

Six new species of *Nesocordulia* McLachlan, 1882 reveal an insular evolutionary radiation of dragonflies on Madagascar (Odonata: Anisoptera: Libelluloidea)

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Abstract

Nesocordulia McLachlan, 1882 is a poorly known dragonfly genus endemic to Madagascar and the Comoros. The genus is revised, and all twelve species are described, including six new ones: *N. coloratissima* **sp. nov.**, *N. evanida* **sp. nov.**, *N. fossa* **sp. nov.**, *N. ipsio* **sp. nov.**, *N. lyricauda* **sp. nov.**, and *N. odonator* **sp. nov.** All are well-defined, with notably distinct male cerci, hamules, and colouration. While an identification key for males of all species is provided, this is based on single specimens for six of them. Females are known for only six species. While several radiations of damselfly genera had been recognised in the Malagasy Region already, *Nesocordulia* is the first to be uncovered in the suborder Anisoptera. Due to the scarcity of data, the exact drivers of their diversification remain unclear, however. While seven species are known from the humid and subhumid forest zone of eastern and north-western Madagascar, and only *N. coloratissima* and *N. villiersi* Legrand, 1984 appear confined to the drier west and to the Comoros respectively, the exact collection localities of three species remain unknown. Although the limited data suggest that most species are localised, the few species with more records appear to be fairly widespread. The species' ecology is almost unknown, with more details provided on the habitat and behaviour of *N. evanida* only, and their conservation status is also largely unknown. Four species have not been recorded for over a century, however, while only *N. coloratissima* and *N. evanida* were confirmed to inhabit anthropogenically influenced landscapes.

Key words: Corduliidae s.l., systematics, species description, taxonomic synopsis, biogeography, endemic species, Malagasy Region, Comoros

Introduction

The Malagasy Region is a renowned biodiversity hotspot (CEPF 2024), with Madagascar alone hosting almost 11,580 known native species of vascular plants with 82% endemic, while the total flora may comprise at least 14,900 species with 90% endemic (Madagascar Catalogue 2024). The fauna is no less spectacular, as manifested not only by iconic groups of vertebrates such as lemurs, tenrecs and vangas, but also by incredibly high rates of endemism (up to 100% in some groups) in amphibians, fishes, and many invertebrate groups, frequently representing endemic genera, families and even higher taxa (e.g., Goodman & Benstead 2005; Goodman 2022; Goodman & Soarimalala 2022; Glaw *et al.* 2022; Spark & Stiassny 2022).

The almost unparalleled levels of species richness and endemism (Goodman & Benstead 2005) are the consequence of Madagascar's isolation since the mid-Late Cretaceous, 88 million years ago (Krause *et al.* 2022), infrequent episodes of later colonisation, and numerous subsequent radiations. The evolutionary factors and

processes behind this spectacular diversification have not yet been fully explained, although Quaternary climatic shifts across the island's numerous separate watersheds must have contributed significantly to the extraordinary levels of micro-endemism today (Wilmé *et al.* 2006).

The level of endemism is also high in dragonflies and damselflies (Odonata), being greater (93%) in Zygoptera than in the generally more widespread and dispersive Anisoptera (65%) (Dijkstra 2022). Although 173 species of odonates are formally named, at least twenty known species still await description (Dijkstra 2022). The taxonomic status of many species and subspecies is unclear, however, with several genera in need of a complete taxonomic revision. As many species probably still await to be discovered, the final number will exceed 200, perhaps even significantly so.

The odonate fauna is comparatively depauperate phylogenetically, however, with some larger groups (Chlorocyphidae, Calopterygidae, Disparoneurinae, Gomphidae) and genera that are well-represented in Africa being (largely) absent (Dijkstra 2022). Nonetheless, five notable radiations in Zygoptera, of which two represent endemic families (Protolestidae and Tatonemididae), gave rise to much of the high level of endemism mentioned. By contrast, no larger radiations were known in Anisoptera, with at most three endemic species described in most genera. The only likely exception was the genus *Nesocordulia* McLachlan, 1882, with five species recognised from Madagascar and one from the Comoros, and the potential for more (see Dijkstra 2022). Although the genus was traditionally included in Corduliidae, that family has long been regarded non-monophyletic, so it is currently considered as Libelluloidea *incertae sedis* (Dijkstra *et al.* 2013; Bybee *et al.* 2021), appearing closest to *Idomacromia* Karsch, 1896 and perhaps *Syncordulia* Selys, 1882 from neighbouring Africa, but more distant to the superficially similar Neotropical genus *Neocordulia* Selys, 1882 and Western Palearctic *Oxygastra* Selys, 1870 (Fleck & Legrand 2006). A close relationship between these genera has long been recognized, so much so that they were all placed in Idomacromiidae by Bechly (1996).

McLachlan (1882) erected the genus with *N. flavicauda* McLachlan, 1882 as the type species, to which *N. rubricauda* Martin, 1900, *N. spinicauda* Martin, 1902, *N. mascarenica* Fraser, 1948, *N. malgassica* Fraser, 1956, and *N. villiersi* Legrand, 1984 were subsequently added. Recent fieldwork by the authors suggested that up to three undescribed species existed, but the original descriptions and Fraser's (1956) synopsis proved so inconsistent and poorly illustrated that a taxonomic survey of the genus and its type material was found to be necessary. Analysis of all available material revealed that the genus is morphologically much more diverse than expected, so we here describe as many as six new species (of which five from recent fieldwork) and redescribe the six species named previously.

Material and methods

The examined material is from the 19th and 20th centuries kept at NHMUK and MNHN (for acronyms, see below), as well as 21st century specimens obtained by Klaas-Douwe B. Dijkstra, Andrianjaka Ravelomanana and colleagues (in the years 2014, 2016 and 2018, all housed at RMNH) and Rafał Bernard and Bogusław Daraż (2023; all in NHC). All specimens were examined, described and photographed in detail by RB and BD. Photographic records were also sourced online from iNaturalist, Observation.org and Wikimedia Commons platforms (downloaded 15 December 2024) or received privately.

Aside from describing six new species, we redescribe the type material of all six previously named species. To further aid comparison, we provide photo collages of most of these types, showing as many diagnostic details as possible, and we also prepared comparative figures of important structures such as the male appendages and hamules. Note that the material is in a variable and sometimes poor state of preservation (some specimens were probably immature), however, and that many distinguishing features could not be verified due to the absence of additional specimens.

All measurements are given in mm. The size of the entire dragonfly, its pterostigma and cerci are described relative to other species of *Nesocordulia*. The terminology of external morphology was based on Dijkstra & Clausnitzer (2014). The following terms are equivalent (to Ris 1921): mesokatepisternum (mesinfraepisternum); metakatepisternum (metinfraepisternum). Abbreviations. A: anal vein; Ax: antenodal cross-veins; Cu: cubital vein; Cux: cross-veins in cubital space; Fw: forewing(s); Hw: hindwing(s); Pt: pterostigma; Px: postnodal cross-veins; S1–10: abdominal segments 1–10.

Acronyms for collections.

MNHN—Muséum National d'Histoire Naturelle, Paris, France;

NHC—Nature History Collections of the Adam Mickiewicz University in Poznań, Poland;

NHMUK—Natural History Museum (formerly BMNH), London, UK;

RMNH—Naturalis Biodiversity Center (formerly Nationaal Natuurhistorisch Museum), Leiden, The Netherlands.

Results

Genus *Nesocordulia*

Nesocordulia McLachlan, 1882—Knifetails

Etymology. From the Ancient Greek νῆσος (*nêsos*)—island (McLachlan 1882) and *Cordulia*—the feminine form of Latinised adjective derived from Greek κορδύλη—club or cudgel (Fliedner & Endersby 2019).

Description. Rather small to medium-sized dragonflies, total length 41–60 mm, Hw 28–41 mm. Arched posterior border of eyes. All male tibiae with whitish tibial keels, contrasting with the dark background. Male with auricles on S2. Abdomen clubbed, S7–10 being expanded (with S8 the widest), although less so in females. Dorsum of male S10 with spine- or keel-like longitudinal tergal process, which ends distally in an acute point. Anal triangle of male Hw with 2 cells (large basal and small apical). Fw with 1 Cux, Hw with 2. Anal loop long and sack-shaped, ending well distal of triangle, with 12–20 (mostly 13–18) cells in males, and 15–22 (mostly 15–20) in females.

Colouration generally dark (partly with metallic reflections) with yellow patterning. Metallic reflections found on synthorax and head, but not on abdomen, and are mostly green, but also blue, violet, bronze, copper and golden. On head these are present regularly on vertex, frons and sides of postclypeus. A yellow centre of clypeus in all but one species. Labrum most frequently dark, labium pale or two-toned. Eyes when alive are purplish brown anterodorsally and blue posteroventrally, sometimes with bright green in between. On synthorax, metallic reflections occupy various areas, from three distinct stripes to almost whole strongly melanised surface. On mesepisternum, a metallic stripe with a non-metallic brown area in various proportions: regularly covers upper parts along the middorsal carina, but in some cases almost the whole surface except the brown anterolateral corner (sometimes with a blurred yellow spot). On mesepimeron, metallic reflections occur especially in its anterior parts, where green is frequently extended down with copper. On metepisternum, variably extensive metallic reflections encircle a yellow spot. On metepimeron, a metallic green stripe covers its anterior region. On synthoracic sides of all but one species, diagnostic pattern of 2–5 pure yellow spots. Poststernum pale (in colour of thoracic spots) or dark (in colour of thoracic background). Legs mostly dark, brown to black, with increasing amounts of yellow (or reddish brown in two reddish brown species) from hindlegs to forelegs, usually found on: (a) coxa in hindlegs, (b) coxa and trochanter in midlegs, and (c) coxa, trochanter and part of femur in forelegs, where spread from its base to two thirds of the length. Except reddish brown species, paired yellow pattern on black abdomen. In most species, S2 on each side with: (a) two yellow spots laterodorsally, and (b) a long lateroventral spot or two smaller spots, rearwards entering at least basally into the genital lobe. On each side of S3–6, the laterodorsal pattern including anterior and posterior stripes, the former frequently on all segments (in some cases reduced to S3–5 or S3–4) while the latter frequently limited to S3 and S4 only. In females, the yellow pattern is more complete. The anterior and posterior stripes differ in their form (best visible on S3): the former has its dorsal margin concave and the latter convex. The S3–6 pattern is interspecifically variable. In many species, paired basal laterodorsal yellow spots on S7, most frequently forming a continuous or broken ring or half-ring. Along the ventral carina of S3–6, pale yellowish lines, in some cases broadened anteriorly.

Descriptions of new species

***Nesocordulia coloratissima* Bernard, Daraž, Ravelomanana & Dijkstra sp. nov.—Flame-tipped Knifetail**
Figs 1, 15–19, 20c,d

<http://zoobank.org/urn:lsid:zoobank.org:act:45F48E7A-7BEE-46C6-9D2C-D585834376C8>

Etymology. A declinable feminine Latin adjective, formed from *colorata*- plus superlative suffix *-issima*, “the most colourful”. This is the most variegated species, with a striking spectrum of black, rusty brown, yellow, and white, as well as metallic with green, blue, golden, bronze, and violet reflections.

Type material. Holotype male (RMNH.INS.1679786) and two paratype males (RMNH.INS.1552533, 1552535), all from Isalo Ranch, 22.5919° S, 45.3921° E, 805 m asl, near Isalo National Park, Ihorombe Region, Madagascar, 09.01.2016, leg. K.-D.B. Dijkstra and A. Ravelomanana. Two paratype females: (RMNH.INS.1679787), Isalo Ranch, 22.5919° S, 45.3921° E, 805 m asl, near Isalo National Park, Ihorombe Region, Madagascar, 09.01.2016, leg. K.-D.B. Dijkstra and A. Ravelomanana, and (RMNH.INS.1679789), Kirindy Forest near lodge and research station, 20.07° S, 44.66° E, 58 m asl, Menabe Region, Madagascar, 14.11.2014, leg. K.-D.B. Dijkstra.

Photographic records. All individuals identified by us from photographs (originally given as *N. malgassica* at the indicated internet platforms). [1] Female, 22.4655° S, 45.2619° E, 968 m asl, Isalo National Park, Ihorombe Region, 25.11.2018, photo by Charles Sharp (https://commons.wikimedia.org/wiki/File:Nesocordulia_malgassica_female.jpg). [2] Male, 22.5583° S, 45.3969° E, 761 m asl, near Isalo National Park, Ihorombe Region, 02.02.2020, photo by Valentina Volkova (<https://www.inaturalist.org/observations/39941193>). [3] Female, 22.5393° S, 45.3776° E, 803 m asl, Isalo National Park, Ihorombe Region, 21.11.2023, photo by user name “augerben” (<https://www.inaturalist.org/observations/195677439>).

Diagnosis. This rather small *Nesocordulia* species is the most colourful and extensively yellow-marked in the genus. The black abdomen marked with yellow up to the base of S7, while the remainder is uniformly rufous, is unique, as are the yellow occipital triangle, yellow frons sides, broadly yellow centre of labrum, and the especially large yellow spot on the mesepimeron and metepisternum (sometimes narrowly divided into two large triangular spots but more frequently fused). The hamule and cerci are also unique (see Figs 15–16 and 17–18, respectively), although the former is similar to that of *N. evanida*.

Description. Holotype male. Total length 45.0, abdomen (excluding appendages) 31.5, Fw 31.9, Hw 31.0, Fw Pt 2.1, cerci 2.2. Fw Ax 12, Fw Px 7–8, Hw Ax 7–8, Hw Px 9–10.

Head. Face dark metallic, marked extensively with yellow (Fig. 1e). Vertex and postfrons metallic blue with some green and violet reflections. Frons sides pure yellow. Antefrons mostly glistening dark bronze with a greyish creamy bar along the clypeus margin. Anteclypeus and centre of postclypeus yellow, sides of postclypeus metallic (green and dark bronze). Labrum glossy brownish black with a large yellow centre and a small dark brown spot in the middle. Labium yellow (Fig. 1f). Occipital triangle yellow. Postgenae black. Eyes in life purplish brown anterodorsally and light blue posteroventrally, with a thin bright green line in between (Fig. 1a).

Thorax. Synthorax brown and dark-metallic (mostly green reflections), with three pure yellow spots on sides: the upper large spot, extending across the mesepimeron and metepisternum and forming two branches around the metastigma, and two spots situated along the lower margin, one smaller on the metakatepisternum below the metastigma and one larger and oblong covering the posterior half of the metepimeron and adjacent to the yellow poststernum (Figs 1a, 19). Middorsal carina mostly yellow, contrasting with the metallic green mesepisternum.

Wings. Membrane partly slightly tinted with brownish amber, especially in anterior parts and at wingtips. Pt medium-sized, black (Fig. 1b).

Abdomen. Colour pattern divided into two sections: S1–6 black with a bright yellow pattern of paired spots, while S7–10 mostly rusty brown (Fig. 1a). The laterodorsal yellow spots on each side of S2 are of similar size, the anterior one being rather angular and the posterior more rounded, while the broad lateroventral spot extends along the whole of the segment (Fig. 1a). The laterodorsal yellow pattern on S3–6 consists of anterior stripes on each segment, and posterior stripes on S3 and S4 only (Fig. 1a). S7 with a basal dorsolateral yellow half-ring covering about 30% of the segment’s length (not crossing the supplementary transverse carina) and including a middorsal pale rusty smudge (Figs 1a,c). Along the ventral carina: (a) on S3–6, pale yellow stripe, broadened anteriorly on each segment; (b) on S7, basal yellow spot, not merged with the yellow half-ring above it (Figs 1a,d).



FIGURE 1. *Nesocordulia coloratissima* **sp. nov.** (a) male habitus in lateral view; (b) female habitus in dorsal view; (c) male S6–8 in dorsal view; (d) male abdomen in ventral view; (e) male head in frontal view (f) male head in ventral view; (g) male terminalia in lateral view. Photos by: a–b, Allan Brandon; c–g, Bogusław Daraż.

Secondary genitalia. In lateral view, the hamule with a shallow but fairly wide rectangular apical incision between its anterior and posterior branch, the latter being only slightly broader and about the same length as the former (Fig. 15). In ventral view, the inner lobe of the anterior branch very broad and broadly rounded inwards; at the apex, the anterior branch shallowly divided from the posterior external branch, which is visible as a rounded flat surface with a thin dark margin (Fig. 16a). Genital lobe relatively narrow, directed slightly obliquely posteriorly (Fig. 15), with ochre hair-like setae.

Caudal appendages. Cerci white with dark brown base (brownish shade to 40–45% of their length) and white hair-like setae (Figs 1g, 17–18). In dorsal view, slightly arched inwards (banana-shaped), with a small bulge visible as a blunt angle near the base of their inner margin (Fig. 18). In lateral view, slightly arched up and not distended in their distal half, being almost equally thick throughout their length (Figs 1g, 17); the small bulge may be visible at 1/3 of the length. Epiproct rusty cream, fairly long, reaching 80% of the cerci length (Figs 1g, 17).

Variation in males. Total length 44.1–45.6, abdomen (excluding appendages) 31.0–32.0, Fw 31.3–32.5, Hw 30.3–31.7, Fw Pt 2.1–2.4, Fw Ax 10–12, Fw Px 7–8, Hw Ax 7–8, Hw Px 8–10. Each of the following slight variations was seen in one individual: (a) more extensive yellow centre of labrum; (b) large upper spot on synthorax narrowly divided into two spots, an anterior one on mesepimeron and a posterior one on metepisternum; (c) an additional but indistinct brownish yellow spot in the anterolateral corner of mesepisternum; (d) the posterior laterodorsal spot on S2 extended ventrally; (e) a short yellow stripe in the posterior part of S5, corresponding to the stripes on S3–4; (f) distal two thirds of S7 only partly rusty brown and partly black laterally and distally.

Paratype females. Total length 42.0–46.4, abdomen (excluding appendages) 30.5–33.0, Fw 32.5–34.4, Hw 31.1, Fw Pt 2.2–2.4, Fw Ax 10–12, Fw Px 6–9, Hw Ax 7, Hw Px 9–10. Colouration similar to that of the males with the following differences: (a) an additional large yellowish spot in the anterolateral corner of mesepisternum; (b) the anterior laterodorsal spot on S2 concave dorsally, and the posterior one enlarged ventrally (Fig. 1b); (c) the yellow pattern on S3–6 complete, i.e., with two paired stripes on each segment (Fig. 1b); (d) wing membrane slightly tinted with amber at its base, but not in its anterior and distal parts. Gonapophyses represented by anterior processes at the end of S8 (subgenital plate) and median processes at the base of S9. The former, a pair of flat ribbon-like arms, are largely covered by corners of the S8 tergites with only their common base discernible (Fig. 20d), but may be visible when tergites are spread apart (Fig. 20c), while the latter have the form of short vertical and triangular projections (Figs 20c, d). Cerci short (0.9–1.0), creamy white (Fig. 1b). Variation in females limited, mostly in their dimensions.

Distribution and ecology. Most records are from (and around) the popular Isalo National Park in south central Madagascar, but one is from Kirindy Forest about 280 km northwest, suggesting the species is fairly widespread (Fig. 21). Indeed, currently it is the only *Nesocordulia* known from the drier west of the island, as both areas are situated in the ecoregion of Madagascar Succulent Woodlands (One Earth 2024) and the hydrographic ecoregion of Western Basins (Sparks & Stiassny 2022). All specimens were collected resting in trees far from water.

Nesocordulia evanida Bernard, Daraž & Dijkstra sp. nov.—Little Knifetail

Figs 2, 15–19, 20e

<http://zoobank.org/urn:lsid:zoobank.org:act:CAAAF98D-D094-462F-BB0E-083C4FFFD58>

Etymology. A declinable feminine Latin adjective meaning “vanishing from sight”, as males are almost impossible to follow for the observer’s eyes due to the combination of their behaviour, disruptive camouflage, and the dappled light in their microhabitat (see Behaviour section).

Type material. Holotype male (NHC-T-INS-000011), and six paratypes, five males (NHC-T-INS-000012, NHC-T-INS-000013, NHC-T-INS-000014, NHC-T-INS-000015, NHC-T-INS-000016) and a teneral female (NHC-T-INS-000017), collected after emergence before maiden flight, all from the Simianona river, a bridge 1.9 km SSE of Antsiatsiaka, 16.3116° S, 48.8541° E, 853 m asl, Sofia Region, Madagascar, 7 and 12.12.2023, leg. R. Bernard, B. Daraž and Mamitiana Rakotohary.

Additional material. 1 male, incomplete, S7–10 missing (RMNH.INS.1552539), the Manantenina river and adjacent rice fields, between Mandena village and the Marojejy National Park border, 14.4690° S, 49.8058° E, 107 m asl, Sava Region, 15.02.2018, leg. K.-D.B. Dijkstra.

Diagnosis. The smallest *Nesocordulia* species, separated from its probable closest relatives (*N. coloratissima* and *N. malgassica*) by the black rather than rufous S7–10 and its slightly, but distinctively distended cerci with black hair-like setae. Differs from other black-tailed species by the shape of the cerci and hamule, as well as the thoracic markings with two triangular and three roundish yellow spots on each side.

Description. Holotype male. Total length 44.3, abdomen (excluding appendages) 30.8, Fw 29.5, Hw 28.5, Fw Pt 1.8; cerci 2.0, Fw Ax 11, Fw Px 7, Hw Ax 6, Hw Px 8–9. Colouration generally dark, black and metallic green with yellow pattern (Fig. 2a).

Head. Face dark metallic with a yellow centre (Fig. 2g). Vertex and frons metallic, with green and blue reflections (Figs 2c,g). Frons sides brownish turning into metallic green with golden and copper reflections. Clypeus largely yellow, with metallic green sides. Labrum black, with two small yellow spots at the base (Fig. 2g). Labium yellow, median lobe paler with a small central darkish spot. Occipital triangle black. Postgenae black. Eyes in life purplish brown anterodorsally, and blue posteroventrally, with a bright green line in between (Fig. 2a).

Thorax. Synthorax mostly metallic (largely green and locally blue and copper), with darker lower parts (purplish-dark brown to blackish), and with five yellow spots on sides (Figs 2a, 19). Two upper spots fairly large, elongated, irregularly triangular, with opposite tips: the mesepimeral pointing dorsally, and the uppermost metepisternal pointing ventrally. Along the lower margin, three small spots, the first on the metakatepisternum below the metastigma and two next on metepimeron, the last spot adjacent to mostly yellow poststernum (with brownish tip). Middorsal carina yellow, contrasting with the metallic green reflections on mesepisternum (Fig. 2c).

Wings. Membrane basally hyaline, without any tint. Pt medium-sized, black.

Abdomen. Black, with paired yellow pattern (Fig. 2f). The laterodorsal yellow spots on each side of S2 are of similar size: the anterior spot broad, with tapered tip directed dorsally, and the posterior one oval (Figs 2a,f). The lateroventral yellow spot stretched along most of the S2 length; narrow anteriorly, broad posteriorly, with a short dorsal branch pointing an auricle (Figs 2a,d). The laterodorsal yellow pattern on S3–6 incomplete, it consists of anterior stripes on S3–5, and posterior stripes on S3 and S4 (vestigial) (Fig. 2a). S7 with a basal dorsolateral yellow half-ring covering one quarter of the segment's length and reaching the supplementary transverse carina; dorsally, the ring is complete, with a small apical notch flanked by two tiny distal projections (Figs 2a,f). Along the ventral carina: (a) on S3–6, a pale yellow line, broadened anteriorly on S3 only; (b) on S7, a small brownish yellow spot basally and a yellow to brownish stripe; (c) on S8, a large brownish spot (thinner distally), visible in lateral view (Fig. 2e).

Secondary genitalia. Hamule in lateral view, with a fairly shallow and rather narrow triangular apical incision between anterior and posterior branches, the former short and tapered and the latter slightly longer, broader and rounded apically (Fig. 15). In ventral view, the inner lobe of the anterior branch broad and slightly tapered inwards; at the apex, the anterior branch shallowly divided from the posterior external branch, which is slightly twisted inwards and visible as pale roundish surface with a broad black margin (Fig. 16b). Genital lobe relatively narrow, directed obliquely posteriorly, with yellow hair-like setae.

Caudal appendages. Cerci fairly short, creamy white, black basally (brownish shade to 40% of the length), with black hair-like setae (Figs 2a,h). In dorsal view, gently arched inwards, with a longer (60%) and slightly distended outward arm (Fig. 18). In lateral view, slightly bent down at one third of their length, further distally slightly distended thus looking hanging down (Figs 2h, 17); the small bulge hardly discernible at one quarter of the length. Epiproct creamy white with a darkish base and blackish apex; fairly long, reaching 70% of the cerci length (Figs 2h, 17).

Variation in males. Total length 43.2–44.6, abdomen (excluding appendages) 29.1–31.0, Fw 29.5–30.8, Hw 28.5–29.9, Fw Pt 1.8–2.0, cerci 2.0–2.2, Fw Ax 10–11, Fw Px 7–8, Hw Ax 6–7, Hw Px 7–9. Differences in colouration limited only to: (a) larger or smaller width of two upper synthoracic spots; (b) laterodorsal yellow pattern on S3–6 more or less developed in individuals from the same local population: the anterior stripes more frequently on S3–6 (Fig. 2f), but also on S3–5 (with that on S5 even vestigial, Fig. 2a), and posterior stripes usually on S3 only, but also on S3–4; (c) the lateroventral spot on S2 without a dorsal branch in one male; (d) the background colour of S7–10 brownish black in one male; (e) various size of two small distal projections of the yellow half-ring on S7, from lacking to quite well developed with disintegrating brownish tips; (f) the brownish shade on cerci reaching their half-length and even three quarters of their length (each version in one specimen).

Paratype female. Teneral, preserved in poor condition. Total length 41.6, abdomen (excluding appendages) 29.6, Fw 31.7, Hw 30.9, Fw Pt 2.0. Fw Ax 13, Fw Px 8, Hw Ax 7, Hw Px 9–10. Although the colouration in this female is not fully developed, it is generally similar to that of the males with the following minor differences (Fig. 2b): (a) two upper thoracic spots, mesepimeral and metepisternal, wider (as in the male from Marojejy); (b) two metepimeral yellow spots partly merged into large one; (c) the laterodorsal pattern on S3–6 more complete, with anterior stripes on all segments (S3–6), and posterior stripes on S3–5 (on S5 vestigial); (d) pattern along the ventral carina: on whole S7, a broad yellow stripe broadened anteriorly, and on S8, a yellow spot, large and rounded in its anterior half, and narrowed in its posterior half. Gonapophyses (Fig. 20e): (a) anterior processes at the end of S8 (subgenital plate) in the form of two short and broad, rounded projections, laterally situated and partly covered by

tergites; and (b) median processes on S9 as vertical, narrow, rather long and tapered warts. Cerci tiny (0.7), white with darkish shade dorsally along the basal half.



FIGURE 2. *Nesocordulia evanida* sp. nov. (a) male habitus in lateral view; (b) female habitus in lateral view; (c) male head and thorax in dorsal view; (d) male secondary genitalia in lateral view; (e) male habitus in ventral view; (f) male abdomen in dorsal view; (g) male head in frontal view; (h) male terminalia in lateral view. Photos by Bogusław Daraż.

Distribution and ecology. Known from two localities situated 229 km apart in northeastern Madagascar (Fig. 21), the type locality being in the ecoregion of Madagascar Subhumid Forests and the second site in the ecoregion of Madagascar Humid Forests (One Earth 2024). Both sites are in the hydrographic ecoregion of Eastern Highlands

(Sparks & Stiassny 2022) at the foot of mountainous protected areas, the type locality lying just below Marotandrano Special Reserve and the second site below Marojejy National Park. The Simianona river originates in extensive foothill marshland and flows through a mosaic of forest, thickets and wetlands with a relatively low degree of human impact. The Manantenina river flows down from the Marojejy range, but the collection locality is in a cultivated landscape two kilometres from closed forest. The Simianona river (Fig. 3) is mostly 7–10 (up to 15) m broad and relatively deep with water clear, but appearing dark brown due to its marshy origin. The flow rate is very low, slightly increasing only where the course narrows and at some small cascades. The banks are mostly overgrown by low trees with their branches and even trunks overhanging the water. Consequently, the river surface is a mosaic of complete shade, half-shade, dispersed light, and sunny clearings, while the shore zone is mostly shaded (Fig. 3). At a few open sections, dense floating mats of ferns and sedges (Cyperaceae) extend over the water surface, with patches of *Nymphaea caerulea* waterlilies along them. The calm river changes its character on short sections with multi-stage cascades and rapids, where habitat conditions become more diverse.

Behaviour. Males were observed (and filmed) at the Simianona river almost only during sunny moments (with one exception), typically remaining for no more than 3–5 minutes. They only flew over shaded and half-shaded sections, never entering larger sunny clearings. Together with their colouration and rapid, erratic flight, this provided disruptive camouflage and made following them for more than a few seconds almost impossible. The areas patrolled covered only 3–10 m², the smallest being in deep shade above foaming water below a cascade, while the largest was occupied during the only observation in overcast weather. Territories were mostly close to the shore (0.2–1.5 m) or along overhanging trees further out; only occasionally males flew even further above open water. The males' flight was highly erratic with rapid sharp turns after every 0.5–1.5 m section covered. Any moments of hovering were brief with the male facing the open river with its abdomen slightly raised. Males mostly flew only 20–30 cm above the water, ranging between 10 and 40 cm. Males of *Hemicordulia similis* (Rambur, 1842) patrolled nearby but favoured more brightly lit sections, including completely sunny ones, and their flight was more predictable, going back and forth at a height of 30–50 cm without sudden turns; they hovered less often but did so for longer periods. A mid-air clash between males of *N. evanida* and *H. similis* ended with the latter being chased from the territory of the former.



FIGURE 3. Habitat at type locality of *Nesocordulia evanida* sp. nov., Simianona river, Antsiatsiaka. Photo by Bogusław Daraż.

***Nesocordulia fossa* Bernard, Daraž, Ravelomanana & Dijkstra sp. nov.—Fossa Knifetail**

Figs 4, 15–19

<http://zoobank.org/urn:lsid:zoobank.org:act:C2B3AC67-AEB0-482B-AD98-99339259908B>

Etymology. The name, a noun in apposition, refers to Madagascar's largest carnivore, the similarly rufous, long-bodied and enigmatic Fossa (*Cryptoprocta ferox* Bennett, 1835).

Type material. Holotype male (RMNH.INS.1552538), Tsakoka trail, 18.7943° S, 48.4267° E, 950 m asl (coordinates approximate), Mantadia National Park, Alaotra-Mangoro Region, Madagascar, 17.01.2016, leg. K.-D.B. Dijkstra and A. Ravelomanana.

Diagnosis. Comparatively large species, easily separated from all congeners except *N. rubricauda* by the reddish brown body, dark brown wing bases, and denser venation, especially between the cubital and anal veins. Aside from unique features, such as the shape of the cerci and hamule (see Figs 15–16 and 17–18, respectively), yellow markings on the largely reddish brown thorax, and black apical smudges laterally on the reddish brown S3–6, differs from *N. rubricauda* by the yellow marking on the clypeus and the single cell rows subtended by Rspl.

Description. Holotype male. Total length 56.6, abdomen (excluding appendages) 39.4, Fw 41.7, Hw 40.6, Fw Pt 2.4, cerci 2.7. Fw Ax 15–16, Fw Px 12, Hw Ax 9, Hw Px 14. Colouration generally reddish brown, with metallic green, yellow and black markings (Fig. 4a).

Head. Face dark in various shades of brown with a yellow triangular centre (Fig. 4e). Postfrons and frons sides olive brown with metallic sheen locally. Frontal shield of antefrons blackish brown with trace of metallic blue; the lower edge of antefrons olive brown with a minute yellow spot in the middle. Anteclypeus and central postclypeus yellow, sides of postclypeus olive brown. Labrum dark reddish brown with a paler amber brown centre (Fig. 4e). Labium pinkish brown with yellowish admixture at the base (Fig. 4b). Occipital triangle reddish- to dark brown. Postgenae yellowish to reddish brown (Fig. 4b). Eyes in live purplish brown anterodorsally and light blue posteroventrally (Fig. 4a).

Thorax. Synthorax reddish brown with three evenly distributed metallic stripes (green with blue reflections) on mesepisternum, mesepimeron and metepisternum, and with adjacent two yellow spots (Figs 4a,b, 19). The mesepimeral yellow spot shorter and together with irregular purplish brown patch situated on the lower extension of the metallic stripe while the metepimeral yellow spot long and extending behind the metallic stripe. Legs dark brown to black with basal parts (coxae, trochanters and parts of femora, the longest on forelegs) ochre to reddish brown (Figs 4a,b).

Wings. Dark brown bases, larger in Fw, reaching farthest in costal and subcostal space (crossing Ax2 in Fw and Ax1 in Hw) and closest in cubital space (Figs 4a,b). Wing membrane also slightly tinted with brownish locally, especially in its anterior and distal parts (Fig. 4f). Pt medium-sized, black, but magnified, with a paler dark brown border along veins. Venation in Hw: (a) row between the cubital and anal veins with 5–8 cells doubled; (b) row between R4 and the median vein with 8–9 cells doubled (even tripled distally) (Fig. 4f). Rspl subtending single row of cells. Membranula whitish.

Abdomen. Reddish brown, most intensively on S8–9, with black rings of posterior field of tergites (beginning from S2). S3–6 each with a posterolateral triangular black smudge bordering the posterior black rings (Figs 4a,d). No yellow pattern, only ochre yellow brush on S3–7 anterolaterally.

Secondary genitalia. Branches of the hamule separated by a deep and wide gap, with the posterior branch pressed against the genital lobe and the anterior branch tapered distally into a triangular and unbent tip (Figs 4b, 15). In ventral view, the inner lobe of the anterior branch bluntly triangular and elongated along the main axis of the body (Fig. 16f). Genital lobe relatively long, bluntly triangular, directed downwards and slightly posteriorly, pinkish brown with rusty ochre hair-like setae (Figs 4b, 15).

Caudal appendages. Cerci medium-length, reddish brown (as the abdomen), basally darker. In dorsal view, with arched base and out-curved tapered tips, thus appearing sinusoidal or lyre-shaped (Figs 4c, 18). In lateral view, gently arched up (with the bent near half of their length), not distended in their distal half, and with an undercut tip (Fig. 17). Epiproct reddish brown and long, reaching 90% of the cerci length (Figs 4c, 17).

Female. Unknown.

Distribution and ecology. Known only from the type locality in central-eastern Madagascar (Fig. 21), in the ecoregion of Madagascar Humid Forests (One Earth 2024) and the hydrographic ecoregion of Eastern Highlands (Sparks & Stiassny 2022). The male was flying in the middle of the day, but in deep shade, cruising very low over a stream under thick tangles and a closed canopy.



FIGURE 4. *Nesocordulia fossa* sp. nov., male. (a) habitus in lateral view; (b) head in ventral view and thorax and S1–2 in lateral view; (c) terminalia in dorsal view; (d) abdomen in ventral view; (e) head in frontal view; (f) left Hw. Photos by: a, Dave Smallshire; b–f, Bogusław Daraż.

***Nesocordulia ipsio* Bernard, Daraž & Dijkstra sp. nov.—Dark Knifetail**

Figs 5, 15–19, 20a,b

<http://zoobank.org/urn:lsid:zoobank.org:act:9627EDCE-FC92-48EC-8839-E629984BDC35>

Etymology. The name, a noun in apposition, refers to the CEPF project Insects and People in the Southern Indian Ocean (IPSIO), initiated by Brian Fisher at the Madagascar Biodiversity Center. K.-D.B. Dijkstra participated in the IPSIO expedition to Marojejy National Park, but all specimens were collected by Alan Gardiner while he was seeking for butterflies.

Type material. Holotype male (RMNH.INS.1552536) and four paratypes: male (RMNH.INS.1552534) and three females (RMNH.INS.1679788, 1679790, 1679791). All from the ridge below Simpona Camp (“camp 3”), 14.4377° S, 49.7544° E, 1,150 m asl, Marojejy National Park, Sava Region, Madagascar, 09–13.02.2018, leg Alan Gardiner.

Photographic records. Female (identified by us from the photograph), vicinity of Mantella camp, 14.4376° S, 49.7756° E (approximate location), 480 m asl, Marojejy National Park, Sava Region, 01.2012, photo by user name “globalherping” (<https://www.inaturalist.org/observations/224246873>).

Diagnosis. Medium-sized *Nesocordulia* species with a uniquely shaped hamule (see Fig. 15) and the most extensive and contrasting dark markings on the labium and cerci in the genus. Only the presumably closely related *N. odorator* is similarly dark, sharing the limited thoracic pattern of small yellow spots, divided yellow lateroventral marking on S2, the laterally long but dorsally interrupted yellowish basal ring on S7, and dark epiproct. *Nesocordulia ipsio* differs from it, however, by a different hamule (see Figs 15 and 16) and mostly blackish brown lateral lobes of labium, and is also significantly smaller.

Description. Holotype male. Total length 46.9, abdomen (excluding appendages) 32.2, Fw 34.9, Hw 33.5, Fw Pt 1.9, cerci 2.2. Fw Ax 11–12, Fw Px 8–9, Hw Ax 7, Hw Px 11. Colouration generally dark, mostly black and locally brown, and with metallic reflections and yellow pattern (Fig. 5a).

Head. Face dark, with rich metallic reflections and a yellow centre (Fig. 5f). Vertex metallic, blue and violet. Frons metallic, with dark bronze frontal shield and green, blue, violet and copper reflections (Figs 5a,f). Clypeus yellow to olive-yellow centrally, and metallic green (with golden and purplish reflections) laterally (Fig. 5f). Labrum glossy black, locally with metallic violet reflections (Fig. 5f). Labium with median lobe brown and lateral lobes largely blackish brown and only narrowly yellow and buff on outer borders, like crescents (Fig. 5g). Occipital triangle black. Postgenae black.

Thorax. Synthorax mostly richly metallic (green, blue, violet, purple, bronze and copper), interspersed with brown, and with small yellow markings (Figs 5a, 19). Mesepisternum metallic (green and blue) in the upper half and brown in the lower half. Mesokatepisternum brown. On the synthoracic sides, four yellow spots in two lines (Figs 5a, 19). In the upper line, the mesepimeral spot, small and triangular, situated opposite the metastigma, and the metepisternal spot, a larger inverted triangle, darker yellow and slightly blurred. In the lower line, two small spots along the lower margin of the synthorax, on the metakatepisternum below the metastigma and on the metepimeron, the latter much less than half as long as the posterior border of metepimeron and not reaching poststernum. Poststernum dark brown.

Wings. Membrane tinted with yellow at base. Pt short, brown.

Abdomen. Black with paired yellow pattern (Fig. 5a). The laterodorsal yellow spots on each side of S2 are of different size: the anterior broad and short, with tapered tip directed dorsally, and the posterior small and oval. Lateroventral yellow marking on each side of S2 divided into two small well-separated spots: the anterior spot additionally split in two uneven parts while the posterior one broad and rectangular (Figs 5a, 16e). The laterodorsal yellow pattern on S3–6 consists of anterior stripes on each segment (the shortest and partly disintegrated on S6) and posterior stripes on S3 only (Fig. 5a). S7 with a basal dorsolateral creamy white ring covering one fifth of the segment’s length and not reaching the supplementary transverse carina, but far-extended laterally; dorsally, the ring is divided by a narrow black line along the dorsal carina (Figs 5a,d). Along the ventral carina (Fig. 5c): (a) on S3–6, a thin yellow line, broadened anteriorly on S3 only; (b) on S7, a rather broad yellow stripe turning brown distally; (c) on S8, a small basal yellow marking broadened distally and laterally into a large rounded brown spot; (d) on S9, a brown basal spot; the brown spots visible in lateral view of S8–9.

Secondary genitalia. In lateral view, the hamule large, with both branches ear-like, broad and rounded, but the posterior branch much shorter and two-coloured, dark with pale margin (Figs 5a, 15). In ventral view, the inner lobe

of the anterior branch of the hamule ear-shaped and broadly rounded inwards, with pale tip of the posterior external branch visible below (Fig. 16e). Genital lobe black, directed straight downwards and almost as the hamule long (Figs 5a, 15), with rusty and buffy hair-like setae.



FIGURE 5. *Nesocordulia ipsio* **sp. nov.** (a) male habitus in lateral view; (b) female habitus in lateral view; (c) male abdomen in ventral view; (d) posterior part of the male abdomen in dorsal view; (e) posterior part of the female abdomen in dorsal view; (f) male head in frontal view; (g) male head in ventral view; (h) male terminalia in lateral view. Photos by Bogusław Daraż.

Caudal appendages. Cerci fairly short, their basal two-thirds dark (black and dark brown), with brownish shade reaching up to 80% of the length and white tips covered with contrasting dark hair-like setae (Figs 5d,h). In dorsal

view, gently arched inwards, with a longer (60%) inward arm and a shorter outward arm bluntly tapered apically (Figs 5d, 18). In lateral view, arched up and slightly distended in their distal half, with tapering tips and cut apices (Figs 5h, 17). Epiproct blackish to dark brown and fairly long, reaching 80% of the cerci length (Figs 5h, 17).

Variation in males. The paratype male is slightly larger and even darker. Total length 47.4, abdomen (excluding appendages) 32.8, Fw 35.3, Hw 34.0, Fw Pt 1.9, cerci 2.1. Fw Ax 11, Fw Px 8, Hw Ax 8, Hw Px 10–11. Minute differences in the colour pattern versus the holotype: (a) the anterior laterodorsal stripes on S5 and S6 vestigial; (b) yellow and brown pattern along the ventral carina of S3–9 partly darkened and disintegrated. Epiproct slightly longer, reaching 85% of the cerci length.

Paratype females. Total length 46.1–48.2, abdomen (excluding appendages) 32.5–33.7, Fw 37.1–38.3, Hw 36.9–37.5, Fw Pt 1.9–2.0. Fw Ax 12–13, Fw Px 8–10, Hw Ax 7–8, Hw Px 10–12. Colour pattern very similar to that of males, with the following minor differences: (a) the anterior lateroventral spot on S2 irregular and not split (Fig. 5b); (b) the posterior laterodorsal stripe on S4 vestigial (Fig. 5b); (c) the basal ring on S7 reduced to two laterodorsal yellow spots broadly separated dorsally (Figs 5b,e); (d) in two females, the darkened yellow pattern along the ventral carina, especially in posterior parts of S3–6. Variation mostly in dimensions and numbers of cross-veins. Anterior processes of gonapophyses on S8 (subgenital plate) take the form of two large triangular arms, dark with yellow edges (Figs 20a,b); their sharp yellow tips touch each other or overlap, and are visible in lateral view as spines protruding below the ventral corners of S8 tergites. Median processes on S9 are shaped like relatively long ‘viking’ horns (Figs 20a,b). Cerci short (1.0), in dorsal view dark basally (one third to half the length) and yellowish white distally (Fig. 5e).

Distribution and ecology. Known only from Marojejy National Park in northeastern Madagascar (Fig. 21), in the ecoregion of Madagascar Humid Forests (One Earth 2024) and the hydrographic ecoregion of Eastern Highlands (Sparks & Stiassny 2022). All individuals collected over path along the top of a mountain ridge with low cloud forest at 1,150 m asl, and one female photographed at much lower elevation at 480 m asl.

Nesocordulia lyricauda Bernard, Daraž & Dijkstra sp. nov.—Lyre-tipped Knifetail

Figs 6, 15–19

<http://zoobank.org/urn:lsid:zoobank.org:act:725EA847-38B0-474E-A984-E2D11FB4228B>

Etymology. A feminine noun derived from Latin “cauda”, a tail, and “lyra”, an U-shaped instrument with two curvy branches, to describe the distinctive lyre-shaped cerci in dorsal view.

Type material. Holotype male and one paratype male (MNHN). Both are labelled “Madagascar” without further details and are part of René Martin’s collection. The species is known only from these two males identified previously as *N. flavicauda*, the holotype by René Martin (as indicated by his handwriting on the label), but the paratype by an unknown person. Martin’s misidentified specimen was thus incorrectly described briefly as *N. flavicauda* in the catalogue of corduliids (Martin 1907): the caudal appendages illustrated there actually belong to *N. lyricauda* sp. nov.

Diagnosis. The largest *Nesocordulia* species, separated by its unique long lyre-shaped cerci, large and uniquely shaped hamule (see Fig. 15), and the basal yellow spots uniquely extending both dorsally and laterally on S7. Also has more Px in Fw (11–13 vs. 7–10) and Hw (13–14 vs. 7–11) than other black species.

Description. Both males, while over a hundred years old, are preserved in a moderate condition, with well-defined markings, although especially the pale colours appear faded. The terms describing these refer to the current state, although they were possibly more intensely yellow (or white) in life.

Holotype male. Total length 57.7, abdomen (excluding appendages) 39.6, Fw 41.2, Hw 39.7, Fw Pt 1.9, cerci 3.1. Fw Ax 13–14, Fw Px 11–12, Hw Ax 8, Hw Px 13–14. Colouration generally dark, black and metallic, with yellow pattern.

Head. Face dark, largely metallic, with a yellow slightly trapezoidal centre (Fig. 6c). Vertex metallic blue with violet reflections. Frons metallic, with blue, green, violet and copper reflections, and narrowly bronze along the lower edge of antefrons (Figs 6a, c). Clypeus largely yellow with metallic (green and copper) sides (Fig. 6c). Labrum glossy black and dark bronze, with a central brownish yellow notch at its base (Fig. 6c). Labium pale yellow with amber tint (Fig. 6c). Occipital triangle black. Postgenae black.



FIGURE 6. *Nesocordulia lyrica* **sp. nov.**, male. (a) habitus in dorsal view; (b) synthorax and S1–2 in lateral view; (c) head in frontal view; (d) abdomen in dorsolateral view (S8–10 twisted, thus brownish yellow spots along the ventral carina visible); (e) secondary genitalia of the paratype, extracted from the body; (f) S7 in lateral view; (g) terminalia in dorsal view. Photos by Bogusław Daraż.

Thorax. Synthorax largely melanized, black, dark brown and metallic (with green, blue, violet, copper and bronze reflections), with large yellow markings (Fig. 6b). Mesepisternum largely metallic: green and blue with violet reflections, in a lower third turning into brown and metallic bronze and copper. Mesokatepisternum pale brownish yellow. Three pale yellow markings on synthoracic sides (Figs 6b, 19): the single upper stripe on the mesepimeron and metepisternum, long, narrow and kinked, and two lower spots, a small one on the metakatepisternum below the metastigma and a long and wide one covering the posterior half of the metepimeron and adjacent to the yellow poststernum.

Wings. Pt very short, brown (Fig. 6a). Membranula half-whitish anteriorly and half-buff.

Abdomen. Black with paired faded yellow pattern. The laterodorsal spots on each side of S2 are of different shape and size: the anterior spot broad, with tapered tip pointing dorsally, and the posterior one small, directed obliquely ventrally (Fig. 6d). The broad yellow lateroventral spot stretched along the whole S2 and penetrating the genital lobe, with a dorsal black ‘bay’ below an auricle (Fig. 6b). The laterodorsal yellow pattern on S3–6 consists of anterior stripes on all segments and posterior stripes on S3 only (Fig. 6d). S7 with a basal large yellow spot, extended laterally where merging with yellowish markings on the ventral carina and also extended dorsally, crossing the blackish supplementary transverse carina and covering one third of the segment’s length (Figs 6d,f). The pale yellow pattern along the ventral carina: (a) on S3–6, a line, broadened anteriorly on each segment; (b) on S7, a broad yellow stripe in the anterior half, basally merged with the dorsolateral ring; (c) on S8, an anterior spot.

Secondary genitalia. In lateral view, the hamule large, with: (a) the dark anterior branch resembling a standing bird (auk), with the anterior margin wavy, and (b) the adjacent posterior branch, broad and almost the same length as the anterior one (Figs 6b, 15). In ventral view, a deep and narrow indentation is visible between the branches, with the inner lobe of the anterior branch broad, and the posterior external branch rounded with a pale margin (Fig. 16c). Genital lobe relatively broad and reaching the hamule tip, and directed downwards; partly yellow with a black apex and posterior margin (Figs 6b, 15), and with yellowish and rusty hair-like setae.

Caudal appendages. Cerci long and narrow, slightly tapering distally, creamy white to amber, basally brown (brownish shade up to a quarter of the length). In dorsal view, sinusoidal, with arched base and out-curved tips, thus recalling a Roman lyre (Figs 6g, 18). In lateral view, horn-like, not distended and arched twice, at first up and then down, thus shallowly sinusoidal (Figs 6d, 17). Epiproct rusty yellowish, medium-length, reaching two thirds of the cerci length (Figs 6d,g, 17).

Variation in males. The paratype is larger, total length 60.5, abdomen (excluding appendages) 41.9, Fw 42.3, Hw 41.1, Fw Pt 2.0, cerci 3.2. Fw Ax 14–15, Fw Px 12–13, Hw Ax 8–9, Hw Px 13. Its colour pattern only slightly different due to: (a) paler, brown dorsal background of S1 and anterior parts of S2 and S3; (b) posterior laterodorsal stripes present also on S4 (as a small spot on each side); (c) cerci mostly with amber tint. Secondary genitalia extracted from the body, dissected and glued to a pad (Fig. 6e).

Female, distribution and ecology unknown.

***Nesocordulia odonator* Bernard, Daraž, Ravelomanana & Dijkstra sp. nov.—Crabshear Knifetail**

Figs 7, 15–19

<http://zoobank.org/urn:lsid:zoobank.org:act:38D61DF9-F45D-4327-B6C1-79955AA5C3FD>

Etymology. The name, a noun in apposition, like those for *Syncordulia legator* Dijkstra *et al.*, 2007, *Syncordulia serendipator* Dijkstra *et al.*, 2007, and *Syncordulia venator* (Barnard, 1933), honours the explorers of Odonata. This species and *N. fossa* were found on the same day of Odonatours’ inaugural trip, whose participants sponsored the first introduction to Malagasy Odonata (Dijkstra & Cohen 2021).

Type material. Holotype male (RMNH.INS.1552537), Rianasoa trail, 18.832° S, 48.435° E, 980 m asl (coordinates and altitude approximate), Mantadia National Park, Alaotra-Mangoro Region, Madagascar, 17.01.2016, leg. K.-D.B. Dijkstra and A. Ravelomanana.

Diagnosis. Fairly large *Nesocordulia* species with unique hamule, in lateral view recalling a crab’s pincer (chelate appendage) with an almost spike-like dactyl, and unique labium with brown median lobe and mostly yellow lateral lobes. Only *N. ipsio* is similarly dark, sharing the limited thoracic yellow pattern of small spots, divided yellow lateroventral marking on S2, laterally long but discontinuous yellow ring on S7, and dark epiproct. *N. ipsio* has an even darker labium and cerci, however, and is also significantly smaller.

Description. Holotype male. Total length 54.5, abdomen (excluding appendages) 38.4, Fw 38.1, Hw 37.0, Fw Pt 1.9, cerci 2.3. Fw Ax 13–14, Fw Px 9–10, Hw Ax 8, Hw Px 10–11. Colouration generally dark, mostly black and metallic green, with yellow pattern (Fig. 7a).

Head. Face dark, richly metallic with an olive yellow rectangular centre (Fig. 7e). Vertex metallic with violet and blue reflections. Frons metallic: blue and violet (postfrons), dark bronze (frontal shield of antefrons), and green and copper (frons sides) (Fig. 7e). Clypeus largely olive-yellow, with metallic green sides with golden and copper reflections. Labrum glossy black (Fig. 7e). Labium yellow with brown base (median lobe) and lateral lobes only

narrowly dark along their inner borders (Fig. 7b). Occipital triangle black. Postgenae black. Eyes in life purple brown anterodorsally and blue posteroventrally (Fig. 7a).

Thorax. Synthorax mostly metallic (green, blue and purplish-dark brown), with some non-metallic brown areas anteriorly and small yellow spots (Figs 7a,b). Mesepisternum with metallic green and blue reflections in the upper half and non-metallic brown in the lower half. Mesokatepisternum yellowish brown. Synthoracic sides with four yellow spots in two lines (Figs 7a,b, 19). In the upper line, a triangular mesepimeral spot opposite to the metastigma, and the uppermost rectangular metepisternal spot. In the lower line, two small spots along the lower margin of the synthorax, on the metakatepisternum below the metastigma and on the metepimeron. The metepimeral spot much less than half as long as the posterior border of metepimeron and not reaching poststernum. Poststernum dark brown (Fig. 7b).

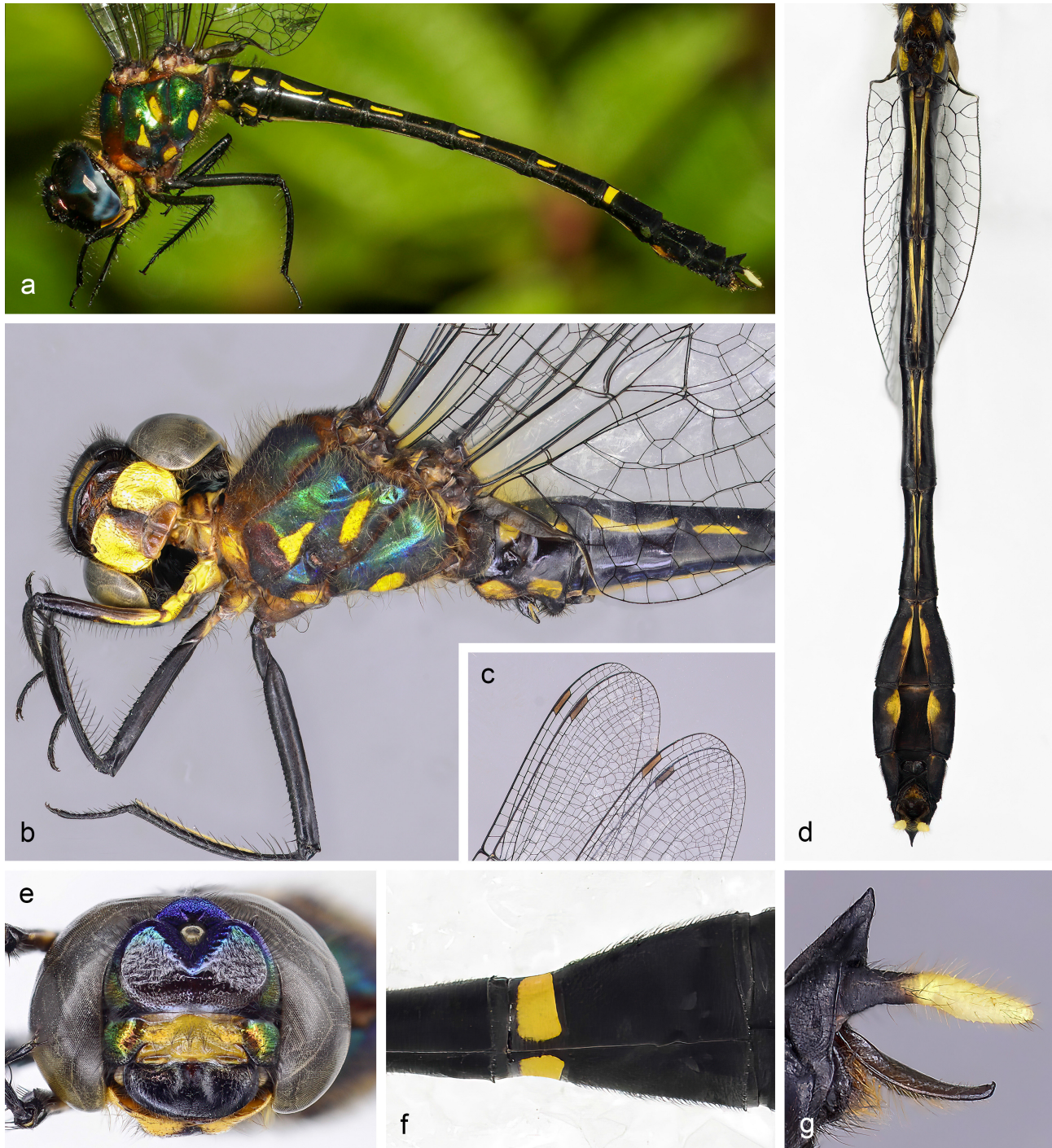


FIGURE 7. *Nesocordulia odonator* sp. nov., male. (a) habitus in lateral view; (b) head in ventral view and thorax and S1–3 in lateral view; (c) wing tips; (d) abdomen in ventral view; (e) head in frontal view; (f) S7 in laterodorsal view; (g) terminalia in lateral view. Photos by: a, Phil Benstead; b–g, Bogusław Daraż.

Wings. Membrane tinted with yellow basally (Fig. 7b). Pt short, brown (Fig. 7c). Membranula dark brown.

Abdomen. Black with paired yellow pattern (Fig. 7a). The laterodorsal yellow spots on each side of S2 are of different size: the anterior spot broad, with tapered tip pointing dorsally, and the posterior one small and angular (Fig. 7a). The lateroventral yellow marking on each side of S2 divided into two small well-separated spots (Figs 7b, 16d). The laterodorsal yellow pattern on S3–6 consists of anterior stripes on each segment and posterior stripes on S3 and S4 only (the last one vestigial) (Fig. 7a). S7 with a basal dorsolateral yellow ring covering one fifth of the segment's length and not reaching the supplementary transverse carina; the ring is extended far laterally and slightly broadened dorsally (Fig. 7a), where it is divided by a broad black line along the dorsal carina (Fig. 7f). The yellow line along the ventral carina (Fig. 7d): (a) on S3–6, continuous and not broadened anteriorly on each segment; (b) on S7, partly broadened into a yellow stripe turning into brown distally; (c) on S8, present in its anterior half and broadened into a brownish yellow spot also visible in lateral view.

Secondary genitalia. In lateral view, the hamule large with two finger-like branches, deeply and narrowly separated and distinctly narrowed and pointed; the posterior branch is much shorter and thinner (Figs 7b, 15). In ventral view, the anterior branch L-shaped with a relatively short and narrow inner lobe (Fig. 16d). Genital lobe black, basally yellow, with black hair-like setae. In lateral view, it is directed downwards and relatively broad and short (Figs 7b, 15), while in ventral view more elongated, with a narrow, finger-like tip (Fig. 16d); this apical part is bent parallel to the body towards the opposite genital lobe and therefore is not visible in the foreshortened lateral view.

Caudal appendages. Cerci fairly short, yellowish, basally black up to 40% of the length, with mostly pale hair-like setae not contrasting with the background (Fig. 7g). In dorsal view, almost straight on the two thirds of the length and further bent outwards and slightly tapering distally (Fig. 18). In lateral view, with lower margin shallowly arched up, and then gently bent at 60% of the length and further straight, appearing thus in their distal half at first slightly distended and then tapering (Figs 7g, 17). Epiproct dark brown and long, reaching 85% of the cerci length (Figs 7g, 17).

Female. Unknown.

Distribution and ecology. Known only from the type locality in central-eastern Madagascar (Fig. 21), in the ecoregion of Madagascar Humid Forests (One Earth 2024) and the hydrographic ecoregion of Eastern Highlands (Sparks & Stiassny 2022). The only known specimen was flying over a fairly large and rocky but very shady forest stream.

Redescriptions of six previously known species

Nesocordulia flavicauda McLachlan, 1882—Yellow-tailed Knifetail

Figs 8, 15, 17–19

Etymology. A feminine noun derived from Latin “flavus”, yellow, and “cauda”, a tail, undoubtedly, to emphasise the extent of yellow on S7–10. Unaware of its unique appearance, Dijkstra & Cohen (2021) called this species the “Yellow-tailed Knifetail”, a translation of the scientific name.

Type material. Holotype male (NHMUK 011253668), just labelled “Madagascar”, but obviously collected no later than 1882.

Additional material. Female (MNHN), also just labelled “Madagascar”, but from René Martin's collection and thus collected before 1921; described by Fraser (1956). *Note:* In the catalogue of corduliids (Martin 1907), *N. flavicauda* is presented erroneously, as Martin must not have seen McLachlan's holotype and thus misidentified a male in his own collection. The male described and illustrated (caudal appendages) by Martin (1907) is described above as the holotype of *N. lyricauda* **sp. nov.** The female described briefly by Martin (1907) as *N. flavicauda* is probably not this species either. Fraser (1956) found two females in Martin's collection labelled as *N. flavicauda*: only one of them was originally identified correctly, but the second was identified and described by him as *N. mascarenica*. We seriously doubt this identification as well, however, see the section on unidentified specimens below. The brief description of a female by Martin (1907) does not allow us to determine precisely which female he described as *N. flavicauda*, although the provided measurements suggest Fraser's ‘*mascarenica*’ rather than true *N. flavicauda*. Therefore, only Fraser's (1956) work can be accepted as the first description of the female *N. flavicauda*.

Uncertain data. 2 males and 1 female (National Museum of Nature and Science, Tokyo, Japan, most probably from the Erich Schmidt's collection): 1 male and 1 female, Sambirano (without closer data), Diana Region, NW Madagascar, 10.1933–01.1934; 1 male, Madagascar (perhaps the same locality?), 02.1934 (Kiyoshi 2024). *Note:* This material was unavailable for study and may well be misidentified.

Diagnosis. Fairly small *Nesocordulia* species, which is the most distinctive in the genus due to the spined cerci and numerous colouration details such as the entirely dark postclypeus, brown and yellow postgenae, two yellow spots on synthoracic sides, yellow central spot on ventrolateral surface of fore femora, evenly narrow and arched anterior dorsal yellow spot on S2, and very large yellow spots on S7–9. Dorsal process (keel) on S10 is shortly pointed and almost horizontal unlike in most other *Nesocordulia* species (except *N. mascarenica*), in which it is more knife-shaped and vertically or at least obliquely protruding.

Description. Holotype male. Preserved in poor condition, in several damaged fragments (Figs 8a,d), but most features still sufficiently recognisable. Additionally, the original description from 143 years ago (McLachlan 1882) has been confronted to make sure of the original colours and other features. Total and abdomen lengths unmeasurable in the present state, McLachlan (1882) gave 35 mm for the abdomen length (caudal appendages included?). Fw length 33.7, Hw 32.7 (34 according to McLachlan, 1882), Fw Pt 1.8, cerci 2.8 ($3\frac{3}{4}$ according to McLachlan, on error). Fw Ax 10, Fw Px 8–9, Hw Ax 7, Hw Px 9–10. Colouration generally dark, black, brown and metallic green, with yellow pattern (Figs 8a–d).

Head. Face dark, largely brown and locally metallic, only with a narrow yellow stripe (Figs 8f–g). Vertex metallic green with golden reflections in posterior parts. Postfrons metallic with green and blue reflections (Figs 8a,f). Frontal shields of antefrons rich brown (Fig. 8f). Antefrons sides yellowish brown to metallic with green, copper and golden reflections (Fig. 8b). Postclypeus entirely dark, glossy black centrally and metallic green and bronze laterally. Anteclypeus yellow (Figs 8f,g). Labrum brown with patina green tint (Figs 8f,g). Labium variegated, with median lobe brown and lateral lobes two coloured: ochre yellow laterally and brown with green patina centrally (Fig. 8g). Occipital triangle brownish to black. Postgenae brown with yellow markings (Fig. 8b).

Thorax. Synthorax dark brown (tinted green patina locally) with metallic reflections locally and yellow spots (Fig. 8b). Middorsal carina brown. Mesepisternum largely metallic green. Synthoracic sides with three pale spots (Figs 8b, 19): a small dull ochre yellow spot on the metakatepisternum below the metastigma and two large yellow spots: an upper oblong, comma-like spot on the mesepimeron, and a lower more oval spot along the posterior margin of metepimeron. Both bright spots encircled with metallic areas, with mostly green, but also blue, violet and reddish copper reflections, the last concentrated in a distinct patch below the mesepimeral yellow spot. No yellow spot on metepisternum. Poststernum brown (Fig. 8b). Legs generally black with (partly) brown coxae and trochanters. Fore femora, on ventrolateral surface, with yellow central spot flanked with brown basally and black distally (Fig. 8b).

Wings. Membrane tinted with yellow in a very small but bright basal spot in all wings (Fig. 8a). Pt short, rich brown (Fig. 8a).

Abdomen. Background dark brown and black, with increasing proportion of the latter from S2 posteriorly, patterned with paired yellow spots (Figs 8a–d). On S2, only anterior laterodorsal spots present, evenly narrow and arched (Figs 8a,c). In place of posterior laterodorsal spots, two paler brown transverse stripes. Lacking lateroventral spot on S2, only a small yellowish brown marking at the base of the genital lobe. Similarly, on S3–6, only anterior laterodorsal stripes, all gently curved with distal tips directed towards the twin stripe; in place of posterior stripes on S3–4, only paler brown irregular shade (Figs 8a,c). S7 with a large dorsal yellow spot covering the anterior half of the segment, with two distal projections reaching 70% of the segment's length (Fig. 8d). S8 dorsally with two large triangular yellow spots, basally fused in a half-ring covering 40% of the segment's length and distally diverging and dissipating in yellow-brown melange, with tips reaching 80% of the segment's length (Fig. 8d). S9 dorsally mostly covered by two large spots, basally yellow and distally brownish, diverged by a blackish stripe along the dorsal carina. Dorsal process (keel) on S10 small, shortly triangular and almost horizontal (Fig. 8e).

Secondary genitalia. Hamule destroyed. Genital lobe rather narrow, directed downwards, brownish black with pale base.

Caudal appendages. Cerci medium-length and relatively stout, creamy yellow with blackish hair-like setae (Figs 8d,e). In dorsal view, almost straight in basal one third of the length and then strongly divergent and tapered into blunt tips (Figs 8d, 18). In lateral view, almost straight, with a sharp triangular spine pointing ventrally at about one third of the length and with tips blunt with an undercut lower edge (Figs 8e, 17). Epiproct chocolate brown, brightened subapically, but with a black apical tooth; short, reaching half of the cerci length, and stout (Figs 8e,

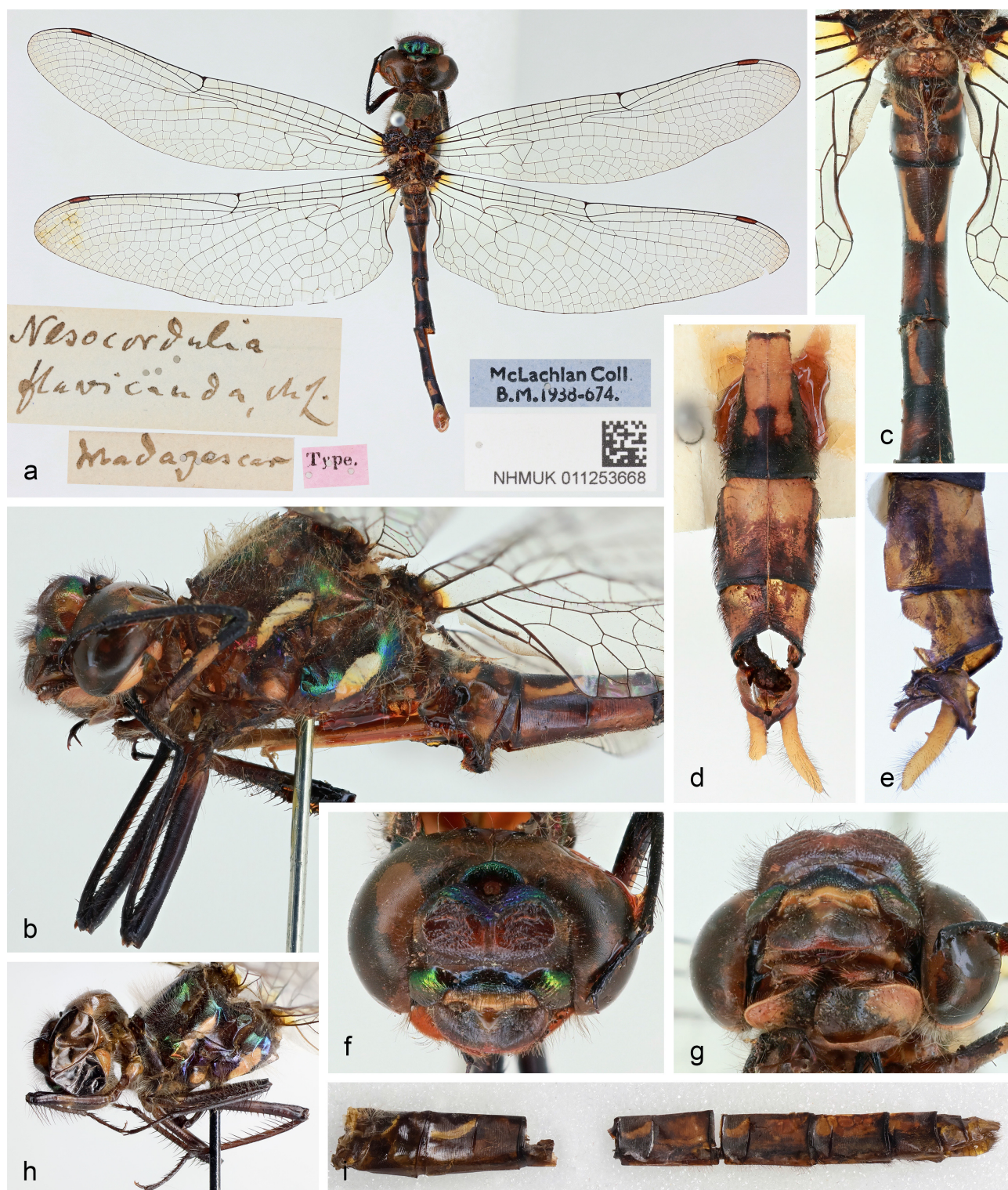


FIGURE 8. *Nesocordulia flavicauda*. (a) male habitus (partial) in dorsal view; (b) male head, synthorax and S1–3 in lateral view; (c) male S1–4 in dorsal view; (d) male S7–10 and caudal appendages in dorsal view (falsely reddish tint, in fact, more yellow); (e) male S8–10 and caudal appendages in lateral view; (f) male head in frontal view (g) male head in anteroventral view; (h) female head and synthorax in lateral view; (i) female abdomen in lateral view. Photos by Bogusław Daraz.

Female. Preserved in poor condition, in several parts (Figs 8h,i). Total and abdomen lengths no longer measurable, Fraser (1956) provided 35 mm as the abdomen length. Fw length 37.2, Hw 35.3, Fw Pt 1.9, cerci 1.2.

Fw Ax 10–12, Fw Px 9–10, Hw Ax 7, Hw Px 10–12. Appears in pre-reproductive period, with pale yellow Pt, and collapsed eyes and synthorax. Many features are difficult to ascertain, although several agree with those of the male, notably the largely brown background colour of the head and synthorax, and the markings on the postgenae, synthorax, fore femora, wing bases, and S2 (Fig. 8h). Central postclypeus not uniform as in the male, but two-toned: brown with an upper yellowish line below the epistomal suture.

Distribution and ecology. Unknown.

Nesocordulia malgassica Fraser, 1956—Rusty-tipped Knifetail

Figs 9, 15, 17–19

Etymology. A feminine adjective indicating the species' Malagasy origin.

Type material. Holotype male and allotype female (MNHN), both from Ambila-Lemaitso, Atsinanana Region, Madagascar, 03.1951.

Photographic records. Male (two photographs), 18.9115° S, 48.4332° E, which lies between the Analamazaotra Special Reserve and Mantadia National Park at 964 m asl, Alaotra-Mangoro Region, 06.02.2001, photo by Ulrich Röder (<https://observation.org/observation/49961334/> erroneously assigned to Zahamena National Park).

Diagnosis. Medium-sized *Nesocordulia* species that appears to be unique by its black abdomen with uniformly rufous S7–10 and its slender cerci. The latter are characteristically wavy in lateral view and abruptly bent inward at their tips, despite diverging for half of their length, in dorsal view. The thoracic markings with two upper and three lower yellow spots on each side are shared only with *N. evanida* (although they differ in detail), as is the labrum with two small yellow basal spots. A potential form of *N. coloratissima* with similarly uniform S7–10 may occur locally, but that species differs in many features such as the cerci, occipital triangle, frons sides, labrum, and thoracic pattern.

Description. Pale colours of specimens in the collection are partly faded and darkened, thus the original species description by Fraser (1956) was helpful in their identification.

Holotype male. Total length 53.2, abdomen (excluding appendages) 36.7, Fw 36.5, Hw 35.4, Fw Pt 2.4, cerci 2.6. Fw Ax 13, Fw Px 9–10, Hw Ax 8, Hw Px 10–11.

Head. Face dark with a yellow centre (Fig. 9c). Frons sides brown and metallic, with bronze, golden and green reflections (Fig. 9f). Vertex, postfrons and central antefrons metallic: green and blue with violet reflections. The rest of antefrons dark brown, with a small yellow triangle in the centre at the clypeus margin (Fig. 9c). Sides of postclypeus dark brown with metallic green reflections, while the centre of it and anteclypeus yellow (Figs 9c,f). Labrum black and dark brown, with two small yellow spots at the base, separated by a diffused brown centre (Fig. 9c). Labium light ochre, possibly ochre yellow in live. Occipital triangle black. Postgenae black.

Thorax. Synthorax largely melanised, metallic reflections (mostly green and locally copper in the lower mesepimeron) interspersed with dark brown (Fig. 9f). Mesepisternum metallic green with the ochre brown anterolateral corner adjacent to similar mesokatepisternum (Fig. 9f). Synthoracic sides with five yellow spots in two lines (Figs 9f, 19). In the upper line, two quite large markings, the irregularly triangular mesepimeral spot, at the level of metastigma and pointing dorsally, and the more rectangular metepisternal spot, with a projection pointing ventrally. In the lower line, three rather small spots along the lower margin of synthorax, the first on the metakatepisternum below the metastigma and two next on metepimeron. Poststernum mostly yellow, its broader region partly brownish. Middorsal carina dark brown.

Wings. Membrane hyaline. Pt medium-sized, brown (Fig. 9a).

Abdomen. Divided into two sections, an anterior part (S1–6), black with paired yellow pattern, and a posterior part (S7–10), mostly reddish brown (Fig. 9a). The laterodorsal yellow spots on each side of S2 are of similar size: the anterior one more angular, with tapered tip pointing dorsally and the posterior one more rounded and tapered anteriorly. The lateroventral yellow spot on each side of S2 stretched along most of the segment's length; narrow anteriorly, broad posteriorly (Fig. 9f). The laterodorsal yellow pattern on S3–6 consists of anterior stripes on each segment, and posterior stripes on S3 and S4 only (Fig. 9e). Basal laterodorsal spots on S7 reddish brown, barely recognisable as almost completely merged with each other and with the similarly coloured rest of the segment; they turn into black in lateroventral parts of the segment (Figs 9a,e). Along the ventral carina of S3–6, a brownish line with an anterior yellow broadening on S3 only; on S7, there is no basal spot adjacent to the ventral carina.



FIGURE 9. *Nesocordulia malgassica*. (a) male habitus in dorsal view; (b) female habitus in dorsal view; (c) male head in frontal view; (d) female distal part of abdomen with caudal appendages in dorsal view; (e) male abdomen in lateral view; (f) male head, synthorax and S1–2 in lateral view. Photos by Bogusław Darż.

Secondary genitalia. In lateral view, the hamule oval to slightly rectangular with rounded distal corners and a hardly recognisable apical incision (Fig. 15); due to the poor quality of the available material, the actual shape of the hamule may differ in detail. Genital lobe relatively narrow, directed downwards, black and basally yellow.

Caudal appendages. Cerci yellow, basally brown, with pale brownish shade up to 40% of their length and with whitish hair-like setae. In dorsal view, slender, straight to their mid-length and gradually diverging distally, but subtly converging at extreme tip, and slightly tapering in the distal third (Figs 9a, 18). In lateral view, shallowly sinusoidal, in the distal half of their length slightly distended, thus looking ‘heavy’, hanging down (Figs 9e, 17); a small ventral bulge visible near their base. Epiproct medium-length, reaching two thirds of the cerci length (Fig. 17), and ochre yellow with the brown apex.

Variation in males. Pale elements in the living male (examined on photographs) clearly brighter than in the specimen in the collection: the abdominal pattern (S2–6) pale yellow and caudal appendages yellowish white. The anterior part of S7 to the supplementary transverse carina not reddish brown similarly to more distal parts as it is in the holotype male, but two-tone, basally darker (reddish black) and further paler, ochre.

Allotype female. Total length 56.4, abdomen (excluding appendages) 40.9, Fw 38.2, Hw 37.4, Fw Pt 2.7–2.8. Fw Ax 12, Fw Px 8–9, Hw Ax 7–8, Hw Px 9–11. The female colour pattern (Figs 9b,d) similar to that of the male holotype with the following differences: (a) frons sides pale brown; (b) labrum black to metallic bronze with less marked yellowish spots forming a diffused central area at the base; (c) colours on S6 not clear (less well preserved), but it seems that intermediate between those on S3–5 and S7–10: blurred and darkened yellow stripes barely visible in the anterior part while the posterior two thirds of the segment mottled rusty on the black background (Fig. 9b); (d) almost the whole wing membrane tinted with amber yellow in all wings, the most intensively, in form of rays, at base (Fig. 9b). Cerci relatively long (1.8), ochre yellow (probably brighter alive) (Fig. 9d).

Distribution. Known from two localities separated by some 75 km in eastern Madagascar (Fig. 21), in the ecoregion of Madagascar Humid Forests (One Earth 2024) and the hydrographic ecoregions of Eastern Lowlands and Eastern Highlands (Sparks & Stiassny 2022).

Nesocordulia mascarenica Fraser, 1948—White-tipped Knifetail

Figs 10, 15, 17–19

Etymology. A feminine adjective, of unknown origin, but probably after the Mascarene Islands. Fraser (1948) did not explain why he named a dragonfly from Madagascar after these islands (Mauritius, Réunion, Rodrigues) or their namesake, the Portuguese navigator Pedro de Mascarenhas. Unaware of the many dark species with pale appendages, Dijkstra & Cohen (2021) called this the “White-tipped Knifetail”.

Type material. Holotype male (NHMUK 012502442), Mandritsara (without further data), Sofia Region, Madagascar, leg. W. Janson. Fraser (1948) described an allotype female (MNHN), just labelled “Madagascar”, from René Martin’s collection, which must thus have been collected before 1921. This does not appear to be conspecific with the holotype (see section on unidentified specimens below).

Diagnosis. Rather small *Nesocordulia* species easily separated by the uniquely slender and almost straight cerci, as well as the hamule with its long posterior branch. The thoracic pattern of yellow spots, crossed supertriangles and wholly yellow genital lobe appear to be distinctive too. The short and down-turned, almost horizontal dorsal process (keel) on S10 is unlike in any other species except the otherwise very distinctive *N. flavicauda*.

Description. Holotype male. Total length 46.1, abdomen (excluding appendages) 31.4, Fw 32.2, Hw 32.3, Fw Pt 1.7, cerci 2.3. Fw Ax 12–13, Fw Px 8–9, Hw Ax 7, Hw Px 8–10. Colouration generally dark, black and metallic, with yellow pattern (Figs 10a,b).

Head. Face dark, metallic with a yellow centre (Fig. 10d). Vertex, frons and sides of postclypeus with metallic reflections: largely green, but also locally blue on vertex and postfrons, and copper on sides of frons and postclypeus (Figs 10b,d). Anteclypeus and central postclypeus yellow. Labrum glossy black (Fig. 10d). Labium ochre yellow. Occipital triangle black. Postgenae black.

Thorax. Synthorax largely metallic green and glossy black (with blue and copper reflections locally), with yellow spots (Fig. 10b). Middorsal carina brown. Mesepisternum metallic green with a brownish yellow spot in the anterolateral corner (Figs 10a,b). Yellowish spot on the mesokatepisternum. Synthoracic sides with four yellow spots in two lines (Figs 10b, 19). In the upper line, two quite large, elongated spots, the mesepimeral triangular spot with a slightly curved and blunt tip obliquely pointing dorsally, and the metepisternal spot, ribbon-like and bluntly pointing ventrally. In the lower line, two markings along the lower margin of synthorax, a small spot on the metakatepisternum below the metastigma and a long and broad (at most slightly incised) spot, stretched along the most of metepimeron and adjacent to the yellow poststernum.



FIGURE 10. *Nesocordulia mascarenica*, male. (a) habitus in dorsal view; (b) head, synthorax and S1–3 in lateral view; (c) abdomen in ventral view (its colour falsely reddish, in fact, it is yellow); (d) head in frontal view; (e) S7–10 and caudal appendages in lateral view. Photos by Bogusław Daraż.

Wings. Membrane hyaline. Pt very short, dark brown (Fig. 10a). Supertriangles crossed in all wings (Fig. 10a).

Abdomen. Black, with paired yellow pattern (Fig. 10a). The laterodorsal spots on each side of S2 are of similar size: the anterior spot broad, with tapered tip directed dorsally, and the posterior one oval (Fig. 10a). The lateroventral yellow spot on each side of S2 stretched along most of the segment's length; narrower anteriorly and broader posteriorly, distally covering the whole genital lobe (Fig. 10b). The laterodorsal yellow pattern on S3–6

consists of anterior stripes on all segments and posterior stripes on S3 only (Fig. 10a). S7 with a basal dorsolateral half-ring, covering one fifth of the segment's length and broadly divided along the black dorsal carina (Figs 10a,e). Along the ventral carina of S3–6, a pale yellow line broadened anteriorly on S3 only (Fig. 10c). On S7, the yellow ventral carina broadened brownish; on S8, ventral carina yellowish to brownish, with a large yellowish spot above; both broadenings on S7 and S8 visible in lateral view (Figs 10c,e). Dorsal process (keel) on S10 weakly defined, short (shortly pointed) and down-turned, almost horizontal (Fig. 10e).

Secondary genitalia. In lateral view, the hamule large, with a significantly longer posterior branch forming a quite long tip like a blunt claw curved towards the front (Figs 10b, 15). An adjacent anterior branch much smaller, nestled at the base of the posterior 'claw'. Genital lobe relatively short, directed obliquely posteriorly, and totally yellow, with ochre yellow hair-like setae (Figs 10b, 15).

Caudal appendages. Cerci fairly short and thin, creamy yellowish, with dark brown base (brownish shade up to one third of the length) and pale hair-like setae (Fig. 10e). In dorsal view, almost straight, slightly divergent in their distal half and not distended (Fig. 18). In lateral view, slightly arched up, with a blunt kink at two thirds of the lower edge, and with straight and gently tapering tips (Figs 10e, 17). Epiproct light brown, darkening towards the black tip, and fairly long, reaching three quarters of the cerci length (Figs 10e, 17).

Distribution. Known only from the type locality in northeastern Madagascar (Fig. 21). Since this site cannot be located precisely, it cannot be assigned to an ecoregion (possibly Madagascar Subhumid Forests, sensu One Earth 2024) or hydrographic ecoregion as both Northwestern Basins and Eastern Highlands (Sparks & Stiassny 2022) are possible.

Nesocordulia rubricauda Martin, 1900—Red-tailed Knifetail

Figs 11, 15, 17–19

Etymology. A feminine noun derived from Latin “*rubrus*”, red, and “*cauda*”, a tail, to emphasise the reddish brown abdomen.

Type material. The male in MNHN, designated as the lectotype by Legrand (1984), should be considered as the holotype by monotypy, being the only specimen examined by R. Martin when he introduced the new species. The specimen is only labelled “Madagascar”.

Diagnosis. Relatively large species, the second largest *Nesocordulia*, easily separated from all but one congener by its reddish brown body, brown wing bases, and dense venation, especially between the cubital and anal veins. Aside from the unique hamule and cerci (Figs 15 and 17–18, respectively), differs from *N. fossa* by the partly doubled cell rows subtended by Rspl in all wings and the absence of yellow markings on the clypeus and thorax as well as of black apical smudges laterally on S3–6.

Description. Holotype male. Possibly immature (pre-reproductive period), with colour pattern most probably fully developed, but not equally intense throughout. Total length 58.0, abdomen (excluding appendages) 40.3, Fw 42.2, Hw 41.1, Fw Pt 2.5, cerci 2.8. Fw Ax 15–16, Fw Px 13, Hw Ax 10–11, Hw Px 16–17. Colouration generally reddish brown, with metallic green thoracic stripes (Fig. 11).

Head. Face dark, in various shades of brown (Fig. 11f). Vertex, postfrons and central antefrons mostly darker reddish brown, and only locally with metallic greenish blue reflections. The rest of frontal shield warm brown (Figs 11a,f). Frons sides yellowish brown, with some admixture of metallic greenish golden reflections. Lower corners and margin of antefrons brown (Figs 11e,f). Clypeus dark brown (Fig. 11f). Labrum reddish brown with paler ochre brown centre (Fig. 11f). Occipital triangle light brown. Postgenae brown.

Thorax. Synthorax brown to reddish brown with three evenly distributed metallic stripes (green, blue and locally copper reflections): the fairly small and rather blue stripe on mesepisternum, along the middorsal carina, and two longer stripes in anterior parts of mesepimeron and metepimeron, with the darkest brown area in between (Fig. 11e). Synthorax lacking yellow spots. Legs two-toned, with basal parts (coxae, trochanters and large parts of femora) paler, ochre brown to reddish brown, and the rest dark brown to black (Fig. 11e).

Wings. Membrane amber brown basally: the darkened wing base larger in Fw, reaching farthest in costal and subcostal space (at level of Ax2 in Fw and Ax1 in Hw), and closest in median space in Fw or median and cubital space in Hw (Figs 11a,d). Apart from the base, membrane clear, without any trace of brownish tint. Pt medium-sized, pale, yellowish buffy (immature?). Venation (Fig. 11a): (a) row between the cubital and anal veins in Hw with

6–7 cells doubled (even tripled or quadrupled distally); (b) row between R4 and the median vein in Hw with 3–4 cells doubled; (c) row subtended by Rspl in all wings with 3–7 cells doubled. Membranula pale buffy to white.



FIGURE 11. *Nesocordulia rubricauda*, male. (a) habitus in dorsal view; (b) abdomen in lateral view; (c) terminalia in dorsolateral view; (d) head, thorax and abdomen in dorsal view; (e) head, thorax and S1–2 in lateral view; (f) head in frontal view. Photos by Bogusław Daraż.

Abdomen. Reddish brown, the most intensively on S7–S9, with four black rings of posterior field of tergites from S3–6; additionally, only an indistinct darkish ‘nail’ there on S2, and a thin dark posterior margin of S7 (Figs

11b,d). On S3–6, no black triangular smudges bordering the posterior black rings. No yellow abdominal pattern, only yellow-ochre tint on S4–6 locally (in their anterolateral regions), like faint remnants of anterior stripes typical of black *Nesocordulia* species (Figs 11b,d). These segments in dorsal view three-tone brown: yellowish brown anteriorly, further rich reddish brown, and terminally dark reddish brown.

Secondary genitalia. In lateral view, branches of hamule separated by deep and wide gap, with the posterior branch fairly narrow and pressed against the genital lobe, and the anterior branch broad and bent down subapically, with beak-like tip (Figs 11e, 15). Genital lobe relatively long, bluntly triangular, directed downwards, reddish brown with rusty ochre hair-like setae (Figs 11e, 15).

Caudal appendages. Cerci fairly long, reddish brown, similar to abdominal colouration (Fig. 11c). In dorsal view, rather straight at base and diverging gradually in distal half, with apices pointing outwards and bluntly tapered (Figs 11c, 18). In lateral view, shallowly arched up, with a blunt kink at 60% of the lower edge, and further with straight and tapering tips (Figs 11b, 17). The lower margin of cerci rather uneven with two greater protrusions: the thickened kink mentioned above and a distinct bulge near their base. Epiproct reddish brown and fairly long, reaching 80% of the cerci length (Figs 11b,c, 17).

Female, distribution and ecology unknown.

Nesocordulia spinicauda Martin, 1902—Pincer-tipped Knifetail

Figs 12, 15, 17–19

Etymology. A feminine noun derived from Latin “cauda”, a tail, and “spina”, a thorn or spine, probably describing the spinelike dorsal process on S10. Dijkstra & Cohen (2021) followed the scientific name in calling the species “Spine-tailed Knifetail”. As the spinelike keel on S10 is found in all *Nesocordulia* males, a new common name recognising the uniquely shaped appendages is proposed above.

Type material. Two males and three females (MNHN), lectotype male and four paralectotypes designated by Legrand (1984); Fort-Dauphin (present Tôlanaro), Anosy Region, Madagascar, leg. Charles Alluaud, January of 1901, the year not given in the original description, but deduced from details known of the expedition (Jeannel 1952).

Diagnosis. Medium-sized *Nesocordulia* species, unique among the black-tailed species by its comparatively long (relative to both abdomen and epiproct) and forcipate cerci, sharply pointed genital lobe, and narrow dorsal yellow markings on S8. By contrast, the undivided hamule has rather a simple form. The markings on the synthorax are similar only to those of *N. lyricauda*, which however also differs by its greater size, distinctive divided hamule (Fig. 15), and both shape and size of basal yellow spots on S7.

Description. All specimens, 124 years ‘old’, preserved at most in a moderate state, with damaged or partly damaged male appendages and partly faded or darkened yellow pattern.

Lectotype male. Total length 52.2, abdomen (excluding appendages) 36.2, Fw 36.5, Hw 35.3, Fw Pt 2.1, cerci 3.5. Fw Ax 11–12, Fw Px 8, Hw Ax 7–8, Hw Px 9. Colouration generally dark, black and metallic, with yellow pattern (Fig. 12).

Head. Face dark, largely metallic, with a yellow slightly trapezoidal centre (Fig. 12c). Vertex metallic blue and violet. Frons with brown background (visible in frontal shield), largely with metallic reflections (green, blue, violet, copper and bronze) (Fig. 12c). Postclypeus broadly yellow centrally with metallic green sides. Anteclypeus yellow (Fig. 12c). Labrum dark, glossy black and bronze (Fig. 12c). Labium yellow (Fig. 12a). Occipital triangle black. Postgenae black.

Thorax. Synthorax largely with metallic reflections, mostly green and blue and locally dark bronze and copper, and with large yellow spots (Figs 12a,b). Mesepisternum with metallic green and blue reflections and yellowish brown anterolateral corner. Mesokatepisternum brown. Three yellow spots on synthoracic sides: (a) a single upper stripe on mesepimeron and metepisternum, long, narrow and kinked; (b) a small spot on the metakatepisternum below the metastigma; and (c) a long and wide rectangular marking covering the posterior half of metepimeron and adjacent to the yellow poststernum (Figs 12a,b, 19).

Wings. Membrane not tinted yellowish, at most a trace at the Hw base. Pt short, brown.



FIGURE 12. *Nesocordulia spinicauda*. (a) male habitus in lateral view; (b) male synthorax in lateral view; (c) male head in frontal view; (d) male hamule and genital lobe in lateral view; (e) male S7–9 in dorsal view; (f) male S7–9 in ventral view; (g) female habitus in dorsolateral view; (h) female head and synthorax in lateral view; (i) female left wings. Photos by Bogusław Daraż.

Abdomen. Black with paired yellow pattern. The laterodorsal spots on each side of S2 are of different shape and size: the anterior patch broad, with tapered tip directed dorsally, and the posterior one small, angular, directed obliquely ventrally. The broad yellow lateroventral spot on each side of S2 stretched along the whole segment and

penetrating the genital lobe, with a dorsal black ‘bay’ below an auricle (Fig. 12d). The laterodorsal paired yellow pattern on S3–6 consists of anterior stripes on each segment and posterior stripes on S3 only. S7 with two basal laterodorsal yellow spots, broadly diverged dorsally and fairly small, covering one fifth of the segment’s length and not reaching far laterally (at most to the segment’s half-height) (Fig. 12e). S8 with two very narrow transverse yellow spots at the base (Fig. 12e). The pale pattern along the ventral carina (yellow to brownish yellow, partly faded/darkened): (a) on S3–7, a line, broadened anteriorly on S3 only, on S7 without any adjacent spot; (b) on S8, a large irregularly triangular spot, the broadest in its anterior half (Fig. 12f); (c) on S9, an anterior broad spot; spots on S8–9 visible in lateral view (Fig. 12a).

Secondary genitalia. In lateral view, the hamule not divided into branches, rectangular, with wavy anterior margin and rounded tips (Figs 12d, 15). Genital lobe exceeding the hamule tip and strongly narrowed terminally, spine-like, with a bent posterior margin thus pointing obliquely posteriorly (Figs 12d, 15); largely dark (brown to black) with a yellow posterobasal area and yellowish ochre hair-like setae.

Caudal appendages. Cerci long and fairly narrow, creamy yellow, basally brown, with brownish shade up to a quarter of the length (Fig. 12a). In dorsal view, arched outwards in their distal half with tips pointing inwards, thus resembling carpenter pincers (Fig. 18), but their arch is more gentle in comparison with the original tool, and also with the cerci illustrated in Fraser (1956). In lateral view, straight, with a strong, wide ventral tooth at 40% of their length and with a tip bent and pointing ventrally (Figs 12a, 17). Epiproct creamy yellow, basally brownish, and short, reaching half of the cerci length (Figs 12a, 17).

Variation in males. The paralectotype is smaller, total length 49.5, abdomen (excluding appendages) 35.1, Fw 34.9, Hw 33.4, Fw Pt 2.0, cerci 3.3. Fw Ax 11, Fw Px 7–8, Hw Ax 8, Hw Px 7–8. The colour pattern almost the same, only the posterior laterodorsal spot on S2 larger, of similar size as the anterior one.

Paralectotypes females. Total length 47.6–49.9, abdomen (excluding appendages) 34.4–36.9, Fw 36.4–37.0, Hw 33.2–35.1, Fw Pt 2.4–2.5, cerci 2.1–2.2. Fw Ax 11–13, Fw Px 7–8, Hw Ax 7–8, Hw Px 8–10. The female colour pattern very similar to that of the males (Fig. 12h) with the following minor differences: (a) abdominal paired yellow pattern on S3–6 complete, although posterior stripes on S5–6 very short in two females (Fig. 12g), and in one female a small posterior spot even on S7; (b) basal laterodorsal spots on S7 longer than wide, slightly trapezoidal (Fig. 12g); (c) broad wing bases tinted with bright yellow to Ax3, including supertriangles in Fw and triangles in Hw (Fig. 12i). Cerci relatively long (2.1–2.2), creamy yellowish (possibly whiter in live) (Fig. 12g).

Distribution. Known only from Tôlanaro in southeastern Madagascar (Fig. 21) in the ecoregion of Madagascar Humid Forests (One Earth 2024) and the hydrographic ecoregion of Eastern Lowlands (Sparks & Stiassny 2022).

Nesocordulia villiersi Legrand, 1984—Comoro Knifetail

Figs 13, 15, 17–19

Etymology. A noun in genitive singular dedicated to André Villiers, the French specialist of Afrotropical bugs and longhorn beetles who animated the new series of *Revue Française d’Entomologie*.

Type material. The holotype male (MNHN), Lac Iconi, Mohéli (Mwali) Island, Comoros, 11.1955, leg. A. Robinson. Iconi is a small watercourse and settlement (present name: Hamavouna), close to Dziani Boundouni Lake. As there are no other lakes nearby, this is probably the same lake as Lac Iconi.

Diagnosis. Rather small species (the second smallest *Nesocordulia*), uniquely occurring on the Comoros, but that is also distinct by its apically clubbed cerci, two-toned brown labium, and subtly different thoracic markings. Hamule similar to that of *N. coloratissima* (especially in lateral view) and *N. evanida* (in ventral view), albeit differing in the proportions and shapes of its anterior and posterior branches and the incision between them.

Description. Holotype male. Total length 45.1, abdomen (excluding appendages) 29.8, Fw 31.2, Hw 29.8, Fw Pt 1.9, cerci 2.1. Fw Ax 12, Fw Px 8, Hw Ax 6–7, Hw Px 11. Colouration generally black, dark brown and metallic, with yellow pattern (Fig. 13).

Head. Face dark, brown to black, partly with metallic reflections, and with a yellow centre (Fig. 13d). Vertex and postfrons metallic green and violet (Figs 13a,d). Frontal shield dark bronze with violet reflections (Fig. 13d). Frons sides mostly melanised with metallic green reflections, but centrally translucent dark yellow. Labrum glossy black (Fig. 13d). Labium two-tone brown, darker centrally, along the inner borders of lateral lobes (Fig. 13e). Occipital triangle black. Postgenae black.

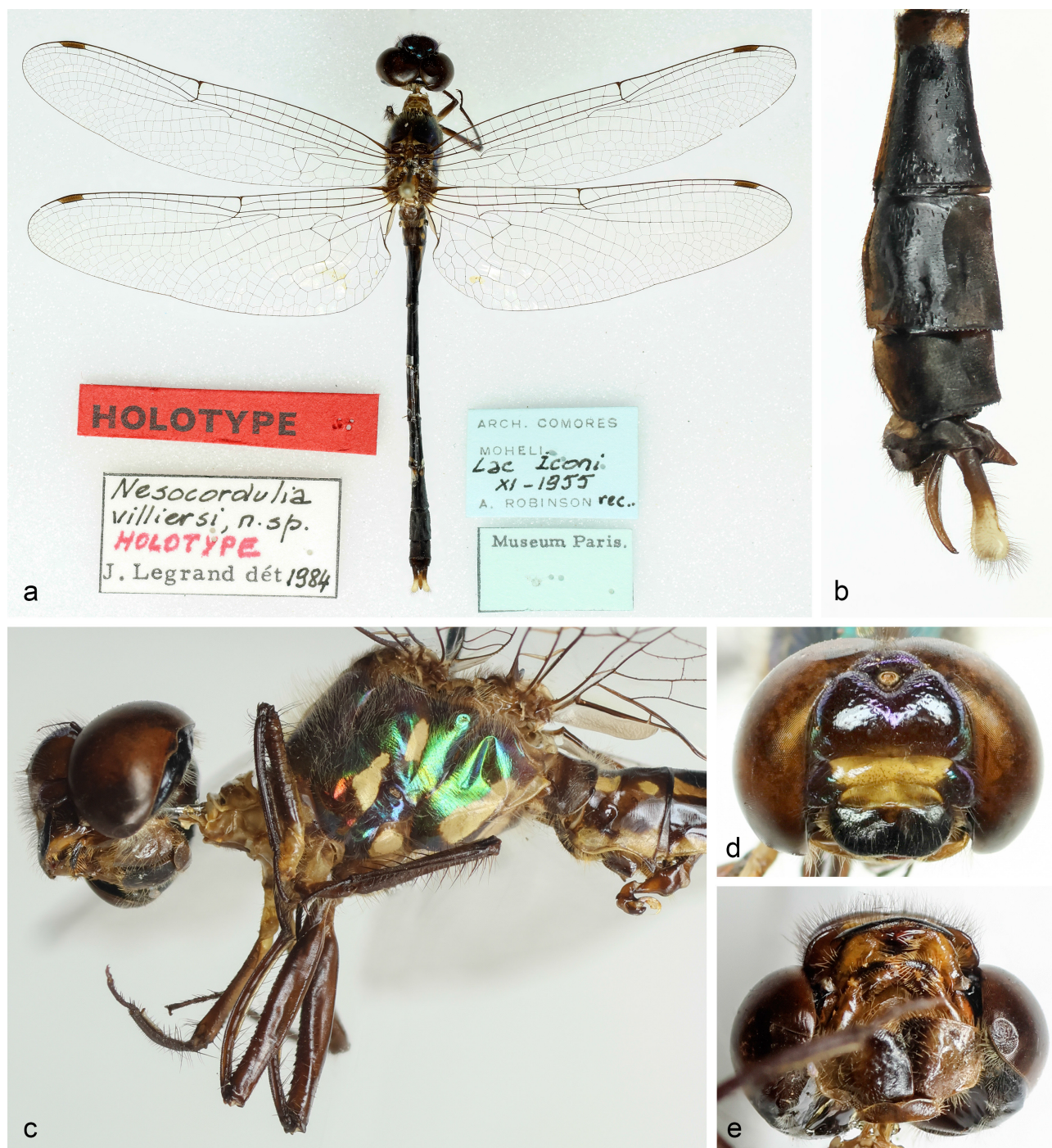


FIGURE 13. *Nesocordulia villiersi*, male. (a) habitus in dorsal view; (b) S7–10 and caudal appendages in lateral view; (c) synthorax and S1–2 in lateral view; (d) head in frontal view; (e) head in ventral view. Photos by Bogusław Daraż.

Thorax. Synthorax largely dark purplish-brown and metallic, with mostly green and blue, and locally copper reflections (Fig. 13c). The whole mesepisternum melanised, metallic blue and green. Mesokatepisternum dark purplish-brown with a small yellow spot. Synthoracic sides with four pale yellow spots in two lines (Figs 13c, 19). In the upper line, a quite large mesepimeral spot, irregularly triangular and pointing dorsally, and the uppermost smaller metepisternal spot, bullet-like and also pointing dorsally. In the lower line, two markings along the lower margin of the synthorax: a small spot on the metakatepisternum, below the metastigma, and a much larger and oblong spot, situated centrally in the posterior half of metepimeron and almost adjacent to the yellow poststernum. Legs mostly chocolate brown (Fig. 13c).

Wings. Membrane hyaline. Pt short, brown (Fig. 13a).

Abdomen. Black and basally dark brown, with paired yellow pattern. The laterodorsal spots on each side of S2 small: the anterior spot rectangular, with tapered tip directed dorsally, and the posterior one oval (Fig. 13c). The lateroventral yellow spot on each side of S2 stretched along the whole segment's length, broader posteriorly (Fig. 13c). The laterodorsal yellow pattern on S3–6 reduced and consisting of anterior stripes on S3 and S4 (narrow), and posterior narrow stripes on S3 only. Two basal laterodorsal yellow spots on S7 roundish and small, covering at most one fifth of the segment's length (Fig. 13b) and broadly diverged along the dorsal carina. Pattern along the ventral carina: (a) on S3–5, an indistinct yellowish brown line, broadened yellow anteriorly on S3 only; (b) on S6–7, the pattern indiscernible; (c) on S8–9, a broad brownish stripe with yellow spots, on S8 in its central and posterior sections, on S9 in its anterior section; on both segments spots visible in lateral view.

Secondary genitalia. In lateral view, the hamule with a shallow and wide, rectangular apical incision between the anterior and posterior branch, the former being short and blunt and the latter slightly longer, much broader and bluntly rounded apically (Figs 13c, 15). In ventral view, the inner lobe of the anterior branch broadly rounded inwards and the posterior external branch twisted inwards and visible as a roundish finger-like projection (see Fig. 2 in Legrand 1984). Genital lobe bluntly triangular, pointing obliquely downwards, with yellowish ochre hair-like setae (Fig. 15).

Caudal appendages. Cerci fairly short, bicoloured, brown in basal half and creamy white in distal half, with buffy greyish hair-like setae (Fig. 13b). In dorsal view, gently arched inwards, with distended tips (Figs 13a, 18). In lateral view, almost straight and apically swollen in a rounded 'head' (Figs 13b, 17); a small lateroventral bulge discernible at a quarter of the length. Epiproct warm brown, long, reaching 95% of the cerci length (Figs 13b, 17).

Female. Unknown.

Distribution. Only known from the type locality on the Comoros, somewhere between the coastal lowlands and hills of southeastern Mohéli, i.e. about 450 km from Madagascar (Fig. 21).

Unidentified specimens of *Nesocordulia*

Several specimens from museum collections and photographs cannot be identified to species with certainty at present (Fig. 14); some of them may represent unnamed species.

Nesocordulia coloratissima?

(Figs 14a–d)

Female (NHMUK), Ankara-fansitra (locality not traced, could be Ankarafantsika), 09.01.1950, leg. A. R. While labelled as *N. rubricauda*, the colouration of Pt (Fig. 14a), frons, labrum (Fig. 14d), labium, and occipital triangle match *N. coloratissima* **sp. nov.**, as does that of the synthorax, the two distinctive triangular yellow spots (Fig. 14c) being found in one of that species' paratype males too. The characteristic yellow basal spot on S7 of *N. coloratissima* is absent, however (Figs 14a,b), being replaced with reddish brown, and the cerci are darker yellow, although both do appear paler than the areas in between. These features may have lost their contrast in preservation or be masked by darker pigmentation. The female could also represent a variety of *N. coloratissima* or a closely similar species, especially if it is indeed from Ankarafantsika National Park, which is also in the drier west of Madagascar but over 450 km north of where that species has been recorded. Total length 47.4, abdomen (excluding appendages) 34.0, Fw 33.7, Hw 32.1, Fw Pt 2.4, cerci 0.9. Fw Ax 11–12, Fw Px 8–9, Hw Ax 7, Hw Px 10.

Nesocordulia mascarenica?

(Figs 14e–h)

Female with no other collection details than 'Madagascar' in MNHN. Although still complete when studied by Fraser (1948) and designated as allotype of *N. mascarenica*, this female is now in poor condition, lacking S6–10. Fraser found that the specimen matched the male holotype in NHMUK, but at least the following features do not correspond with it: (a) Pt (Fig. 14g) 0.7–1 mm longer, length 2.4–2.7 mm versus 1.7 mm in the male, while typically it is just as long in females as in males (three known species of *Nesocordulia*) or at most 0.4 mm longer (two species); (b) supertriangles not crossed in all wings (Fig. 14e) versus crossed in the male; (c) two metepimeral spots

(larger and smaller) (Fig. 14f) versus one large spot in the male, while in other species the number of spots is the same in both sexes (except *N. evanida*, however, where female has one spot versus males' two); (d) the metepisternal spot (Fig. 14f) of different shape and not arched as in the male, while in this genus, the shape of this spot is largely similar in both sexes; (e) upper sides of femora dark chocolate brown (Fig. 14f) versus black in the male, while the dark colours of female legs follow those of the male ones in *Nesocordulia*. Although these differences seem to rule *N. mascarenica* out, this combination of features does not correspond to any other named species either. Thus, an unnamed species may also be considered. Fw length 37.4, Hw length 36.8, Fw Pt 2.4–2.7. Fw Ax 13, Fw Px 8–10, Hw Ax 8, Hw Px 10–12.



FIGURE 14. Four females of *Nesocordulia* that cannot be identified. (a–d) possible *N. coloratissima* **sp. nov.** in NHMUK; (e–h) doubtful *N. mascarenica* described by Fraser (1956) in MNHN; (i) possible *N. mascarenica* from Masoala National Park; (j) possible *N. spinicauda* from the Palmarium Reserve. Photos by: a–h, Bogusław Daraż; i, Callan Cohen; j, Michiel Van de Velde.

Nesocordulia mascarenica?

(Fig. 14i)

Photographic record. Female, 15.7029° S, 49.9619° E, Masoala National Park, Analanjirofo Region, northeastern Madagascar, 13.12.2013, photo by Callan Cohen. The short brown Pt and yellow markings (particularly on upper synthorax and S5–7) are suggestive of *N. mascarenica*, but other features are not visible.

Nesocordulia spinicauda?

(Fig. 14j)

Photographic record. Female, Palmarium Reserve, 18.606° S, 49.2118° E, Atsinanana Region, central-eastern Madagascar, 08.12.2023, photo by Michiel Van de Velde: <https://www.inaturalist.org/observations/194048870> (also photographed and submitted without details by Yenthe Van Puyenbroeck: <https://www.inaturalist.org/observations/247478087>). The long cerci and the shape of the yellow spots on S7 and on the synthorax (the latter poorly visible) suggest *N. spinicauda*, but that species' diagnostic yellow markings on S8 are not apparent, while other informative features are not visible.

Nesocordulia sp. (not illustrated)

Photographic record. Male (in flight), 21.2301° S, 47.4013° E, Ranomafana National Park, Vatovavy Region, central-eastern Madagascar, 02.12.2013, photo by Callan Cohen. The number and size of thoracic yellow spots recall *N. evanida*. Their form differs slightly, however, while other features are not visible or unclear due to motion blur.

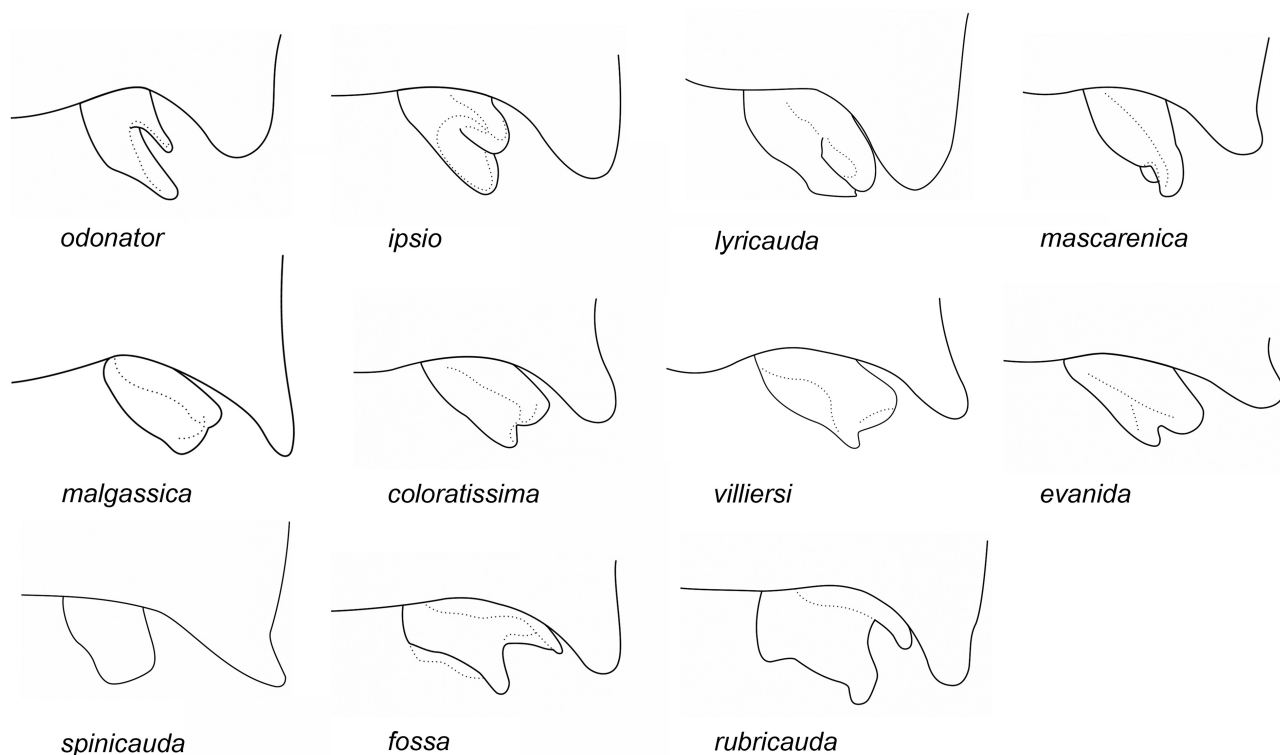


FIGURE 15. Lateral view of hamule and genital lobe of all species of *Nesocordulia* except *N. flavicauda*. Arranged according to similar form to aid comparison. Due to the poor quality of the available material, the actual shape of the *N. malgassica* hamule may differ in detail.



FIGURE 16. Secondary genitalia in ventral view of the six new species of *Nesocordulia*: (a) *N. coloratissima*, (b) *N. evanida*, (c) *N. lyricauda* (only right side recognisable, the left one damaged), (d) *N. odonator*, (e) *N. ipsio*, and (f) *N. fossa*. Arranged vertically (head upwards) to aid comparison. Photos by Bogusław Daraż.

Key to males of *Nesocordulia*

The key is to males only, as females are available for only half of the twelve species. Caution is advised, moreover, as for six of the species characters are based on single specimens.

- 1 Abdomen largely reddish brown, without distinct yellow markings. Cerci and epiproct reddish brown, similar to abdominal colouration. Wing membrane with brown markings at base. Branches of hamule separated by deep and wide gap, with posterior branch pressed against genital lobe. Venation dense; 15–16 Ax in Fw; row between cubital and anal veins in Hw with 5–8 cells doubled (to multiplied) **2**
- Abdomen at least partly black with contrasting yellow markings. Cerci at least on tips white to yellowish, contrasting with darker abdomen, in some species epiproct paler too. At base, wing membrane hyaline or at most tinted with yellow. Branches of hamule, if recognisable, closely apposed, with only slight or, if deep, narrow incision between them. Venation more open; 10–13 Ax in Fw, rarely up to 15; single row of cells between cubital and anal veins in Hw, with at most 2 cells doubled . . . **3**
- 2 (1) Clypeus all brown. Thorax without distinct yellow markings. S3–6 entirely reddish brown except for the black posterior field of tergites forming contrasting rings. Anterior branch of the hamule broad and bent down subapically, with beak-like tip. Cerci in dorsal view rather straight at base and diverging gradually in distal half. Rspl subtending doubled cell row for 3–7 cells . . . *N. rubricauda* **Martin, 1900**
- Clypeus yellow at centre. Thoracic mesepimeron and metepimeron each with yellow spot contrasting with surrounding darker colouration. S3–6 each with a triangular black posterolateral smudge bordering the posterior black rings. Anterior branch of the hamule tapered distally into a triangular and unbent tip. Cerci in dorsal view with arched base and out-curved tips, thus appearing sinusoidal or lyre-shaped. Rspl subtending single row of cells *N. fossa* **sp. nov.**

- 3 (1) Each of S7–10 largely yellow dorsally, only marked distally with black. Ventrolateral side of fore femora dark with contrasting yellow spot at about mid-length. Postclypeus entirely dark and glossy. Postgenae brown with contrasting yellow markings. Cerci ventrally at about third of their length from base with distinct downward spine. Anterior laterodorsal spots on S2 evenly narrow and arched. *N. flavicauda* McLachlan, 1882
- Each of S7–10 largely black or reddish brown dorsally, at most with yellow markings basally on S7–8. Ventrolateral side of fore femora with some yellow extending from their base. Postclypeus with broad yellow centre. Postgenae wholly black. Cerci ventrally smooth, without downward spine. Anterior laterodorsal spots on S2 broad, typically narrowing distally into a curved point. 4
- 4 (3) Poststernum dark brown, like the thoracic background. Epiproct dark brown to black. Lower yellow spot on metepimeron small, much less than half as long as posterior border of metepimeron and not reaching poststernum. Lateroventral yellow marking on S2 divided into two small well-separated spots. Lateral lobes of labium two-coloured, yellow with contrasting blackish markings. Wing membrane tinted with yellow at base. 5
- Poststernum predominantly yellow, like the thoracic spots. Epiproct largely white, yellow or pale brown. Lower yellow spot on metepimeron large, at least half as long as posterior border of metepimeron and reaching poststernum. Lateroventral marking on S2 single and large, at most narrowed. Lateral lobes of labium yellow, at most with faint dark smudges; brown in the Comoros. Wing membrane hyaline at base. 6
- 5 (4) Both branches of hamule broad and rounded, ear-like. Labium with lateral lobes largely blackish brown, only narrowly yellow on outer borders, like crescents. Basal two-thirds (up to 80%) of cerci dark, their pale tips covered with contrasting dark hair-like setae. Total length about 47 mm, Hw 33–34 mm. *N. ipsio* sp. nov.
- Both branches of hamule distinctly narrowed and pointed, like fingers. Labium with lateral lobes largely yellow, only narrowly dark along their inner borders. Basal third (up to 40%) of cerci dark only, remainder yellowish white covered mostly with similarly pale hair-like setae. Total length about 54 mm, Hw 37 mm. *N. odorator* sp. nov.
- 6 (4) Cerci broadest apically, with clearly swollen tips, appearing clubbed. Labium brown, distinctly darker centrally. Only known from Mohéli, Comoros. *N. villiersi* Legrand, 1984
- Cerci not distended apically, even if broadest subapically, always gradually tapering towards apices. Labium pale (yellow, ochre yellow), at most with faint darker smudges. Only on Madagascar. 7
- 7 (6) S8 black with pair of narrow dorsolateral yellow spots at base. Cerci angled at 40% of their length from base with a broad downward tooth (visible in lateral view) and with down- and in-curved tips, like an earwig's forceps in dorsal view. Epiproct reaches about halfway cerci. Genital lobe pointed. *N. spinicauda* Martin, 1902
- S8 entirely black or reddish brown. Cerci without a strong ventral tooth and gradually curving outwards distally. Epiproct reaches at least two-thirds of the cerci length. Genital lobe rounded. 8
- 8 (7) Cerci in dorsal view sinusoidal, with arched base and out-curved tips, recalling a Roman lyre. Basal yellow spot on S7 extends dorsally beyond the supplementary transverse carina and also extends laterally, merging with the yellowish markings on the ventral carina. Mesepimeron and metepisternum marked with a single narrow and kinked yellow stripe. Total length 58–60 mm, Hw 40–41 mm, Fw Ax 13–15, Fw Px 11–13, Hw Px 13–14. *N. lyricauda* sp. nov.
- Cerci in dorsal view diverging gradually, rather straight at base. Basal spot on S7 more limited, not extending beyond the supplementary transverse carina and not reaching the yellowish markings on the ventral carina, or spot is absent. Mesepimeron and metepisternum with two distinct spots, which may be fused into one broad irregular marking. Total length 43–53 mm, Hw 28–35 mm, Fw Ax 10–13, Fw Px 7–10, Hw Px 7–11. 9
- 9 (8) S7–10 mostly reddish brown, contrasting with black remainder of abdomen. 10
- S7–10 mostly black, like rest of abdomen. 11
- 10 (9) S7 dorsally reddish brown with large basal yellow spot (may be absent locally). Mesepimeron and metepisternum marked with single large, broad and irregular yellow spot, sometimes narrowly divided into two spots. Metepimeron with single long yellow marking. Occipital triangle yellow. Frons laterally pure yellow. Labrum with extensively yellow centre. In dorsal view, cerci fairly thick, basally converging and then diverging, with inner margin slightly angled near base. *N. coloratissima* sp. nov.
- S7 uniformly reddish brown. Mesepimeron and metepisternum with two broadly separated spots. Metepimeron with two distinct yellow spots. Occipital triangle black. Frons laterally dark metallic (at most partly yellowish brown). Labrum with two small yellow spots at base. In dorsal view, cerci more slender, basally straight and while diverging for distal half subtly converging at extreme tips, with smooth inner margin. *N. malgassica* Fraser, 1956
- 11 (9) Dorsal process (keel) on S10 long and rather erect. Supertriangles free of cross-veins. Metepimeron with two small and widely separated yellow spots. Yellow spot at base of S7 continuous across dorsal carina. In lateral view, posterior branch of hamule broader but not much longer than anterior branch. At least tip of genital lobe black. In dorsal view, cerci slightly arched inwards and relatively thick with slightly distended distal half. *N. evanida* sp. nov.
- Dorsal process (keel) on S10 short and almost horizontal, directed posteriorly. Supertriangles crossed in all wings. Metepimeron with one large (at most slightly incised) yellow spot. Yellow spot at base of S7 interrupted by black on dorsal carina. In lateral view, posterior branch of hamule much longer than anterior branch. Genital lobe completely yellow. In dorsal view, cerci almost straight, thin, and not distended. *N. mascarenica* Fraser, 1948

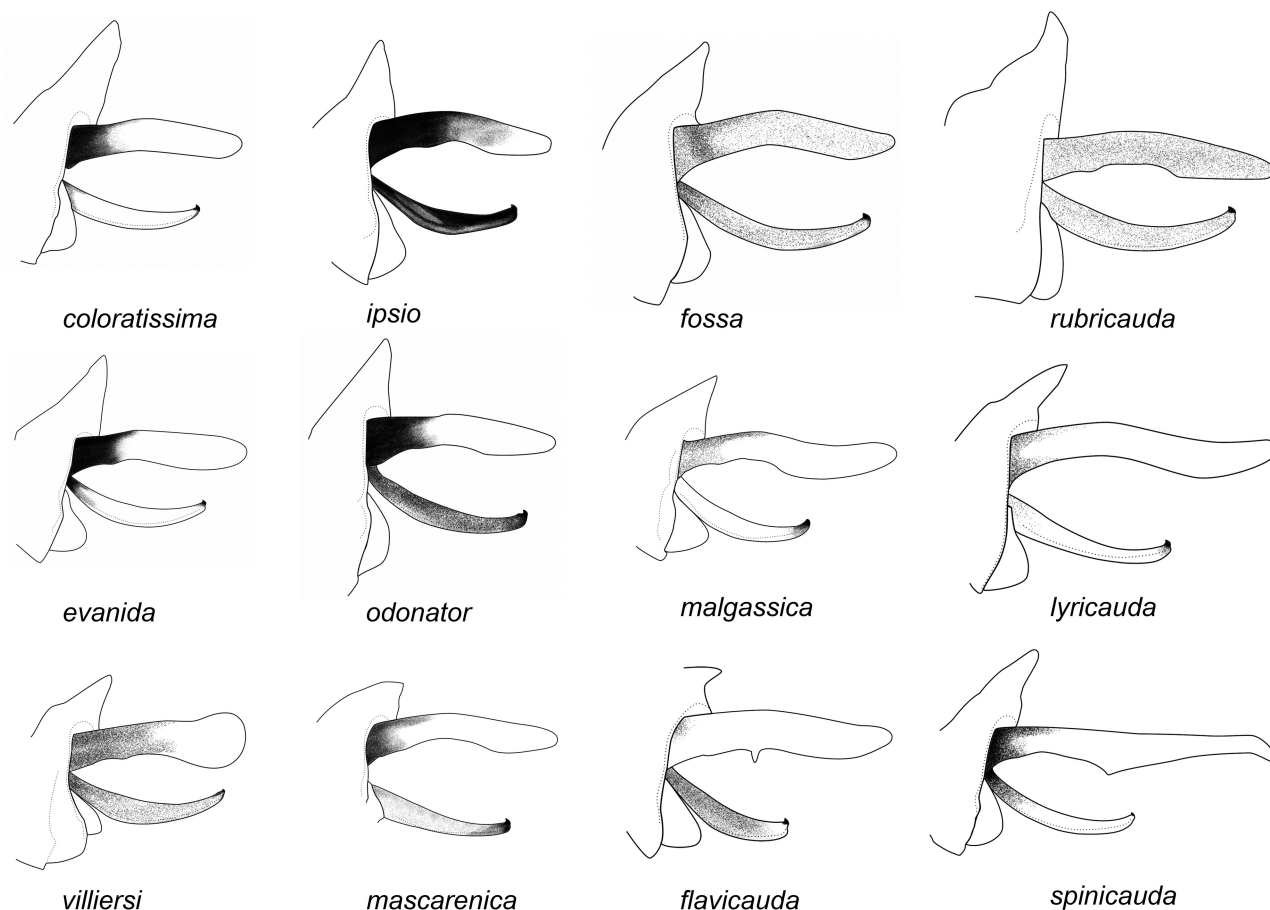


FIGURE 17. Lateral view of caudal appendages of all known species of *Nesocordulia*. Showed to scale. Hair-like setae not illustrated. Arranged according to similar form and size to aid comparison.

Discussion

Distribution. Knowledge of the genus' distribution remains exceptionally poor. Only 29 records of imagines (i.e., a species per locality per day) were obtained, with the species identity confirmed for 22. These pertain to as many as twelve species, but locality details were clear for only nine of them (Fig. 21). Consequently, few biogeographical conclusions can be drawn. The high diversity (currently almost every second record is a new species) and the wide scatter of the species across the island might suggest some regional endemism. As many taxonomic groups show, Madagascar provides exceptional circumstances for micro-endemism (Goodman & Benstead 2005; Wilmé *et al.* 2006), although endemism at such a limited spatial scale seems improbable for taxa with greater dispersal abilities as dragonflies. Nonetheless, even the three species with at least two quite distant records seem restricted to specific regions on the island, with *N. coloratissima* in the west of the island only, *N. evanida* in the northeast, and *N. malgassica* in the central east (Fig. 21). Even if possible records of *N. mascarenica* and *N. spinicauda* females (see above) prove to be correct, these species may also have rather restricted ranges, being limited to the northeast and eastern coast respectively.

Most *Nesocordulia* species occur in the east of the island, while only *N. coloratissima* is confirmed to occur in, and probably limited to, the west. The disproportionate richness of the wetter east and north-west relative to the drier west is typical of Madagascar, the former having many more endemic species in numerous groups, especially those dependent on water, including the five damselfly radiations (Dijkstra & Cohen 2021; Dijkstra 2022), mayflies (Elouard *et al.* 2022), freshwater shrimps (Short 2022), and amphibians (Vences *et al.* 2022).

Morphological diversity and species relationships. The twelve known species are very well-defined, with no doubt as to the species identity of each of them. Male sexual characters, notably the shape and colour of the cerci

(Figs 17–18) and the shape and size of the hamule (Figs 15–16), are most informative. Colouration is also diagnostic, especially the pattern of yellow markings on the synthorax (Fig. 19). The background colour as well as markings on the labium, S2, S7, and S8 are also useful to separate some species or small groups of them. While Fraser (1956) considered the yellow markings on S3–6 important, those proved to be variable and thus taxonomically not informative.

The colour differences appear to largely apply to females too. As in the presumably related genera *Idomacromia* and *Syncordulia* (Dijkstra & Kisakye 2004; Dijkstra *et al.* 2007), marked differences in female sexual characters (especially subgenital plate) were also noted (Fig. 20), although this could only be examined in the recently collected species, *N. coloratissima*, *N. evanida* and *N. ipsio*.

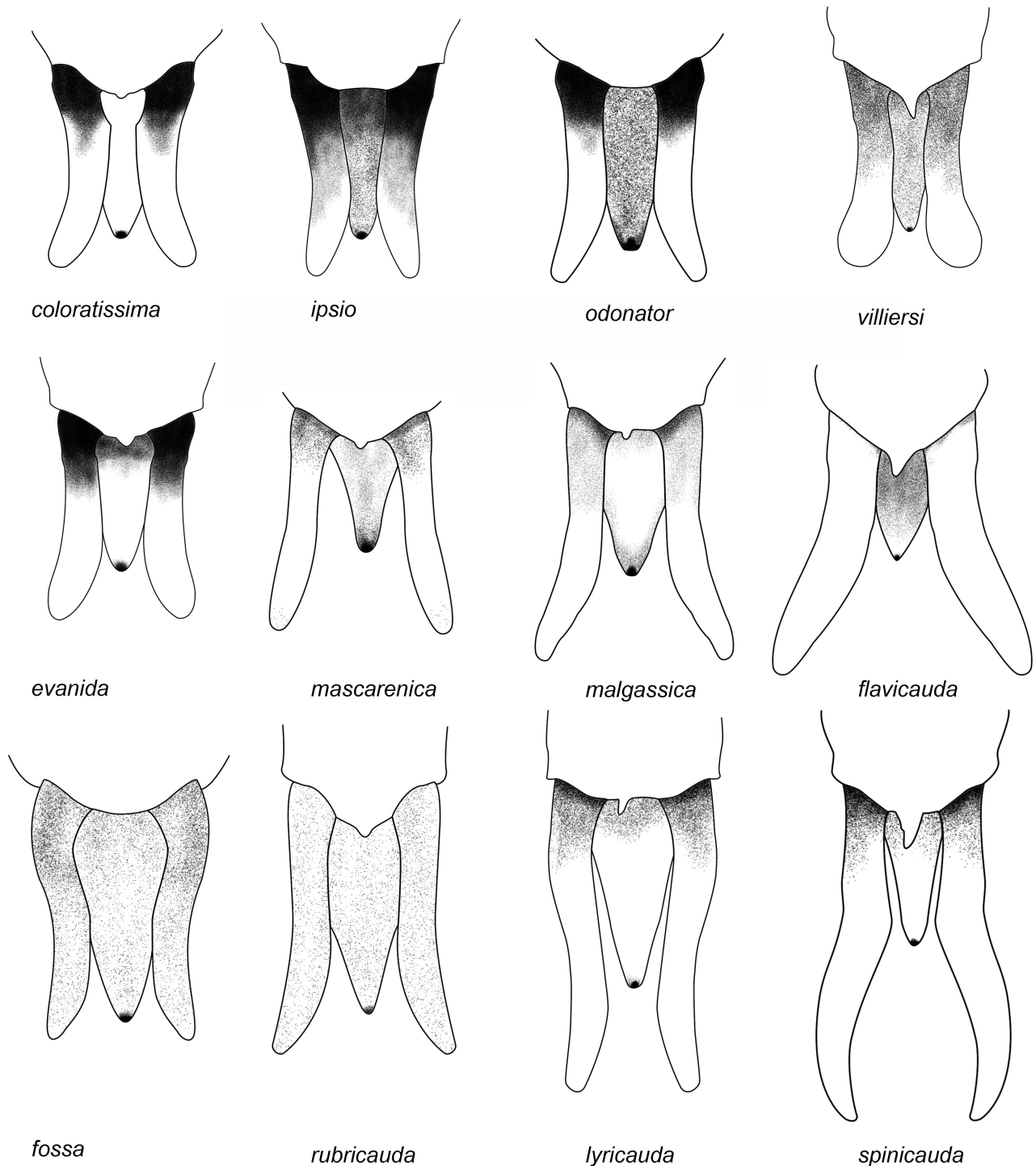


FIGURE 18. Dorsal view of caudal appendages of all known species of *Nesocordulia*. Shown to scale. Hair-like setae not illustrated. Arranged according to similar form and size to aid comparison.

Because the species are so distinct and molecular data are lacking, it is impossible to say much about relationships and delimit species-groups. Based on their morphology, we suspect that *N. coloratissima*, *N. evanida* and *N. malgassica* are quite close, while *N. villiersi* and *N. mascarenica* seem to be close to them too in some features but more distant in others. *Nesocordulia ipsio* and *N. odonator* probably form a species-pair. So do *N. fossa* and *N. rubricauda*, but their unique appearance, hamule and dense venation suggest they are rather distinct from all other species. Although *N. lyricauda* and *N. spinicauda* seem rather similar, their very different hamules suggest they are not closely related and other species may be more related. *N. flavicauda*, finally, is probably the most distinct species of all.

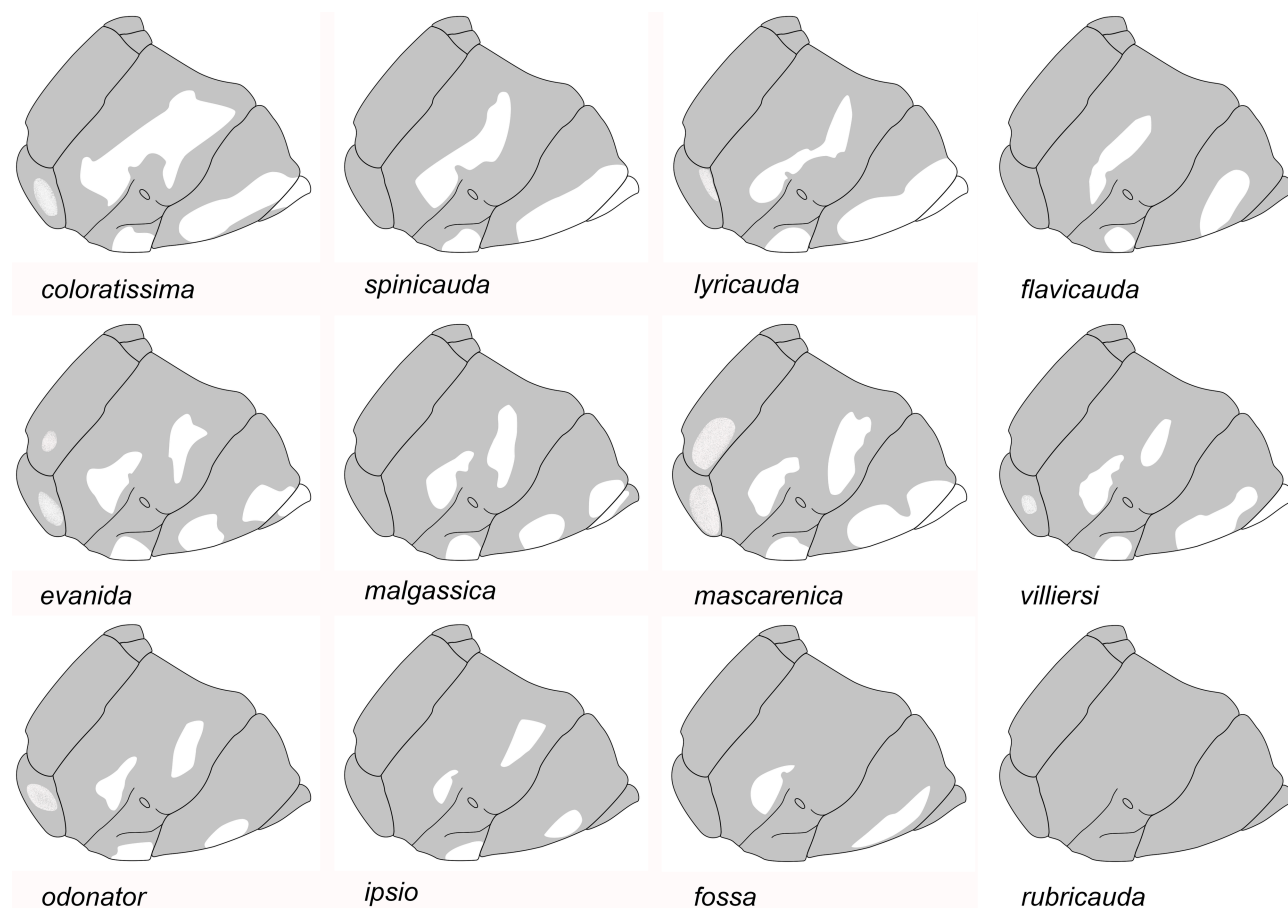


FIGURE 19. Lateral view of synthorax of all known species of *Nesocordulia*. Arranged by extent and form of clear yellow spots (but not the indistinct brownish-yellow ones indicated by a slightly darker shade) to aid comparison. All darker colouration (i.e. more or less melanised, from reddish brown to black) is indicated by the dark shading.

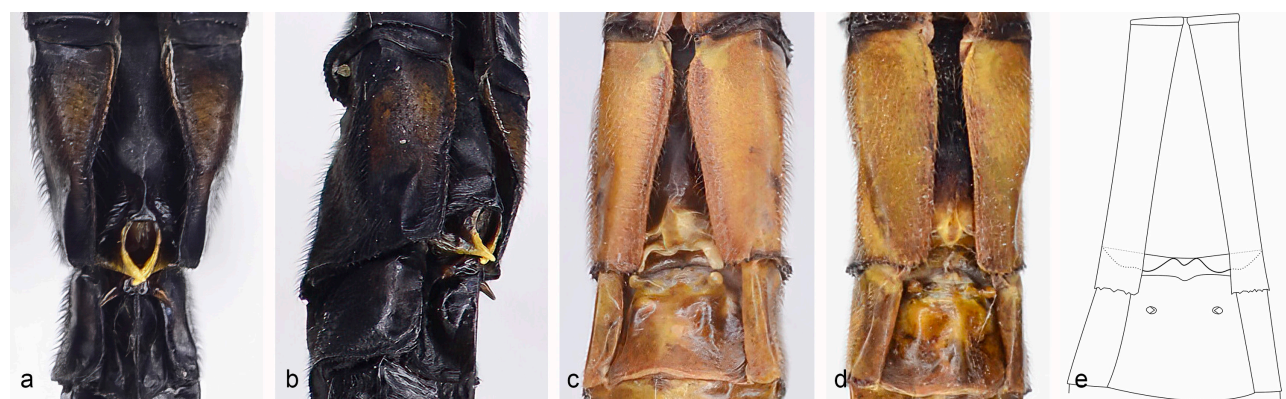


FIGURE 20. S8–9 of female *Nesocordulia* in ventral view, with gonapophyses: anterior processes (subgenital plate) on S8 and median processes on S9. a–b, *N. ipsio*; c–d, *N. coloratissima*, on figure d the anterior processes (subgenital plate) covered by tergites and only their common base discernible; e, *N. evanida* (the teneral female preserved in poor condition), the anterior processes (subgenital plate) partly covered by tergites (dotted line). Photos by Bogusław Daraż.

Larvae of *Nesocordulia* were described for the first time based on several specimens collected in a small forest stream (14.4339° S, 49.7630° E) at Marojejija Camp, Marojejy National Park, Sava Region, in north-eastern Madagascar (Fleck & Legrand 2006). Two different species were suggested, and one of them was tentatively identified (with a question mark) as *N. rubricauda* based on the larval wing pads venation. In the light of the present revision and discovery of *N. fossa*, this identification appears even more uncertain, and these larvae should be treated as unidentified. In this area, only *N. ipsio* and *N. evanida*, described in this synopsis, have been recorded so far.

Diversification. The six new species have doubled the number of known species to twelve, of which eleven are restricted to Madagascar and one to the Comoros. Given that many areas are still poorly explored and some species may occur only locally, we assume that the actual number is higher still. Evidently, *Nesocordulia* represents an evolutionary radiation; the first to be uncovered from the Malagasy Region in the suborder Anisoptera. The five previously known radiations, in five families of Zygoptera, are the genera *Nesolestes* Selys, 1891 (Argiolestidae), *Protolestes* Förster, 1899 (Protolestidae), *Tatocnemis* Kirby, 1889 (Tatocnemididae), and *Proplatycnemis* Kennedy, 1920 (Platycnemididae), plus the M-group of *Pseudagrion* Selys, 1876 (Coenagrionidae). The latter forms the largest radiation with over 30 species in running waters, although *Nesolestes* may prove to be richer once that genus is revised and complemented with expected species discoveries (Dijkstra & Cohen 2021; Dijkstra 2022).

With so little knowledge of the species' distribution and phylogeny (see above), it is hard to say how *Nesocordulia* diversified. Studying terrestrial vertebrates, Wilmé *et al.* (2006) posited that Madagascar's exceptional species richness is linked to endemism in its many river catchments, as organisms could easily become isolated there with Quaternary climatic shifts and diverge. Only in catchments that extend to the island's highest reaches, taxa could retreat upward during the most extreme shifts, and once conditions improved again disperse back and also expand into adjacent catchments, thus eventually occupying larger ranges.

Species arising by such non-adaptive speciation should be largely allopatric and can be similar ecologically, as resource-partitioning is not the main driver of their diversification (Czekanski-Moir & Rundell 2019). On one hand, distribution of seven *Nesocordulia* species, according to very limited data, match the areas of endemism identified by Wilmé *et al.* (2006); only *N. coloratissima* was recorded out of them. On the other hand, three (*N. fossa*, *N. malgassica*, *N. odonator*) and two species (*N. evanida*, *N. ipsio*) were found in close proximity around Mantadia and Marojejy National Parks respectively (Fig. 21). *Nesocordulia fossa* and *N. odonator* are among the most disparate species in appearance, suggesting they have quite distinct ecologies. Although the former's eyes are not notably large, its reddish brown body and brown-marked wings recall crepuscular dragonflies in genera such as *Gynacantha* Rambur, 1842 (Aeshnidae) and *Tholymis* Hagen, 1867 (Libellulidae), and it was indeed found flying in very deep shade. *Nesocordulia ipsio* and *N. evanida* are more alike, but while the former inhabits wet forest within the massif, the latter was found in the half-open landscape at the foot of the forested mountains, suggesting their ecologies differ substantially too. The more extensive yellow thoracic and abdominal markings of *N. evanida* support this, as the yellowest species (*N. coloratissima*) inhabits the driest and most open areas. Indeed, the proximity of *N. evanida* to *N. ipsio* at Marojejy may well have followed deforestation by humans.

Overall, the dozen species now known and their often strong differences in morphology and colouration are more suggestive of a comparatively ancient radiation into ecologically rather distinct species, than of the numerous species with small ranges and rather slight ecological and morphological differences that the Wilmé *et al.* (2006) micro-endemism hypothesis predicts. However, the non-adaptive evolution of more similar species (e.g. *N. ipsio* versus *N. odonator*, or *N. fossa* versus *N. rubricauda*) cannot be excluded.

Conservation status. Virtually nothing is known of the population status of the species and possible threats to their survival. While five of the twelve species (*N. coloratissima*, *N. evanida*, *N. fossa*, *N. ipsio*, and *N. odonator*) were found only in the past decade, four were not recorded with certainty for over a century (*N. flavicauda*, *N. lyricauda*, *N. rubricauda*, and *N. spinicauda*). Like the latter, *N. mascarenica* and *N. villiersi* are only known from their original discovery, before 1948 and in 1955 respectively. Only *N. malgassica*, first obtained in 1951, was recorded again, being photographed half a century later. All but one of the previously known six species were thus assessed as Data Deficient on the IUCN Red List of Threatened Species, the status that must apply to the six new species too. Only *N. villiersi* could be assessed as Endangered (Schütte & Clausnitzer 2020) because, assuming that it is restricted to Mohéli, its area of occupancy is smaller than 500 km² and the extent and quality of potential habitat continue to decline at this single locality. Many of the species may nonetheless be under threat, with only *N. coloratissima* and *N. evanida* confirmed to occur in human-impacted habitats, although in the vicinity of protected areas.



FIGURE 21. Distribution of known localities of *Nesocordulia*. For further details see the species texts. “*flavicauda* ?”—unconfirmed records in the Sambirano area; “*Nesocordulia* sp.”—several unidentified specimens from collections and photographs (see Fig. 14 and section “Unidentified specimens of *Nesocordulia*”).

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