacodes* were still being confused, a problem even reflected in the type specimens. Moreover, I concluded that the monotypic genus *Philonomon* Förster, 1906 represents a large relative of African *Diplacodes*.

MATERIAL AND METHODS

Relevant specimens in the BMNH, ISNB, MRAC, NMBZ, NMKE, RMNH, ZMHB, ZMMU and the collection of J. Lempert, Hamburg, were examined. Age-related variation was assessed (Table 1) and morphology of appendages and secondary genitalia was investigated using scanning electron microscopy (Figs 1-4). Terminology of the penis follows Miller (1991). Acronyms for collections:

BMNH	Natural History Museum, London
ISNB	Institut Royal des Sciences Naturelles de Belgique, Brussels
MRAC	Musee Royal de l'Afrique Centrale, Tervuren
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

Diplacodes deminuta Lieftinck, 1969
(Figs 1a, 2a, 3a, 4a, Plate 1a, 1b)

Diplacodes exul nec (Selys) — Grünberg (1903: 720).

Diplacodes deminuta Lieftinck, 1969: 32 [type: Samfya, Zambia; MRAC].

Diplacodes okavangoensis Pinhey, 1976: 579 [type: Four Rivers, Botswana; NMBZ]; new synonymy.

Hoping to settle the confusion about *D. exilis*-like specimens from continental Africa, Lieftinck (1969) described *D. deminuta*, based on extensive material from NE Zambia. Pinhey (1976) realised that there was a second small species with an overlapping range: he described *D. okavangoensis* from N Botswana and Zambia, providing a key to separate it from *D. deminuta*, *D. exilis*, *D. lefebvrii* and *D. trivialis*. Lieftinck (1969) also referred to a male from Sibweza: this specimen and additional W Tanzanian specimens from Mpanda and Mukuyu (RMNH) were treated as *D. deminuta* by Pinhey & Pinhey (1984). I examined these specimens and others from Albertville (= Kalemie), Bambesa, Bomboma, Eala, PN Garamba and Lubumbashi in Congo-Kinshasa (ISNB, MRAC), Rumbek in S Sudan and Ajai, Katera (= Kyotera), Murchison Falls NP and Tororo in Uganda (NMKE, ZMMU). All were similar and agreed with the holotype (NMBZ), paratype males (BMNH, NMBZ) and topotypical specimens of *D. okavangoensis* (Okavango Delta, leg. J. Kipping, RMNH). Grünberg's (1903) "*D. exul*" specimens in ZMHB belonged to the same species. Gambles (unpubl. manuscript: "The Nigerian dragonflies") stated that *D. exilis* from Nigeria "can be recognised by the mature males developing a pruinosity on the basal segments of the abdomen and sometimes the thorax": two teneral males from Vom and a mature male and female from Lagos (BMNH) also agreed with *D. okavangoensis*, as did one rather dark male and two females from three sites in Liberia (coll. J. Lempert).

These findings showed that *D. okavangoensis* is more widespread than its name and earlier records suggested (Fig. 6), and much more so than *D. diminuta* and *D. exilis*, under which names specimens were usually placed. The close similarity and overlapping ranges of *D. okavangoensis* and *D. diminuta* implied that the latter's type series could be mixed. Examination of the specimens in MRAC revealed that the *D. diminuta* holotype agreed with *D. okavangoensis*, while all paratypes (9 ♂, 7 ♀) conformed with Pinhey's (1976) diagnosis of *D. diminuta*. Lieftinck's (1969) figures 5a-d are all of the latter species, while his figure 5f of a penis assigned to *D. lefebvrii* from Samfya, is that of the real *D. diminuta*. Nonetheless, the section "Male (adult)" of Lieftinck's description perfectly matches the holotype of *D. diminuta* – with the exception of the reference to figure 5a –, and therefore its redescription is not required. The provided collection data, including the unique sample number, also conform fully with the examined male. Lieftinck selected as holotype one of the few mature males amongst the available material. Although this is generally a sensible action in Odonata, it is not so in *Diplacodes*, where mature males are among the most difficult adult specimens to identify. *D. okavangoensis* is a junior synonym of *D. diminuta*, while the species represented by Lieftinck's paratypes and accurately diagnosed by Pinhey (1976) is unnamed. A male from Lieftinck's series was selected as holotype.

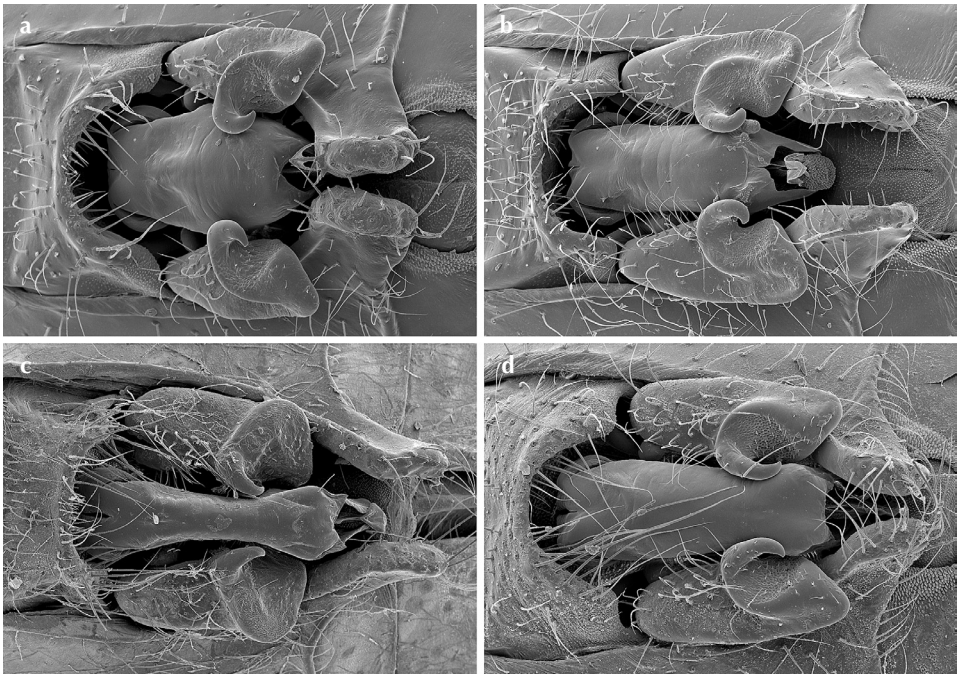


Figure 1: *Diplacodes* secondary genitalia, ventral view — (a) *D. diminuta* (PN Garamba, Congo-Kinshasa); (b) *D. lefebvrii* (origin unknown, probably from Congo-Kinshasa); (c) *D. luminans* (Tumbwe, Congo-Kinshasa); (d) *D. pumila* sp. nov. (Samfya, Zambia).

Diplacodes pumila sp. nov.

(Figs 1d, 2d, 3d, 4d, Plate 1c-f)

Diplacodes deminuta nec Lieftinck. — Pinhey (1976: 578).*Diplacodes pumila* sp. nov. [type: Ndoaba, Zambia; MRAC].

Specimens studied

Holotype ♂ (paratype of *deminuta*): Zambia, Ndoaba (sample 10014a), 27 i 1963, leg. J.J. Symoens, MRAC. — 1 ♀: Congo-Kinshasa, Marais-Mulita, 26 vi 1928, leg. Ch. Seydel, MRAC. — 1 ♀: Congo-Kinshasa, Kifoko, 3 ix 1928, leg. Ch. Seydel, MRAC. — 1 ♂: Congo-Kinshasa, Elisabethville (= Lubumbashi), 23 i 1935, leg. Ch. Seydel, MRAC. — 2 ♂, 3 ♀ (all paratypes of *deminuta*, as well as allotype): Zambia, Samfya (samples 9110, 9960, 10296), 29 xii 1961 - 17 iv 1963, leg. J.J. Symoens, MRAC. — 1 ♂ (paratype of *deminuta*): Zambia, 5km SSE of Chilubula (sample 9542), 02 vi 1962, leg. J.J. Symoens, MRAC. — 1 ♀ (paratype of *deminuta*): Zambia, Chipundu, Livingstone Memorial (sample 10714a), 24 xii 1963, leg. J.J. Symoens, MRAC. — 4 ♂, 3 ♀ (all paratypes of *deminuta*): Zambia, Ndoaba (samples 9134, 10014a), 30 xii 1961 - 27 i 1963, leg. J.J. Symoens, MRAC. — 1 ♀: Tanzania, Sao Hill, 23 ix 2001, leg. and collection V. Clausnitzer. — 5 ♂, 1 ♀: Tanzania, Iringa, Kisolanza Farm, 30 ix 2001, leg. and collection V. Clausnitzer.

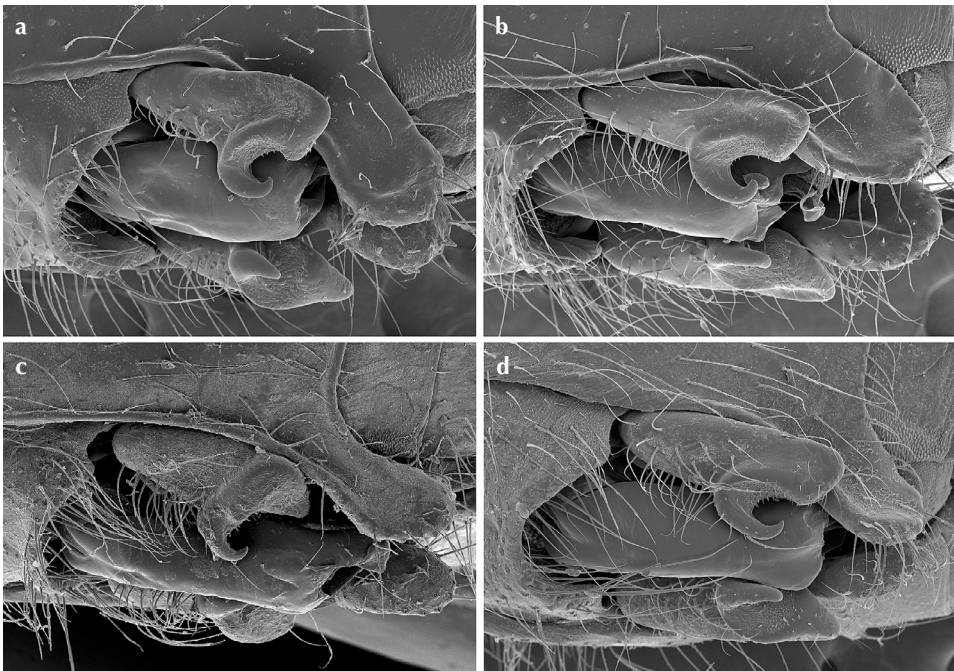


Figure 2: *Diplacodes* secondary genitalia, ventro-lateral view — (a) *D. deminuta* (PN Garamba, Congo-Kinshasa); (b) *D. lefebvreii* (origin unknown, probably from Congo-Kinshasa); (c) *D. luminans* (Tumbwe, Congo-Kinshasa); (d) *D. pumila* sp. nov. (Samfya, Zambia).

Etymology

Because its small size has always been emphasised, I propose the feminine Latin noun in apposition *pumila* (dwarf) as name for the species formerly known as *D. deminuta*.

Diagnosis

Small *Diplacodes* with short Pt and extensive pale abdominal markings and russet front of synthorax in both sexes, which becomes obscured by complete blackening of body in mature male. Long hook of hamule (Figs 1d, 2d) and short epiproct (Fig. 4d) are diagnostic in male.

Description of holotype male

Preserved dry, in cellophane. Rather teneral and crushed, S6 lost, but diagnostic coloration clear.

Head: labium yellowish cream, with central lobe and inner halves of lateral lobes blackish. Face (mandibles, genae, labrum, clypeus and frons) brown, becoming slightly darker dorsally and more yellow laterally; base of frons and vertex blackish brown. Antennae black. Occipital triangle brown becoming yellowish anteriorly. Back of head entirely brownish black with indistinct yellowish markings on post-genae: circular spot halfway along eye margin with streak along lower margin. **Thorax:** prothorax somewhat concealed by fore legs, brownish black, laterally yellowish, posterior lobe large with broad hind-margin slightly incised centrally,

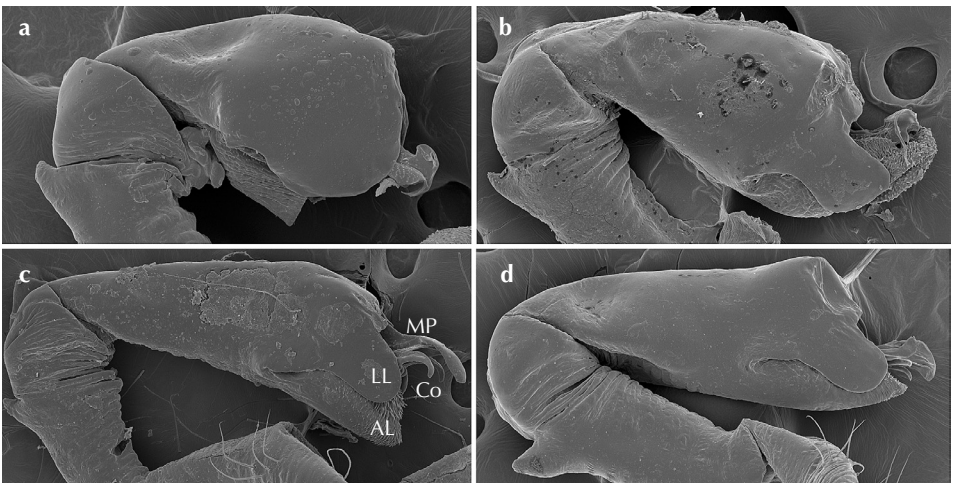


Figure 3: *Diplacodes* penes, lateral view — (a) *D. deminuta* (Eala, Congo-Kinshasa); (b) *D. lefebvrei* (Kagera, Rwanda); (c) *D. luminans* (Manjenene, Malawi); (d) *D. pumila* sp. nov. (Ndoba, Zambia). The structures at the apex of the terminal segment (see 3c) are the inflatable and bristly apical lobe (AL), the paired and curved cornua (Co), the similarly shaped but single extension of the medial process (MP), and the rounded lateral lobes (LL).

with pale long fine hairs. Synthorax yellow, but mesepisterna uniformly and contrasting warm brown, with black marking as follows: thick black stripe over entire humeral suture, an indistinct smudge extends onto mesepisternum from about half-way along this stripe; thick stripe running from ventral mesepimeron to about half-way between metastigma and dorsal end of mesepimeron; black stripe that incorporates metastigma and extends slightly further dorsad than mesepimeral stripe, with which it is narrowly fused; stripe on entire metapleural suture distinctly widest in fossa and at ventral end, from where it extends faintly onto central metepimeron. Venter of synthorax brown, somewhat paler on central poststernum. Legs entirely black, save for indistinct pale smudge at base of fore femora and yellow sides of coxae.

Wings: clear, Fw very faintly yellow at extreme base, Hw clearly yellow at base to beyond Cux and almost to Ax1; venation brown, but anterior face of costa and more basal cross-veins yellowish; Pt cream with thick black margins. Arculus half-way between Ax 1-2. In Fw $6\frac{1}{2}$ Ax, in Hw 5, in Fw 5-6 Px, in Hw 6. Bridge and cubital spaces each with a single cross-vein in all wings. All triangles, subtriangles and supratrangles uncrossed. Fw discoidal field parallel-sided and of two cell-rows for 4-5 cells at base. Rspl subtends single row of 4-5 cells in all wings. Anal loop of 11-12 cells.

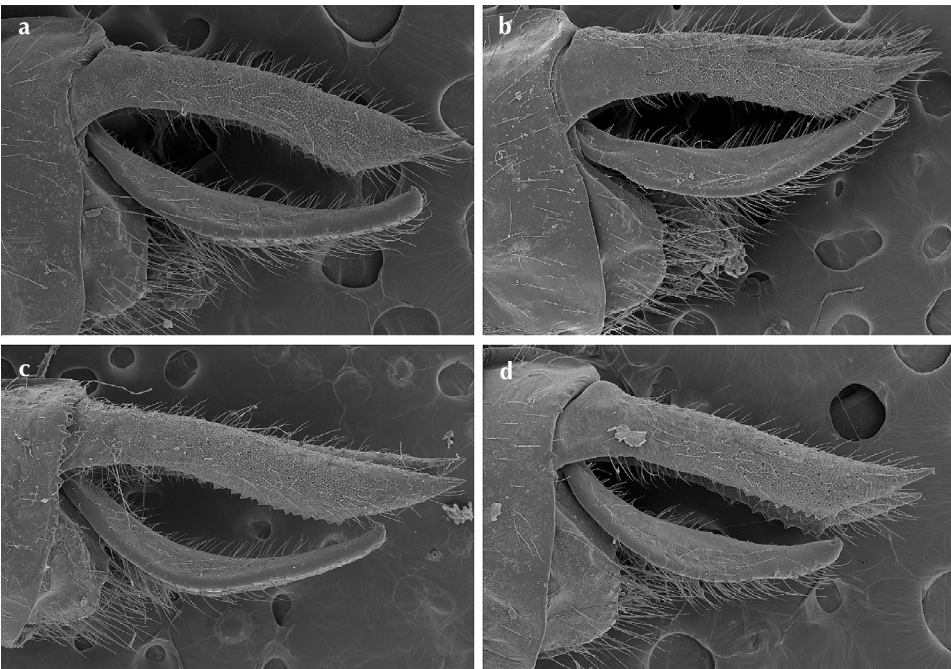


Figure 4: *Diplacodes* male appendages, lateral view — (a) *D. deminuta* (PN Garamba, Congo-Kinshasa); (b) *D. lefebvrei* (unknown, probably in Congo-Kinshasa); (c) *D. luminans* (Tumbwe, Congo-Kinshasa); (d) *D. pumila* sp. nov. (Samfya, Zambia).

Abdomen: brownish black, tergites marked with yellow as follows: S1-3 largely yellow laterally, fairly narrowly black along dorsal carina and lateral carinae; ventral area dark. Dark areas expanded distally on S4-10, leaving a series of lateral pale streaks on segments: streak on S4 reaches from base almost to apex; on S5 falling just short of base and apex; on S6 unavailable for study; on S7 and S8 falling just short of base, respectively two-thirds and half length of whole segment; S9 with tiny subbasal spot; S10 entirely black. Sternites all brownish black. Cerci slender, yellowish beige with dark brown tip and blackish ventral teeth; epiproct dark brown, just surpassing most distal ventral tooth ('ventral angle') of cerci (cf. Fig. 4d). Secondary genitalia dark brown, as illustrated, with relatively long hamular hook and long straight-sided terminal segment of penis (cf. Figs 1d, 2d, 3d).

Measurements [mm]: entire length (reconstructed) 22.5, abdomen length (reconstructed, excl. appendages) 13.5, Fw length 17.4, Hw length 16.3, Pt in Fw 1.8.

Variation and identification

Males of the continental African *Diplacodes* species can most reliably be separated by secondary genitalia; *D. diminuta* by the stout 'glans' of the penis (Figs 1a, 3a) and *D. pumila* sp. nov. by the relatively long and straight hamular hooks (Figs 1d, 2d). The differences in the penis were already correctly, although crudely, illustrated by Pinhey (1967: fig. 4c "*exilis* Chirinda Forest" is *pumila*; 4d "*exilis* Sepopa" is *diminuta*). The length of the male epiproct relative to the cerci separates the two small species (Table 1, Figs 4a, 4d), but *D. lefebvreii* may show both their conditions (Fig. 4b). Age-related and individual variation may make both sexes of the two small *Diplacodes* difficult to separate from each other and from *D. lefebvreii* by coloration (see Key and Table 1). Extremely teneral and very old specimens are most difficult to identify with confidence. *D. lefebvreii* is especially variable in size and markings (Plate IIa-f). Specimens from Madagascar and Mauritius, for instance, are relatively large and have broad, brown, wing markings, while those from dry areas may have almost no black on the thorax – and sometimes also very little on the face, legs and abdomen – when teneral (Plate IIb). Among the abundant *D. lefebvreii*, the two smaller and much scarcer species are usually first noticed by their size and also (especially) by the relatively smaller Pt. Unlike *D. lefebvreii* the Hw base does not develop a brown patch with maturity, but remains clear or yellow, while the thorax and abdomen base may become pruinose grey (Plate Ia, Ic). Females and immature males of the two are easily separated by the colour of the mesepisternum and the extent of pale markings on the abdomen: in *D. pumila* sp. nov. more extensive than in *D. lefebvreii* but in *D. diminuta* less than in *D. lefebvreii* (Plate Ib, Id, If). When mature, the males become difficult to distinguish. The face of *D. pumila* sp. nov. turns black like the rest of its body (Plate Ic). In *D. diminuta* it remains largely yellow (Plate Ia), but the extent varies: Garamba and Uganda specimens have a slightly darkened frons dorsum, the holotype has a rather brown face and the Lagos male only has the sides of antefrons and postclypeus yellow. Note that *D. diminuta* is much more like the Madagascan *D. exilis* than *D. pumila* sp. nov., differing only in minor details, of which the fragmented thoracic markings and extensive male pruinosity are most conspicuous (Lief-tinck 1969; Pinhey 1976; own unpubl. obs.).

Range and ecology

D. pumila sp. nov. occurs from KwaZulu-Natal (see photograph in Silsby 2001) through Zimbabwe and Zambia to S Katanga (Fig. 6). Pinhey (1984) noted under *D. deminuta* (i.e. *D. pumila* sp. nov.) that “probably those records for *exilis* from Kenya and Uganda [are this species]”, but these more likely pertain to the true *D. deminuta*. Pinhey (1984) also listed Malawi, despite doubting the location of Grünberg’s (1903) “*D. exul*” specimens from Langenburg previously (Pinhey 1979). The site lies on the Tanzanian shore of Lake Malawi; the specimens belong to true *D. deminuta*. The Tanzanian specimens examined thus constitute the first reliable records of *D. pumila* sp. nov. for East Africa. The real *D. deminuta* ranges from N Botswana at least to S Sudan, Uganda and Liberia (Fig. 6), although it seems localised, always being greatly outnumbered by *D. lefebvrii* in collections. Pinhey (1984) emphatically distinguished between the habitats of the two small species: while *D. pumila* sp. nov. is “local at swampy margins of pools, but not palustrine”, *D. deminuta* is “a palustrine or swamp species”. This seems to be a distinction of scale, *D. deminuta* occurring in larger swamps, such as the Okavango Delta. Moreover, localities suggest that *D. pumila* sp. nov. is found especially in highlands (e.g. at 1,780-1,850 m altitude in Tanzania). Lieftinck’s (1969) Zambian records at 1,150-1,260 m, however, demonstrate that the two can occur together, even on the same date.

Diplacodes luminans (Karsch, 1893) comb. nov.

(Figs 1c, 2c, 3c, 4c, 5b, Plate IIg, IIh)

Sympetrum luminans Karsch, 1893: 22 [type: Bismarckburg, Togo; ZMHB].

Philonomon erlangeri Förster, 1906: 310 [type (not seen): Haro Ali, Ethiopia; UMMZ]; junior synonym (Ris 1908: 340).

Philonomon luminans (Karsch) — Ris (1911: 697).

Diplacodes croceata Selys — label name; nomen nudum.

Diplacodes [?] *bicellularis* Selys — label name; nomen nudum.

The genus *Philonomon* has been associated with *Sympetrum* Newman, 1833: Förster (1906b) compared it with that genus and the only species, *P. luminans*, was described in it by Karsch (1893). The large size and predominance of red must have been the main incentive for this. On the other hand, in his classification of African libellulid genera, Förster (1906a) placed *Philonomon* closest to *Diplacodes*. When only venation is considered – as Förster (1906a) did – the subtriangle of 1-2 cells (with short anterior margin), the Fw discoidal field of normally 2 cells at base, the shape of the anal loop (“mit der eigenartigen Konfiguration der Schleife” of Ris 1911) and the separate origin of CuP and A1 in *Philonomon* are more like *Diplacodes* than *Sympetrum* (Figs 5a, 5b). Ris (1911) admits that for these characters *luminans* would stand alone “in der grossen Gattung *Sympetrum*”, which is why he must have deviated from his earlier decision to leave *luminans* in *Sympetrum* when he discovered the synonymy of *erlangeri* (Ris 1908). Förster’s (1906a, b) remarks suggest that the “ungewöhnlich bunte Färbung” was the main

Table 1. Comparison of small *Diplacodes* species. The applicability of characters for sexes and three developmental stages of males is indicated — t: teneral (shortly after emergence, thoracic markings crisp); y: young (abdominal markings well-visible, but thorax darkening, its markings smudged and merging); o: old (entire abdomen black); exclamation marks denote characters that are preferably used only in direct comparison of both species.

Character	<i>D. deminuta</i> = <i>D. okavangoensis</i>	<i>D. pumila</i> sp. nov. = <i>D. deminuta</i> auctt.
Hw length		
♀ ♂ t y o	15.0 - 20.5 mm	16.0 - 18.5 mm
Colour of face		
♂ o !	Usually at least some yellow on sides of frons (Plate Ia)	All black when mature (Plate Ic)
Mesepisternum		
♀ ♂ t	Yellowish, like sides of synthorax; often with central dark streak (Plate Ib)	Rufous, in contrast with sides of synthorax; at most with short smudge extending from humeral black stripe (Plate Id, If)
Pterostigma		
♂ y o !	Whitish (Plate Ia)	Becomes brown (Plate Ic)
Hook of hamule		
♂ t y o !	Shorter (Figs 1a, 2a)	Longer (Figs 1d, 2d)
Terminal segment of penis		
♂ t y o	Short and swollen with large lateral lobes (Figs 1a, 3a)	Long and slender with small lateral lobes (Figs 1d, 3d)
Pale marking S8		
♀ ♂ t y	At most small or indistinct spot, in contrast with streak on S7 (Plate Ia)	Streak extending over more than half length of segment, like on S7 (Plate Ic)
Pale marking S9		
♂ t y	None	Distinct spot or streak
Pale marking S10		
♂ t y	None	Often distinct spot or streak
Tip of epiproct		
♂ t y o !	Closer to tips of cerci (Fig. 4a)	Closer to ventral angle of cerci (Fig. 4d)
Colour of appendages		
♂ y o !	Seldom more than tips of cerci and epiproct dark	Epiproct and underside cerci with strong tendency to darken
Vulvar scale		
♀ !	More deeply notched	Shallowly notched

reason to describe the separate genus. The bold abdominal pattern of *P. luminans* is reminiscent of that seen in females and immature males of African *Diplacodes*. Other markings, secondary genitalia (Figs 1c, 2c, 3c), male appendages (Fig. 4c), vulvar scale, and head and prothorax morphology are also like *Diplacodes*. The nearly identical penis of *D. pumila* sp. nov. is especially striking in this respect (Figs 2c, 2d). Altogether *Philonomon* has the appearance of a large, red-bodied and broad-winged *Diplacodes* (Plate IIg, IIIh). The ecology of *P. luminans* also fits *Diplacodes*, it being a migratory species that breeds in open, temporary waters. The larvae of *Diplacodes* and *Philonomon* are similar to each other and to possibly close relatives like *Sympetrum fonscolombii* (Selys, 1840), *Bradinopyga* Kirby, 1893 and *Crocothemis* Brauer, 1868 (Pinhey 1961; von Hagen 1996; Hawking & Theischinger 1999).

Interestingly, a teneral female from “Nossibe” (Nosy Bé, Madagascar) in ISNB bears a label in Selys’ handwriting “*Diplacodes* n. sp. *croceata* Selys”. A note with the same handwriting pinned nearby reads “*bicellularis* de Selys”. Neither name was published, but both refer to distinctive features of the species: the broadly yellow Hw base and the Fw triangle that – unlike most species of similar size – is usually bordered by two cells, both in the subtriangle and discoidal field. The holotype of *P. luminans* carries a poorly legible note “sector trianguli ... *lefebvrei* ... (n. g.?)”. This suggests Karsch too initially considered the species close to *Diplacodes* by the configuration of CuP and A1, although possibly representing a new genus.

Worldwide the genus *Diplacodes* demonstrates a greater diversity of body and wing coloration, venation and genitalia than seen in Africa alone. For instance, *D. haematodes* (Burmeister, 1839) is all-red and also has broad Hw bases marked extensively with yellow. If the close relationship between *P. luminans* and African *Diplacodes* is acknowledged, recognition of *Philonomon* would probably make *Diplacodes* paraphyletic. Genetic analysis consistently groups *P. luminans* as the sister species of *D. lefebvrei* and *D. nebulosa* (Fabricius, 1793), while *D. bipunctata* and *D. trivialis* group more distantly within a clade that includes, amongst others, members of the genera *Bradinopyga*, *Crocothemis*, *Erythrodiplax* Brauer, 1868 and *Neurothemis* Brauer, 1867 (E. Pilgrim and D.C. von Dohlen unpubl.).

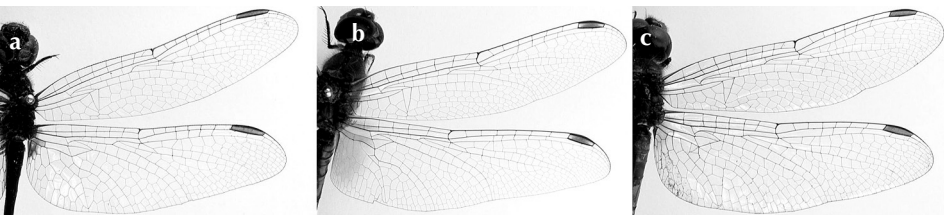


Figure 5: Wings of *Diplacodes* spp. compared with *Sympetrum navasi* Lacroix, 1921, dorsal view — (a) *D. lefebvrei*; (b) *D. luminans*; (c) *S. navasi*.

Classifying the single species as *Diplacodes luminans* is more inclusive and potentially stable than maintaining the monotypic *Philonomon*, as it groups more closely with the type species *D. lefebvreii* than some other species now placed in *Diplacodes* do. As argued by Dijkstra & Vick (2006), the separation of monotypic libellulid genera based solely on conspicuous apomorphies – in the present case merely of size and colour – has led to many superfluous taxa in the family.

EPILOGUE

On 7 February 1964 Maurits Lieftinck, rightly considered as one of the greatest taxonomists of Odonata, wrote to Jean-Jacques Symoens, collector of both the *Diplacodes deminuta* and *D. pumila* sp. nov. holotypes, how (translated from Dutch) “the specialists engaged in this work [on Odonata of tropical Africa] are proceeding very hurriedly, ... hampering the study of the fauna more and more, making it so unattractive that accurately working specialists will need years to create order in the existing chaos.” The case of the small *Diplacodes* species shows that also the most experienced specialists may require correction.

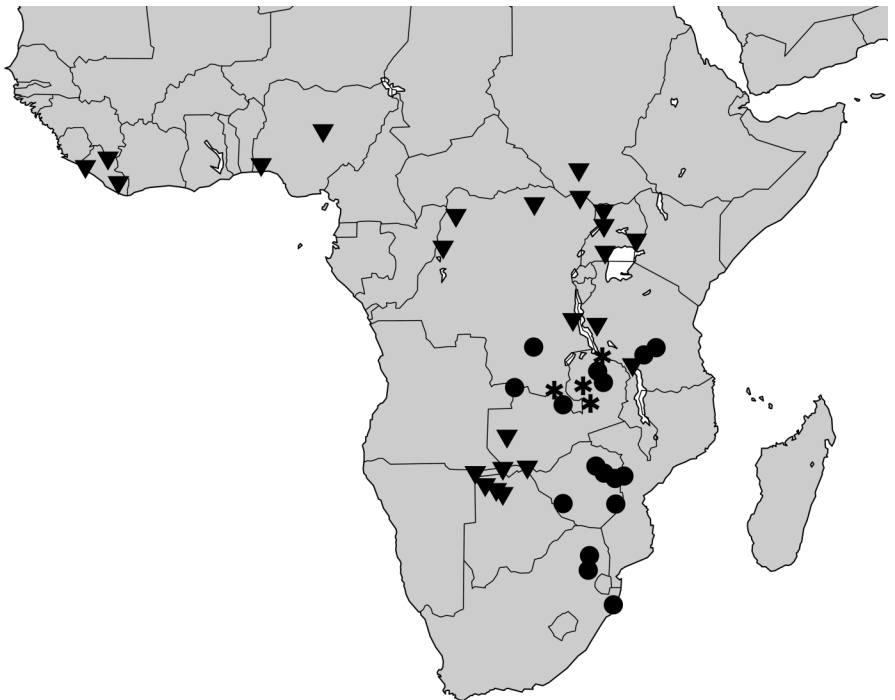


Figure 6: Distribution of the small continental African *Diplacodes* species, based on records in this paper supplemented by Pinhey (1984) and the Southern Africa Odonata Database (J. Kipping pers. comm.) — ▼: *D. deminuta*, ●: *D. pumila* sp. nov., *: both species.

KEY TO *Diplacodes* SPECIES OF CONTINENTAL AFRICA

1. Hw base broad and rectangular, orange reaching approximately to triangle (Fig. 5b); undersides of S5-8 with well-defined pale spots between black lateral and ventral carinae; Hw 25-31 mm. Male: face and abdomen base red when mature (Plate IIg); terminal segment of penis in ventral view narrower than hamule and with concave sides (Fig. 1c); lobe of hamules smaller, protruding less over base of genital lobe, their hooks directed more inwards (Figs 1c, 2c) *luminans*
- 1'. Hw base narrower and rounded, extreme base with yellow to dark brown patch or clear (Fig. 5a); undersides of S5-8 unspotted, including ventral carinae if pale; Hw 15-24 mm, seldom reaching 28 mm. Male: never red, mostly black when old (Plate Ia, Ic, Ie, IIa); terminal segment of penis in ventral view at least as wide as hamule, with rather straight or convex sides (Figs 1a, 1b, 1d); lobe of hamules larger, protruding more over base of genital lobe, their hooks directed more outwards (Figs 1a, 1b, 1d, 2a, 2b, 2d) 2
2. Female* or younger male: abdomen black with distinct pale spots 3
- 2'. Old male: abdomen all dark, without pale markings 5
3. Mesepisternum rufous, contrasting with sides of thorax (Plate Id); S8 with pale streak more than half as long as segment, S9 with pale spot or streak, S10 may have pale spot; Hw 15-19 mm; Pt about 2 mm. Male: hook of hamule long (Figs 1d, 2d) *pumila* sp. nov.
- 3'. Mesepisternum yellowish, like sides of thorax (Plate Ib); S8 at most with pale spot about half as long as segment, S9 all black or with indistinct pale spot, S10 black; Hw 15-28 mm; Pt 2-4 mm. Male: hook of hamule short (Figs 1a-b, 2a-b) 4
4. Pt 2.5-4.0 mm; Hw 20-28 mm; S8 with distinct pale spot about half as long as segment, S9 all black or with indistinct pale spot (Plate IIa-f). Male: terminal segment of penis in ventral view about as wide as hamule and with rather straight sides (Fig. 1b), in lateral view more than 2x as long as high, its lateral lobes small and distinct, about half as high as apex (Fig. 3b); its apical lobe usually extends well beyond apex when relaxed, enclosing cornua and visible as a whitish mass between the bases of the genital lobes in ventral view (Figs 1b, 3b) *lefebvrii*
- 4'. Pt about 2.0 mm; Hw 15-21 mm; S8 at most with small or indistinct pale spot, S9 all black. Male: terminal segment of penis in ventral view wider than hamule and with convex sides (Fig. 1a), in lateral view less than 2x as long as high, its lateral lobes encompassing entire apex (Fig. 3a); its apical lobe shorter and therefore not visible in ventral view (Figs 1a, 3a) *deminuta*
5. Pt 2.5-4.0 mm; Hw 20-28 mm; patch at Hw base dark brown, wings may be tinged brown near Pt; apical lobe of penis usually extends well beyond apex of terminal segment when relaxed, enclosing cornua and visible as a whitish mass between the bases of the genital lobes in ventral view (Figs 1b, 3b); face all black; thorax and abdomen matt black *lefebvrii*

5'. Pt 2.0-2.5 mm; Hw 15-21 mm; patch at Hw base yellow or absent, wings always clear near Pt; apical lobe of penis shorter and therefore not visible in ventral view (Figs 1a, 1d, 3a, 3d); face black or yellow; thorax and dorsum of abdomen base may be (partly) pale grey pruinose 6

6. Face entirely black; Pt brown; hook of hamule long (Figs 1d, 2d); epiproct and underside of cerci largely dark; tip of epiproct usually closer to ventral angle than tip of cerci (Fig. 4d); terminal segment of penis in ventral view about as wide as hamule and with rather straight sides (Fig. 1d), in lateral view more than 2x as long as high, its lateral lobes small and distinct, about half as high as apex (Fig. 3d) *pumila* sp. nov.

6'. Face usually yellow at least laterally or anteriorly; Pt whitish; hook of hamule short (Figs 1a, 2a); usually only tip of epiproct and tips of cerci dark; tip of epiproct usually closer to tip than ventral angle of cerci (Fig. 4a); terminal segment of penis in ventral view wider than hamule and with convex sides (Fig. 1a), in lateral view less than 2x as long as high, its lateral lobes encompassing entire apex (Fig. 3a) *deminuta*

* Rare all-dark females (see Plate III) may tentatively be identified by measurements and coloration characters.

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REFERENCES

- Dijkstra, K.-D.B. & G.S. Vick, 2006. 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). *International Journal of Odonatology* 9: 51-70.
- Förster, F., 1906a. Die Libellulidengattungen von Afrika und Madagaskar. *Jahresbericht des Vereins für Naturkunde zu Mannheim* 71/72: 1-67.
- Förster, F., 1906b. Libellen. In: "Forschungsreise durch Südschoa, Galla und die Somaliländer von Carlo Freiherr von Erlanger." *Jahrbücher des Nassauischen Vereins für Naturkunde* 59: 299-344, 1 pl.
- Grünberg, K., 1903. Zur Kenntniss der Odonatenfauna des ost-afrikanischen Seengebiets. Ergebnisse der Nyassa-See- und Kinga-Gebirgs-Expedition der Hermann und Elise geb. Heckmann-Wentzel-Stiftung. *Zoologische Jahrbücher (Abteilung für Systematik, Ökologie und Geographie der Tiere)* 18: 695-726.
- Hawking, J. & G. Theischinger, 1999. Dragonfly larvae (Odonata). A guide to the identification of larvae of Australian families and to the identification and ecology of larvae from New South Wales. AWT Identification Guide 3. CRCFE Identification Guide 24: 1-217.
- Karsch, F., 1893. Libellen – Odonata – von Adeli. In: "Die Insecten der Berglandschaft Adeli im Hinterlande von Togo (Westafrika)". *Berliner Entomologische Zeitschrift* 38: 17-48.
- Lieftinck, M.A., 1969. Odonata Anisoptera. *Scientific Results of the Hydrobiological Survey of the Lake Bangweulu and the Luapula River Basin* 14 (4): 1-61.
- Miller, P.L., 1991. The structure and function of the genitalia in the Libellulidae (Odonata). *Zoological Journal of the Linnean Society* 102: 43-73.
- Pinhey, E., 1961. Notes on African Odonata nymphs – 2. *Journal of the Entomological Society of South Africa* 24: 165-172.
- Pinhey, E., 1967. Odonata of Ngamiland (1967). *Arnoldia Rhodesia* 3 (15): 1-17.
- Pinhey, E., 1976. Dragonflies (Odonata) of Botswana, with ecological notes. *Occasional Papers of the National Museums and Monuments of Southern Rhodesia (B)* 5: 524-601.
- Pinhey, E., 1979. Additions and corrections to the 1966 check-list of dragonflies (Odonata) from Malawi. *Arnoldia Zimbabwe Rhodesia* 8 (38): 1-14.
- 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. Lieftinck. *Odonatologica* 13: 129-138.
- Ris, F., 1908. Odonata. Nach den Sammlungen L. Schultze's und Katalog der Odonaten von Südafrika. *Denkschriften der Medizinisch-Naturwissenschaftlichen Gesellschaft, Jena* 13: 303-346.
- Ris, F., 1911. Libellulinen monographisch bearbeitet, Vol. II. Libellulinen 5. *Collections Zoologiques du Baron Edm. de Selys Longchamps. Catalogue Systématique et Descriptif* 13: 529-700, pl. V.
- Silksby, J., 2001. *Dragonflies of the world*. CSIRO Publishing, Collingwood.
- von Hagen, H., 1996. Notiz zu den Exuvien von *Diplacodes lefebvreii* und *Selysiothemis nigra* (Anisoptera: Libellulidae). *Advances in Odonatology, Supplement* 1: 47-51.



Colour plate I. Habitus of *Diplacodes* species — (a) mature male *D. deminuta* (Okavango Delta, Botswana, 1 February 2006) with pruinosity, notably pale face, Pt and appendages, and pale streaks up to S7; (b) female *D. deminuta* (Okavango Delta, Botswana, 1 February 2006) with notably pale appendages and pale streaks up to S7; (c) mature male *D. pumila* sp. nov. (Kisolanza Farm, Tanzania, 21 September 2001) with notably dark face, Pt and appendages, and pale streaks up to S9; (d, f) female *D. pumila* sp. nov. (Kisolanza Farm, Tanzania, 21 September 2001) with contrasting rufous thoracic dorsum and pale streaks extending to notably dark appendages; (e) immature male *D. pumila* sp. nov. (Kisolanza Farm, Tanzania, 21 September 2001), showing an intermediate development between immature and mature condition (rather like Plate IIc and II d). Photos by Jens Kipping (a, b) and Viola Clausnitzer (c-f).



Colour plate II. Habitus of *Diplacodes* species — (a) mature male *D. lefebvreii* (Nouil, Tunisia, 16 June 2002); (b-f) female *D. lefebvreii* show age-dependend darkening: (b) teneral (Nouil, Tunisia, 26 May 2001); (c) immature (Jemna oasis, Tunisia, 25 May 2001); (d) mature (same data as c); (e) fully mature (Blidet, Tunisia, 16 June 2002); (f) aged (same data as c); (g) mature male *D. luminans* (South Luangwa NP, Zambia, 4 January 2002); (h) female *D. luminans* ovipositing (Ghanzi, Kalahari, Botswana, 17 January 2006). Photos by Bernd Kunz (a-f), KD Dijkstra (g) and Jens Kipping (h).