



Paragomphus matroka sp. nov.—a new Hooktail species from the rainforests of eastern Madagascar (Odonata: Gomphidae)

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Abstract

Paragomphus matroka sp. nov. (holotype ♂: Madagascar, Taolagnaro District, Iaboakoho, Réserve de Ressources Naturelles de la Forêt Naturelle de Tsitongambarika, Ampasy; Lat. -24.57840°, Lon. 47.14493°; 4.xii.2024; to be deposited in RMNH, Leiden), is described as new to science. The new endemic species is known only from the holotype, the paratype deposited in the MNHN, Paris, and an additional specimen deposited in NHRS, Stockholm. It has been recorded from three localities in the eastern part of the island, scattered over a distance of 1,033 km, within the Madagascar Humid Forests ecoregion. Despite the pronounced variation in the colour pattern, the three known specimens are interpreted as conspecific based on concordant diagnostic morphological characters, particularly the nearly identical structure of the secondary genitalia and cerci. The new species is related to *P. fritillarius* (Selys, 1892) and *P. sofiae* Bernard & Daraž, 2026. From these two more brightly coloured, spotted Hooktail species, *P. matroka* sp. nov. differs in its considerably darker colouration, a reduced pattern of smaller light markings on the synthorax, and clearly different secondary genitalia. The discovery of a new species underlines the need for additional intensive odonatological studies in Madagascar. Improving knowledge of species distributions, taxonomy, phenology and ecological requirements is crucial, especially in the context of threat assessments and conservation of endemic odonate fauna.

Key words: dragonflies, Anisoptera, endemic, new species, *Paragomphus fritillarius*, taxonomy, biogeography, Malagasy Region

Introduction

Renowned as a paradise for biologists, Madagascar is characterized by exceptional biodiversity and a high degree of endemism (Antonelli *et al.* 2022; Goodman 2022, 2023). This large island off the east coast of Africa harbours 180 formally erected species of Odonata representing 14 families. Eighty percent of these species are endemic—in Zygoptera the endemism exceeds 90%, while among Anisoptera nearly 66 % of species are confined to the island (Dijkstra 2022; Bernard *et al.* 2025; Goodman *et al.* 2025; Bernard & Daraž 2026).

The exceptional endemism levels and species diversity make the dragonflies and damselflies of Madagascar a compelling group for biogeographical, phylogenetic, evolutionary and ecological studies. However, despite considerable recent advances, including the publication of the book *Dragonflies and Damselflies of Madagascar and the western Indian Ocean Islands* (Dijkstra & Cohen 2021) and encouraging recent descriptions of new species (Bernard *et al.* 2025; Bernard & Daraž 2026), the knowledge of the island's odonate fauna remains insufficient.

The family Gomphidae in Madagascar is no exception regarding knowledge gaps, with its ten endemic representatives, currently placed in the genera *Isomma* Selys, 1892, *Onychogomphus* Selys, 1854 and *Paragomphus* Cowley, 1934. The latter genus, with 50 described species worldwide (Paulson *et al.* 2026), is known from Madagascar by five endemic species so far. *P. madegassus* (Karsch, 1890), *P. fritillarius* (Selys, 1892) and *P. obliterated* (Selys,

1892) were described at the end of the 19th century, while *P. z-viridum* Fraser, 1955 was added to the island's odonate fauna in the mid-20th century. Recently, after several decades, another new endemic species from the lowlands of northern Madagascar, *P. sofiae* Bernard & Daraž, 2026, was described. This species is related and superficially very similar to *P. fritillarius*.

The latest study by Bernard & Daraž (2026) provided valuable morphological details of the genitalia not only of *P. sofiae* but also of *P. fritillarius*, based on its lectotype from the Selys collection housed at the Royal Belgian Institute of Natural Sciences in Brussels. This new information on an otherwise very fragmentarily known group of Madagascan dragonflies enabled thorough comparison and conclusive determination of *Paragomphus* material, collected in southeastern Madagascar in 2024 in the framework of the Slovenian scientific expedition to Madagascar. An unusually dark-coloured specimen from the protected Tsitongambarika Natural Resources Reserve, which had already been tentatively ascribed in the field to an undescribed species, has indeed proved to be new to science and is described in this paper.

Nearly simultaneously, in early February 2026, the Polish co-authors of the present study made an exciting discovery in the entomological collection of the Muséum National d'Histoire Naturelle in Paris. They identified a single male specimen of an undescribed *Paragomphus* species, collected by the late French odonatologist Jean Legrand around the turn of the millennium in central-eastern Madagascar. Subsequent intensive information exchange and comparative analyses soon led to the understanding that we were most likely dealing with the same species. We present here the combined results and conclusions of our study.

Material and methods

Within the framework of the Slovenian scientific expedition to Madagascar, entitled *Continuous Contribution to Understanding the Spider and Dragonfly Diversity in Madagascar*, organised by researchers from the National Institute of Biology (NIB) and the Research Centre of the Slovenian Academy of Sciences and Arts (ZRC SAZU), the odonate fauna of the island was investigated between 18.xi.2024 and 14.xii.2024. Fieldwork activities were conducted in different parts of the island with a special focus on the region north of Taolagnaro (formerly Fort Dauphin), southeastern Madagascar. One of the areas visited by the research team between 3.xii. and 5.xii.2024 was Tsitongambarika.

This large protected area, officially named *Réserve de Ressources Naturelles de la Forêt Naturelle de Tsitongambarika*, is located in Madagascar's southeastern Anosy Region. It encompasses ca. 58,600 ha of lowland and medium altitude moist evergreen forests spanning from near sea level to more than 1,350 m a.s.l. The reserve represents one of the largest remaining blocks of humid evergreen forest in the southeast of the island, with a complex altitudinal zonation of forest types and numerous streams and tributaries that support diverse aquatic and terrestrial fauna (Goodman *et al.* 2018). Fieldwork was conducted in the vicinity of the Ampasy Research Station, situated at the edge of the protected area on the banks of the Ampasy River, approximately 9 km upstream from the village of Iaboakoho and approximately 52 km northeast of Taolagnaro. The area around the research station is characterized by the pristine Ampasy River and its smaller tributaries and is surrounded by secondary forest and shrubland. Some remaining patches of lowland rainforest are already considerably disturbed due to illicit logging. The altitude in the study area ranges between 20 and 100 m a.s.l.

Collected holotype specimen was preserved in a vial containing absolute ethanol and properly labelled. In the laboratory, the holotype was examined, measured, and imaged using a Keyence VHX-7000 digital microscope (Keyence Corporation, Japan). Prior to examination, the specimen was air-dried overnight and was subsequently stored in a polypropylene envelope. Photographs of living specimens were taken in the field using a Sony DSC-RX10 IV camera.

The paratype was discovered in the MNHN collection, examined and described in detail by R. Bernard and B. Daraž. It was photographed using a Canon EOS R7 camera equipped with a Canon RF 100mm Macro lens. Measurements were taken using the DLTCamViewer (Delta Optical) computer program (in the photographs).

We also accessed iNaturalist platform (<https://www.inaturalist.org/>) in December 2025 to screen for potential photographic records of the new species. One of the photographed specimens available on this platform, potentially attributable to the new species described herein, was subsequently located in the entomological collections of the Swedish Museum of Natural History (Naturhistoriska Museet) in Stockholm. Photographs sent by Professor Johannes Bergsten, the Senior Curator at this museum, allowed us to confirm its species identity.

All measurements (lengths) are given in millimetres (mm) with an accuracy of 0.1 mm. The terminology of external morphology follows Dijkstra & Clausnitzer (2014). Colouration in new species description is given as detectable from the preserved material, supplemented with photographs and notes on colouration in life where available.

Necessary fieldwork permits were issued by the Direction des Aires Protégées, des Ressources Naturelles renouvelables et des Ecosystèmes: N°359/24/MEDD/SG/DGGE/DAPRNE/SCBE.Re. and N°352N-EA12/MG24.

Abbreviations. Ax: antenodal cross-veins; Px: postnodal cross-veins; Fw: forewing(s); Hw: hindwing(s); Pt: pterostigma; S1–10: abdominal segments 1–10.

Acronyms for collections. RMNH—Naturalis Biodiversity Center (formerly Nationaal Natuurhistorisch Museum), Leiden, The Netherlands; MNHN—Muséum National d'Histoire Naturelle, Paris, France; NHRS—Naturhistoriska Museet, Stockholm, Sweden (entomological collections).

Results

Paragomphus matroka sp. nov.

Common name (en): Dark Hooktail / Nom commun (fr): Paragomphe sombre

<https://zoobank.org/urn:lsid:zoobank.org:act:AA7C1577-11F9-4ED9-BA8C-9F009C3CFC2F>

Figs 1a–h, 2b, 2d, 3b, 3d, 4b, 4d, 4f, 5a–h, 6a–b

Holotype: 1♂ (mature) (RMNH.INS.1555270; dry specimen, ex. ethanol; right middle and hind legs removed and preserved in absolute ethanol for future studies at the National Institute of Biology, Ljubljana, Slovenia): Right tributary of Ampasy River 700 m NW of Ampasy Research Station; Réserve de Ressources Naturelles de la Forêt Naturelle de Tsitongambarika, Andrahanjato, Iaboakoho, Taolagnaro District, Anosy Region, southeastern Madagascar; Lat. -24.57840°, Lon. 47.14493°; alt. 40 m; 4.xii.2024; leg. M. Bedjanič. **Paratype:** 1♂ (mature) (MNHN, dry specimen), unnamed watercourse, near the road to Lakato, Moramanga District, Alaotra-Mangoro Region, central-eastern Madagascar; Lat. -19.05830°, Lon. 48.36388°; alt. 1,053 m; 5.i.1999; leg. J. Legrand.

Additional material. 1♂ (mature) (NHRS-JLKB000072760, dry specimen), tributary of Bedinta Stream, Masoala National Park, Antalaha District, Sava Region, northeastern Madagascar; Lat. -15.6742°, Lon. 49.9945°; alt. 497 m; 27.ii.2025; leg. J. Bergsten & A. de Jong. (<https://www.inaturalist.org/observations/327001344>).

Etymology. The species epithet is to be treated as a noun in apposition. It is derived from the Malagasy word “*matroka*”, meaning “*dark-coloured*” and it refers to the relatively dark colouration of the new species in comparison to its congeners.

Description. Holotype male. Head. Face brown, vertex dark brown to black, dorsal surface of frons with two rounded triangular light yellow-greenish spots (Fig. 1d). Maxilla and labium with greyish brown base and bordered with brown, tips of maxillae dark brown. Mandibles light brown, with diffuse yellowish spot in basal part, apical fourth dark brown. Labrum brown. Anteclypeus brownish, with a faint greenish tint. Postclypeus brown, its dorsolateral angles diffusely bordered light greenish to yellowish. Anterior surface of frons dark brown, dorsal yellow-greenish spots with straight anterior and broadly rounded posterior borders. Bases of antennae light yellow-greenish, scapus dark brown, other segments brown. Vertex and the ocelli crest black. Occiput completely black with a row of straight light hair-like setae (Fig. 1d). Rear of the head behind occiput dark brown with two small yellow spots on each side. Laterally, rear of the head mostly brown with an isolated median elongated semicircular-oval yellow spot, lower third entirely yellowish, sharply demarcated from the brown upper part with oval spot. Eyes light ochre in preserved specimen, green in life (Fig. 6).

Thorax. Prothorax entirely black dorsally to dark brown lateroventrally. Posterior border of prothorax with semicircular protrusion and long light hair-like setae. Dorsum of synthorax black, sides dark brown, becoming reddish brown ventrally, with narrow yellow stripes and light yellow to greenish-yellow spots (Figs 1a, b). Mesepisternum black, with only a shade of dark brown towards humeral suture. Crest and tooth of the middorsal carina black. Collar yellow, two spots separated from each other in the middle, anterior border with long hairs. The postdorsal stripe fairly narrow, around 4–5 times as long as wide, well-separated from the collar. Antehumeral stripe reduced, divided into a small dorsal spot and a narrow stripe situated more ventrally (Figs 1a, b). Mesokatepisternum reddish brown, mesepimeron and metepisternum chocolate brown. Mesepimeron with three isolated pale yellowish spots of unequal shape; upper spot distinct, of rounded triangular shape, followed below by hardly visible diffuse light

marking and also very diffuse but clearly visible oval lower spot. The metepisternum with two well-separated spots, the upper yellow oval spot just below dorsal synthorax border and lower greenish-yellow diffuse oval spot in the middle above the metastigma (Figs 1a, b). Similar pattern and position of two spots present on metepimeron, both of light greenish-yellow colour, very diffuse. Poststernum brown with yellowish brown anterior corner. Under surface of thorax light brown.

Legs. Coxae and trochanters reddish brown. Femora reddish brown, darker, almost black at distal end (Fig. 1a). Foreleg femur with light yellowish stripe on its inner posterior side. Short strong spines on flexor surface of femora and trochanters black. Tibiae and tarsi very dark brown to black with two rows of strong bristle-like setae.

Wings. Wings hyaline, with a barely recognisable amber tint. Venation black and dark brown. Forewings with 16/15 Ax and 10 Px, hindwings with 9/10 Ax and 9/10 Px. More than half of antenodal cross-veins incomplete. Costa black. Pt elongated, nearly 6 times longer than wide, coloured very dark brown, braced by thick black veins, covering 5 underlying cells in both Fw and Hw. Anal triangle with 4 cells, its proximal side almost rectangularly incised in its lower third, tornus strongly angulated (Figs 1a, c).

Abdomen. Colouration of S1–6 predominantly black, S2–6 with laterodorsal yellow spots. S7–10 predominantly reddish-brown, forming a distinct club, with pronounced ventrolateral foliations on S8 and S9 (Figs 1a, h). The anterior half of S7 with conspicuous paired elongated dorsal yellow spots and the posterior half of S7–9 with blurred blackish dorsal stripe (Fig. 1h). The detailed abdominal colouration pattern as follows: S1 dark brown, with small diffuse greenish-yellow spot in the distal ventrolateral portion and a narrow yellowish T-stripe dorsally. S2 brown laterally, auricles citron yellow above and brown below, with 4–5 strong denticles on ventrolateral margin, blurred yellowish spot in the apical ventrolateral portion and a larger blurred yellowish spot in the distal ventrolateral portion, dorsum of the segment black, with a very narrow fusiform yellow stripe along almost the entire segment length. S3 black, with a basal elongate triangular yellowish spot dorsolaterally on each side of the dorsal carina, a basal triangular yellow spot ventrolaterally and a larger elongate yellow spot medially. S4 black, with very similar pattern of slightly smaller yellow markings. S5 black, with yellow markings already very reduced. S6 black, with only two narrow basal yellow spots separated mediodorsally and mediolaterally by black ground colour. S7 with an anterior dorsolateral yellow marking, reaching 45 % of the segment's length dorsally; in basal half the yellow marking semi circularly broadened laterally, forming a ring, that becomes blurred ventrally; the remainder of S7 reddish-brown, apical half with blurred blackish mediodorsal longitudinal stripe, apical segment carina finely bordered with black (Fig. 1h). S8 and S9 reddish to rusty brown, with a somewhat blurred blackish mediodorsal longitudinal stripe and narrowly blackish apical carina. On S7–9, a small black spot situated laterally on rings of posterior field of tergites. Ventrolateral rounded foliations large, reddish-brown, diffusely bordered with blackish brown towards segment margin, being much larger on S8 than on S9, the former overlapping approximately one fourth of S9 in side view. S10 uniformly orange-brown (Figs 1a, h). Otherwise, S1–6 ventrally greyish, S7–10 coloured ventrally in different shades of orange. Small denticles along dorsal carina in all abdominal segments, with denser rows of black denticles along apical segment margins; blackish dorsal stripe on S7–9 with distinctly roughened surface, bearing with minute denticles and short hair-like setae.

Secondary genitalia. In lateral view, the anterior hamule evenly sickle-shaped, tapering markedly towards the apex, and directed posteriorly. Posterior hamule elongated in lateral view, narrowing distally, and ending in a blunt apex slightly bent anteriorly. The penial peduncle with straight ventral margin and rounded distal portion (Figs 1c, e, 3b and 4d). Ventral aspect as shown in Figs 3d and 4f. Distal hook of posterior hamule strongly bent inward and downward, thus not visible in lateral view (Figs 3b, d and 4d, f). Penis as illustrated in Fig. 1e.

Caudal appendages. Uniformly pale reddish-orange (Figs 1f–h, 2b, d). In lateral view, cerci stout at base and gradually narrowing distally, tapering to finely pointed apices (Figs 1f, 2b, 4b). In the distal third, they are gently curved downward, forming an obtuse angle (approximately 135°) between the straight anterior portion and the curved posterior portion. Ten very small black denticles present along the ventral inner ridge of cerci tips, with spacing between them increasing distally. Cerci tips clearly divergent (Figs 1g, h, 2d). Epiproct approximately half as long as cerci. In ventral view, the basal third of epiproct undivided, apical two thirds deeply divided into two short clavate branches with swollen, rounded apices that are closely adjacent on a short distance before their margins diverge again; opening between epiproct branches elliptical and slightly tapering distally (Figs 1g, 2d). In lateral view, epiproct curved upwards before the middle of its length, with a slightly obtuse angle (about 105°). Apices on each side with a slightly protruding dorsolateral dark brown crenate margin (Figs 1f, 2b).

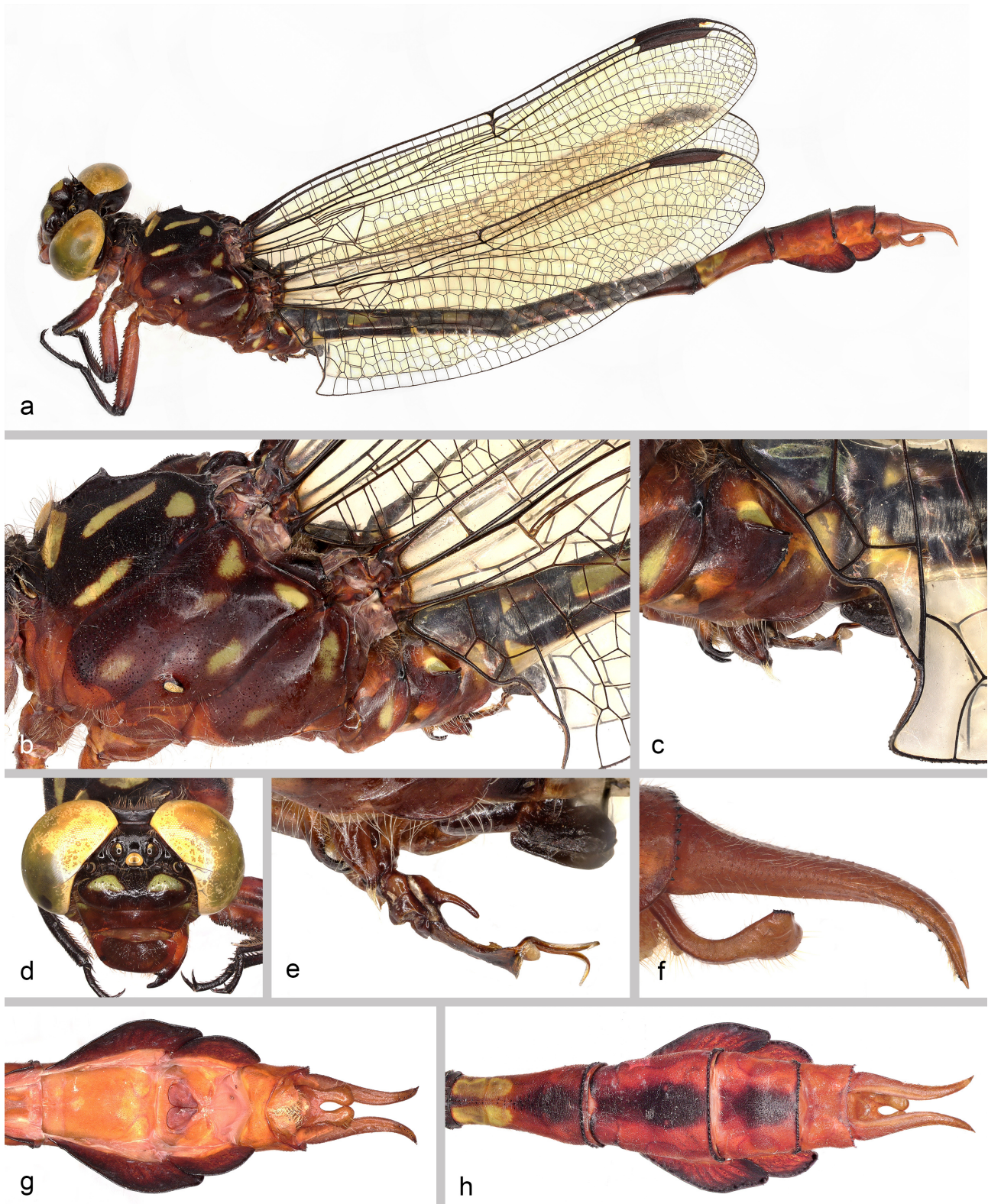


FIGURE 1. Male of *Paragomphus matroka* sp. nov. (holotype, type locality); (a) habitus in lateral view; (b) synthorax in lateral view; (c) secondary genitalia and part of proximal portion of hind wing with anal triangle and tornus; (d) head in dorsofrontal view; (e) penis in lateral view, subsequently expanded; (f) caudal appendages in lateral view; (g) S7–10 and caudal appendages in ventral view; (h) S7–10 and caudal appendages in dorsal view. Photographs by Kuang-Ping Yu & Matjaž Bedjanič.

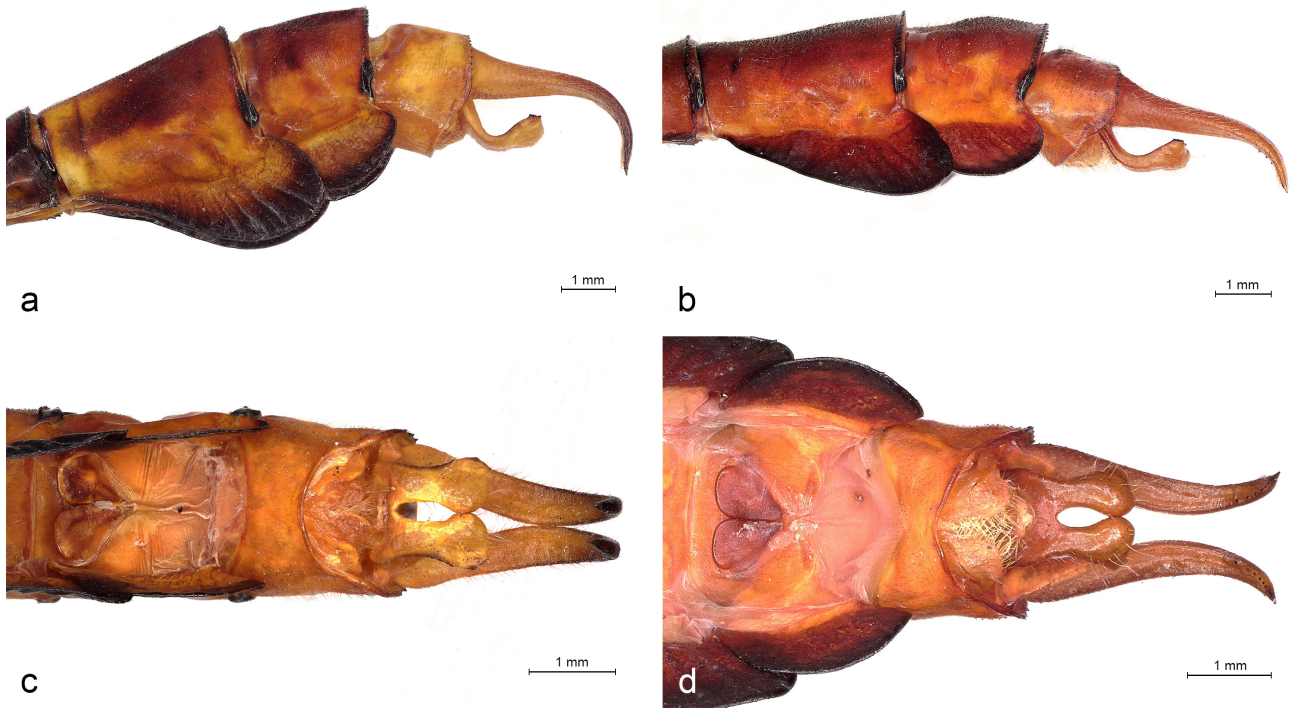


FIGURE 2. Male caudal appendages in lateral view (a, b), and ventral view (c, d), of *Paragomphus fritillarius* (a, c—left column; Domaine de la Cascade—Plantation Lansargues 8 km NW of Taolagnaro, Anosy Region, southeastern Madagascar) and *Paragomphus matroka* **sp. nov.** (b, d—right column; holotype, type locality). Photographs by Kuang-Ping Yu & Matjaž Bedjanič.

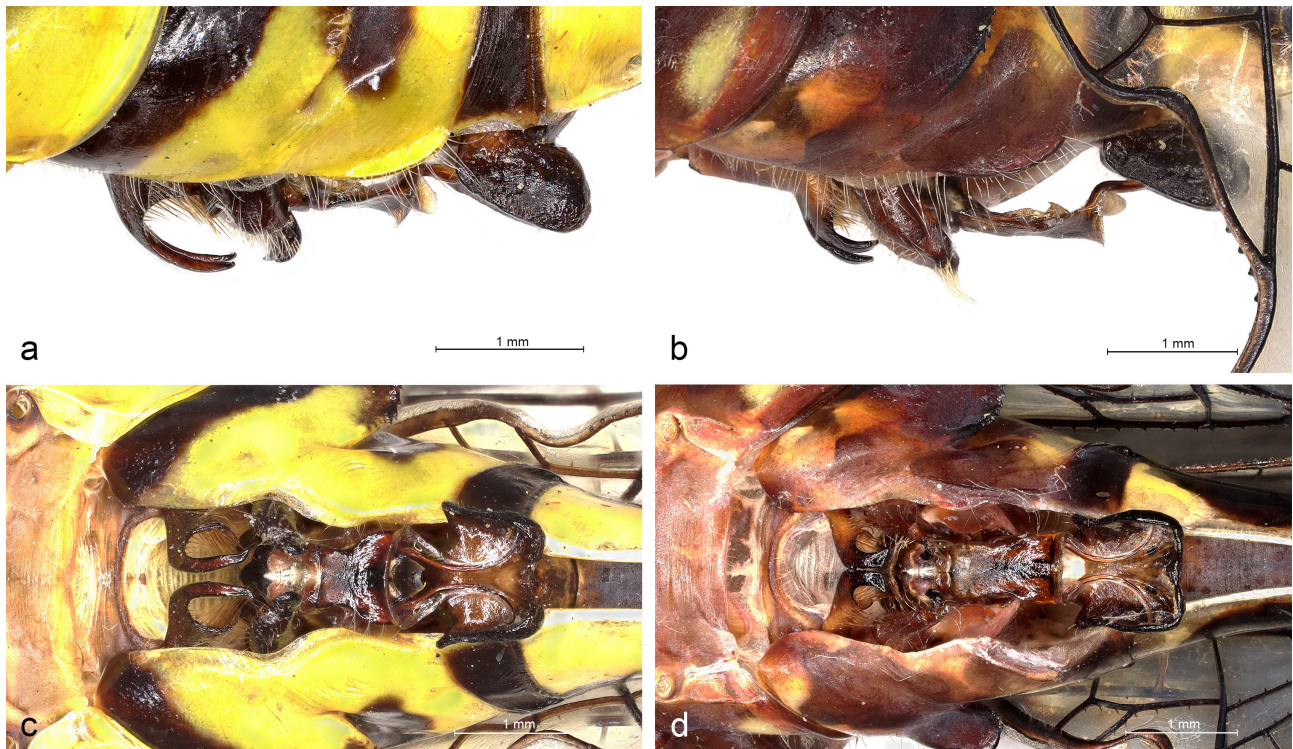


FIGURE 3. Male secondary genitalia in lateral view (a, b), and ventral view (c, d), of *Paragomphus fritillarius* (a, c—left column; Domaine de la Cascade—Plantation Lansargues 8 km NW of Taolagnaro, Anosy Region, southeastern Madagascar) and *Paragomphus matroka* **sp. nov.** (b, d—right column; holotype, type locality). Photographs by Kuang-Ping Yu & Matjaž Bedjanič.

Measurements. Total length 54.7 mm, abdomen, incl. appendages 41.1 mm, Fw 31.9 mm, Hw 29.6 mm, Fw Pt 4.4 mm, Hw Pt 4.3 mm, cerci 3.0 mm, epiproct 1.5 mm.

Notes on colouration in life. The holotype male was the only specimen observed at the type locality. Prior to collection, it was photographed from two slightly different aspects (Figs 6a, b). In life, the dark colouration of the species is more pronounced, with the dorsum and sides entirely black and brown shades restricted to the lower ventrolateral and ventral portions. Markings on the head, thorax and abdomen light yellow, lacking any greenish lustre, and more sharply defined than in the preserved specimen. The dorsal surface of the synthorax between the wing bases, posterior to the base of the tooth of the middorsal carina, with light yellow spots. Eyes grass-green, the face dark brown. Ground colouration of segments S7–9 reddish-brown to reddish-orange, S10 reddish-orange. Cerci of a lighter reddish orange colour (Figs 6a, b).

Variation in the paratype male. Total length 53.6 mm, abdomen (including appendages) 41.1 mm, Fw 33.5 mm, Hw 31.3 mm, Fw Pt 4.5 mm, Hw Pt 4.5 mm, cerci 3.3 mm, epiproct 1.5 mm; Fw Ax 16/14, Fw Px 10/12, Hw Ax 12/11, Hw Px 12/13. The paratype male differs little in size from the holotype, being slightly shorter in total length but having greater wing length. It is noticeably lighter on the sides of the synthorax than the holotype. This is due to the more extensive warm and ferrugineous-brown background (in relation to black) and, above all, to the larger, more distinct, and more intensely yellow spots (Fig. 5b). The latter difference is striking on the mesepimeron, which has two large spots, whereas in the holotype these are reduced to three small, diffuse remnants. A similar pattern is observed on the metepimeron, where the two large spots are almost fused in the paratype, but remain small and widely separated in the holotype (Figs 5b *versus* 1b, respectively). In contrast, on the abdomen, the yellow markings are slightly smaller (on S3–5) or even hardly recognisable (S1–2) in the paratype compared to the holotype. The colour differences in the paratype are further complemented by a brown anteclypeus *versus* a yellowish-brown anteclypeus in the holotype. Variation in secondary genitalia and caudal appendages is mostly minute: in the paratype, (a) the tip of the anterior hamule is slightly more hooked in lateral view; (b) the hook of the posterior hamule is a bit more curled and less acute; and (c) cercus bears four minute black denticles along the ventral inner ridge of the tip *versus* 10 slightly stronger denticles in the holotype. The only substantial difference concerns the epiproct: its branches are clearly distended distally in the holotype compared to the paratype. This is evident in both ventral and lateral view; in the latter the difference between the bulbous ‘head’ of the epiproct in the holotype and the gradually widening tip in the paratype is pronounced (Figs 5d *versus* 1f).

Female. Unknown.

Differential diagnosis. *Paragomphus matroka* is a large, dark endemic representative of the genus, belonging to a group of two additional endemic Madagascan species with a “spotted” thorax—*P. fritillarius* and *P. soflae*—which closely resemble each other and are characterized by brighter, predominantly yellow-and-black colouration.

The new species remotely resembles *P. fritillarius* in the pattern of yellow spots on the synthorax and abdomen, the reddish-brown terminal abdominal segments, and the general shape of the cerci. However, it is readily distinguished by its overall darker colouration and the unique morphology of the hamules. The most significant colouration differences occur on the face, which is predominantly brown in *P. matroka*, *versus* interspersed yellow and black in *P. fritillarius*, and on the dark brown synthorax sides, where the yellow spots within the mesepimeral and metepimeral stripes are distinctly smaller in *P. matroka*, and may be nearly obsolete (Figs 1a, b, d and Fig. 5b *versus* Fig. 1b and Fig. 7a, c in Bernard & Daraz 2026 for *P. fritillarius*). Additional diagnostic features of the new species include a completely black occiput, which is yellow in *P. fritillarius*, and reduced yellow abdominal spots on segments S1–6. The anterior hamule of *P. matroka* differs in having a much shorter decurved distal section, resulting in a distinctly smaller overall appearance compared to that of *P. fritillarius*. In lateral view, a prominent distal claw on the posterior hamule of *P. matroka* is not visible; in fact, the claw is present but is directed inwards and downwards and thus remains concealed within the outline of the structure if only inspected from the side. In contrast, *P. fritillarius* exhibits a strong, anteriorly directed distal claw that is clearly visible in lateral view (Figs 3 and 4c–f). The cerci of *P. matroka* are uniformly reddish-orange and downcurved at an obtuse angle with shorter distal downcurved part, whereas in *P. fritillarius* they are black-tipped and abruptly bent ventrally at approximately a right angle, with longer distal downcurved part (Figs 2 and 4a, b).

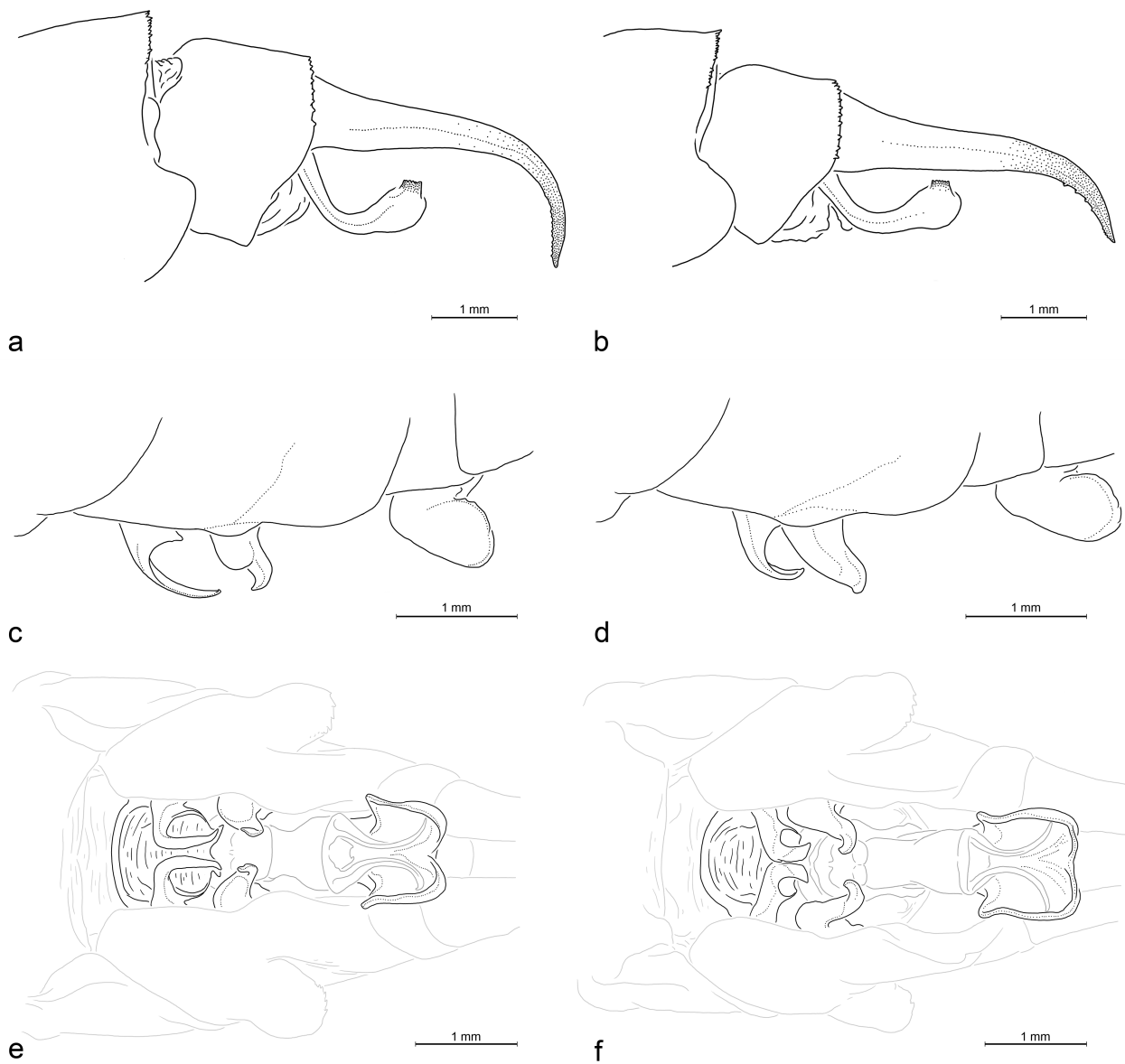


FIGURE 4. Male caudal appendages in lateral view (a, b), male secondary genitalia in lateral view (c, d), and in ventral view (e, f), of *Paragomphus fritillarius* (a, c, e—left column; Domaine de la Cascade - Plantation Lansargues 8 km NW of Taolagnaro, Anosy Region, southeastern Madagascar) and *Paragomphus matroka* **sp. nov.** (b, d, f—right column; holotype, type locality). Illustrations by Kuang-Ping Yu.

In addition to the same differences in the head, synthorax and abdomen colouration (as described in the comparison with *P. fritillarius* above), *P. matroka* also clearly differs from *P. sofiae* in a distinct shape of posterior hamule. In lateral view, this structure is unbranched in *P. matroka* versus provisionally branched, with a dominant anterior branch, in *P. sofiae* (Figs 3b, 4d versus Figs 2e, 3a in Bernard & Daraz 2026). Ventral view of the same structure reveals a strong hooked claw directed inwards and downwards in *P. matroka*, while posterior hamule of *P. sofiae* lacks any distal claw elongation (Figs 3d, 4f versus Fig. 3c in Bernard & Daraz 2026).

While the size difference of new species is not so evident in comparison to *P. fritillarius*, the size difference between *P. matroka* and *P. sofiae* is greater, with the total length 53.6–54.7 mm versus 47.0–48.5 mm and Hw 29.6–31.3 mm versus 24.2–25.6 mm.

The other described insular representatives of the genus—*P. madegassus*, *P. z-viridum* and *P. obliteratus*—remain taxonomically insufficiently understood, but they differ more strongly from *P. matroka* by their more “striped” than “spotted” pattern of thoracic markings, more extensive bright markings on abdominal segments, and clearly different hamules and/or cerci.

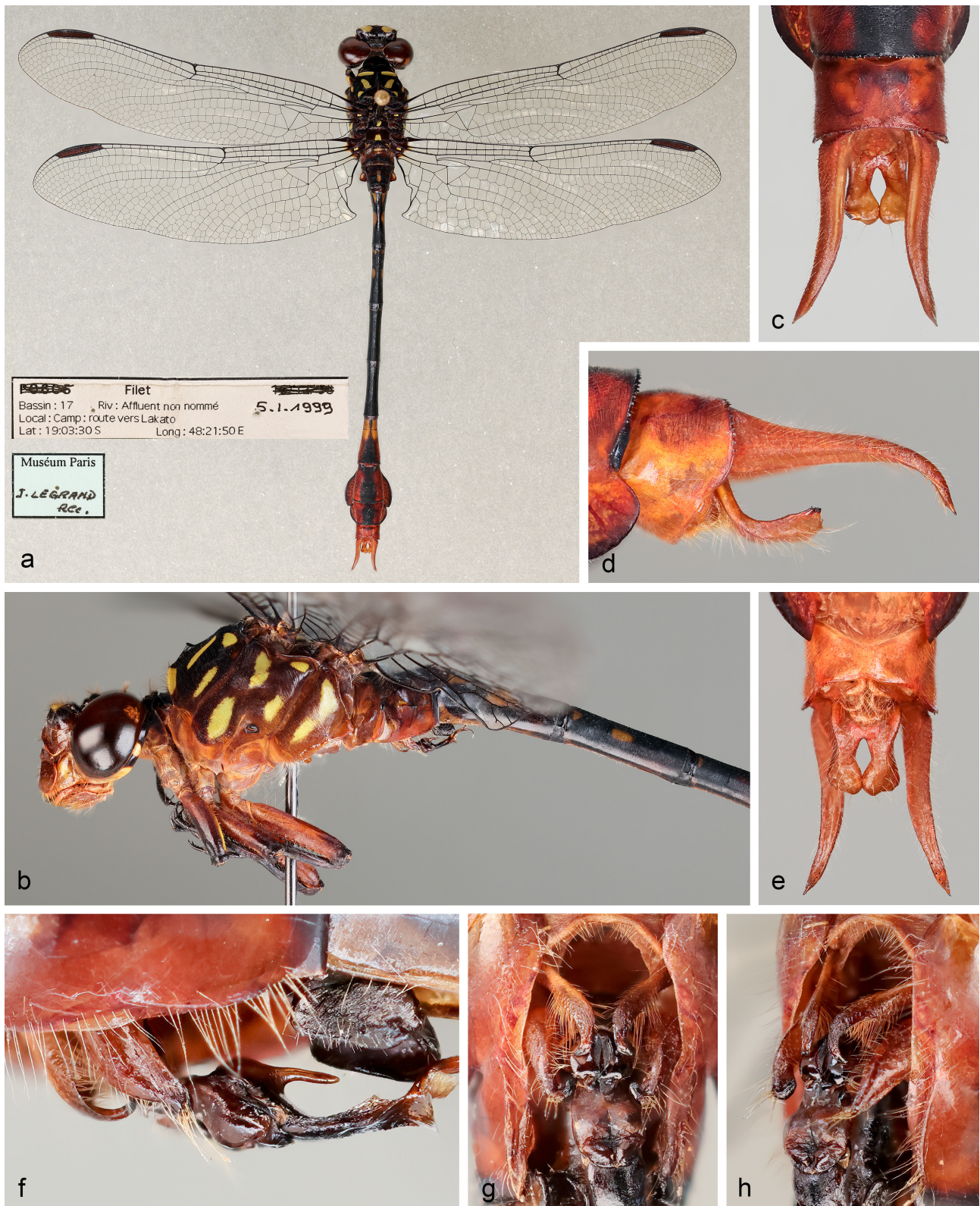


FIGURE 5. *Paragomphus matroka* sp. nov., male (paratype, MNHN Paris; Moramanga District, central-eastern Madagascar). (a) habitus in dorsal view and labels; (b) head, thorax and anterior part of abdomen (S1–4) in lateral view; (c), (d), and (e) S10 and caudal appendages in dorsal, lateral and ventral view, respectively; (f) secondary genitalia in lateral view, with penis partly exposed; (g) secondary genitalia in ventral view; (h) secondary genitalia in lateroventral view to show hook of the posterior hamule hidden behind its outline. Photographs by Bogusław Darąż.



FIGURE 6. *Paragomphus matroka* sp. nov., male holotype, colouration in life: (a) dorsolateral view; (b) frontolateral view (Right tributary of the Ampasy River 700 m NW of Ampasy Research Station, Tsitongambarika, Anosy Region, southeastern Madagascar; 4.xii.2024). Photographs by Matjaž Bedjanič.



FIGURE 7. Localities of *Paragomphus matroka* sp. nov. (red circles) and specimens likely conspecific but not verifiable (blue circles) in Madagascar. The unconfirmed specimens from iNaturalist are indicated with their identification codes as used on the platform. Map by Bogusław Daraż.

Distribution and ecology. The new species is known with certainty from three localities along a 1,033 km stretch in eastern Madagascar, from Tsitongambarika in the South-East to Masoala National Park in the North-East (Fig. 7), within the ecoregion of Madagascar Humid Forests (One Earth 2026), and in the hydrographic ecoregions of Eastern Lowlands and Eastern Highlands (Sparks & Stiassny 2022). The citizen-science platform iNaturalist contains two other photographic records of a dark *Paragomphus* species from other areas that may be tentatively attributed to *P. matroka*, however, the photographs lack the necessary diagnostic details, and without voucher specimen the species attribution cannot be confirmed. The most likely candidate is a male strikingly similar to the *P. matroka* holotype, shown by “ethankistler” in the photo from central eastern Madagascar, 30 km NNE of the

paratype locality (<https://www.inaturalist.org/observations/14630218>, Mantadia National Park, Alaotra-Mangoro Region). The photograph shared by “angelomg” from southeastern Madagascar (<https://www.inaturalist.org/observations/67192293>; Ambatokasa, Anosy Region) shows rather incomplete picture, however, it was taken at a place only around 22 km northwest of the type locality of *P. matroka*.



FIGURE 8. Type locality of *Paragomphus matroka* sp. nov.—Right tributary of the Ampasy River 700 m NW of Ampasy Research Station, Réserve de Ressources Naturelles de la Forêt Naturelle de Tsitongambarika, Anosy Region, southeastern Madagascar. Photograph by Matjaž Bedjanič.

Based on a single observed specimen at the type locality and due to the fact that the description of the paratype locality is not available, the conclusions regarding the habitat of *P. matroka* remain tentative and presently only refer to the type locality. The right tributary of the Ampasy River (Fig. 8) where the male was photographed and collected, is a medium-size natural forest stream with a coarse, gravel-rocky substrate and a total width of approximately 4–6 m. The section where the new species was observed is situated approximately 400–500 m upstream from the confluence with the Ampasy River. At the time of our visit, at the beginning of the rainy season, the water level in the stream was low, averaging 10–20 centimetres in depth and becoming deeper in occasional pools formed below larger boulders. The current was rather slow and the water was crystal clear. The stream is bordered by primary lowland rainforest and is shaded to varying degrees by the canopy, forming a mosaic of shaded, partially shaded, and sunlit patches. The observed specimen perched in a typical hooktail manner on large sunlit boulders, relatively low above the water surface (Figs 6a, b). Prior to being photographed on two occasions and subsequently collected, it patrolled an approximately 20–30 m stretch of the stream in fairly rapid flight.

Discussion

The fauna and flora of Madagascar are unique to our planet. With one of the highest levels of endemism across multiple taxonomic levels of any country, the island ranks among the hottest of the biodiversity hotspots on Earth (Antonelli *et al.* 2022; Goodman 2022, 2023). Among the various faunal groups, the Odonata are no exception in this respect and the endemism at the species-level of 80 % is remarkable. Within the Zygoptera, several endemic radiations in the Malagasy Region have long been recognised, including ancient and isolated lineages at the family level (e.g., Protolestidae, Tatocnemididae). In contrast, the endemic Anisoptera fauna is less diverse; nevertheless, with approximately two thirds of its species restricted to the island, it remains highly distinctive and of considerable biogeographic interest. The new *P. matroka*, described herein increases the number of endemic Anisoptera to 57 and raises the total number of species currently known from the island to 181 (Dijkstra 2022; Bernard *et al.* 2025; Bernard & Daraž 2026).

In comparison with the African mainland, the Gomphidae of Madagascar are considerably less diverse, comprising only eleven described species assigned to three genera (Dijkstra & Clausnitzer 2014; Dijkstra & Cohen 2021; Dijkstra 2022; Bernard & Daraž 2026; present paper). However, as already noted by Dijkstra & Cohen (2021), and clearly demonstrated by the recent revision of the genus *Nesocordulia* McLachlan, 1882 of the family Idomacromiidae (Bernard *et al.* 2025; Goodman *et al.* 2025), the true diversity of endemic Madagascan odonates is substantially underestimated. Within Gomphidae, the recent addition of two new species in the genus *Paragomphus*, the first by Bernard & Daraž (2026) and the second presented herein, together with additional taxa descriptions in the subfamilies Phyllogomphinae and Onychogomphinae currently in preparation (Bedjanič *et al. in prep.*; Bernard & Daraž *in prep.*), suggest that a similar pattern applies. The taxonomy and true insular diversity of the family remain far from being adequately documented. Regarding the island's representatives of the genus *Paragomphus*, it should be noted that the original historical descriptions and literature are incomplete and lack adequate illustrations which in some instances appear to have been conflated (e.g., Karsch 1890; Selys-Longchamps 1892; Fraser 1955, 1956; RBINS 2025). This has contributed to persistent taxonomic confusion and delays in recognizing taxa new to science. The description of the new *P. matroka* was only made possible after detailed figures of the lectotype of *P. fritillarius* from the Selys collection, housed at the Royal Belgian Institute of Natural Sciences, Brussels, became available (Bernard & Daraž 2026).

The described specimens of *P. matroka* differ to some extent, primarily in their colour pattern, with the paratype representing a brighter form of the holotype. In contrast, the secondary genitalia and caudal appendages are nearly identical in both specimens. Furthermore, also in the third known specimen from Masoala National Park, which is the darkest of all, with prevailing blackish colouration and even more reduced yellow markings on thorax and abdomen, the secondary genitalia and caudal appendages are likewise nearly identical to those of the holotype. The cause of the observed colour differences remains unknown, and it is unclear whether their individual age may contribute to this variation. However, these differences may reflect a situation in which less conservative traits, such as somatic colouration, evolve more rapidly under slightly different selective pressures (e.g., varying habitat conditions), whereas more conservative reproductive structures remain unchanged or change more slowly. We therefore hypothesize that *P. matroka* may represent a variable species undergoing ongoing diversification (incipient

speciation). However, due to the limited material available and the lack of molecular data, it is not possible to assess the extent to which this process has progressed. Given the most diagnostic characters, namely the secondary genitalia and cerci, we currently interpret the available specimens as conspecific, despite the pronounced variation in colour pattern. This hypothesis should be tested in the future using more extensive material, particularly molecular data. The documented intraspecific colour variation in *P. matroka*, together with the striking interspecific similarity in colouration between *P. sofiae* and *P. fritillarius* (Bernard & Daráz 2026), further demonstrates that somatic colour pattern alone may be insufficient for reliable species delimitation within *Paragomphus* species.



FIGURE 9. A stark contrast between (a) pristine beauty of the Réserve de Ressources Naturelles de la Forêt Naturelle de Tsitongambarika in southeastern Madagascar—scenic view from above the waterfall in the upper reach of the Ampasy River; and (b) the results of anthropogenic pressures at the border of the protected area—the main threats to the reserve are advancing slash-and-burn agriculture and illicit logging of forest trees. Photographs by Matjaž Bedjanič.

The general knowledge gap regarding the odonate fauna of Madagascar is highlighted by the fact that at least 50 endemic species have not been recorded since their original discovery, mostly between 1900 and 1950. Furthermore, for over 50% of endemic species the data are insufficient for the IUCN Global Red List of Threatened Species assessment (Dijkstra & Cohen 2021; Dijkstra 2022; Bedjanič & Dijkstra 2024). For the endemic species of *Paragomphus*, with the exception of the widespread *P. madegassus*, virtually nothing is known of their population status and possible threats to their survival. The same applies to the newly described *P. matroka*, for which a preliminary assessment as Data Deficient under the IUCN Red List of Threatened Species would be appropriate, given the currently fragmented information. Despite its protected status, and still well-preserved upper course of the Ampasy River and its tributaries, Tsitongambarika's forests are under pressure from slash-and-burn agriculture, selective logging, and expanding human settlements along its margins (Goodman *et al.* 2018; Fig. 9). Nevertheless, this protected area remains a critical refuge for the southeastern rainforest fauna of Madagascar and constitutes an important stronghold for the discovery and conservation of endemic freshwater and forest-associated species, including Odonata. During our brief visit to the northern part of Tsitongambarika, several additional endemic damselfly and dragonfly species were recorded and will be described in due course (Bedjanič *et al.*, *in prep.*).

Unfortunately, Madagascar's natural wealth and highly sensitive ecosystems—including wetland habitats that support a remarkable endemic odonate fauna—are severely threatened by a combination of factors, including direct human impacts such as overexploitation of natural resources and unsustainable agriculture, as well as natural disasters and climate change (Ralimanana *et al.* 2022). For comparatively well-studied taxa, such as lemurs, amphibians, reptiles, and birds, existing biodiversity data are generally sufficient to characterize major conservation challenges and to inform robust conservation strategies. In these groups, effective management and the expansion of biodiversity monitoring within protected areas remain key priorities. However, despite the umbrella effects of conservation initiatives and protected area management, which is largely centred on endemic vertebrates, the risk of extinction remains acute in understudied ecosystems and taxonomic groups. Odonata, in particular, must be recognized among those taxa for which conservation status, distribution, and ecological requirements remain insufficiently understood. The urgent need to address basic knowledge gaps in this charismatic insect group is particularly pressing given that dragonflies and damselflies are among the best environmental sentinels, sensitive to both aquatic and terrestrial habitat quality (Dijkstra 2022; Dijkstra & Cohen 2021; Samways *et al.* 2025).

In conclusion, the discovery of the new endemic *Paragomphus* species underscores the urgent need for intensified odonatological research in Madagascar. Accelerating studies on species distributions, taxonomy, phenology, and ecological requirements is crucial, particularly for informing threat assessments and the conservation of endemic odonate fauna. Equally important are initiatives aimed at promoting interest in odonatology, engaging citizen scientists, and raising awareness of the conservation importance of Madagascar's wetlands and rainforest ecosystems.

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