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## Research article

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# A new species and first record of *Vates* Burmeister, 1838 from the Atlantic Rainforest (Mantodea: Vatinae)

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**Abstract.** A new species of praying mantis, *Vates phoenix* sp. nov. (Mantidae, Vatinae), is described from localities within Rio de Janeiro and São Paulo states, Brazil. This is the first record of *Vates* from the Atlantic Rainforest biome. The new species is unique among its congeners in having, among other features, strongly reduced cuticular projections above the lateral ocelli, structures otherwise well developed and produced in all other species of *Vates*. Remarks on the natural history and biogeography of *Vates*, in relation to this new finding, are further discussed.

Keywords. Atlantic Rainforest, new species, Mantodea, Vatinae, natural history.

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# Introduction

The Vatini Stål, 1877 (Mantidae Latreille, 1802) is a relatively diverse clade of cernomantodean (hearing) praying mantises found mostly in the Neotropical region. Members of this clade are plant mimics and can be distinguished from other Neotropical taxa by: i) having strong longitudinal carinae along the meso- and metathoracic legs, often developed into produced lobes — in taxa lacking lobes, the carinae confer legs with a curvy appearance; ii) ocellar tubercle with cuticle extending above margins of ocelli

to varying lengths, often in the form of two parallel or divergent, conical projections, sometimes as long as the insect's head. Their various foliaceous, cuticular processes on head, limbs and abdomen vary in number, size and arrangement, defining the different genera. Other character states include males with asymmetric antennomeres and margins of pronotum denticled.

Svenson *et al.* (2015) proposed a new higher-level classification for the subfamily Vatinae Stål, 1877 after conducting a total-evidence phylogenetic analysis, granting with tribal rank (Vatini) the clade comprising Vates Burmeister, 1838, Pseudovates Saussure, 1869, Alangularis Svenson et al., 2015, Callivates Roy, 2003 and Zoolea Serville, 1839. Following their comparative analysis of male genital structures, Schwarz & Roy (2019) provided further evidence for the validity of this clade, although they granted Vatini sensu Svenson et al. (2015) subtribal rank as the Vatina, which along with Heterovatina Svenson et al., 2015 formed their tribal concept of Vatini. Whether as a tribe or subtribe, this clade includes five genera and 44 species. Two genera, *Callivates* and *Alangularis*, are monotypical, whereas Zoolea is the only genus that has been the subject of recent revisionary work (Roy & Ehrmann 2009). Members of this clade are distributed in tropical and subtropical regions within the Neotropics and southern Nearctic. Most species within the tribe prefer tropical, wet forest, although some members of Pseudovates and Zoolea can be found in more seasonal biomes across their area of distribution. Vates is the second most diverse genus of its clade only after *Pseudovates* (13 spp vs 24 spp, sensu Svenson et al. 2015). Since Giglio-Tos' (1914) first species-level revision, Vates has never been subject of a modern taxonomic treatment. Nevertheless, species-level identification is straightforward for the most common species.

Distributed from Southern Mexico to north of Patagonia, the taxonomic concept of *Vates* has remained relatively stable since its original formulation (Burmeister 1838) and following redefinitions (e.g., Rehn 1911; Giglio-Tos 1914, 1927; Terra 1995). In its most recent definition (Svenson *et al.* 2015), *Vates* was characterized by the following combination of characters: i) males with pectinate antennae, ii) mesothoracic tibiae with two median lobes, iii) ocellar tubercle cuticle above lateral ocelli forming contiguous or divergent conical projections, and iv) male genitalia with posterior process (Pda) of the ventral left sclerite (L4A) acuminate or 'scimitar-like'. According to Svenson *et al.* (2015), *Vates* currently comprises 13 species, including *Vates chopardi* (Deeleman-Reinhold, 1957), formerly placed in *Lobovates* Deeleman-Reinhold, 1957, but synonymized under *Vates* in the same publication.

In this study, we report and describe a new and elusive species of *Vates* from the Atlantic Rainforest of Rio de Janeiro, Brazil. The new species is readily distinct from all other known congenerics by unique character states and for being the first member of *Vates* described from this rich but highly endangered biome. This new finding ultimately enabled us to highlight some biogeographic aspects of praying mantis taxa associated with tropical rainforest biomes across South America.

# Material and methods

Examined specimens were either collected in the field or borrowed from a museum depository. We examined a total of 15 adult specimens — 13 males and 2 females — from various localities within the Atlantic Rainforest biome. Nine specimens (eight males, one female) were borrowed from Museu Nacional, Rio de Janeiro, with collecting dates ranging from 1915 to 1936. The remaining six specimens (five males, one female) were collected between the years 2016 and 2018 at the following localities:

**Jardim Botânico do Rio de Janeiro – JBRJ** (Fig. 1A) (22°96′73.717″ S, 43°22′50.381″ W; elevation ca 5 m). A federal conservation and research area within Rio de Janeiro municipality, the JBRJ extends over 137 hectares, 54 of which consist of an arboretum housing thousands of plant representatives from all over the world. This area is contiguous to Parque Nacional da Tijuca (Tijuca National Park) and Parque da Cidade (City Park), two Atlantic Rainforest reserves. The single female specimen collected at JBRJ

was incidentally found while walking along a pathway within the arboretum. The area is surrounded by numerous old and tall tree species.

**Fazenda Recanto** (Fig. 1B) (22°07′15.3″ S, 43°51′01.2″ W; elevation ca 560 m). A privately owned farmland in Valença municipality, Rio de Janeiro state, Brazil. The area consists of a mix of secondary Atlantic Rainforest, exotic eucalyptus forests, cattle pasture and gardens. Three adult males were collected there, lured by lights (two on a white cloth light trap and another one on an outdoor light at the house's balcony). The house's backyards, where the light trap was set, consisted of gardens with many ornamental and fruit plants, both native and exotic.

**Reserva Ecológica do Guapiaçu** – **REGUA** (Fig. 1C) (22°27'10.309" S; 42°46'13.011" W; approx. elevation 50 m). A private conservation area in Cachoeiras de Macacu municipality. The reserve consists of several well-conserved secondary forest patches, including lowland Atlantic Rainforest and wetlands, the latter among the most diverse ecosystems within this biome. The two males collected there were lured to a light trap set near the reserve's headquarters.

The light traps used for field collections consisted of a white cloth with a 250W mixed mercury vapor bulb (Fig. 1D). All collected specimens were kept in captivity inside glass terrariums fitted with twigs and leaves as perching sites and large enough to enable free movement. Specimens were kept alive and maintained on a diet of wild-caught insects (mostly grasshoppers) until natural death. All specimens were photographed and observed to document behaviour. Morphological nomenclature, specimen preparation and genital dissection procedures followed Brannoch *et al.* (2017); body measurements were taken on right side structures using a pachymeter. Photographs of the holotype, allotype and live specimens were made using a DSLR camera with a 100 mm macro lens, and then edited using Adobe Photoshop and Adobe Lightroom. Genitalia captures were done using a Leica MZ16 stereo microscope connected to a Leica DMC4500 camera.

All specimens examined are deposited at the Museu Nacional, Rio de Janeiro, Brazil.

### Repositories

MNRJ = Museu Nacional, Rio de Janeiro, Brazil

### Location abbreviations in Table 1

- FR01 = *Vates phoenix* from Fazenda Recanto, Valença. Collected 15 Nov. 2015 (MNRJ-ENT6-28441)
- FR02 = *Vates phoenix* #02 from Fazenda Recanto, Valença. Collected 30 Dec. 2016 (MNRJ-ENT6-28443)
- FR03 = *Vates phoenix* #03 from Fazenda Recanto, Valença. Collected 15 Nov. 2015 (MNRJ-ENT6-28445)
- JB01 = *Vates phoenix* #01 from Jardim Botânico do Rio de Janeiro. Collected 29 May 2018 (MNRJ-ENT6-28442)
- JB02 = *Vates phoenix* #02 from Jardim Botânico do Rio de Janeiro. Collected May 1935 (MNRJ-ENT6-28455)
- RG01 = *Vates phoenix* #01 from Reserva Ecológica de Guapiaçu, Cachoeiras de Macacu. Collected 18 Dec. 2017 (MNRJ-ENT6-28446)
- RG02 = *Vates phoenix* #02 from Reserva Ecológica de Guapiaçu, Cachoeiras de Macacu. Collected 18 Dec. 2017 (MNRJ-ENT6-28447)
- CO = *Vates phoenix* from Corcovado, Rio de Janeiro. Collected Jan. 1936 (MNRJ-ENT6-28448)
- JU01 = Vates phoenix #01 from Jussaral, Angra dos Reis. Collected Sep. 1935 (MNRJ-ENT6-28449)
- JU02 = *Vates phoenix* #02 from Jussaral, Angra dos Reis. Collected Sep. 1934 (MNRJ-ENT6-28450)



**Fig. 1.** Habitat of *Vates phoenix* sp. nov. in the Atlantic Rainforest, highlighting variation across collecting sites. **A**. Jardim Botânico do Rio de Janeiro. **B**. Fazenda Recanto, Valença. **C**. Reserva Ecológica de Guapiaçu, Cachoeiras de Macacu. **D**. Customized white cloth light trap used to lure adult males.

JU03	=	<i>Vates phoenix</i> #03 from Jussaral, Angra dos Reis. Collected Sep. 1935 (MNRJ-ENT6-28451)
JU04	=	Vates phoenix #04 from Jussaral, Angra dos Reis. Collected Sep. 1935 (MNRJ-ENT6-28452)
JU05	=	Vates phoenix #05 from Jussaral, Angra dos Reis. Collected Sep. 1934 (MNRJ-ENT6-28453)
JU06	=	Vates phoenix #06 from Jussaral, Angra dos Reis. Collected Sep. 1934 (MNRJ-ENT6-28454)
AN	=	Vates phoenix from Angatuba, São Paulo. Collected Nov. 1917 (MNRJ-ENT6-28456)

#### Abbreviations for structures

afa	=	anterior process (left phallomere)
an	=	anterior apodeme
bm	=	dextral extension
fda	=	main posterior lobe (with R1 sclerotization)
L4A	=	sclerite extending over the ventral wall (ventral phallomere)
L4B	=	sclerite extending over the dorsal wall (left phallomere)
loa	=	posteromesal lobe (left phallomere)
Paa	=	posterior process (left phallomere)
Pda	=	posterior process (ventral phallomere)
Pia	=	process posterolateral to Pva (right phallomere)
Pva	=	process anteromesal to Pia (right phallomere)

R3 = anteriorly extending sclerite (right phallomere)

# Results

Class Insecta Linnaeus, 1758 Order Mantodea Burmeister, 1838 Family Mantidae Latreille, 1802 Subfamily Vatinae Stål, 1877 Tribe Vatini Stål, 1877 Genus *Vates* Burmeister, 1838

# *Vates phoenix* sp. nov. urn:lsid:zoobank.org:act:EB7BB1D8-786F-401C-B408-2D41260C7797 Figs 2–5, 6A–H, 8–9; Table 1

#### Diagnosis

The new species can be easily recognized by the following combination of characters: i) cuticular projections above lateral ocelli strongly reduced (almost entirely missing in some specimens); ii) antennomeres of males asymmetrical (s-shaped); iii) hindwing of females with large, yellowish white and partially opaque area that spreads over most or part of the membrane; iv) anterodorsal lobe of hind tibiae at least 50% the length of tibial length (i.e., not narrowly restricted to its middle section).

### Etymology

The specific epithet refers to the Phoenix, a mythical, immortal creature that is born again from its own ashes after being consumed by fire. The new species is a homage to the Museu Nacional of Rio de Janeiro, which was destroyed during a massive fire on September 2, 2018. The entire entomological collection, representing more than 5 million specimens, was destroyed, including all praying mantis specimens. Only a few specimens of *Vates* borrowed in the context of this study, including our new species, survived the event. *Vates phoenix* sp. nov. thus symbolically attempts to link the past and the future of the Museu Nacional, as it represents the rebirth of the Mantodea collection and our hopes for the revival of an even stronger institution in the not too distant future.

#### Material examined

#### Holotype

BRAZIL •  $\mathcal{J}$ ; Rio de Janeiro, Valença, Fazenda Recanto; 22°07′15.3″ S, 43°51′01.2″ W; alt. 560 m; 15 Nov. 2015; Projeto Mantis leg.; white cloth light trap; MNRJ-ENT6-28441.

#### Allotype

BRAZIL • 1 ♀; Rio de Janeiro, Rio de Janeiro City, Jardim Botânico do Rio de Janeiro; 22°96′73.717″ S, 43°22′50.381″ W; alt. 7 m; 29 May 2018; M.L.F. Teixeira leg.; manual collection; MNRJ-ENT6-28442.

#### Paratypes

BRAZIL – **Rio de Janeiro** • 1 3; same collection data as for holotype; MNRJ-ENT6-28445 • 1 3; same collection data as for holotype; 31 Dec. 2016; white cloth light trap; William Moura leg.; MNRJ-ENT6-28443 • 2 33; Reserva Ecológica de Guapiaçu, Cachoeiras de Macacu; 22°27'10.309" S, 42°46'13.011" W; alt. 37 m; 18 Dec. 2017; Projeto Mantis leg.; white cloth light trap; MNRJ-ENT6-28446, MNRJ-ENT6-28447 • 1 3; Rio de Janeiro City, Corcovado; 22°57'06" S; 43°12'37" W; alt. 600 m; Jan. 1936; D. Mendes leg.; MNRJ-ENT6-28448 • 3 33; Angra dos Reis, Jussaral Train Station (note: now in ruins, the station closed down in 1996); 22°56'26" S, 44°16'26" W; alt. 351 m; Sep. 1934; D. Mendes leg.; MNRJENT6-28450, MNRJ-ENT6-28453, MNRJ-ENT6-28454 • 3 33; same collection data as for preceding; Sep. 1935; D. Mendes leg; MNRJ-ENT6-28449, MNRJ-ENT6-28451, MNRJ-ENT6-28452 • 1 2; same collection data as for allotype; May 1935; MNRJ-ENT6-28455. – São Paulo • 1 3; Angatuba; 22°56'26" S, 44°16'26" W; alt. 7 m; Nov. 1917; A. Marques leg.; MNRJ-ENT6-28456.

### Description

**Male** (holotype; MNRJ-ENT6-28441) HABITUS. Live specimen (paratype) in Fig. 2A; pinned specimen (holotype) in Fig. 2C.

MEASUREMENTS. See Table 1 (specimen FR01).

HEAD. Eyes rounded (Fig. 3A). Vertex flat, higher than imaginary line connecting dorsal margin of compound eyes. Juxtaocular bulges flat, aligned to vertex. Ocellar tubercles (Fig. 3A) bearing two poorly developed conical projections, one over each lateral ocellus, only scarcely spaced (variation of this character across examined specimens is shown in Fig. 3B–E). Central ocellus elliptical, lateral ocelli rounded. Antennae (Fig. 3F–H) with scape and pedicel light brown, rest of antennae dark brown, proximal-most antennomeres cylindrical, eventually turning strongly asymmetrical, conferring antennae with a pectiniform appearance, distal-most antennomeres more or less filiform. Lower frons (Fig. 3A) sub-pentagonal, wider than high and with upper margin arcuate, surface smooth, concave and medially darkened. Maxillary palps light brown. Inner margin of labial palpi dark, basal-most segment with dark spots.

THORAX. Pronotum (Fig. 3I) elongated, metazona triangular in cross-section. Supracoxal dilation moderately pronounced and broadly rounded; ratio metazona/prozona = 4.12 (variation across specimens 4.5–3.75). Distal margin of prozona uniformly curved, margins with small, spine-like, blunt tubercles, denser along prozona than along metazona and mostly absent proximally. Dorsal surface of metazona keeled along its midline (keel more pronounced proximally). Pronotum predominantly green, except for darkened prozone and lateral margins of metazona. Variation in pronotal size and shape across examined specimens shown in Fig. 3J–L.

PROTHORACIC LEGS. Forecoxae triangular in cross-section; ventral margin pale green, except for a small and distally positioned dark spot on its anterior aspect, and a larger preapical spot posteriorly;

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Character	FR01	JB01	FR02	FR03	RG01	RG02	CO	JU01	JU02	JU03	JU04	JU05	90Nf	AN	JB02
Sex	F0	0+	r0	60	F0	F0	r0	F0	60	60	F0	F0	F0	F0	0+
Body length	64.0	67.5	66.0	66.0	64.0	64.5	64.0	67.0	68.0	64.0	68.5	67.5	68.5	66.0	65.0
Head width	5.0	6.9	6.0	6.0	6.0	6.0	5.5	6.0	6.0	6.0	6.0	6.0	6.5	6.0	7.0
Head length	2.5	3.0	2.5	2.5	2.5	2.5	2.0	2.0	2.5	2.5	2.5	2.5	2.5	2.3	3.0
Lower frons width	1.5	2.5	1.5	1.5	1.5	1.5	damaged	1.5	1.0	1.0	2.0	1.5	1.0	1.0	2.5
Lower frons length	1.0	1.4	1.0	1.0	1.0	1.0	1.5	1.0	1.0	0.6	1.0	1.0	1.0	1.0	2.5
Pronotal length	20.5	23.2	22.5	21.3	20	19	19.5	21.5	20.5	19.5	21.5	21.5	21.5	21	23
Prozone	4.0	4.2	4.5	4.0	4.0	4.0	3.5	3.5	3.5	3.5	4.0	4.0	4.0	4.0	4.1
Metazone	16.5	19	18.0	17.3	16.0	15.0	16.0	18.0	17.0	16.0	17.5	17.5	17.5	17.0	18.9
Pronotal width	4.0	5.2	4.0	4.5	4.0	4.0	4.0	4.5	4.0	4.0	4.3	4.0	4.0	4.0	5.0
Ratio metazone/prozone	4.12	3.65	4.50	3.85	4.00	3.75	4.00	4.00	4,25	4.00	04.05	4.37	4.37	4.37	3.78
Forewing length	42.0	40.3	44.0	42.3	41.0	43.5	40.0	43.0	43.5	43.0	44.0	43.0	43.5	40.5	40.0
Forewing width	9.0	10.0	9.0	8.5	8.0	8.5	ı	ı	ı	ı	·	ı	ı	ı	
Hindwing length	37.5	35.2	38.0	37.6	39.5	39.0	ı	ı		ı	·	ı	·	ı	·
Hindwing width	17.0	18.6	16.0	17.5	16.0	16.0	·	ı	ı	ı	ı	ı	ı	ı	
Forecoxal length	11.0	14.4	11.0	11.0	11.0	11.0	11.0	11.0	11.0	10.6	11.0	11.5	11.5	11.5	13.5
Forecoxal width	1.5	2.5	1.5	1.6	1.5	1.5	2.0	2.0	1.5	1.5	2.0	2.0	2.0	1.6	2.0
Forefemoral length	14.0	15.3	14.5	12.5	12.5	11.5	12.0	13.0	13.0	12.3	12.6	13.0	12.6	12.5	15.0
Forefemoral width	1.6	2,3	2.0	1.6	1.6	1.6	1.5	2.0	2.0	2.0	2.0	2.0	2.0	1.6	3.0
Foretibial length (D1)	5.0	6.0	5.5	5.0	4.6	4.5	4.5	5.0	5.0	5.0	5.0	5.0	5.0	4.5	5.5
Foretibial length (D2)	7.0	9.0	7.5	7.33	7.0	7.0	7.0	7.5	7.0	7.0	7.5	7.0	7.33	7.33	8.0
Mesocoxa	4.0	6.5	5.5	4.0	4.0	4.0	4.0	4.0	4.5	4.0	4.5	4.5	5.0	4.5	6.0
Mesofemur	11.0	12	11.0	11.0	10.0	10.0	10.0	10.0	10.0	10.0	11.0	11.0	11.0	11.0	12.3
Mesotibia	8.3	9,6	9.0	8.6	9.0	8.0	8.0	8.0	8.5	9.0	9.0	8.5	8.6	8.6	10.0
Mesotarsus	6.0	7,7	6.0	6.0	6.0	6.0	6.0	5.0	6.0	6.5	6.0	5.5	6.5	6.0	7.0
Metacoxa length	4.0	5.7	4.0	4.5	4.5	4.0	4.0	4.0	4.0	4.0	4.5	4.5	5.0	4.5	5.5
Metafemur length	13.5	14,3	15.0	13.5	13.5	13.0	12.0	13.0	12.0	12.0	14.0	13.5	13.66	13.6	15.3
Metatibia length	11.5	14,3	11.5	12.0	12.0	11.5	11.0	12.0	11.5	12.0	12.5	12.0	12.0	11.6	13.0
Metatarsus length	6.0	8.5	7.0	7.5	7.0	7.5	6.5	7.0	7.0	7.5	8.5	8.0	8.5	8.5	8.0

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dorsal margin bearing five spine-like, darkened tubercles interleaved with smaller, paler ones; anterior aspect of forecoxae light colored, darked apically, rest of structure dark brown. Spination formula: F=4DS/14AvS/4PvS; T=14AvS/8(R)-10(L)PvS. Forefemora light brown, three-banded, with a small dark spot near trochanter; dorsal margin of forefemora slightly sinuous; discoidal spines I, II and III mostly pale with darkened apex, spine IV entirely dark; anteroventral spines II, IV, VI, X and XII slightly reclined and entirely dark, spine XV larger than the others, entirely dark and not curved; remaining spines smaller, pale and with darkened apex; genicular spines developed and present on both sides of femora; tibial spur groove located in proximal  $\frac{1}{4}$  of femora. Foretibiae light brown, dorsally three-banded.

WINGS. Forewings (Fig. 2C) surpass abdomen by <sup>1</sup>/<sub>4</sub> of its length in resting position. Costal area distally tapering, membrane opaque and predominantly green, with a yellowish longitudinal strip along margin of costal vein; discoidal area entirely hyaline with yellowish to brownish longitudinal veins, apex slightly darkened, with more densely reticulate venation. Hindwings (Fig. 2C) hyaline and colorless, yellowish to brownish longitudinal veins, apex of discoidal area densely reticulated and dark brown.



**Fig. 2.** Adults of *Vates phoenix* sp. nov. **A**–**B**. Live specimens photographed in a studio. **A**. Paratype,  $\Diamond$ , from Reserva Ecológica de Guapiaçu (MNRJ-ENT6-28446). **B**. Allotype,  $\heartsuit$ , from Jardim Botânico do Rio de Janeiro (MNRJ-ENT6-28442). – **C**–**D**. Pinned adults. **C**. Holotype,  $\Diamond$ , from Fazenda Recanto (MNRJ-ENT6-28441). **D**. Allotype,  $\heartsuit$  (MNRJ-ENT6-28442). Scale bars: C–D = 10 mm.



**Fig. 3.** *Vates phoenix* sp. nov., male morphology. **A**. Head, frontal view, holotype (MNRJ-ENT6-28441). – **B**–**E**. Variation in ocellar tubercles across localities (not to scale). **B**. Fazenda Recanto, holotype (MNRJ-ENT6-28441). **C**. Reserva Ecológica de Guapiaçu, paratype (MNRJ-ENT6-28447). **D**. Jussaral, paratype (MNRJ-ENT6-28449). **E**. Corcovado, paratype (MNRJ-ENT6-28448). – **F**–**H**. Antenna, highlighting sectional variation of antennomeres. **F**. Basal section. **G**. Mid section. **H**. Apex. – **I**–**L**. Pronota, highlighting size variation. **I**. Fazenda Recanto, holotype (MNRJ-ENT6-28441). **J**. Reserva Ecológica de Guapiaçu, paratype (MNRJ-ENT6-28441). **J**. Reserva Ecológica de Guapiaçu, paratype (MNRJ-ENT6-28447). **K**. Jussaral, paratype (MNRJ-ENT6-28449). **L**. Angatuba, paratype (MNRJ-ENT6-28456). Scale bars: A = 1 mm; I–L = 5 mm.

MESO- AND METATHORACIC LEGS. Mesothoracic femora (Fig. 4A) with a marked posteroventral keel that forms two evident lobes: a proximal, elongated but scarcely produced lobe, and a pre-apical, short and produced lobe whose shape resembles that of a shark's dorsal fin (variation of this character across specimens can be seen in Fig. 4B–D). Metathoracic femora (Fig. 4E) with a marked posteroventral keel that forms a single, preapical lobe, also shaped like a shark's dorsal fin (variation of this character across specimens can be seen in Fig. 4F). Mesothoracic tibiae (Fig. 4G) with two medial lobes: a produced, anterodorsal lobe almost as long as tibia itself, and an anteroventral one, almost equally produced but clearly shorter (variation of this character across specimens can be seen in Fig. 4K) with two elongated lobes, anterodorsal one longer and wider than anteroventral one, and also more prominent than its homologue on mesothoracic tibiae (variation of this character across specimens can be seen in Fig. 4L–M).

ABDOMEN. Slightly compressed dorsoventrally, widest between segments III–V. Tergites I–III with a whitish coloration, remaining tergites darkened. Supraanal plate triangular in shape, wider than longer, apex medially notched, forming two small, lateral lobes. Cerci cylindrical and elongated, not surpassing apex of subgenital plate, last cercomere conical.

GENITALIA (note: holotype was not dissected; the following description corresponds to genital structures of paratypes). Left phallomere (Fig. 5A–E): sclerite L4B longer than wide, its left margin projects anteriorly; anterior process (afa) glabrous, sinuous, basal half broad but tapering distally, apex more strongly sclerotized, with sharp, pointy apex; posteromesal lobe (loa) elongated and sinuous, glabrous, lacking projections; posterior process (Paa) elongated, slightly curved left, apex curved anteriorly. Ventral phallomere (Fig. 5F–I): sclerite L4A roughly oval, proximal left margin slightly sinuous and strongly sclerotized, forming a small, medial projection followed by a membranous notch; posterior process (Pda) elongated, apex strongly scletorized and tapering distally, uniformly curved right, although its distal third curves anteriorly. Right phallomere (Fig. 5J–N): roughly triangular, distal margin folded anteriorly; anterior apodeme (an) of sclerite R3 elongated, distally broadened, bearing a small, basal process near its articulation to main posterior lobe (fda), the latter with a relatively short and broad dextral extension (bm); process anteromesal to Pia (Pva) elongated and finger-like, slightly curved ventrally, strongly sclerotized, with a moderately truncated apex; process posterolateral to Pva (Pia) elongated and well sclerotized.

Female (allotype; MNRJ-ENT6-28442)

HABITUS. Live specimen (allotype) in Fig. 2B; pinned specimen (allotype) in Fig. 2D.

MEASUREMENTS. See Table 1 (specimen JB01).

HEAD. Eyes rounded (Fig. 6A). Vertex flat, higher than imaginary line connecting dorsal margin of compound eyes. Parietal suture darkened, juxtaocular bulges flat and aligned to vertex. Ocellar tubercles (Fig. 6B) bearing two poorly developed conical projections, one over each lateral ocellus and barely spaced (variation of this character across specimens can be seen in Fig. 6C). Ocelli rounded, lateral ocelli twice as large as central ocellus. Antenna filiform, scape and pedicel light brown, flagellomeres dark brown. Lower frons sub-pentagonal, wider than high, smooth, medially darkened, upper margin arcuate, smooth and concave. Maxillary palps light brown; inner margin of labial palpi darkened, basal-most segment with dark spots.

THORAX. Pronotum elongated (Fig. 6D), metazona triangular in cross-section. Supracoxal dilatation moderately pronounced and broadly rounded; ratio metazona/prozona = 3.65 (additional paratype female = 3.78). Distal margins of prozona uniformly curved, margins with small, spine-like, blunt tubercles, denser along prozona than along metazona and mostly absent proximally. Dorsal surface of



Fig. 4. Mid- and hind legs of *Vates phoenix* sp. nov., highlighting variation across male specimens. A–D. Mid femora. A. Holotype from Fazenda Recanto (MNRJ-ENT6-28441). B. Paratype from Reserva Ecológica de Guapiaçu (MNRJ-ENT6-28447). C. Paratype from Jussaral (MNRJ-ENT6-28449). D. Paratype from Angatuba (MNRJ-ENT6-28456). – E–F. Hind femora. E. Holotype from Fazenda Recanto (MNRJ-ENT6-28441). F. Paratype from Angatuba (MNRJ-ENT6-28456). – G–J. Mid tibiae. G. Holotype from Fazenda Recanto (MNRJ-ENT6-28441). H. Paratype from Reserva Ecológica de Guapiaçu (MNRJ-ENT6-28447). I. Paratype from Jussaral (MNRJ-ENT6-28449). J. Paratype from Angatuba (MNRJ-ENT6-28447). L. Paratype from Jussaral (MNRJ-ENT6-28441). L. Paratype from Jussaral (MNRJ-ENT6-28449). M. Paratype from Angatuba (MNRJ-ENT6-28456). – K–M. Hind tibiae. K. Holotype from Fazenda Recanto (MNRJ-ENT6-284456). – K–M. Hind tibiae. K. Holotype from Angatuba (MNRJ-ENT6-284456). – K–M. Hind tibiae. K. Holotype from Angatuba (MNRJ-ENT6-284456). – K–M. Hind tibiae. K. Holotype from Fazenda Recanto (MNRJ-ENT6-284456). – K–M. Hind tibiae. K. Holotype from Angatuba (MNRJ-ENT6-284456). – K–M. Hind tibiae. K. Holotype from Fazenda Recanto (MNRJ-ENT6-284456). – K–M. Hind tibiae. K. Holotype from Fazenda Recanto (MNRJ-ENT6-284456). – K–M. Hind tibiae. K. Holotype from Fazenda Recanto (MNRJ-ENT6-284456). Scale bar: A–M = 5 mm.



Fig. 5. Male genital structures of *Vates phoenix* sp. nov., highlighting variation across specimens. A–B. Left phallomere, paratype (MNRJ-ENT6-28445). A. Dorsal view. B. Ventral view. – C–E. Left phallomere, partial ventral view. C. Paratype (MNRJ-ENT6-28445). D. Paratype (MNRJ-ENT6-28443). E. Paratype (MNRJ-ENT6-28446). – F–I. Ventral phallomere. F. Dorsal view, paratype (MNRJ-ENT6-28445). G. Partial ventral view, same as in F. H. Partial dorsal view, same as in F. I. Partial ventral view, paratype (MNRJ-ENT6-28446). – J–L. Right phallomere, dorsal view. J. Fazenda Recanto, paratype (MNRJ-ENT6-28445). K. Reserva Ecológica de Guapiaçu, paratype (MNRJ-ENT6-28446). L. Fazenda Recanto, paratype (MNRJ-ENT6-28443). – M–N. Right phallomere, details of ventral structures. M. Fazenda Recanto, paratype (MNRJ-ENT6-28443). N. Reserva Ecológica de Guapiaçu, paratype (MNRJ-ENT6-28446). Scale bars: A–B, F, J–L = 2 mm; C–E, G–I = 1 mm; M–N = 500 µm.

metazona keeled along its midline (keel more pronounced proximally). Pronotum predominantly green, except for darkened prozone and lateral margins of metazona.

PROTHORACIC LEGS. Forecoxae triangular in cross-section, ventral margin pale yellowish brown, except for small dark spot on its anterior end, and a larger, preapical one on its posterior aspect; dorsal margin with nine spine-like, darkened tubercles interleaved with smaller, paler ones; color patterning in general similar to that of males. Forefemora light brown, three-banded, and with a small spot in anterior region of each femur near trochanter. Dorsal margin of forefemora slightly sinuous. Spination formula of forelegs: F=4DS/15AvS/4PvS; T=15(R)-16(L)AvS/13(R)-11(L)PvS. Discoidal spines I, II and III pale with dark spots at their base and apex, spine IV entirely dark. Anteroventral spines II, IV, VI, VIII and X slightly reclined, spines I–XII entirely black, XIII and XIV black laterally and at apex, XV with black base and apex, spine XV largest, straight and darkened at its base and its tip; posteroventral spines black at their base and tips; a well developed genicular spine on each sides of femora; tibial spine groove located in proximal <sup>1</sup>/<sub>4</sub> of femora. Foretibiae light brown, dorsally three-banded.

WINGS. Forewings (Fig. 2D) surpass abdomen by <sup>1</sup>/<sub>4</sub> of their length in resting position. Forewings with membrane of costal area opaque and predominantñy green, with a yellowish longitudinal strip along margin of costal vein, distal-most portion of costal vein and membrane around radial vein darkened; discoidal area with green and opaque membrane, longitudinal veins mostly yellow, veins densely reticulated distally, stigma with a darkly pigmented spot; anal area small, mostly opaque, veins and membrane withish. Hindwing with narrow costal area, tapering distally and partially opaque, proximal half with membrane and veins whitish, although cells become dark brown distally; discoidal area largely hyaline with yellowish veins, proximal region of membrane whitish, distal portion smoky brown, opaque and heavily reticulated; anal area largely hyaline, veins and proximal area of membrane whitish, distal portion below discoidal area faint brown.

MESO- AND METATHORACIC LEGS. Mesothoracic femora (Fig. 6E) with a marked posteroventral keel that forms two evident lobes: a proximal one that is elongated but scarcely produced, and a pre-apical one that is short and produced, shaped like a shark's dorsal fin. Metathoracic femora (Fig. 6F) with a marked posteroventral keel that forms a single preapical lobe, also shaped like a shark's dorsal fin. Mesothoracic tibiae (Fig. 6G) with two medial lobes: a produced but clearly shorter. Metathoracic tibiae (Fig. 6H) with two elongated lobes, anterodorsal one longer and wider than anteroventral one, and also more prominent than its homologue on mesothoracic tibiae.

ABDOMEN. Fusiform, slightly flattened dorsoventrally, widest between segments III–V, brownish with some contrasting spots in middle of each tergite. Cerci elongated, surpassing apex of subgenital plate, cercomeres cylindrical.

# **Differential diagnosis**

Svenson *et al.* (2015) listed all species of *Vates* they considered valid, totaling 13 spp. All these species are herein discussed in relation to our new species. The males of *V. phoenix* sp. nov. share with those of *V. biplagiata* Sjöstedt, 1930, *V. luxuriosa* Beier, 1958, *V. amazonica* (Westwood, 1889), *V. pectinicornis* (Stål, 1877), *V. foliata* (Lichtenstein, 1802) and *V. lobata* (Fabricius, 1798) the asymmetrical, s-shaped antennomeres, whereas the females share with those of *V. serraticornis* Stål, 1877, *V. festae* Giglio-Tos, 1914, *V. weyrauchi* Beier, 1958, and likely also *V. boliviana* Giglio-Tos, 1914 (which remains known from males only) the yellowish white tinge of the hindwing membrane. None of the preceding species has both males with s-shaped antennomeres and females with yellowish white hindwings. Therefore, *V. phoenix* sp. nov. possesses a unique combination of character states unknown in other species of *Vates*, making its identification straightforward. In the absence of either one of the sexes for effective



**Fig. 6.** *Vates phoenix* sp. nov., female morphology (both specimens are from Jardim Botânico do Rio de Janeiro), and head morphology of *Vates* spp. **A**. Head, frontal view, allotype (MNRJ-ENT6-28442). – **B**–**C**. Variation in ocellar tubercles (not to scale). **B**. Allotype (collected in 2018; MNRJ-ENT6-28442). **C**. Paratype (collected in 1935; MNRJ-ENT6-28455). – **D**. Pronotum, dorsal view, allotype (MNRJ-ENT6-28442). **E**. T6-28442). – **E**–**H**. Mid- and hind legs, allotype (MNRJ-ENT6-28442). **E**. Mid-femur, detail of distal section. **F**. Hind femur, detail of distal section. **G**. Mid-tibia. **H**. Hind tibia. – **I**. *Vates biplagiata* Sjöstedt, 1930, head, frontal view (male specimen from Peru). **J**. *Vates weyrauchi* Beier, 1958, head, frontal view (male specimen from Peru). **S**–**H** = 5 mm.

comparisons, the reduced ocellar tubercles of V. phoenix sp. nov. represent a distinct character state for the species, common to both sexes, and unique among members of the genus (compare, for instance, with Fig. 6I–J). Our new species can also be easily distinguished from V. pectinata Saussure, 1871 and V. chopardi (Deeleman-Reinhold, 1957) for lacking the dorsal, preapical lobe of the forefemora, a distinct character shared by the latter two species (Fig. 7) — which Roy (2012) suggested as likely synonyms. Additionally, we were unable to compare V. phoenix sp. nov. with the type specimen of Vates lobata (Fabricius, 1798). This species was originally described from "Cajennae" (= Cayenne, French Guiana) as Mantis lobata (Fabricius 1798) in the 'Supplementum' to 'Entomologica Systematica' - not to be confused with Mantis lobata Fabricius, 1781, a synonym of Harpagomantis tricolor (Linnaeus, 1758) (Galinthiadidae) sensu Beier (1934). Examination of the Banks collection (JR) housed by the Natural History Museum, London (containing a sizable portion of Fabricius types) did reveal the presence of Mantis lobata Fabricius, 1781, though no specimen attributable to Mantis lobata Fabricius, 1798 (i.e., Vates) was found there. The taxa that Fabricius (1798) described from "Cajennae" in his 'Supplementum' were owned by Louis Augustin Guillaume Bosc d'Antic (N. Kristensen, pers. com. 2011), a French naturalist whose insect collection, in part studied by Fabricius, dispersed across European natural history institutions after his death in 1828 (Notton 2007). A good portion of this material eventually made it to Paris and Geneva; however, examination of these and other European collections also containing some of Fabricius' types, such as the Zoological Museum in Copenhagen (N. Kristensen, pers. com. 2011) and the Hunterian Museum in Glasgow (online catalogue: http://collections.gla.ac.uk/) did not turn up any specimen attributable to the type of *Mantis lobata* Fabricius, 1798. This specimen is most likely lost. Regardless of the fate of the type specimen, the new species can be distinguished from Vates lobata on the basis of its distribution, as French Guiana and Rio de Janeiro are biogeographically distant and unrelated regions that do not share any praying mantis species. Finally, *Vates obscura* Toledo Piza, 1983, listed as valid in Svenson et al. (2015), had already been synonymized with V. biplagiata in an earlier publication (Agudelo & Rivera 2015), and thus we conclusively remove this species from the Vates checklist.

#### Systematic remarks

Morphological comparison of male genitalia provided insights on the affinities of the new species. The only species whose male genital structures are known are *Vates chopardi* (Lombardo 2000: figs 25–27), and *V. biplagiata* and *V. festae* (Medellín & Salazar 2011: fig. 14). Morphological comparisons between *V. phoenix* sp. nov. and *V. biplagiata* genitalia showed that both species share a strong, proximally bent afa, whereas the accentuated sigmoidal shape of the same can also be observed in *V. chopardi*, though in the latter the afa is not bent to the same degree as in *V. biplagiata*. Differences in genital structures are more accentuated between *V. phoenix* sp. nov. and *V. festae*, the latter with a much straighter afa and, and a shortened and robust Pda on the ventral phallomere. Coincidently, the phylogeny of Vatini proposed in Svenson *et al* (2015) recovered three main clades within *Vates*: one containing *V. chopardi*, sister to another clade comprised of *V. festae* and *V. weyrauchi*, altogether sister to a more diverse clade containing *V. biplagiata*. Our analysis of external morphology and existing reports of male genital structures thus suggests a closer affinity to members of this latter clade, which in Svenson *et al.* (2015) also included *V. luxuriosa*, *V. amazonica*, *V. pectinicornis* and two additional, unidentified species. Further phylogenetic studies are necessary to test this hypothesis and resolve evolutionary affinities with all members of *Vates*.

With the description of our new species and the clarification of previous records, the following species are considered valid: 1) *V. amazonica* (Westwood, 1889); 2) *V. biplagiata* Sjöstedt, 1930; 3) *V. boliviana* Giglio-Tos, 1914; 4) *V. chopardi* (Deeleman-Reinhold, 1957); 5) *V. festae* Giglio-Tos, 1914; 6) *V. foliata* (Lichtenstein, 1802); 7) *V. lobata* (Fabricius, 1798); 8) *V. luxuriosa* Beier, 1958; 9) *V. pectinata* Saussure, 1871; 10) *V. pectinicornis* (Stål, 1877); 11) *V. serraticornis* Stål, 1877; 12) *V. weyrauchi* Beier, 1958;



**Fig. 7. A**. *Vates pectinata* Saussure, 1871, holotype,  $\mathcal{S}$ , and labels (Muséum d'histoire naturelle de la Ville de Genève, Geneva, Switzerland); note: the male and female specimens portrayed in fig. 8d–c of Svenson *et al.* (2016) and reported as *Vates pectinata* cannot be attributed to this species. **B**. *Lobovates chopardi* Deeleman-Reinhold, 1957, holotype,  $\mathcal{S}$ , and labels (National Museum of Natural History, Leiden, the Netherlands); note: wings are colorless and hyaline in the actual specimen, whitish tinge is due to a photo originally taken against a white background.

13) *V. phoenix* Rivera *et al.* sp. nov. The possible synonymy between *V. pectinata* and *V. chopardi*, as suggested by Roy (2012), is pending confirmation.

### Natural history and behavior

Rehn (1935) noted that species of *Vates* were difficult to come across in nature. Things have not changed much since Rehn's times, as there still is very little information in the literature regarding the biology of *Vates*. Below we present natural history information of *Vates* spp resulting from our own observations and literature accounts, and summarize this information to place it in the context of our new species.

Neither nymphs nor adults of V. phoenix sp. nov. were ever found in their natural habitat. Unlike members of other sympatric genera, all broadly sampled across Rio de Janeiro by Projeto Mantis' research team, we were unable to locate specimens of *Vates* in any manually sampled plant formations in the three years that this project spanned. This suggest that *Vates* spp. likely prefer higher layers within the vegetation as perching and hunting grounds, thus making their collection at ground level difficult. In fact, Dantas et al. (2008) reported Vates spp. flying to canopy light traps 45 m above the ground near Manaus, Brazil. Interestingly, the latter study reported collecting a few females, thus evidencing enhanced flying capabilities of this sex in Vates. Behavioral observations conducted on the only wild-caught female indeed showed that this sex is able to sustain controlled gliding for short distances while moving across perching sites. Our anatomical examinations of *V. phoenix* sp. nov. revealed that females have relatively larger ocelli compared to other non-Vatini females, a pattern consistent with flying capabilities in female praying mantises and other insects (Battiston et al. 2018). Further, reduced sexual dimorphism in wing size and shape is evident in the examined specimens (e.g., Fig. 2C–D). This likely explains why females of Vates are sometimes lured to light traps, as shown by Dantas et al. (2008) and corroborated by some of us through field work (JR, pers. obs.). Collecting efforts using this sampling method could eventually result in collecting additional female specimens of V. phoenix sp. nov.

Angatuba (São Paulo) and Reserva Ecológica de Guapiacu (Rio de Janeiro) represent the westerneasternmost limits of Vates phoenix sp. nov. based on the available data. Unfortunately, it is difficult to determine the extent of the original distribution of V. phoenix sp. nov. and other sympatric species, as the original Atlantic Rainforest circumscribed by these localities is now heavily altered by urban development and farming, thus affecting this and likely other praying mantis species (Rodrigues & Cancello 2013). Sampled localities showed that V. phoenix sp. nov. ranges from 7 to 600 m. Distributional records compiled from the literature revealed that several species of *Vates* are found at mid- to higher elevations. For instance, the dominant species along the oriental slopes of the Peruvian/Ecuadorian Andes and neighbouring lowlands are V. weyrauchi (100-1000 m), V. luxuriosa (400-1000 m), V. biplagiata (180-2900 m) and V. festae (1000-1700 m) (Lombardo & Agabiti 2001; Rivera & Vergara-Cobián 2017), with the latter also found on the eastern slopes of the central and oriental cordilleras of central Colombia (450–2400 m) (Medellín & Salazar 2011; Svenson et al. 2015) and in the vicinity of Manaus, Brazil (ca 90 m) (Dantas et al. 2008). The relatively narrow vertical distribution of V. phoenix sp. nov. is comparable to that of V. amazonica and V. chopardi, both predominantly lowland species mostly found below 500 m, the former across the Amazon basin and the latter along the Mexican Pacific and Atlantic lowlands (Svenson et al. 2015). All this information suggests that several species of Vates have a broad altitudinal range (e.g., V. biplagiata), and that the genus has a tendency to be more diverse at higher elevations. However, distributional records across the Amazonian lowlands are still scarce for most species and more surveys are necessary to infer patterns of vertical distribution across the genus.

Reared specimens preferred perching clinging upside-down, often keeping their raptorial forelegs stretched forward to form a 90° angle relative to the body (Fig. 8). This posture was assumed either *de novo* or enhanced in response to a nearby observer the insect possibly perceived as a potential threat. Robinson (1969) reported a similar behavior in *Pseudovates chlorophaea* (Blanchard, 1836) (cited as



**Fig. 8.** Habitus of *Vates phoenix* sp. nov. Adult female is portrayed upside-down with raptorial legs stretched forward, perching on *Licania tomentosa* (Benth.) Fritsch. ('oiti'), an arboreal species distinct from the Atlantic Rainforest and abundant within the general area where the female allotype was found. A male specimen is depicted flying, as they often are on the wings through adulthood. Scientific illustration executed by Paulo Ormindo, based on observations of wild specimens.

*Phyllovates chlorophaea* therein) in Panama, regarding it as a combination of leaf and stick mimicry. More efforts are necessary to unveil further aspects of the natural history of *Vates* spp, and of Vatini in general.

# Discussion

The Atlantic Rainforest of southern Brazil is a global biodiversity hotspot that supports the highest rates of endemism on Earth (Ribeiro et al. 2009). This unique, yet severely threatened ecosystem is the home of several praying mantis taxa that are only (or predominantly) found there. Representative mantis genera include Miobantia Giglio-Tos, 1917, Chloromiopteryx Giglio-Tos, 1915 (Thespidae Saussure, 1869, Miobantiinae Roy, 2013), Fuga Svenson, 2014 (Liturgusidae Giglio-Tos, 1915) and Hicetia Saussure & Zehntner, 1894 (Photinaidae Giglio-Tos, 1915, Photinainae Giglio-Tos, 1915). Besides these endemisms, the Atlantic Rainforest also harbors a number of species from various other genera otherwise well diversified within the Amazon and Central America, but with only one or a few representatives in the Atlantic Rainforest. Notable examples are Acanthops falcataria (Goeze, 1778) (Acanthopidae Burmeister, 1838), Acontista concinna (Perty, 1833) (Acontistidae Giglio-Tos, 1915), Stenophylla cornigera Westwood, 1843 (Stenophyllidae Saussure, 1869), Stagmatoptera praecaria Linnaeus, 1758 (Mantidae, Stagmatopterinae Burmeister, 1838), and the new species of Vates herein described, a genus until now thought to be mostly Amazonian. The discovery of V. phoenix sp. nov. exemplifies this asymmetrical pattern of praying mantis diversity between rainforest ecosystems in South America, suggesting that this lineage has a more complex biogeographic history in the area than previously acknowledged.

The Atlantic and Amazonian Rainforests are physically separated by the "South American dry-diagonal", a xeric and highly seasonal corridor of open vegetation that extends from the Caatinga biome, in Brazil's north-eastern region, to the Chaco in Argentina, Bolivia and Paraguay, to the eastern slopes of the Andes, passing through the Cerrado biome in central Brazil (Fig. 9) (Prado & Gibbs 1993). Multiple lines of evidence point to paleoecological scenarios where dramatic vegetation turnovers, caused by cyclical climate fluctuations, favored repetitive events of connection and isolation between the Atlantic Rainforest and other South American forested areas, such as the Amazon and the Andean region (Ledru 1993; Ledru et al. 1996; Sobral-Souza et al. 2015). These episodic events of forest contraction and expansion resulted in allopatric speciation and intense biological interchange between the Atlantic and Amazon Rainforests which, at times, formed a continuous forest unit, although with some degree of regional differentiation (Sobral-Souza et al. 2015). Several biogeographic studies of selected taxa have also found support for such historical connectivity among today's South-eastern Amazon, the Chacos and the Atlantic Rainforest regions: small mammals (Costa 2003), the Diptera family Muscidae Latreille, 1802 (Lowenberg-Neto & Carvalho 2009), the bee genera Partamona Schwarz, 1939, Geotrigona Moure, 1943 and Paratrigona Schwarz, 1938 (Camargo 1996; Camargo & Moure 1996; Camargo & Pedro 2003), triatominae true bugs of the tribe Rhodniini Pinto, 1926 (Paula et al. 2007) and microhylid frogs (de Sá et al. 2019), among others. The analyses of different taxa, and their diversification patterns in relation to major geographical changes, such as the Andean uplift, marine transgressions and river reconfigurations, or the Serra do Mar and Serra da Mantiqueira formation in the Atlantic Rainforest, add to the complexity of this paleobiological scenario.

The pattern of distribution of *Vates*, and other genera such as *Acanthops* Audinet-Serville, 1831, *Stenophylla* Westwood, 1843, and *Acontista* Saussure, 1869, points to the Amazon Rainforest as the likely ancestral source of at least part of the praying mantis diversity found in the Atlantic Rainforest. Since *Vates* is mostly diversified and distributed across the Amazon basin, the presence of *V. phoenix* sp. nov. in the Atlantic Rainforest could have resulted from the dispersal of an ancestral species during a time when both ecosystems constituted a continuous formation, followed by local speciation in allopatry. Another hypothesis could be dispersal through gallery forests. These habitats have been shown to play

a role in the dispersal of forest-dwelling taxa occurring both in the Atlantic and Amazon Rainforests, as these form networks of interconnected patches of relatively dense vegetation associated with rivers and wetlands across otherwise xeric and open habitats (Oliveira-Filho & Ratter 1995; Vivo 1997; Costa 2003). However, it is likely that multiple processes were involved in shaping current patterns of distribution of praying mantises in the Atlantic Rainforest. In fact, many authors (e.g. Bush 1994; Bates *et al.* 1998; Marks *et al.* 2002; Costa 2003; Nihei & Carvalho 2007) point to complex and dynamic processes, where vicariant and dispersal events occurred repeatedly, ultimately shaping the pattern of distribution we see today. The few phylogenetic studies available addressing evolutionary relationships among Neotropical Mantodea (Rivera & Svenson 2016; Svenson *et al.* 2015; Rodrigues *et al.* 2017) included only few representatives from the Atlantic Rainforest, and thus available data remains insufficient for inferring the timeline of their likely origin. Sampling genetic diversity from those populations, to be analyzed along with existing data from Amazonian lineages, is therefore of paramount importance to test the biogeographic scenarios herein proposed.

# Conclusions

Despite being a severely threatened biome, and having lost more than 85% of its original extension (Rezende *et al.* 2018), endemic organisms unknown to science still wander the Atlantic Rainforest of southern Brazil. European naturalists, who intensely surveyed this region through the 19<sup>th</sup> century (Browne 2001), collected most of the praying mantis species originally described from this biome,



**Fig. 9.** Map of South America highlighting Brazilian biomes and the known distribution of *Vates phoenix* sp. nov. in the Atlantic Rainforest. The highly disrupted state of this biome can be seen in the satellite image (lower right), where some of the last remains of primary forest can be appreciated along the coast. See Material and methods for detailed locality information. Maps not to scale.

particularly from Rio de Janeiro. The majority of species were described by German, Austrian, Swedish, Swiss and Italian entomologists between the 1830s and early 20<sup>th</sup> century; several decades of scant scientific production have followed since. Reinvigorated interest in the Neotropical praying mantis fauna has resulted in the discovery of new species associated to this biome, or in the clarification of their taxonomic status (Scherrer 2014; Svenson 2014; Agudelo & Rivera 2015; this study), whereas phylogeographic studies are beginning to emerge (Santos *et al.* 2018). The discovery of *Vates phoenix* sp. nov. joins other large-sized species discovered in recent times (Rodrigues *et al.* 2017; Schwarz *et al.* 2018), whereas current collecting efforts in tropical and extratropical areas of the globe, previously thought to be relatively well-sampled, have revealed both unrecognized praying mantis taxa as well as numerous new regional records (e.g., Helmkampf *et al.* 2007; Ehrmann 2011; Schwarz & Konopik 2014; Wieland *et al.* 2014; Tedrow *et al.* 2015; Moulin *et al.* 2017; Moulin 2018; Shcherbakov & Anisyutkin 2018). These studies showe that regional surveys in poorly explored regions, including the Atlantic Rainforest of southern Brazil, still have a lot to reveal. An important diversity of new mantodean taxa is surely awaiting discovery.

Considerable efforts to taxonomically and systematically characterize the Neotropical Mantodea fauna are underway. However, more systematized collecting efforts are necessary to increase geographic coverage. Regional surveys are needed on most biomes to gain a better picture of the real diversity of the group and their ecological associations. These efforts must include the analysis of smaller regional insect collections across Latin America, which in recent times have yielded interesting specimens, helping to fill some of the gaps (e.g., Maldaner & Rafael 2017). Limited distributional data on most Neotropical taxa of Mantodea compromises our understanding of the evolution and diversification of these insects in the region, and the elucidation of their biogeographic patterns. Thorough geographic sampling, coupled with time-calibrated molecular phylogenies, could help to identify the time frame, and likely sequence, of historical events leading to regional patterns of diversity (Morrone 2014). Further research focusing on *Vates*, as well as other taxa shared by the Amazon and Atlantic Rainforests, represent good prospects to shed new light on the processes promoting biological diversification in these two global biodiversity hotspots.

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## References

Agudelo A.A. & Rivera J. 2015. Some taxonomic and nomenclatural changes in American Mantodea (Insecta, Dictyoptera) – Part I. *Zootaxa* 3936 (3): 335–356. https://doi.org/10.11646/zootaxa.3936.3.2

Bates J.M., Hackett S.J. & Cracraft J. 1998. Area-relationships in the Neotropical lowlands: an hypothesis based on raw distributions of Passerine birds. *Journal of Biogeography* 25 (4): 783–793.

Battiston R., Correas J., Lombardo F., Mouna M., Payne K. & Schuette K. 2018. Morphological convergences in *Ameles* Burmeister and *Pseudoyersinia* Kirby: Taxonomic implications of wing reduction and flight predisposition in some West-Mediterranean Amelini (Insecta: Mantodea). *Zootaxa* 4377 (1): 21–38. https://doi.org/10.11646/zootaxa.4377.1.2

Beier M. 1934. Mantodea. Subfamilie: Hymenopodidae. *In*: Wytsman P. (ed.) *Genera Insectorum*. Fasc. 196: 1–37. Tervuren.

Brannoch S.K., Wieland F., Rivera J., Klass K.D., Béthoux O. & Svenson G.J. 2017. Manual of praying mantis morphology, nomenclature, and practices (Insecta, Mantodea). *ZooKeys* 696: 1–100. https://doi.org/10.3897/zookeys.696.12542

Browne J. 2001. Natural history collecting and the biogeographical tradition. *História, ciências, saúde-manguinhos* 8 (Suppl.): 959–967. https://doi.org/10.1590/S0104-59702001000500009

Burmeister H.C. 1838. Handbuch der Entomologie. Fangschrecken, Mantodea. *In: Handbuch der Entomologie*. Vol. 2: v–viii, 517–522. Theodor Christian Friedrich Enslin, Berlin.

Bush M. 1994. Amazonian Speciation: A Necessarily Complex Model. *Journal of Biogeography* 21: 5–18. https://doi.org/10.2307/2845600

Camargo J.M. 1996. Meliponini neotropicais (Apinae, Apidae, Hymenoptera): biogeografia histórica. *Anais do Encontro sobre Abelhas* 2: 107–121.

Camargo J.M. & Moure J.S. 1996. Meliponini neotropicais: o gênero *Geotrigona* Moure, 1943 (Apinae, Apidae, Hymenoptera), com especial referência à filogenia e biogeografia. *Arquivos de Zoologia (São Paulo)* 33 (2–3): 95–161. https://doi.org/10.11606/issn.2176-7793.v33i2-3p95-161

Camargo J.M. & Pedro S.R. 2003. Meliponini neotropicais: o gênero *Partamona* Schwarz, 1939 (Hymenoptera, Apidae, Apinae) – bionomia e biogeografia. *Revista brasileira de Entomologia* 47 (3): 311–372. https://doi.org/10.1590/S0085-56262003000300001

Costa L.P. 2003. The historical bridge between the Amazon and the Atlantic Forest of Brazil: a study of molecular phylogeography with small mammals. *Journal of Biogeography* 30 (1): 71–86. https://doi.org/10.1046/j.1365-2699.2003.00792.x

Dantas Y.K.L.A., Rafael J.A., Motta C.d.S., Agudelo A.A. & Xavier Filho F.F. 2008. Records of Mantodea (Insecta) collected with light trap at 45 meters height over an Amazon forest canopy, at ZF-2 nucleus, Manaus, Brazil. *Acta Amazonica* 38 (2): 317–320. https://doi.org/10.1590/S0044-59672008000200015

de Sá R.O., Tonini J.F.R., van Huss H., Long A., Cuddy T., Forlani M.C., Peloso P.L.V., Zaher H. & Haddad C.F. 2019. Multiple connections between Amazonia and Atlantic Forest shaped the phylogenetic and morphological diversity of *Chiasmocleis* Mehely, 1904 (Anura: Microhylidae: Gastrophryninae). *Molecular Phylogenetics and Evolution* 130: 198–210.

Ehrmann R. 2011. Mantodea from Turkey and Cyprus (Dictyoptera: Mantodea). Articulata 26 (1): 1-42.

Fabricius J.C. 1798. Supplementum entomologiae systematicae. Proft & Storch, Kopenhagen [Hafniae].

Giglio-Tos E. 1914. Mantidi esotici (VII, Vatinae). Bolletino dei Musei di Zoologia e di Anatomia comparata della Reale Università di Torino 29 (684):1–87.

Giglio-Tos E. 1927. Orthoptera (Mantidae). *In: Das Tierreich* Vol. 50: 1–707. Walter de Gruyter & Co., Berlin/Leipzig.

Helmkampf M.E., Schwarz C.J. & Beck J. 2007. A first look at the biodiversity of praying mantids (Insecta: Mantodea) in Sabah, Borneo. *Sepilok Bulletin* 7: 1–13.

Ledru M.-P. 1993. Late quaternary environmental and climatic changes in central Brazil. *Quaternary Research* 39: 90–98. https://doi.org/10.1006/qres.1993.1011

Ledru M.-P., Braga P.I.S., Soubiès F., Fournier M., Martin L., Suguio K. & Turcq B. 1996. The last 50,000 years in the Neotropics (Southern Brazil): evolution of vegetation and climate. *Palaeogeography, Palaeoclimatology, Palaeoecology* 123 (1–4): 239–257. https://doi.org/10.1016/0031-0182(96)00105-8

Lombardo F. 2000. Remarks on some American mantids of the Museum für Naturkunde, Berlin, and a description of a new species of *Xystropeltis* Rehn from Ecuador. *Deutsche entomologische Zeitschrift* 47 (1): 87–93. https://doi.org/10.1002/dez.200000009

Lombardo F. & Agabiti B. 2001. The mantids from Ecuador, with some biogeographic considerations. *Journal of Orthoptera Research* 10 (1): 89–105.

Löwenberg-Neto P. & De Carvalho C.J.B. 2009. Areas of endemism and spatial diversification of the Muscidae (Insecta: Diptera) in the Andean and Neotropical regions. *Journal of Biogeography* 36 (9): 1750–1759. https://doi.org/10.1111/j.1365-2699.2009.02112.x

Maldaner C. & Rafael J.A. 2017. A new species of *Decimiana* Uvarov from Brazil, with updated key to species and remarks on their geographic distribution (Mantodea: Acanthopidae, Acanthopinae). *Zootaxa* 4291 (3): 521–530. https://doi.org/10.11646/zootaxa.4291.3.5

Marks B.D., Hackett S.J., & Caparella P.A. 2002. Historical relationships among Neotropical lowland forest areas of endemism as determined by mitochondrial DNA sequence variation within the Wedgebilled Woodcreeper (Aves: Dendrocolaptidae: Glyphorynchus spirurus). *Molecular Phylogenetics and Evolution* 24: 153–167. https://doi.org/10.1016/S1055-7903(02)00233-6

Medellín C. & Salazar J.A. 2011. Notas sobre mántidos colombianos con énfasis en la subfamilia Vatinae (Insecta). *Boletín Científico Centro de Museos de Historia Natural* 15 (1): 134–150.

Morrone J.J. 2014. Cladistic biogeography of the Neotropical region: identifying the main events in the diversification of the terrestrial biota. *Cladistics* 30 (2): 202–214. https://doi.org/10.1111/cla.12039

Moulin N. 2018. Liste commentée et catalogue illustré des Mantodea du Gabon. *Les Cahiers de la Fondation Biotope* 24: 2–60.

Moulin N., Decaëns T. & Annoyer P. 2017. Diversity of mantids (Dictyoptera: Mantodea) of Sangha-Mbaere Region, Central African Republic, with some ecological data and DNA barcoding. *Journal of Orthoptera Research* 26 (2): 117–141.

Nihei S.S. & de Carvalho C.J.B. 2007. Systematics and biogeography of *Polietina* Schnabl & Dziedzicki (Diptera, Muscidae): Neotropical area relationships and Amazonia as a composite area. *Systematic Entomology* 32 (3): 477–501. https://doi.org/10.1111/j.1365-3113.2006.00376.x

Notton D.G. 2007. A catalogue of types of the smaller taxa of Proctotrupoidea (Hymenoptera) in the Museum national d'Histoire naturelle, Paris, with notes on the history of the insect collection of LAG Bosc d'Antic. *Zoosystema* 29 (3): 457–470.

Oliveira-Filho A.T. & Ratter J.A. 1995. A study of the origin of central Brazilian forests by the analysis of plant species distribution patterns. *Edinburgh Journal of Botany* 52 (2): 141–194. https://doi.org/10.1017/S0960428600000949

Paula A.S., Diotaiuti L. & Galvão C. 2007. Systematics and biogeography of Rhodniini (Heteroptera: Reduviidae: Triatominae) based on 16S mitochondrial rDNA sequences. *Journal of Biogeography* 34: 699–712. https://doi.org/10.1111/j.1365-2699.2006.01628.x

Prado D.E. & Gibbs P.E. 1993. Patterns of species distributions in the dry seasonal forests of South America. *Annals of the Missouri Botanical Garden* 80 (4): 902–927.

Rehn J.A.G. 1911. Orthoptera (Mantidae, Vatinae). *In*: Wytsman P. (ed.) *Genera Insectorum*. Vol. 119: 1–28. Verteneuil & Desmet, Brussels.

Rehn J.A.G. 1935. The Orthoptera of Costa Rica, Part I: Mantidae. *Proceedings of the Academy of Natural Sciences of Philadelphia* 87: 167–272.

Rezende C.L., Scarano F.R., Assad E.D., Joly C.A., Metzger J.P., Strassburg B.B.N., Tabarelli M., Fonseca G.A. & Mittermeier R.A. 2018. From hotspot to hopespot: An opportunity for the Brazilian Atlantic Forest. *Perspectives in Ecology and Conservation* 16 (4): 208–214.

Ribeiro M.C., Metzger J.P., Martensen A.C., Ponzoni F.J. & Hirota M.M. 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation* 142 (6): 1141–1153. https://doi.org/10.1016/j.biocon.2009.02.021

Rivera J. & Svenson G.J. 2016. The Neotropical 'polymorphic earless praying mantises' – Part I: molecular phylogeny and revised higher-level systematics (Insecta: Mantodea, Acanthopoidea). *Systematic Entomology* 41 (3): 607–649. https://doi.org/10.1111/syen.12178

Rivera J. & Vergara-Cobián C. 2017. A checklist of the praying mantises of Peru: new records, one new genus (*Piscomantis* gen. n.) and biogeographic remarks (Insecta, Mantodea). *Zootaxa* 4337 (3): 361–389. https://doi.org/10.11646/zootaxa.4337.3.3

Robinson M.H. 1969. The defensive behaviour of some orthopteroid insects from Panama. *Transactions of the Royal Entomological Society of London* 121 (7): 281–303. https://doi.org/10.1111/j.1365-2311.1969.tb00521.x

Rodrigues H.M. & Cancello E.M. 2013. Mantodea (Insecta) collection in the Museu de Zoologia da Universidade de São Paulo: taxonomic and geographical coverage. *Check List* 9 (5): 957–965. https://doi.org/10.15560/9.5.957

Rodrigues H.M., Rivera J., Reid N. & Svenson G.J. 2017. An elusive Neotropical giant, *Hondurantemna chespiritoi* gen. n. & sp. n. (Antemninae, Mantidae): a new lineage of mantises exhibiting an ontogenetic change in cryptic strategy. *ZooKeys* 680: 73–104. https://doi.org/10.3897/zookeys.680.11162

Roy R. 2012. Une curieuse ressemblance entre des espèces des genres voisins *Zoolea* Audinet Serville, 1838, et *Vates* Burmeister, 1838 (Dict., Mantidae, Vatinae). *Bulletin de la Société entomologique de France* 117 (3): 380.

Roy R. & Ehrmann R. 2009. Révision du Genre *Zoolea* Audinet-Serville [Mantodea, Mantidae, Vatinae]. *Revue française d'Entomologie* 31 (1): 1–22.

Santos B.F., Scherrer M.V. & Loss A.C. 2018. Neither barriers nor refugia explain genetic structure in a major biogeographic break: phylogeography of praying mantises in the Brazilian Atlantic Forest. *Mitochondrial DNA Part A – DNA Mapping, Sequencing, and Analysis* 29 (8): 1284–1292. https://doi.org/10.1080/24701394.2018.1445242

Scherrer M. 2014. A revision of *Miobantia* Giglio-Tos, 1917 (Mantodea: Thespidae, Miobantiinae), with molecular association of dimorphic sexes and immature stages. *Zootaxa* 3797 (1): 207–268. https://doi.org/10.11646/zootaxa.3797.1.15

Schwarz C.J. & Konopik O. 2014. An annotated checklist of the praying mantises (Mantodea) of Borneo, including the results of the 2008 scientific expedition to Lanjak Entimau Wildlife Sanctuary, Sarawak. *Zootaxa* 3797 (1): 130–168. https://doi.org/10.11646/zootaxa.3797.1.12

Schwarz C.J. & Roy R. 2019. The systematics of Mantodea revisited: an updated classification incorporating multiple data sources (Insecta: Dictyoptera). *Annales de la Société entomologique de France (N.S.)* 55 (2): 101–196. https://doi.org/10.1080/00379271.2018.1556567

Schwarz C.J., Ehrmann R. & Shcherbakov E. 2018. A new genus and species of praying mantis (Insecta, Mantodea, Mantidae) from Indochina, with a key to Mantidae of South-East Asia. *Zootaxa* 4472 (3): 581–593. https://doi.org/10.11646/zootaxa.4472.3.10

Shcherbakov E. & Anisyutkin L. 2018. Update on the praying mantises (Insecta: Mantodea) of South-East Vietnam. *Annales de la Société entomologique de France (N.S.)* 54 (2): 119–140. https://doi.org/10.1080/00379271.2018.1447394

Sobral-Souza T., Lima-Ribeiro M.S. & Solferini V.N. 2015. Biogeography of Neotropical Rainforests: past connections between Amazon and Atlantic Forest detected by ecological niche modeling. *Evolutionary Ecology* 29 (5): 643–655. https://doi.org/10.1007/s10682-015-9780-9

Svenson G.J. 2014. Revision of the Neotropical bark mantis genus *Liturgusa* Saussure, 1869 (Insecta, Mantodea, Liturgusini). *ZooKeys* 390: 1–214. https://doi.org/10.3897/zookeys.390.6661

Svenson G.J., Medellin C. & Sarmiento C.E. 2015. Re-evolution of a morphological precursor of crypsis investment in the newly revised horned praying mantises (Insecta, Mantodea, Vatinae). *Systematic Entomology* 41 (1): 229–255. https://doi.org/10.1111/syen.12151

Tedrow R., Nathan K., Richard N. & Svenson G.J. 2015. A survey of the praying mantises of Rwanda, including new records (Insecta, Mantodea). *Zootaxa* 4027 (1): 67–100. https://doi.org/10.11646/zootaxa.4027.1.3

Terra P. 1995. Revisão sistemática dos gêneros de louva-a-deus da região Neotropical (Mantodea). *Revista brasileira de Entomologia* 39 (1): 13–94.

Vivo M. 1997. Mammalian evidence of historical ecological change in the Caatinga semiarid vegetation of northeastern Brazil. *Journal of Comparative Biology* 2 (1): 65–73.

Wieland F. 2013. The phylogenetic system of Mantodea (Insecta: Dictyoptera). *Species, Phylogeny and Evolution* 3: 3–222. https://doi.org/10.17875/gup2013-711

Wieland F., Schütte K. & Goldberg J. 2014. A review of the research on Canary Islands praying mantises (Mantodea). *Zootaxa* 3797 (1): 78–102. https://doi.org/10.11646/zootaxa.3797.1.9

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