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A new species of social wasp from Madagascar with an inverted nest architecture (Hymenoptera, Vespidae)

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Abstract

Ropalidia jemmae **sp. nov.** is described from the protected Ankafobe evergreen forest in central Madagascar. This species is characterized by a variable black and green body colour pattern and a unique nest architecture within the genus *Ropalidia*. The nests of this species have an inverted cell opening orientation that exposes the cell bottoms outwardly, mimics the tree bark, and provides excellent visual nest concealment.

Keywords

Nest, new species, protected areas, social wasp, Vespidae

Introduction

Social insects occasionally have very welcome features that supplement the taxonomic work. In addition to their morphology, some species have unique nest architecture. This reflects their life cycle, and adaptive mechanisms that can contribute to speciation (Invernizzi and Ruxton 2019). Numerous evolutionary effects can be reflected in the nest architecture and nesting behaviour (Jeanne 1975), which prevents catastrophic brood loss (Furuichi and Kasuya 2015). Interestingly, the nesting architecture in vespid wasps is considered to have evolved predominantly in response to another group of social insects, the ants (Richards 1971; Jeanne 1975). Stalked nests, the outer envelope or adding the pulp to larva cocoon tops were developed to repel or reduce invertebrate access to the brood (Jeanne 1975; Furuichi and Kasuya 2015). In contrast to adaptations protecting against invertebrate predators, visually masking or concealing nests in the envelopes or tree hollows are believed to have evolved due to vertebrate nest predation, primarily driven by visual cues (Jeanne 1975).

Among social wasps, the most diverse nest architecture was reported in the genus *Ropalidia* (Kojima 1982; Spradbery and Kojima 1989; Wenzel 1998). Members of the former subgenus *Icarielia*, present in Asia and Australia, build enveloped nests with complex structures (Kojima 1982). On the other hand, most species in this genus build gymnodomous stelocyttarous nests, characterized by the stalked nest without any envelope (Jeanne 1975; Wenzel 1998). Most African mainland species build simple discoid nests (Polašek et al. in press), while Malagasy *Ropalidia* exhibit much greater nest architecture diversity (Vesey-Fitzgerald 1950; Blommers 2012).

All 43 Malagasy *Ropalidia* species are endemic (Carpenter and Madl 2009; Blommers 2012). Despite substantial obstacles in their separation due to the lack of a taxonomic revision, some species were shown to have unique nest architecture, which provides a valuable supplement to species determination (Blommers 2012). Notably, some Malagasy species build visually concealed nests directly on the tree trunks (Vesey-Fitzgerald 1950), a feature described in only one African mainland species (Polašek et al. 2022). In addition, *R. cocoscola* Blommers was reported to build entirely concealed nests within the tree trunk cavities, while *R. merina* Blommers (previously considered as *R. formosa* de Saussure) and *R. favulorum* Blommers create large nesting colonies of hundreds of nests that provide an additional layer of security (Wenzel 1987; Blommers 2012).

The aim of this study was to identify and describe a taxon that was recently observed in a protected area of the Ankafobe forest. The Tampoketsa de Ankazobe, including the Ambohitantely forest, is one of the last and the largest remaining fragmented forests on the highlands of Madagascar, a mosaic of forest and grassland. Ambohitantely forest consists of about around 80 sections of the subhumid, high plateau evergreen forest at an altitude between 1,300 and 1,650 metres. With about 1800 hectares of surface area, it harbours many endemic and critically endangered species of insects (Wesener et al. 2010; Wiorek et al. 2021; Moravec and Trzna 2022), frogs and mammals (Stephenson et al. 1994; Barata et al. 2022), requiring careful management, protection and restoration efforts.

Materials and methods

This study was based on the field observation of the wasps on a nest in the Ankafobe forest in October and November 2022. The initial observation prompted a wider-scale search for the corresponding specimen in the accessible entomological collections. In total, 18 collections were examined, including the American Museum of Natural History, New York, US [**AMNH**], Centre for Biodiversity Genomics, Guelph, Ontario, Canada [**CBCG**], Centrum für Naturkunde, Zoological Museum, Universität Hamburg, Germany [**CeNaK**], Entomological Collection, ETH Zurich, Switzerland [**ETH**], Hungarian Natural History Museum, Budapest, Hungary [**HNHM**], Museo di Storia Naturale di Venezia, Italy [**MSNV**], Muséum d'Histoire Naturelle, Geneva, Switzerland [**MHNG**], Museum für Naturkunde, Berlin, Germany [**MFNB**], National Museum of Natural History, Naturalis, Leiden, the Netherlands [**NNM**], Natural History Museum London, UK [**NHM**], National Museum Kenya, Nairobi, Kenya [**NMK**], National Museums Scotland, Edinburgh, Scotland [**NMS**], Oberösterreichisches Landesmuseum, Linz, Austria [**OLM**], Royal Museum for Central Africa, Tervuren, Belgium [**RMCA**], Swedish Museum of Natural History, Stockholm, Sweden [**NHRS**], Statens Naturhistoriske Museum, Copenhagen, Denmark [**SNM**], Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany [**ZFMK**] and Zoologische Staatssammlung München, Munich, Germany [**ZSM**].

All specimens were examined under a Leica S9i stereomicroscope and photographed with an integrated camera. Images were stacked using Helicon Focus version 6.8.0 (Kharkiv, Ukraine). All terga and sterna were denoted as T or S, while the flagellomeres were denoted as AF1–AF10.

Results

Taxonomy

Ropalidia jemmae **Polašek & de Beer, sp. nov.**
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Figs 1–5, holotype labels Fig. 6

Material. ***Holotype*****:** "Ankafobe/Ambohitantely", 1♀. ***Paratypes*****:** the same location as the holotype, 2♀♀. The nest from the same series also has an additional label "5. 52/ (RP)", [nest A] (all in MSNV).

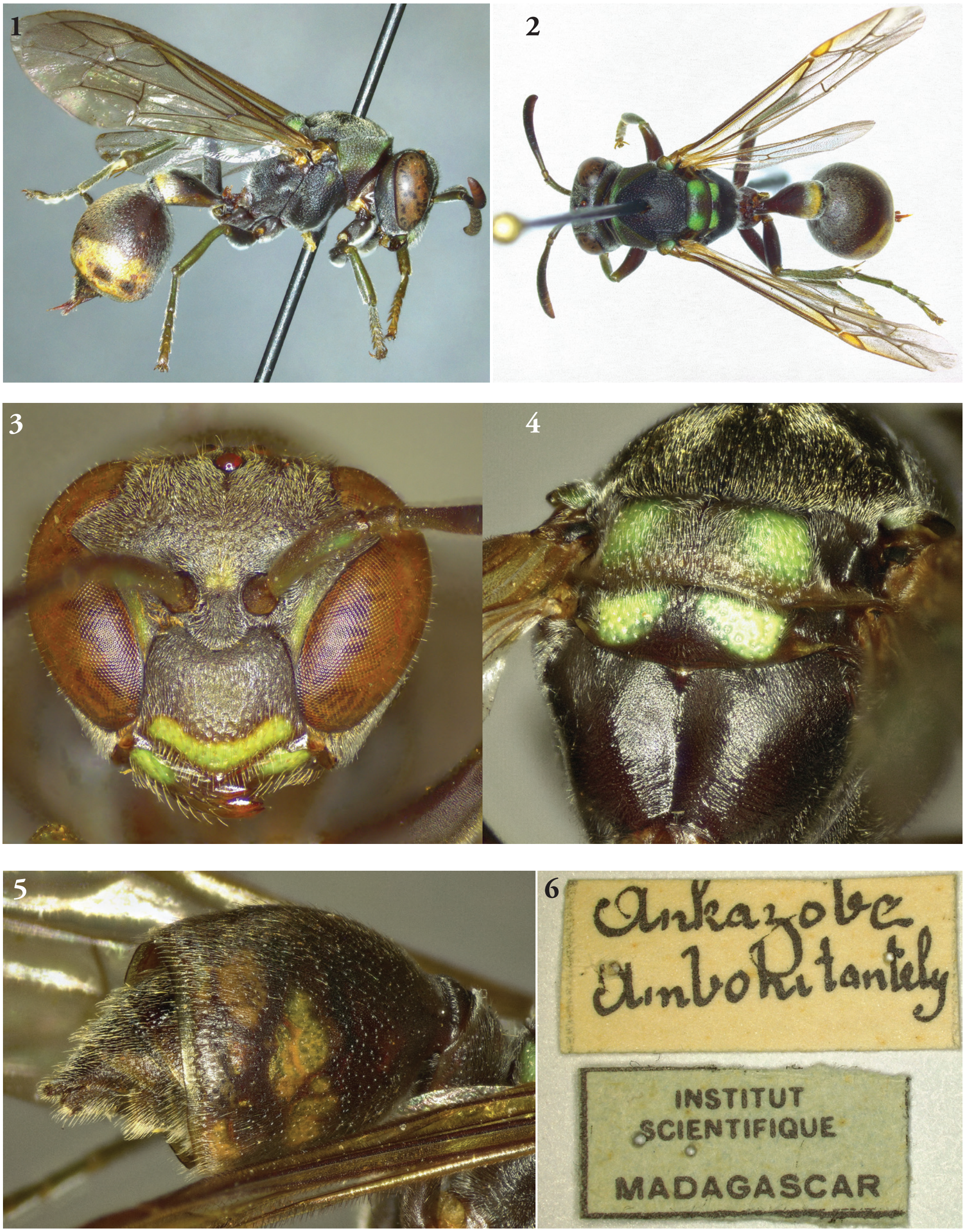
Observation data. Ankafobe [-18.10492, 47.187227], 27 Oct 2022 and 10 Nov 2022, 2♀♀ and a nest [nest B], obs. Len de Beer [https://www.inaturalist.org/observations/141686572, https://www.inaturalist.org/observations/140282514].

Diagnosis. This species is characterized by the combination of the following characters: T1 shape streamlined, propodeal excavation impunctate, black basal colour and variably expressed whitish-green markings on the head and mesosoma, green markings only on coxa II, widened posterior yellow-green bands on T1 and T2, and overall longer pilosity. ***Wing length*****:** 7.9 [7.8–8.0] mm.

Description. Female. ***Colour.*** Basal body colour black (Figs 1, 2). Head black, with green line in apical fourth of clypeus (Fig. 3). Interantennal area and inner orbits with faint green markings, mandible with basal green spot (Fig. 3). Gena and tempora suffused brown-green (Fig. 1). Antennal scape, pedicel and AF1 green ventrally, flagellum dorsally black, remaining flagellomeres ventrally orange (Fig. 1). Pronotum suffused green, with stronger green hue close to carina; inferior angle darker; mesonotum without green markings (Fig. 2). Suffused green spot high on mesopleuron, posterior third of tegula green (Figs 1, 2). Scutellum with two green spots; metanotum with two green spots that have stronger margins than those on scutellum (Fig. 4). Propodeum black (Fig. 4). Coxa I and III black, coxa II with lateral green quadrant (very faint in one specimen). Femora black with elongated or circular green spot near distal margin on femora II and III. Tibia with two shades of green; tarsi green, distally light brown (Figs 1, 2). Wings translucent, with some yellowing anteriorly; nervature yellow to brown, stigma yellowish and translucent, apical spot faintly developed in anterior third of marginal cell (Fig. 1). T1 with posterior yellow band that occupies about half of the total surface, thin connecting green suffused area and a dorsal remaining black diamond-shaped area (one paratype has mainly black T1, with thin remaining green band). T2 with posterior widened band, characterized by two larger attached areas and two remaining spots in basal colour near posterior margin, located close to T2/S2 suture (Fig. 1; band substantially reduced in one paratype, shown in Fig. 5). This pattern extends on S2 as short and smaller yellow-green spot, integrated with posterior band (very reduced in one specimen). Remaining terga and sterna in basal colour or somewhat brownish.

Head. Head frontally 1.2× as wide as high; clypeus 1.15× as wide as long (Fig. 3). Clypeal base elongated, lateral margins parallel, juxtamandibular lobe moderately developed, apex pointy and projecting (Fig. 3). Clypeus surface with basal sculpture and evenly spaced and well-defined small punctures, obscured by pubescence; punctures on apex coarser and converting into poorly defined craters (Fig. 3). Frons with dense, moderately sized and comparatively shallow punctures, vertex behind ocelli with diminishing punctures, area close to occipital carina impunctate and shiny. Gena and tempora with equally sized, but shallower punctures. Gena posteriorly 0.6–0.8× as wide as eye, mainly parallel to posterior eye margin; occipital carina complete, reaches mandible. Clypeus and frons covered by dense and straight silvery-yellowish pubescence and yellowish protruding setae, about equally long as forward ocellus diameter (Fig. 3). Compound eyes setose (Fig. 3). Ocellar triangle equidistant; distance between lateral ocelli about 0.6× of ocelli-eye distance. Scape equally long as AF1, AF1 equally long as AF2+3+4, AF2 about 1.4–1.5× as long as wide.

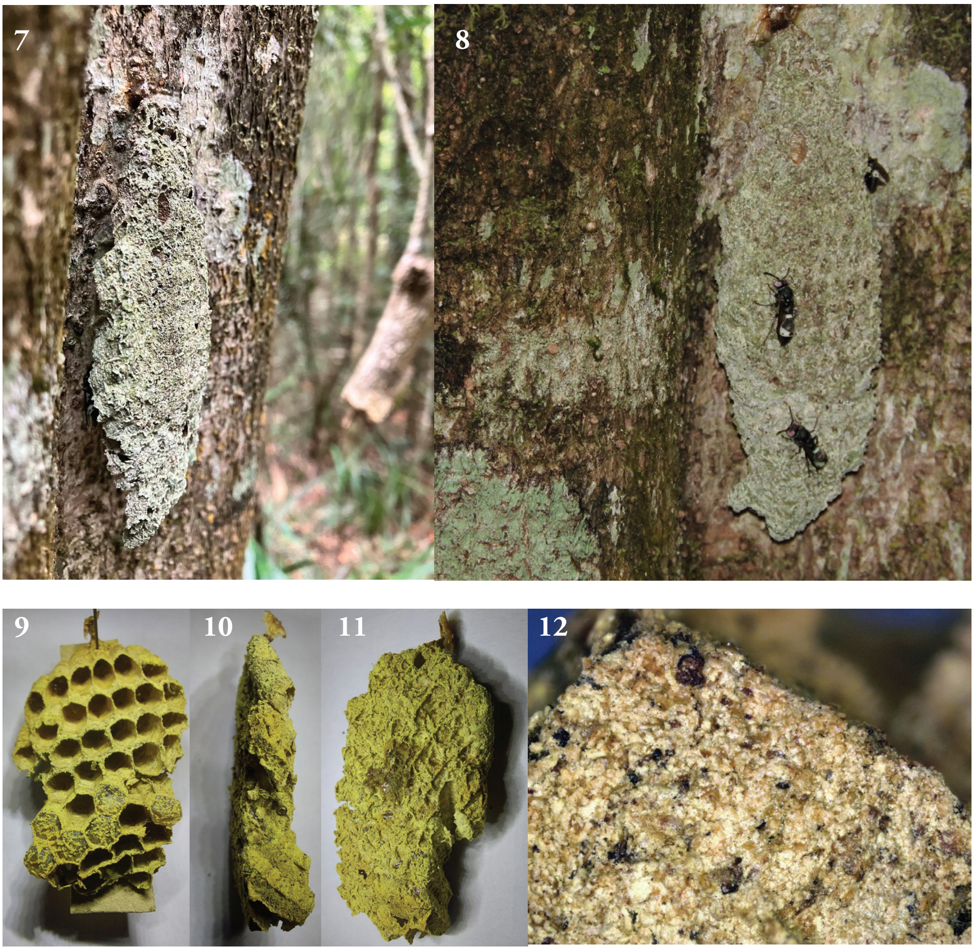
Mesosoma. Mesosoma about 1.8× as long as wide in dorsal view, mesonotum 1.2× as long as wide (Fig. 2). Head wider than pronotal carina width (Fig. 2). Pronotal carina developed as translucent rim, twice wider dorsally than laterally; entire pronotum covered by shallow and very dense punctures separated from each other by their diameter; inferior pronotal corner with increasingly larger punctures (Fig. 1). Mesonotum punctures less dense and shallow, somewhat denser close to scutellum. Mesopleuron densely punctate. Metapleuron shiny, with an occasional very weak punctum that can only be visualized in specimen rotation. Scutellum densely punctate, with shallower punctures than those on mesonotum. Median scutellar carina developed and thin, reaches about half of scutellar length. Metanotum dorsally punctate, with shiny impunctate posterior triangle with small projecting area towards propodeum. Propodeal excavation shallow, without strong carina; upper half with cuticular surface, lower with minute striae; entire propodeal excavation completely impunctate (Fig. 4). Entire mesosoma covered by silvery-yellowish pubescence and some protruding setae; setae



Figures 1–6. *R. jemmae* sp. nov., female, habitus **1** lateral view **2** dorsal view **3** head in frontal view **4** propodeal excavation **5** distal margin of T2 **6** label of the holotype.

on dorsal side of pronotum silvery, those on mesonotum yellowish. Propodeal excavation covered by longer silvery setae.

Metasoma. T1 pyriform and elongated, with developed dorsal part, but not globular in shape; posterior sulcus very weak (Figs 1, 2). T1 shallowly punctate, punctures poorly defined. T2 shiny, with shallow, dense and small punctures, covered by silvery pubescence and longer silvery-yellowish protruding setae that extend well over lamella (Fig. 5). T2 somewhat shorter than S2, visible in dorsally oblique lamella (Fig. 4). Remaining metasomal segments with weakly developed punctures and pubescence longer than that on T2 and S2.



Figures 7–12. *R. jemmae* sp. nov. nest **7** nest B, in situ, lateral view **8** with wasps **9** nest A, cell openings **10** lateral view **11** outer view (notably, the spot in the middle is the glue that connected the nest to the underlying cardboard) **12** greater magnification, showing a brittle paper structure.

Males are unknown (two more pre-hatching larvae were recovered from the cocoons of nest A, macerated and examined, but both were females). Notably, at least one male was observed on nest B (Fig. 8), with entirely yellow clypeus. However, in the absence of the specimen, the male remains undescribed.

Similar species. Several Malagasy species have a similar morphology and a general colour pattern. In order to provide sufficient support to separating *R. jemmae* sp. nov. from previously described species, a partial key is provided here. The key is designed to separate the four similar species from others (key couplet 1). The key couplet 2 can be treated as 25b in the previous key to Malagasy species (Giordani Soika 1991).

Nest. The nest is the single most interesting feature of this species, with unique architecture in the entire genus *Ropalidia*. Instead of the cell openings oriented outwardly, the nests *of R. jemmae* sp. nov. are inverted, with the cell openings oriented towards the nesting surface and the cell bottoms oriented outwardly (Fig. 7). The loosely built cell bottoms thus correspond to the rugged texture of the tree bark or the lichen and provide excellent concealment of the nest (Fig. 8). In addition, the nest is built with greenish-grey material, mostly homogenous, without streaks of different colours integrated into the cell walls, which are common in some other species.

The first examined nest, nest A, has a total of 43 cells, arranged in the 7*9 cells maximum. The nest is somewhat elongated, with six enclosed cells (Fig. 9). The paper structure is brittle, visible in several collapsed cells (Fig. 9). Approximately 50%–75% of the cell length overlap between the cell rows (Fig. 10). The stalk of the same nest is also inverted, suggesting attachment on the cell openings side (Fig. 10). The outer (bottom-exposed) side of the cells has a very textured surface with numerous arches, which do not reflect the cell wall structure but are located much more densely, providing a heavily textured outer surface (Fig. 11). The greater magnification shows no elongated fibres, but only clumps of heavily masticated and mostly rounded chips (Fig. 12).

The second, nest B, was only observed *in situ* (Figs 7, 8). The nest was on the tree trunk, 1.3 m above the ground. The nest colour and shape resemble the nearby greyish-green lichen patch (Fig. 7).

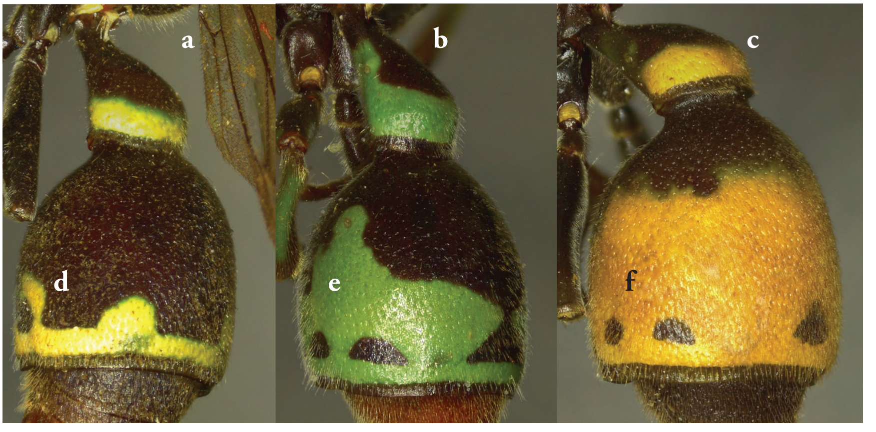
In comparison, the nests of *R. ranavali* are elongated with a pointy tip, suspended from similarly coloured branches (https://www.inaturalist.org/observations/63188743, https://www.inaturalist.org/observations/9173358). The nests of *R. venustula* and *R. scottiana* are unknown.

Etymology. The name is given after Jemma de Beer, who participated in the nest B discovery.

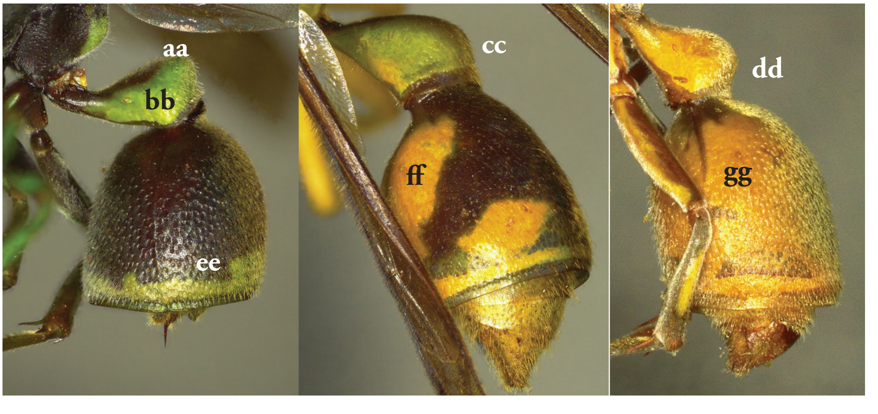
Distribution. All the examined specimens and observations originated from a narrow area (of no more than 16 km of distance) in central Madagascar near Ankafobe, at the edge of the Ambohitantely forest.

Partial key to species

1 T1 streamlined and posteriorly rounded, with poorly defined punctures (**a–c**). Basal body colour black(ish)-olivaceous, T2 with obligate posterior green or yellow band on T1 and T2, with additional four attached spots on T2 that can be small in size (**d**), intermediate and merged (**e**) or occupy most of T2 surface (**f**). Femora II and III black, sometimes with distal green or yellow spot. Mesonotum black. Wing length 7.5–10.3 mm **2**



– T1 differently shaped, dorsally developed (**aa**) and distally punctate (**bb**), more angulate (**cc**) or with stronger posterior sulcus (**dd**). Basal body colour variable; if there are green or yellow markings on T2 then those are either just a posterior band (**ee**), bilateral green-yellow spot near base (**ff**) or entire T2 surface green or yellow (**gg**). Femora II and III variably coloured (if T2 has wider posterior band, then femora are green). Mesonotum variably coloured (if T2 has wider posterior band, then mesonotum always with a pair of green longitudinal lines) .... **other species**, according to the Giordani Soika (1991) key

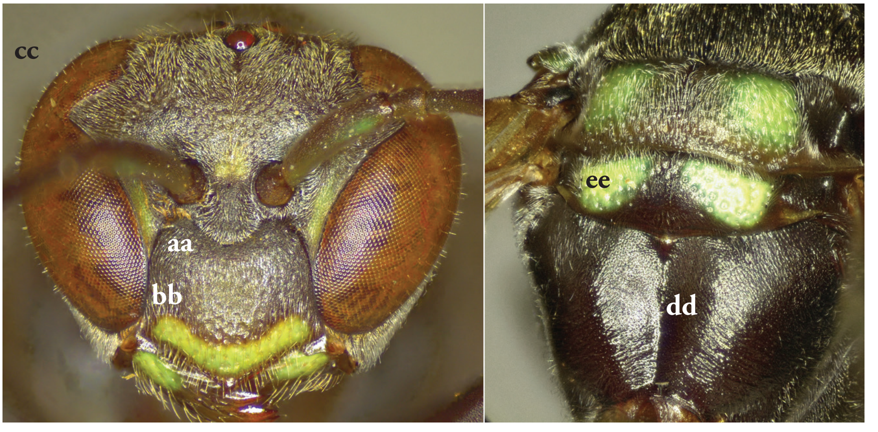


2 Head and mesosoma with numerous green or yellow markings (**a**). Pronotal carina twice broader dorsally than laterally, commonly with a fine translucent rim (**b**). Base of clypeus with poorly defined punctures (**c**). Femora II and III black with distal yellow or green spot (**d**) **3**

– Clypeus, interantennal area, pronotum, scutellum, mesopleuron and metanotum commonly black, at most with olivaceous suffused greenish colouration (**aa**). Pronotal carina equally wide dorsally and laterally, without translucent rim (**bb**). Base of clypeus with large and well-defined punctures (**cc**). Femora II and III at most with a very faint suffused olivaceous spot, commonly entirely black (**dd**) **4**

3 Face with numerous yellow markings, clypeus entirely yellow (**a**). Clypeus wider apically, pentagonal (**b**). Eyes asetose (**c**). Propodeal excavation shiny, with more developed striae, present in upper half (**d**); markings on body yellow-green (**e**). AF2 as long as wide.................. ***R. scottiana* (de Saussure)**

– Face mostly black, with lesser amount of greenish-white markings (**aa**). Clypeus elongated, with parallel sides (**bb**). Eyes covered by numerous straight setae (**cc**). Propodeal excavation shiny, upper half without punctures or striae (**dd**); markings greenish-white (**ee**). AF2 about 1.4–1.5× as long as wide .... ***R. jemmae* sp. nov.**



4 T2 with broad posterior yellow band (**a**). Distal margin of T2 towards lamella evenly rounded and straight; lamella with linear digitations, impunctate (**b**). .... ***R. ranavali* (de Saussure)**

– T2 with thin posterior whitish-yellow band with integrated spots (**aa**). Distal margin of T2 towards lamella serrated, with translucent rim; lamella coarsely punctate (**bb**) .... ***R. venustula* (de Saussure)**

Discussion

The new *Ropalidia* species exhibits an interesting case of an inverted nest, which can be considered an evolutionary reversal. Instead of favouring economically and structurally stronger ancestral nest type, with regular cell size and shared adjacent walls, this species evolved a trade-off by favouring visual concealment. Such architecture requires more founder and worker effort than ancestral nests, which might directly contribute to the low abundance and scarcity of collected or observed specimens. This kind of concealing of the nest is unique in *Ropalidia*, but a similar example of visual concealment is known from the Neotropical species of *Mischocyttarus* (Milani et al. 2021; O'Donnell 2021), suggesting that visual predation of social wasps nests is a common evolutionary pressure across continents.

The biology of *R. jemmae* sp. nov. remains unknown, but this is similar to almost all Malagasy *Ropalidia*, with only a handful of documented field observations (Vesey-Fitzgekald 1950; Wenzel 1987; Blommers 2012). Lastly, the declining habitat undoubtedly presents another negative factor towards species abundance, suggesting the need to reverse this trend, propelled by the restoration of the native forests.

The green cuticular colour in Malagasy Vespidae is a strong indicator of the selective pressure exerted on the nests and the adult wasps. Interestingly, the same feature is known not only for numerous *Ropalidia* species, but also for several *Belonogaster* species (Hensen and Blommers 1987), and at least one eumenid species (Giordani Soika

1941). This pattern of local camouflage can be viewed as both colour matching (fitting the background colour) and disruptive colouring (the pattern of green and black areas on the body that cause visual confusion and break the expected body contour). It seems that the adaptive radiation in Madagascar has taken more concealed pathway in vespid wasps, as opposed to bright black-and-yellow species present in temperate regions or brown- red-black predominant colour in tropical regions.

The conservation efforts in Malagasy forests are of utmost importance in maintaining their biodiversity. The restoration efforts, while present in the area, are hampered by cultural practices, exploitation of the forests, and invasive species. Additional effort is warranted, in order to retain the known and unknown biodiversity of this irreplaceable area. The mosaic of forest and grassland called the Tampoketsa d' Ankazobe, which is the only proven habitat for *Ropalidia jemmae* sp. nov., has the disadvantage of proximity to Madagascar's capital city and has been subject to years of exploitation for wood in an area, where the use of fire regularly during the dry period, has almost totally decimated what was once a diverse mix of trees and grass.

Protective and restorative efforts focused on the remaining fragments of evergreen forests in the Tampoketsa, namely Ankafobe and Ambohitantely are of paramount importance in retaining their utterly unique elements of biodiversity that are not found anywhere else, including in some cases not even anywhere else in Madagascar. Several NGOs are undertaking restorative reforestation under challenging conditions.

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