

A New Species of Praying Mantis from Peru Reveals Impaling as a Novel Hunting Strategy in Mantodea (Thespidae: Thespini)

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Abstract

A new species of lichen-mimicking praying mantis, *Carrikerella simpira* n. sp., is described from Tingo María region in Peru. The new species differs from its congeners in having reduced tergal lobes, a relatively sinuous pronotum, and it is found in the highland tropical rainforest of the Central Andes. Behavioral observations conducted on captive individuals revealed that juveniles and adults hunt by impaling prey using modified foretibial structures. Anatomical examinations of the incumbent trophic structures revealed functional adaptations for prey impaling in the foretibiae, primarily consisting of prominent, forwardly oriented, barbed spines. We provide an overall description of this novel hunting behavior in Mantodea and hypothesize on its evolutionary origin and adaptive significance for the Thespidae.

Introduction

The predatory praying mantises are among the most distinct and charismatic insects. From leaf mimics to floral simulants, praying mantises have evolved a wide array of morphological and behavioral strategies to both secure prey and avoid their own predators. The Neotropical region is home of about 20% of the world praying mantis fauna, comprising about 2500 species (Wieland & Svenson 2018). One family remarkable for their rich diversity of ecomorphological and behavioral adaptations is the Thespidae. From the small and stout-bodied *Pseudomiopteryx* Saussure (Pseudomiopteryginae) to the slim and gracile *Thesprotia* Stål (Thespinae), the thespids are distinct for their morphological disparity, diverse array of cryptic adaptations, and for being one of the most species-rich families among the Neotropical Mantodea (Rivera & Svenson 2016). Because of their usual small size, dull coloration, and secretive lifestyles, thespids are often overlooked by collectors and thus are rare in collections. Although the last decade or so has witnessed and increased research focus on Mantodea, thanks in part to comprehensive phylogenetic,

faunistic, and nomenclatural studies (e.g., Ehrmann 2002, Svenson & Whiting 2009, Wieland 2013, Rivera & Svenson 2014, Roy 2014), the greatest majority of the 30 or so thespid genera remain, with few recent exceptions (e.g., Rivera *et al* 2011, Agudelo & Rafael 2014, Scherrer 2014, Maldaner *et al* 2015), largely understudied.

Carrikerella Hebard is a little known genus of Thespidae distributed in Central and northwestern South America. Classified among the Thespini (Rivera & Svenson 2016), it includes three species, all known from single, female specimens: *Carrikerella ceratophora* Hebard, 1922 (Colombia; type species), *Carrikerella empusa* Rehn, 1935 (Costa Rica), and the recently described *Carrikerella amazonica* Salazar & Dias, 2018 (Colombia). The following character states define the genus: (1) postocellar region of head with a forked projection; (2) pronotum slightly sigmoidal in lateral view; (3) foretibiae with its two distal most anteroventral spines (AvS) strongly dorsally positioned, and with a single posteroventral spine (PvS); (4) forefemora with three discoidal spines (DS); (5) mid abdominal terga of adult females distally with lobe-like, cuticular projections. *Carrikerella* spp. have

been reported inhabiting among epiphytic moss, lichen, liverwort, and ferns in lowland tropical rainforest (Rehn 1935, Salazar-E & Gomes-Dias 2018) (Fig 1, inset).

Carrikerella, along several other genera from subfamilies Thespiinae and Bantiinae, are unusual for their diverse configuration of foretibial structures (Fig 1). These include dorsolateral displacement of anteroventral spines, hyper-development, and/or atrophy of certain spines, spineless gaps, forwardly oriented spines, shortened tibiae, among other features (Wieland 2013). This variation, of great utility for thespid taxonomy, is otherwise unique among Mantodea (Rivera & Svenson 2016). It is unknown how such diversity of structural variation interplays during prey capture, or whether it reflects

some form of prey specialization. Saussure & Zehntner (1894) and Beier (1964) were perhaps the only researchers in ever wondering about the unusual diversity of foretibial configurations across Thespidae. Saussure & Zehntner (1894: 161) suggested that—in reference to the dorsolaterally displaced distal AvS—“...if caught, the struggling prey must fatally impale itself on these spines by its own movements” and added—in reference to *Oligonyx* Saussure and *Thesprotia*—“...and perhaps also the other allied species, hunt very small prey only, probably soft insects.” Beier (1964) went further and, perhaps inspired by Saussure & Zehntner’s elucubrations, suggested that these structures enable these type of mantises to catch small, slow-moving prey—such as aphids. Though no particular

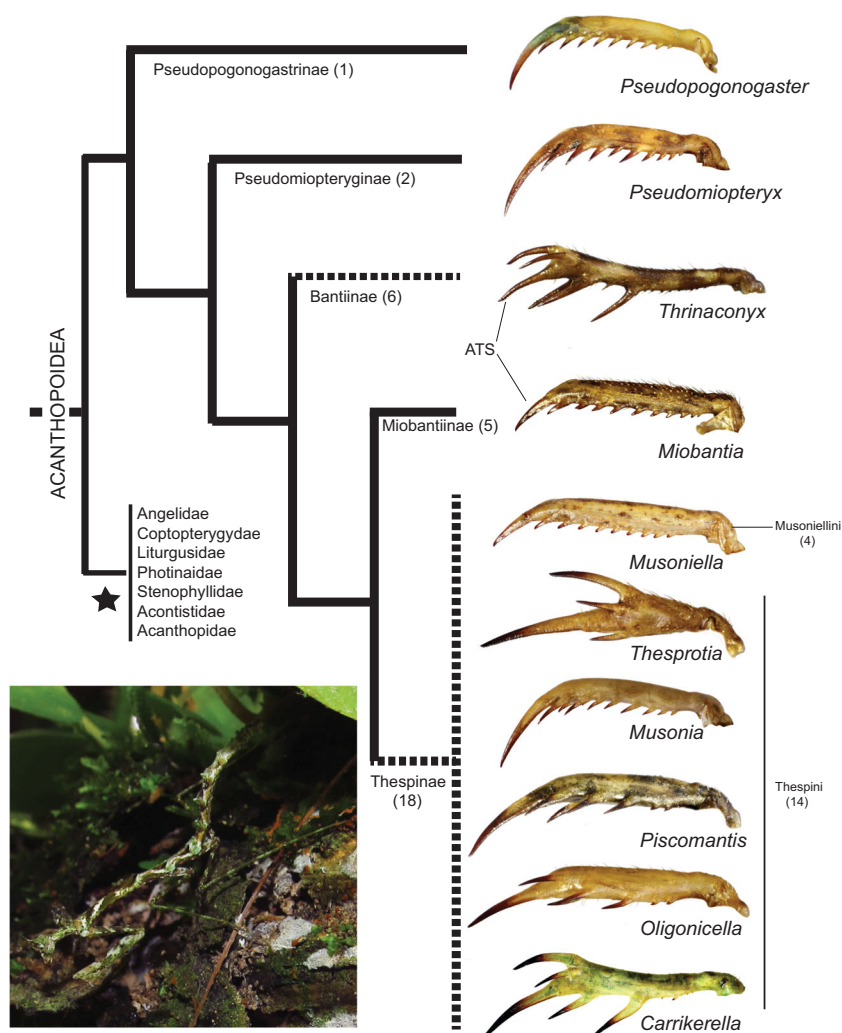


Fig 1 Higher-level phylogeny of Thespidae. The thespids form a clade sister to another containing the remaining families of Acanthoipoidea (marked with a star, branches collapsed for simplicity). The “standard” generalist tibial morph of *Pseudopogonogaster* (representative of most Mantodea) and the aberrant spines of *Thesprotia* are extreme expressions of an otherwise complex character trait system. The degree of displacement of the anteroventral foretibial spines, the tendency for the shortening of the tibiae, and the magnitude of straightness of the apical tibial spur (ATS) are only some of the most observable characters within this system. Only the Bantiinae and Thespini (Thespiinae) (dashed branches in phylogeny) exhibit such variation among its members. Figures in parenthesis indicate number of genera we accept as valid for each taxon. All tibiae are shown from their anterior aspect; thus, the anteroventral set of spines is visible. Inset in lower left portrays an adult female of *Carrikerella simpria* in its natural habitat in Tingo María, Peru (photo by Y. Callohuari). Tibiae not to same scale. See Rivera & Svenson (2016) for further details on the phylogeny of Thespidae.

functional prey capture mechanism was proposed, both Saussure & Zehntner (1894) and Beier (1964) coincided in that tibial modifications across Thespididae likely represented a form of prey specialization. To the best of our knowledge, no attempt has ever been undertaken, in 125 years, to corroborate the “impaling hypothesis” of Saussure & Zehntner (1894).

In this study, we report and describe a new species of *Carrikerella* from Peru on the basis of both male and female specimens, making of this the first species of the genus with unambiguously associated sexes. Behavioral observations conducted on living specimens enabled us to document a novel hunting strategy never reported before in Mantodea, offering the opportunity to appraise Saussure & Zehntner’s (1894) “impaling hypothesis” for the first time. We provide a general description of this newly discovered hunting behavior, highlight morphological adaptations related to its functionality, and hypothesize on its adaptive and evolutionary value.

Material and Methods

Specimens and morphological nomenclature

All studied specimens are part of the Mantodea holdings of the Museo de Entomología Klaus Raven Büller (MEKRB), Universidad Nacional Agraria la Molina in Lima, Peru. Morphological nomenclature and specimen handling procedures follow Brannoch *et al* (2017). We also studied the type specimens of *C. cerathophora* Hebard, 1922, and *C. empusa* Rehn, 1935, both deposited at the Academy of Natural Sciences of Drexel University (ANSP) in Philadelphia, USA.

Rearing conditions and behavioral observations

Subadults specimens (one male and two females) submitted to the senior author (JR) for examination on July 2017 were reared on “kokedamas.” Otherwise known as “japanese moss balls,” kokedamas are commercially available, ornamental plants cultivated within a matrix of soil wrapped on living moss. The kokedamas used each supported a single plant of either *Syngonium podophyllum* Schott or *Anthurium andreaeanum* Linden ex André (both Araceae), while the soil matrix was wrapped on a matt of *Sphagnum* L. moss, which was naturally infested with a small population of fungus gnats (Sciaridae: *Bradysia* sp.). This set up provided the mantises with a proper environment—similar to its natural epiphyte microhabitat within the Amazon rainforest—and a convenient source of self-regenerating prey of adequate size—fungus gnats were mating on site. The kokedamas were kept indoors at room temperature, hanging from a wire at eye level (1.70 m above ground). These semi-captive conditions allowed for close monitoring of the mantises with

minimum handling. Though the goal of rearing juvenile mantises was to obtain adult specimens for taxonomic examination, casual observations on their predatory behavior provided intriguing evidence of a novel hunting strategy never before documented in Mantodea: prey impalement by means of the apical tibial spur (ATS). To confirm this behavior and to learn more about its particularities, we moved the mantises to separate Styrofoam containers for more controlled observations during approximately 30 min every 2 days. We offered different types of prey of various sizes, including flies (*Drosophila*, tephritids, muscoids), small lepidopterans, and spiders. Although repetitive observations under naked eye conditions confirmed this unusual behavior, we recorded several hunting events using video film and photography to gain further insights on its functional details, as well as to provide a broad description of the same. To accomplish this, we placed a praying mantis on a simple, artificial hunting arena consisting on an open cardboard box with background color set to white for enhanced contrast; we used natural light conditions and implemented an infinite horizon effect to minimize shadows. Once at the center of the arena, we presented the mantis with a disabled prey item (a fly) and filmed it. Offered prey were positioned on the ground within reaching distance in front of the mantis—mantises were previously starved for 3 days to encourage active hunting during filming. We used a Sony RX100 Mark 5 hand camera to produce video footage in full HD (image resolution 1920 × 1080 pixels) at 120 frames/s. For more careful observation of the impaling technique of *Carrikerella*, we used Adobe Premiere 2018 ver. 12.1 to reduce original playback speed from 120 to 29.97 frames/s using the “modify footage” function, and then implemented the “function rate” tool to reduce speed down to 60% of the original footage. We then compared our observations with the “standard” predatory strike sequence of praying mantises as outlined in Oufiero *et al* (2016) to highlight divergent components of the strike conducive to impaling prey. We finally examined specimens under the microscope to pinpoint anatomical features of forelegs associated to this behavior. Our morphological examinations also included first instar individuals obtained from egg cases collected in a previous occasion near the type locality. Behavior and anatomical elements divergent from those associated to the standard strike (Oufiero *et al* 2016) are discussed from a functional and evolutionary perspective.

Imaging and 3D rendering

Photos of whole specimens (living and pinned) were taken using a Canon EOS Rebel T5i DSLR camera using Canon EF 100 mm f/2.8 L Macro IS USM lens. A Macro rail (WeMacro rail, 100 mm type) was incorporated to capture images of pinned specimens only. Structural details were photographed using a Canon EOS 5D Mark III camera mounted

on a Leica S8 APO stereoscope with a Leica KL300 LED as light source, or a Canon PowerShot SX130IS mounted on a Carl Zeiss Axiostar Plus 1169-149 microscope. Photo stacking software was Helicon Focus v6.8.0, with Method B (depth map) used as rendering technique. For 3D modeling, we took photographs of the anterior, posterior, ventral, and dorsal aspects of the left foreleg (femur and tibia) of a female specimen. We used the same settings for structural details and photo stacking software as detailed above. The resulting images were then uploaded to Blender v2.79 (freely available at: blender.org) as referential background images to build a 3D model of the foreleg. Both tibia and femur were built from cubes using the “loop cut and slide,” movement of vertices, extrusion, and scale and rotation of faces, tools. The model was smoothed through “subdivision surface” modifier with 3 levels of subdivision, and then exported to .STL format for printing in Acrylonitrile Butadiene Styrene (ABS) on a DaVinci 1.0 printer.

Results

Taxonomy

Carrikerella simpira Rivera & Callohuari sp. nov. (Figs 2, 3, 4, and 7, Table 1).

Description male

Habitus. (Fig 2a) Body slender, cuticle brown to greenish brown in preserved specimens, predominantly green when alive.

Head. (Fig 2b) Compound eyes prominent, rounded. Vertex straight, rising above imaginary line connecting the dorsal margin of compound eyes, but lower than the moderate, but noticeably produced, juxtaocular bulges. Postocellar projection elongated, distally forked, sides of shaft almost

Table 1 Standard body measurements of *Carrikerella simpira* (in mm). Measurements labeled as “forefemur prediscoidal” and “forefemur postdiscoidal” are taken, respectively, from the proximal margin to discoidal spine 1, and from discoidal spine 1 to distal margin. Foretibial measurement D1 does not include the tibial spur, whereas D2 does. Standard measurements sensu Brannoch *et al* (2017), except for those marked with (*), which are herein introduced. Measurements under MO1 correspond to the holotype. CS coxosternite (*subgenital plate* of authors); F female, M male.

Character	F01	F02	F03	F04	M01	M02	M03	M04
Body length	37.30	35.30	38.20	36.10	27.30	31.20	29.00	28.50
Head width	2.94	2.88	2.84	2.80	2.58	2.48	2.33	2.40
Head length	1.90	1.88	1.92	1.94	1.66	1.58	1.53	1.58
Lower frons width	0.85	0.88	0.80	0.84	0.73	0.69	0.69	0.73
Lower frons length	0.28	0.30	0.30	0.29	0.28	0.28	0.31	0.26
Postocellar projection*	0.98	1.23	1.03	0.97	0.96	0.85	0.81	0.75
Pronotal height	1.02	1.26	Damaged	0.93	0.96	0.90	0.75	0.78
Pronotal length	12.80	12.00	12.00	11.60	8.70	8.40	7.90	8.10
Pronotal width	2.60	2.50	2.43	2.38	1.52	1.82	1.84	1.75
Prozone	3.60	3.30	Damaged	3.30	2.70	2.70	2.50	2.50
Metazone	9.20	8.70	–	8.30	6.00	5.70	5.40	5.60
Ratio metazone/prozone	2.60	2.60	–	2.50	2.20	2.10	2.20	2.20
Forewing length	N/A	N/A	N/A	N/A	16.00	16.50	16.10	15.40
Forewing width	N/A	N/A	N/A	N/A	3.80	–	–	–
Hindwing length	N/A	N/A	N/A	N/A	16.70	–	–	–
Hindwing width	N/A	N/A	N/A	N/A	8.00	–	–	–
Forecoxal length	7.90	7.20	7.40	7.10	5.40	5.70	5.40	5.60
Forefemoral length	9.20	8.50	8.60	8.20	6.70	6.60	6.20	6.50
Forefemoral width	0.84	0.76	0.73	0.69	0.61	0.61	0.55	0.55
Foretibial length (D1)	2.40	2.04	2.12	1.88	1.84	1.76	1.68	1.84
Foretibial length (D2)	3.80	3.52	3.60	3.32	2.88	2.60	2.60	2.76
Foretarsal length		4.25	4.40	4.28	3.20	3.12	4.16	4.16
Forefemur prediscoidal*	5.30	4.90	5.10	4.70	3.70	3.60	3.40	3.60
Forefemur postdiscoidal*	3.90	3.60	3.50	3.50	3.00	3.00	2.80	2.90
Mesocoxa	2.23	2.13	2.18	2.00	1.80	1.78	1.58	1.78
Mesofemur	8.40	8.00	7.80	7.60	6.80	6.70	6.50	–
Mesotibia	7.50	6.80	7.00	6.70	5.50	5.60	5.20	–
Mesotarsus	6.00	5.90	–	5.40	5.45	5.40	5.15	–
Metacoxa	2.33	2.25	2.25	2.03	1.90	1.80	1.70	1.83
Metafemur	9.60	8.70	8.60	8.20	7.50	7.60	7.10	–
Metatibia	9.60	8.50	8.60	8.30	7.20	7.20	6.80	–
Metatarsus	7.80	7.50	–	–	7.25	7.25	6.75	–
Male CS9 length	N/A	N/A	N/A	N/A	1.50	1.45	1.48	–
Male CS9 width	N/A	N/A	N/A	N/A	1.98	1.80	1.63	–
Female CS7 length	1.30	1.05	1.18	1.15	N/A	N/A	N/A	N/A
Female CS7 width	0.73	0.58	0.58	0.58	N/A	N/A	N/A	N/A

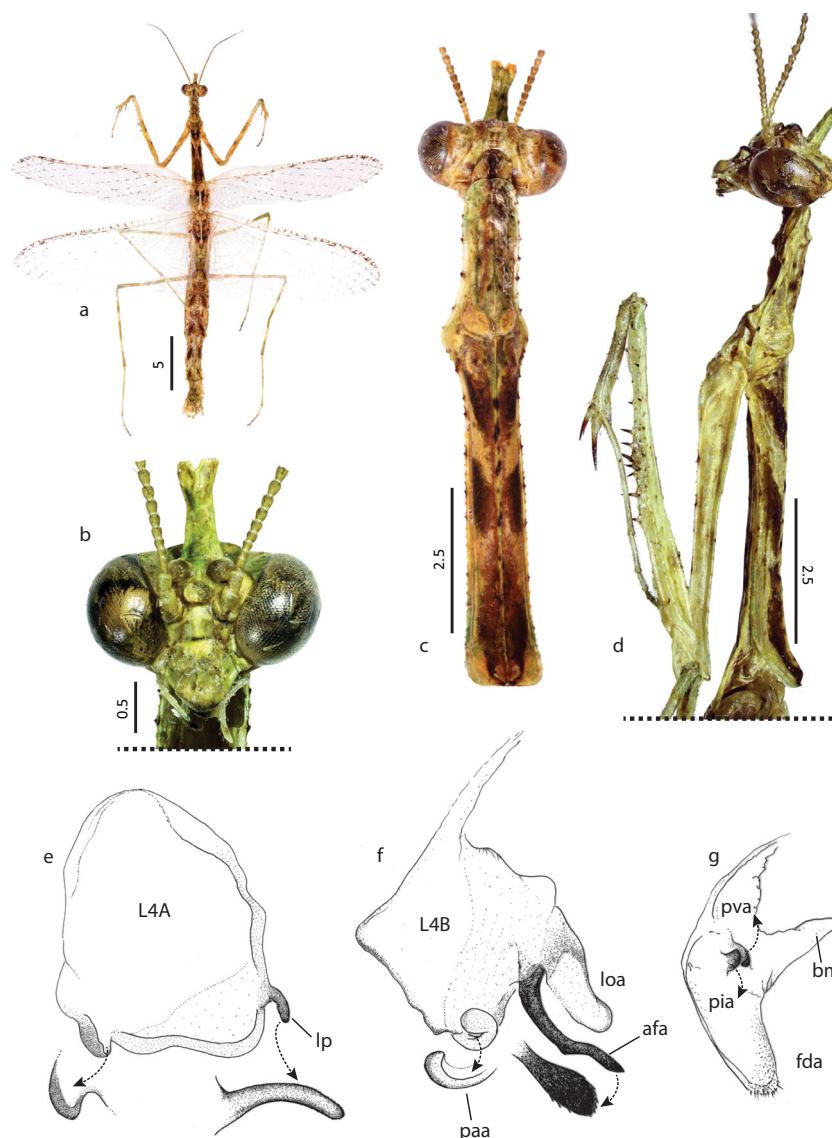


Fig 2 *Carrikerella simpira*, male. **a**, dorsal habitus (holotype); **b**, head, frontal view; **c**, head and pronotum, dorsal view; **d**, head and prothorax, lateral view; **e–f**, male genitalia: **e**, ventral phallomere, dorsal view (structural details in lateral view); **f**, left phallomere, dorsal view (structural details in lateral view); **g**, right phallomere, ventral view. Abbreviations: *afa*, apofisi falloide; *bm*, dextral extension; *fda*, main posterior lobe; *loa*, lobo membranoso; *lp*, lateral process; *paa*, processo apicale; *pda*, proceso distale; *pia*, piastra ventrale; *pva*, proceso ventrale. Genital structures not to same scale. Scale bars in millimeters.

parallel and appearing dilated in the lateral view, carined posteriorly. Ocelli large, median ocellus rounded, lateral ones slightly elliptical, and separated from each other by a gap twice as long as the gap between either and the median ocellus. Lower frons pentagonal, medially with a longitudinal carina that does not reach the lower side. Antennal segments covered with minute setae, conferring each antennomere with a rough surface, each antennomere bearing a preapical crown of dark setae.

Thorax. (Fig 2c–d) *Pronotum* narrow and elongated, prosternum narrowly visible in lateral view, also appearing slightly sigmoid; supracoxal dilation pronounced, longitudinal carina

null on prozona, well-defined along metazona; ratio metazona/prozona = 2.1–2.2; lateral margins of pronotum slightly produced, forming a ledge. Prozona strongly rectangular, distal margin straight, lateral margins almost parallel, dorsal surface with a small preapical tubercle on its midline. Pronotal margins bearing denticles, with 1 to 3 darker denticles alternating with one or more pale ones (darker denticles might appear larger); all denticles bear a minute, preapical seta. Pronotal surface with contrasting markings and spots, prozona often with a few punctiform marks in the middle and along its midline, whereas on the metazona, they are located along the longitudinal carina. Metazona surface with three distinct and contrasting dark brown bands whose

intensity varies across specimens: distal and median bands often V-shaped, proximal one ellipsoidal, the latter extending into and surrounding the well-defined, proximal tubercles, the latter paler than surrounding cuticle.

Forelegs. (Fig 2d) Coxa slightly shorter than metazona, dilated proximally but tapering distally, anterior margin with minute denticles, surface with scattered brown marks. Trochanter pale with a large dark brown, circular spot anteriorly. Forefemora narrow, dorsal margin sigmoid, proximal half thicker relative to distal half; cuticle with dark, contrasting bands, both external and internally, a darker longitudinal strip is often present between anteroventral spines 3–4; setae of femoral brush golden. Foretibiae with dark, irregular bands, its largest proximal spine straight or slightly curved, but always forming a clear open angle with the tibial margin. Both forefemora and tibiae bearing minute dorsal and ventral setae, and all their spines with dark tips (sometimes the proximal, smallest spines are fully brown). Spination formula: $F = 3DS/5-9AvS/4PvS$; $T = 2-5[+2]AvS/1PvS$. Surface of largest foretibial spines bearing microserrations, appearing barbed. Mid- and hindlegs rather slender, femora and tibiae tri-banded in brown, hind metatarsus almost as long as corresponding tibia; tarsomeres 2–5 darker than corresponding metatarsus.

Wings. (Fig 2a) Membrane iridescent, hyaline and overall colorless, longitudinal and crossveins light brown, both with dark brown marking at intersection points; forewings with light brown costal vein, mostly spotless except distally; costal area hyaline, distalmost cells bearing dark brown markings. Hindwings with some dark brown markings restricted to costal area and distal portion of discoidal area. When at rest, forewings do not reach tip of hindwings, whereas the latter do not reach the tip of the subgenital plate, leaving terminalia exposed.

Abdomen. (Fig 2d) Brown, with multiple darker markings; sternites with median, darker mark; tergites bearing a small lobe on their posterior angles. Subgenital plate trapezoidal, styli oblong and short, cerci short, barely projecting beyond subgenital plate.

Genitalia. (Fig 2e–g) Ventral phallomere (in dorsal view) roughly rectangular in shape, bearing a strongly sclerotized and evenly curved process near its right distal corner that projects dorsally, and a short, broad, and curved lobe-like process on its left, distal corner (Fig 2e). Left phallomere (in dorsal view) overall shape rhomboidal; sclerite *L4B* with tapering process projecting anteriorly; *paa* strongly recurved anteriorly; *afa* strongly sclerotized, its proximal $\frac{3}{4}$ evenly curved, distal $\frac{1}{4}$ bent, curving in the opposite direction, apex spoon-shaped, broader than its shaft, its distal margin and neighboring lateral

edges bearing minute spines; *loa* mostly membranous, broad, thumb-like (Fig 2f). Right phallomere with elongated *fa*, its apex bearing minute, distal setae (Fig 2g).

Description female

Habitus. (Fig 3a–b) Body slender, cuticle brown to greenish brown in preserved specimens, predominantly green when alive (Fig 1, inset).

Head. (Fig 3c) Similar to male but antennae much shorter and glabrous, alternating pale and brown antennomeres (the latter from partially to fully dark brown). Postocellar process more robust and prominent than males.

Thorax. (Fig 3d–e, f) Similar to males but much more robust, prosternum visible in lateral view thus cross-section is ellipsoidal; lateral margins more densely denticled than males. Ratio metazona/prozona = 2.5–2.6; meso- and metanotum with a central, oval brown spot. Wings visible as pterotecas, lobiform, and laterally projected. Mid- and hind femora basally swollen. Foreleg spines prominent, largest, foretibial ones with strongly barbed surface (Fig 3f, 4a). Spination formula as in males.

Abdomen. (Fig 4b–c) Terga with a single, small medial tooth-like lobe, those on terga 1–4 are relatively more developed than those on distal most terga. Supraanal plate linguiform, medially carined, cerci short. Caudogyne (*CG8*) defined as a well-sclerotized sclerite with a rounded and smooth anterior margin, but with a truncated and irregular posterior margin (Fig 4d). Coxa 8 (*CX8*) well sclerotized, its surface and margins are smooth, laterally narrowly connecting to *CG8* (Fig 4d). Spermathecal bulge (*sbu*) trapezoidal, its posterior margin bearing a small, narrow process. Accessory gland supporting lobe (*agsl*) well-sclerotized and narrowly transversal (Fig 4d). Gonapophysis 8 (*gp8*) each internally bearing a weak row of laterodorsal setae, in addition to numerous other stronger setae densely covering most of its apical lobe's (*gpal8*) dorsal surface, as well as along the dorsal surface of its outer, longitudinal fold (Fig 4d); shaft of *gp8* with a medial swell (visible in lateral view). Ventral margin of gonoplac 9 (*gl9*) bearing long setae.

Ootheca. (Fig 4e–h) Small, rectangular, and laterally compressed. Attached to flat surfaces by its ventral aspect. External coating typical of thespid oothecae, i.e., soft and extensive, covering the ootheca completely except ventrally. The coating consists of a loosely cemented, light brown, sponge-like matter embedded with multiple, minute air bubbles. The ootheca itself has a thick, yet flexible, external wall that is carmine red in color. Residual process present, short and filiform, projecting dorsally. Ootheca has 11–12 egg

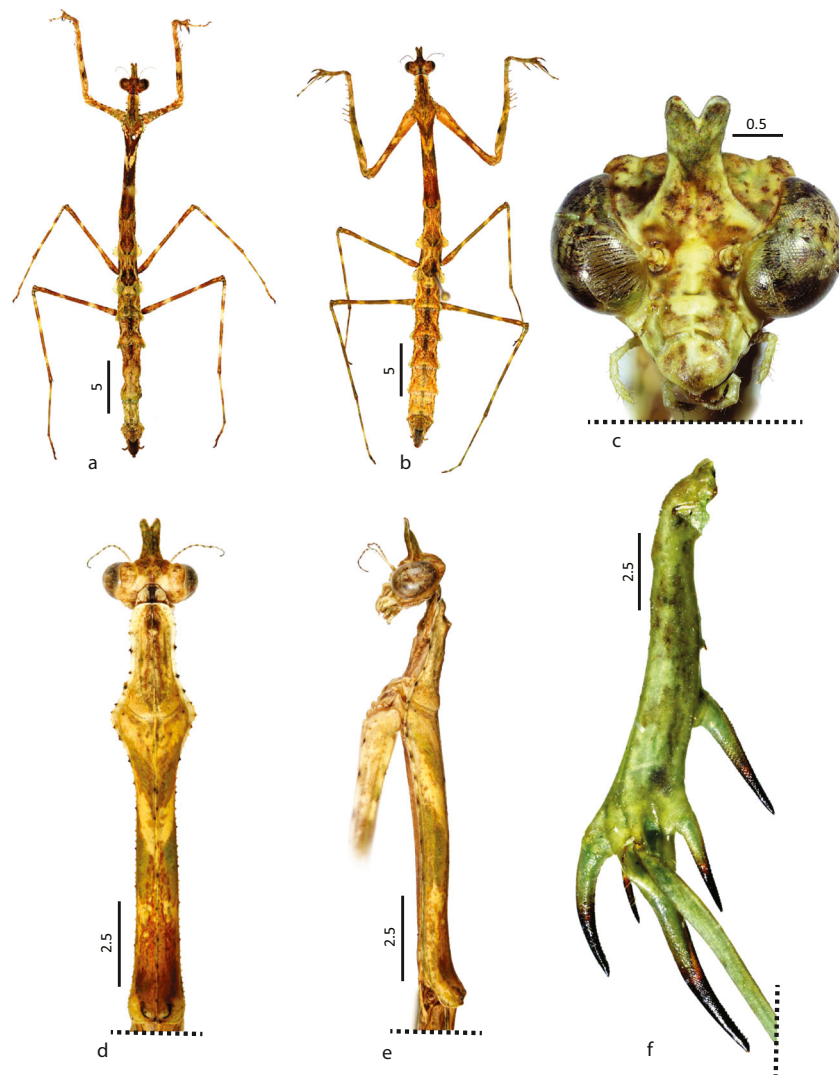


Fig 3 *Carrikerella simpira*, female. **a**, **b**, dorsal habitus (paratypes); **c**, head, frontal view; **d**, head and pronotum, dorsal view; **e**, head and prothorax, lateral view; **f**, left foretibia, posterolateral view. Scale bars in millimeters.

chambers with clearly delimited boundaries, lateral wall of each egg chamber projects dorsally thus conferring ootheca with a crested outline. Emergence area dorsal, comprised of 11–12 openings. Measurements in mm (figures in parenthesis correspond to coated ootheca): length at base, 6 (7.2); height, excluding residual process, 4.5 (4.9); width, 3.5 (3.8).

Etymology. The specific epithet refers to the “simpira,” a horned, mythological amazonian entity. According to local shipibo-conibo cosmivision, the simpira can stretch one of its arms to snare its victims, a behavior that evokes that of *Carrikerella*.

Material examined. PERU: HOLOTYPE (male) and PARATYPES (3 males, 2 females) from Huánuco, Leoncio Prado province, Tingo María, vicinity of Clorinda Matto de Turner village, IX.2017 (P. Sabino leg.), 1 additional female (PARATYPE), also from Huánuco, Distrito de Mariano Dámaso Beraún, –

9.320438°, –76.033504°, 667 m, 30.VI.2018 (Y. Callohuari leg.). Additional material. Perú: 1 male, Huánuco, Leoncio Prado province, Tingo María, Jardín Botánico Universidad Nacional Agraria de la Selva, 20.X.1991 (L. Gil leg.); 2 females (one of which is a subadult), “Tingo Maria” (no additional data). All deposited at MEKRB.

Distribution. Perú, Huánuco.

Natural history. The species can be found among epiphytic vegetation growing on tree trunks.

Comparative taxonomy

All three known species of *Carrikerella* remain known only from their respective female holotype and thus male-based comparisons are not yet possible. *Carrikerella simpira* differs from Colombian *C. amazonica* in having a Y-shaped

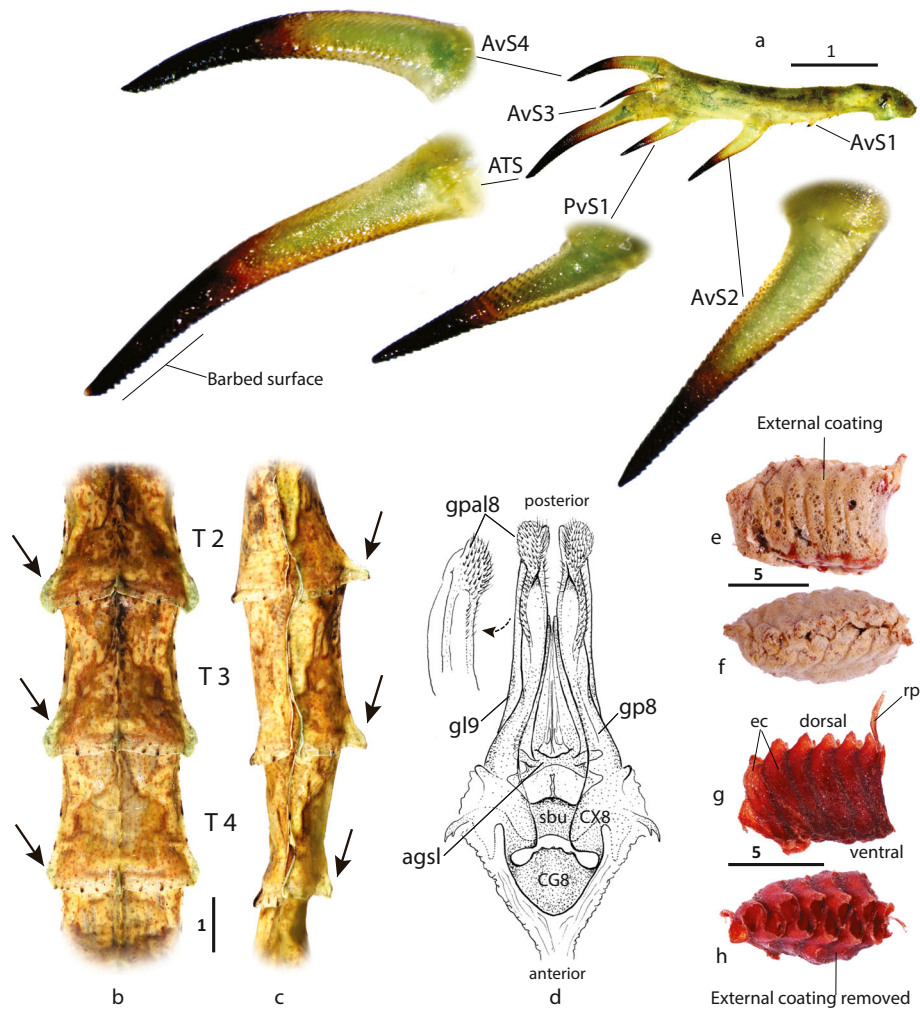


Fig 4 *Carrikerella simpira*, female. **a**, foretibia and detail of main spines (notice barbed surface); **b**, partial dorsal view of abdominal terga 2–4; **c**, same as **b**, but in lateral view (arrows point to tergal lobes); **d**, female genitalic complex, dorsal view, and detail of distal section of gonoplac 8 in lateral view; **e**, egg case, coated, lateral view; **f**, same as **e**, but in dorsal view; **g**, egg case, external coating removed, lateral view; **h**, same as **g**, but in dorsal view. Abbreviations: agsl, accessory gland supporting lobe; ATS, apical tibial spine; AvS, anteroventral spine; CG8, caudogyne; CX8, coxa 8; ec, egg chamber; gl9, gonoplac 9; gp8, gonapophysis 8; gpa8, apical lobe of gonapophysis 8; rp, residual process; PvS, posteroventral spine; sbu, spermathecal bulge; T, tergite. Scale bars in millimeters (Fig 4d not to scale).

postocellar process, which in the latter is V-shaped, a unique character state in *Carrikerella*. From the also Colombian *C. ceratophora*, the new species differs in having poorly developed tergal lobes, as the same are well-developed and produced in *C. ceratophora* (as well as in *C. amazonica*). The new species differ from Central American *C. empusa* in having a relatively more sinuous pronotum (as seen in the lateral view), prozona with lateral sides less parallel, and a postocellar process with a much deeper bifurcation (shallower in *C. empusa*). The holotype of *C. empusa* had its abdomen missing at the time of description and no more specimens have been reported since, and thus, further comparisons are not possible. Beier (1942) provided the description of what he assumed to be the male of *C. ceratophora*, a single male specimen from Balzapamba (=Balsapamba) in Ecuador, deposited in the

Naturhistorisches Museum Wien, Austria. However, Beier (1942) did not provide convincing evidence to support conspecificity of this male specimen with the known female of *C. ceratophora*, and thus, it cannot be confidently attributed to this species nor compared to the one herein described. Our own analysis of this specimen could not confirm its actual identity either. The ventral phallomere of *C. simpira* exhibits a unique feature not documented before in other Thespinae: a strongly sclerotized process near its right distal corner; all other members of Thespini lack this feature or have, at most, a short and poorly sclerotized process (see Fig 10E–M in Rivera & Svenson 2016 for further anatomical details and comparisons). It is difficult to determine whether this process represents the functional homologous of the *pda* or *posterior process* of the ventral phallomere, as defined in Brannoch *et al* (2017), and thus, we refrain from



Fig 5 *Carrikerella* spp., type specimens. **a**, *Carrikerella ceratophora*, female holotype from Andagoya, Colombia (lateral view) and labels (T2–T4 are indicated for comparison with *Carrikerella simpira*); **b**, *Carrikerella empusa*, female holotype from Peralta, Costa Rica (lateral view) and its labels; **c**, same as **b**, but in dorsal view (abdomen missing). Both holotypes deposited at ANSP. All scale bars = 5 mm.

labeling it as such until its embryological origin can be confidently established. The female genitalic complex depicted in Fig 4d is the first ever described for any member of Thespidae.

Systematics

Following their phylogenetic analyses of the Neotropical Acanthopoidea, or polymorphic earless praying mantises, Rivera & Svenson (2016) proposed a new phylogenetic classification for the Thespidae. Based on a well-supported topology and observed phylogenetic patterns of male genital morphology, Rivera & Svenson (2016) granted subfamily status to each of the five main clades comprising this family: Pseudopogonogastrinae, Pseudomiopteryginae, Bantiinae, Miobantiinae, and Thespinae, with the latter further subdivided into sister tribes Musoniellini and Thespini. More recently, Schwarz & Roy (2019) proposed a

new classification system for Mantodea. They largely derived their system from a comprehensive comparative morphological analysis of male genital structures across the order, which they contrasted against published phylogenies (Svenson & Whiting 2009, Rivera & Svenson 2016, Rodrigues *et al* 2017) for further validation of their groupings. Schwarz & Roy's scheme for Thespidae largely echoed that of Rivera & Svenson (2016); however, one of the few divergent points pertained to their treatment of Thespinae sensu Rivera & Svenson. Schwarz & Roy (2019) chose to grant Rivera & Svenson's Musoniellini and Thespini the rank of subfamily instead, as the Musoniellinae and Thespinae. Schwarz & Roy justified their procedure based on the relative diversity of both lineages: 4 genera in Musoniellini vs. 16 genera (including the recently formulated *Piscomantis* Rivera & Vergara-Cobián, 2017, and *Bistanta* Anderson, 2018) in Thespini, further claiming that such upgrading (i.e., from tribe to subfamily) best accounted for the thespid

phylogenetic patterns. We find these arguments untenable for two main reasons. First, their proposal does not fundamentally contradict or improve upon Rivera & Svenson's, as generic composition remains identical under both definitions. Secondly, resorting on relative diversity between sister clades constitutes a weak argument in support of taxonomic, systematic, and/or nomenclatural decisions, particularly because Schwarz & Roy (2019) did not present additional phylogenetic evidence to justify their differential treatment of Rivera & Svenson's Thespinae. The same rationale applies to Schwarz & Roy's proposal of subdividing Thespinae into Thespini and Oligonychini, two tribes they ambiguously defined based on rather variable foretibial character state distribution. Although we regard Schwarz & Roy's proposal valuable in many respects, such as their exclusion of Thespidae from Acanthopoidea to conform its own superfamily, the Thespoidea, we regard their overall treatment of Thespinae sensu Rivera & Svenson (2016) as merely cosmetic and thus unjustified. We therefore choose to adhere to Rivera & Svenson (2016) empirically derived classification, maintaining subfamily Thespinae and its two tribes Musoniellini and Thespini, with *Carrikerella* assigned to the latter.

Biology

Description of "Impaling Strikes" in *Carrikerella Simpira*

The well-camouflaged and stealthy praying mantises use their spiny forelegs to both catch their prey and restrain them during consumption. The predatory strike of the praying mantis essentially consists of two main components: the *approach* and the *sweep*. During the approach, the mantis first positions itself within striking distance, then elevates the coxae, and extends the tibiae towards the prey, whereas the sweep involves the forward protraction of the femur while the curved apical spur of the rapidly flexing tibiae sweeps the prey in for a firm grasp against the femur (Corrette 1990, Maldonado *et al* 1967). These two differential, yet integrated components are versatile enough to allow mantises to adapt their strike to different hunting scenarios (Oufiero *et al* 2016). Our observations on *C. simpira* showed that, although the elements of the approach are recognizable, the sweep itself is significantly different from what it is known to be the norm in Mantodea.

After *C. simpira* has positioned itself within striking distance, its body (or at least its pronotum) is more or less aligned with its target. At this point, the forelegs are fully or partially retracted, with the coxae held near or pressed against the prosternum, and the tibiae fully flexed against the femora—that is, in the distinct "praying" position (Fig 6a). In *C. simpira*, the *approach* consists in slowly extending the coxae forward, forming an angle with the prosternum

(Fig 6b). Almost simultaneously, the tibiae begin to extend, forming an increasingly wider angle with their corresponding femora, while the tarsi are flexed backwards and out of the way (Fig 6c). The approach ends when the mantis has fully positioned its body and the tibiae are pointing in the direction of the prey. The mantises often use their mid- and hind legs to move its body slightly forward and/or down before the strike, depending on the location of the prey—presumably to optimize prey capture by either reducing the distance to it, or improving the striking angle. The *sweep* component, however, was not such. After the approach, and following the forward extension of the forefemora, the mantis rapidly thrusts its tibiae in the direction of the prey, normally impaling it with a single ATS (Fig 6d), or both when catching larger prey. Less often other spines acted as impaling device. Once the prey is secured, the mantis brings it to its mouth and starts consuming it while still lodged in its ATS (Fig 6e–f). We noticed that during the strike, the mantises procured forming a relatively perpendicular angle between its ATS and the prey's resting grounds, likely to aid the piercing action of the ATS on the exoskeleton. Successful strikes often resulted in prey being impaled with the ATS (Fig 6g), although less often a different spine acted as impaling device (e.g., Fig 6h). In many observations, the mantises often got one or both ATS embedded on the surface beneath the prey or (when missing) next to it; however, they always managed to free themselves after repetitive and coordinated jerking movements of their body and foreleg.

Discussion

Foretibial adaptations related to hunting by impaling strikes

Closer examination of foretibial structures revealed several morphological adaptations consistent with impaling strikes as hunting strategy. For instance, the ATS in *Carrikerella* are strongly sclerotized only moderately curved and somewhat more aligned with the tibial axis; in contraposition, the foretibiae themselves are dorsally bent (Fig 4a). This design contrasts with the condition observed in praying mantises where sweeping strikes have been documented, with strongly and evenly curved ATS, and straight foretibiae, thus making impaling mechanically incompatible with such design (see, for example, the foretibiae of *Pseudopogonogaster*, *Pseudomiopteryx*, and *Musonia* in Fig 1). Impaling strikes performed with the latter could result in forces damaging the structure, especially if the impaling ATS is prone to pierce through the prey and hit the surface beneath. Therefore, these foretibial modifications likely represent adaptations to facilitate not only the impaling of prey, but also to buffering mechanical forces resulting from thrusting the ATS through the latter. The slight, but definite distal, upward

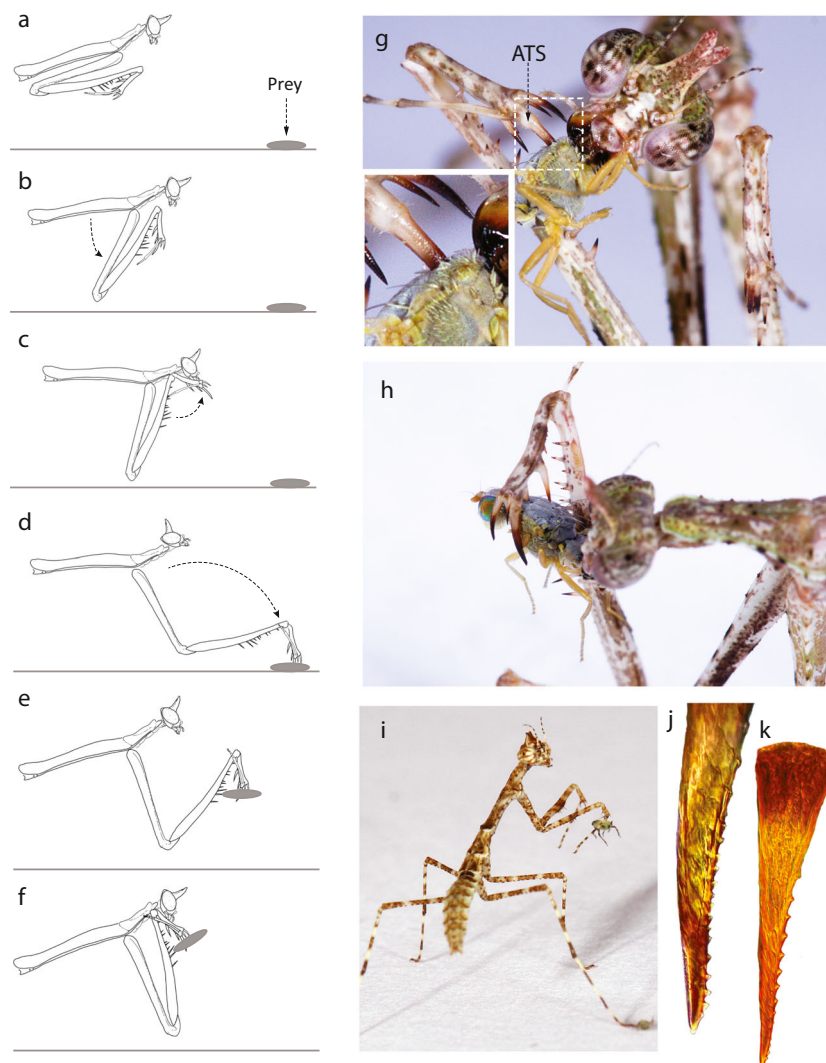


Fig 6 Hunting behavior of *Carrikerella simpira*. **a–f**, overall schematic representation of impaling strike sequence (traced from video frames). After the approach (**a–c**), the rapid forward extension of the forefemora during the strike (**d–f**) launches the foretibiae in the direction of the prey, impaling it; the impact forces resulting from piercing prey with the ATS often causes the mantis head to backlash (**d**); **g**, adult female specimen feeding on a specimen of *Trupanea* sp. (Tephritidae, approx. 5.5 mm) (inset shows ATS deeply embedded with the prey's body); **h**, same mantis specimen with a different prey, in this case impaled by the large, distal PvS; **i**, first instar *Carrikerella simpira* with juvenile aphid (possibly *Rhopalosiphum maidis*) lodged in its ATS; **j**, detail of the ATS of first instar specimen of *Carrikerella simpira* showing its barbed ventral edge (barbed surface becomes more extensive in subsequent instars); **k**, ATS of first instar specimen of *Musonia margharethae* (Battiston & Picciau), where barbed edges and dorsolateral displacement of foretibial distalmost AvS are both distinct characters in early nymphs; however, adults lose these traits through ontogeny (see adult foretibia of *M. margharethae* in Fig 1).

bend of the ATS probably also contributes to minimize such effect. The functionality of the ATS is further enhanced by its edged tip and, in particular, its barbed ventral surface (Fig 4a). This remarkable adaptation is analogous to certain hunting weapons that incorporate barbed edges into their design, such as harpoons and spears, for both piercing and holding prey. These barbed spines are evidently an adaptation to prevent prey items from slipping off the ATS while “picking” them off the ground. Impaled prey were consumed while still lodged in the ATS (Fig 6h). Interestingly, impaled prey did not interfere with mantis locomotion, as these were capable of walking on all six legs—a praying mantis holding a prey

between tibia and femur can normally use as many as five legs for locomotion. The ATS were not the only barbed spines. All largest foretibial spines, which are distinctly pointing forward and more or less aligned with the ATS (altogether resembling a sort of trident), are barbed to some degree (Fig 4a), suggesting a role in capturing and retaining prey. We were able to verify this in two occasions: when an adult female impaled a fly using its tibial PvS, and a first instar nymph using its ATS in addition to one dorsal AvS to impale an aphid. Despite this versatility, *C. simpira* used the ATS as its main prey capture device, whereas the other spines seemingly play a complementary role, perhaps as assisting,

secondary impaling structures. Summarizing, foreleg design, including shape and orientation of the ATS, and the barbed nature of this and other associated spines are thus best explained as adaptations concomitant with the impaling strikes of *C. simpira*.

Hunting behavior

From the minute fungus gnats *Bradysia* sp. (2-mm length) to the relatively much larger and sturdy skipper butterfly *Hylephila phyleus* (Drury) (12-mm length), impaling strikes proved effective for catching all prey items tested. In many occasions, we observed the mantises impaling and retrieving fungus gnats from crevices and other secluded places the mantises themselves were unable to walk in. The most remarkable observation consisted in the hunting of a minute mite approx. 0.5 mm long. This mite was not offered by us, but fortuitously detected on the kokedama, walking slowly along a plant stem right in front of one of the mantises. Although almost imperceptible to the naked eye, and about three orders of magnitude smaller than *C. simpira* itself, the mantis successfully tracked the mite and impaled it with one of its ATS with uncanny precision, and then proceeded to consume it. Impaling strikes also proved effective at catching prey crawling over vertical surfaces (e.g., plant stems), and even over obstacles (e.g., moss stems positioned in between the mantis and its targeted prey), all scenarios that rendered sweeping strikes unfeasible because of the structural complexity of the habitat. In one single occasion, the mantis was observed using grasping instead of impaling to secure its prey. This occurred when a small theridiid spider offered as prey clinged from a silk line in front of the mantis; upon detection, the mantis quickly snatched the spider off the air, holding it between tibia and femur as most mantises handle their prey. Overall, our observations showed that impaling strikes allowed *C. simpira* to acquire a wide array of prey items under different scenarios. Particularly revealing was the remarkable ability of the adult mantis to use their ATS to impale and consume comparatively minute arthropods that would have otherwise been ignored by other, equally sized praying mantises that hunt using sweeping strikes instead.

Ecological and evolutionary implications

Juvenile thespids consume minute, soft-bodied arthropods, such as springtails (Collembola) and mites (Acari) (Travassos Filho & Urban 1954, Terra 1980). Epiphyte formations therefore constitute ideal hunting grounds for an early instar praying mantis, as these provide moist, shelter, and ovipositing grounds to a great variety of small-sized invertebrates, particularly in tropical, humid environments (Gerson 1982). In fact, these microhabitats are dominated by soft-bodied

arthropods with average median body length of approx. 0.35 mm (Yanoviak *et al* 2003, Yanoviak *et al* 2004), among them springtails and mites, the latter comprising up to 65% of the total community (Yanoviak *et al* 2007). Our anatomical and behavioral observations showed that first instar and adults of *C. simpira* use their forelegs structures to “strike and impale” small, soft-bodied arthropods, a seemingly obvious choice of prey given their preferred habitat and reduced body size. Although the relatively much larger adults demonstrated the ability to impale prey as large as domestic flies and skipper butterflies, the fact that they actively aim for minute arthropods, and the precision with which they impale them, indicates that they are naturally adapted to target this type of prey as well. This observation resulted enthralling because the breadth of prey size typically expands as the predator—and its energetic needs—grow. However, optimal foraging theory predicts that a growing predator could incorporate prey items several orders of magnitude smaller into their diet as long as the combined effect of its hunting strategy, and favorable local probabilities of prey encounter, supersede the energetic costs incurred in handling and processing this type of prey (Pyke 1984, Scharf *et al* 2000). In our view, a sit-and-wait predator hunting minute but abundant arthropods, swiftly picking them up from the surrounding environment using a built-in tibial “spear,” arguably represents such energetically profitable strategy. What mechanism enabled the evolution of such unusual life strategy?

Following their molecular phylogenetic analysis and reclassification of the Thespidae, Rivera & Svenson (2016) inferred that juvenile tibial structures of several genera undergo considerable reconfiguration during post-embryonic development. Moreover, they noticed that certain juvenile tibial features are lost at various grades in the adults of several taxa, but not in others. For instance, Rivera & Svenson (2016) reported that the forwardly oriented distal postero- and anteroventral spines (the latter dorsolaterally displaced) of first instar *Pseudomiopteryx* (Pseudomiopteryginae) and *Macromusonia* (Thespinae), otherwise very similar to the condition observed in *Carrikerella* spp., progressively transition into a tibial configuration more consistent with the mechanics of sweeping strikes, with much smaller and ventrally positioned postero- and anteroventral spines in the adults. In others, tibial configuration remains consistent across instars and into adulthood; *C. simpira* belongs to this latter group. This pattern of morphological transformation prompted Rivera & Svenson (2016) to suggest that heterochronic processes could be responsible for the uneven expression of juvenile features across adult Thespidae.

Heterochrony is defined as the phylogenetic change in the timing or rate of growth and developmental events relative to the same events in the ancestor (Alberch *et al* 1979, McKinney & McNamara 2013). In *paedomorphosis*, a form of heterochrony, a decreased degree of development often

results in the retention of juvenile traits in adults (McNamara 2012). Under the right selective regimen, heterochrony often results in novel evolutionary trends at various hierarchical levels, from single and multiple morphological traits to complex behavioral expressions (Wobber *et al* 2010, McNamara 2012), and thus is generally regarded as a powerful driver of macroevolution (McNamara & McKinney 2005). We posit that pedomorphic traits of adult *C. simpira* (i.e., juvenile foretibial morphology optimized for the acquisition of small prey items by means of impaling strikes) arguably represent the evolutionary adaptive response to heterochronic processes arresting the development of such traits. These pedomorphisms seemingly confer *C. simpira* with the unusual ability to continue profiting off not only from significantly smaller and potentially abundant arthropods through their post-embryonic development, but also from much larger prey as these become increasingly accessible for the growing mantis. This versatility presumably enables *C. simpira* to considerably expand its trophic niche as it grows. In contrast, full ontogenetic transitions in foretibial anatomy and hunting strategy of certain taxa—i.e., from impaling nymphs to sweeping adults—would indicate that adjustments in predatory behavior are necessary to facilitate niche transitions during growth, perhaps as an adaptation to prevent the loss of fitness during seasonal shifts in prey availability. *Pseudomiopteryx* and *Macromusonia* Hebard—and also *Musonia* Stål (Fig 6k)—are examples of taxa where it would be expected to see these ontogenetic shifts in habitat and prey preference. If this hypothesis is proven true, then it will provide an evolutionary background to explore the remarkable ecomorphological disparity across Thespidae, especially in regards of their rich and unique diversity of foretibial anatomy.

The case for the study of Thespidae

Thespidae is arguably one of the most interesting families of Mantodea, from both ecological and evolutionary perspectives. Although recent and ongoing contributions are helping to pave the road for more advanced studies focusing on this family (Rivera *et al* 2011, Agudelo & Rafael 2014, Scherrer 2014, Maldaner *et al* 2015, Santos *et al* 2018), limited historical interest has greatly impacted our understanding of their actual taxonomic diversity and evolutionary relationships. Their highly cryptic adaptations, and especially their small size, make of these microhabitat specialists difficult to find and observe in their natural habitats (Rivera 2010, Rivera & Vergara-Cobián 2017), a serious disadvantage when compared to their larger, and more ubiquitous, showy relatives. This unfortunate blend of circumstances has hardly sparked the interest of specialists, let alone casual collectors and natural historians in search for new stories to tell among insect collections and wild habitats. In a time when a renewed

interest for praying mantis natural history has yielded remarkable discoveries on their hunting prowess, such as their appetite for birds (Nyffeler *et al* 2017) and even fish (Battiston *et al* 2018), finding novel ways to communicate about thespid morphological and ecological diversity is key to fostering scientific inquiry, especially in young researchers on the lookout for new biological models to tackle old questions in ecology and evolutionary biology.

It is with this rationale that we supply readers with a 3D printable file to reproduce a physical model of the unique foretibia of *C. simpira* (Fig 7a–c). 3D modeling has proven useful in many aspects of biodiversity exploration, scientific dissemination, and education. For example, 3D modeling could help to shed light on the functional properties of anatomical parts (Li *et al* 2011, Wulff *et al* 2015, Zimmermann *et al* 2011), or as supporting media in taxonomic descriptions to complement two-dimensional images of complex structures (Friedrich *et al* 2014, Qing & Bert 2018, this study). Further, it has been argued that 3D models, in the form of “cybertypes,” could reduce or even suppress the need to deliver invaluable and often fragile type specimens, thus assuring their long-term preservation (Godfray 2007, Nguyen *et al* 2014). Though this relatively new technology still requires significant amount of time and specialized equipment, efforts are underway to automate and simplify this task (Nguyen *et al* 2014, Ströbe *et al* 2018, Kelly *et al* 2019). Charismatic insects like praying mantises, with their rich diversity of anatomical structures and complex functionality, are particularly well suited for this kind technological exploration. We anticipate that once 3D modeling becomes cheaper and more widely used, this emerging form of “biodiversity sharing” will have a positive impact in taxonomic discovery and communication of biological data in Mantodea.

The description of *C. simpira*, in addition to our observations of their behavior, resulted in the discovery of a novel hunting strategy in Mantodea and confirmed, at least partially, the “impaling hypothesis” that Henri de Saussure & Leo Zehntner formulated 125 years ago. Interestingly, this newly described behavior is analogous to that observed in some species of mantis shrimps (Stomatopoda), which use their second maxilliped, modified into a powerful raptorial appendage, to impale fish and crustacean prey with uncanny speed and precision (Murphy & Patek 2012, Van Der Wal *et al* 2017). Besides certain predatory heteropterans, dipterans, and most neuropteran larvae, which impale their prey using their piercing, suctorial mouthparts, this is, to the best of our knowledge, the first confirmed case of trophic structures, other than mouthparts, used to impale prey in carnivorous insects. Though herein documented for the first time in *C. simpira*, other thespid taxa with similar, and even more extensive foretibial modifications, within subfamilies Bantiinae and Thespiinae (Rivera & Svenson 2016), including

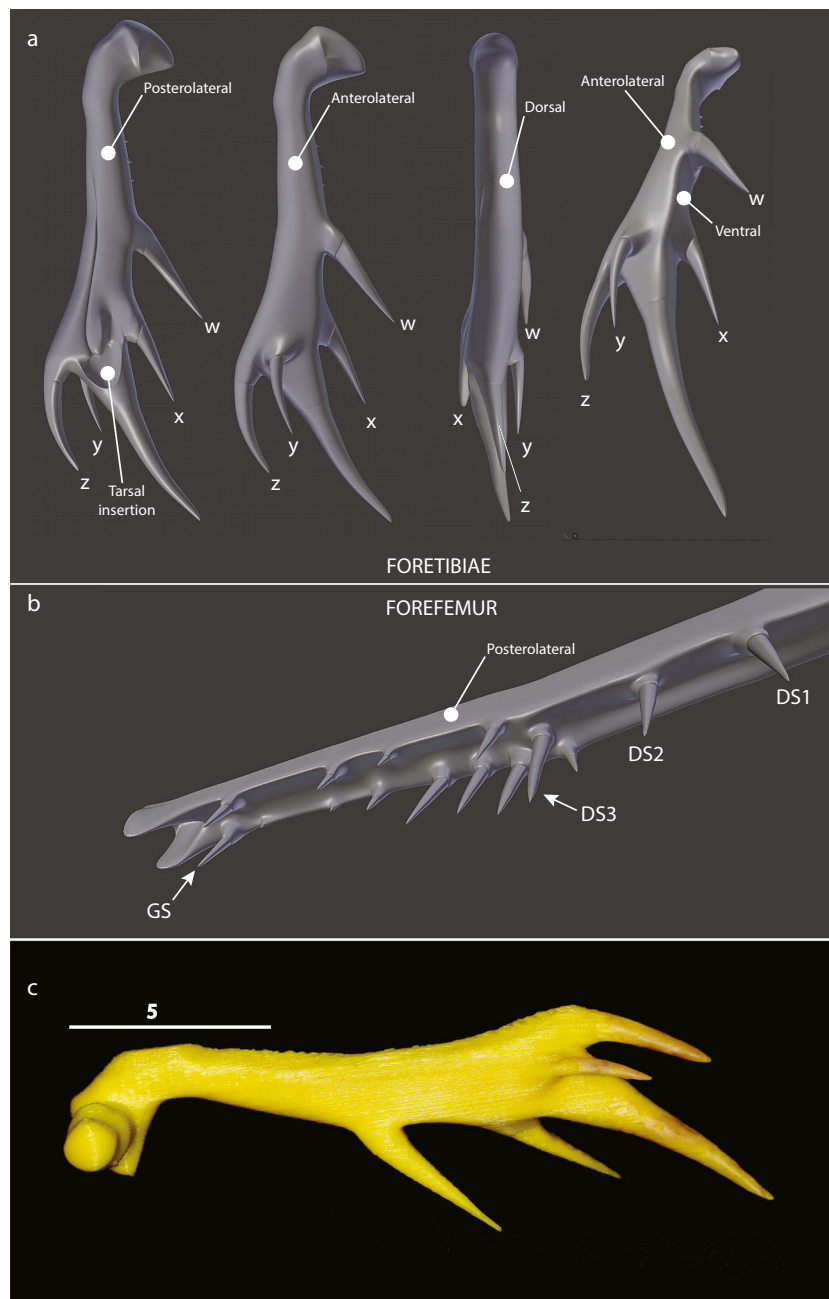


Fig 7 3D digital rendering of foreleg structures of *Carrikerella simpira*. **a**, 3D model of the foretibia showing structures in different views (from left to right): posterolateral, anterolateral, dorsal, and anterolateral ventral, in all cases equivalent spines are labeled w to z; **b**, forefemur, posterolateral ventral view, highlighting positioning of discoidal spines (DS); **c**, 3D printed foretibia of *Carrikerella simpira*. 3D images and modeling allow effective manipulation of anatomical structures for comparative analysis in multiple views using a single model, thus offering a clearer and unrestricted panorama of the morphological landscape under study. The included printable 3D model of the foretibia of *Carrikerella simpira* is fitted with a T-handle so readers can interact with the structure to enhance understanding of its functional properties (see [supplementary material](#)). Scale bar in centimeters. Note: printed model may vary depending on the type of device used, accuracy and printing material

the remaining species of *Carrikerella*, are all most likely hunting by means of impaling strikes during part or most of their development. The same must hold true for *Haania* Saussure and *Astape* Stål, two Asian genera of lichen-mimicking mantises, unrelated to Thespidae (Rivera & Svenson 2016), but possessing remarkably similar, yet convergent, foretibial anatomy (Wieland 2013). This discovery now permits

categorizing praying mantises into two discrete, functional categories based on their hunting method: the “sweepers” and the “impalers,” with the latter clearly representing a specialized, derived condition within Mantodea.

The specific mechanism behind the evolution of such remarkable morphological diversity in Thespidae remains unknown. However, we hypothesize that heterochrony, and

more specifically, paedomorphosis, could be plausible explanations for the disparate retention of juvenile tibial and behavioral traits in this lineage. Sampling complete developmental series across thespid taxa to contrast specific ontogenetic trajectories would be necessary as a test for heterochrony, as well as to identify the specific process responsible for this distinct evolutionary trend in Thespidae—and possibly other mantodean lineages. Coupling ontogenetic trajectories of foretibial morphology and hunting behavior with their specific ecological context could also shed light on the selective mechanisms behind thespid diversification and niche specialization.

This study highlights the importance of behavioral observations to understand functional anatomy, encourage scientific enquiry and hypothesis formulation in the context of Mantodea research.

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Author Contribution Statement JR planned the study, conducted taxonomic procedures, and wrote the manuscript; JR and YC conducted behavioral observations; YC generated images, digital renderings, 3D models, and contributed to writing the manuscript.

Nomenclature ZooBank registration can be found at: <http://zoobank.org/urn:lsid:zoobank.org:pub:64D19F6F-DA96-4667-A34C-8C087663DFC6>

References

- Agudelo AA, Rafael JA (2014) Genus *Mantillica* Westwood, 1889: rediscovery and review of the Amazonian “ant-mantis” (Mantodea: Thespidae: Oligonictinae). *Entomol Sci* 17:400–408
- Alberch P, Gould S JG, Oster F, Wake DB (1979) Size and shape in ontogeny and phylogeny. *Paleobiology* 5:296–317
- Battiston R, Puttaswamaiah R, Manjunath N (2018) The fishing mantid: predation on fish as a new adaptive strategy for praying mantids (Insecta: Mantodea). *J Orthop Res* 27:155–158
- Beier M (1942) Neue und seltene Mantodeen aus deutschen Museen. *Ann Nat Hist Mus Wien* 52:126–154

- Beier M (1964) Blattopteroidea-Mantodea. In: Bronn HG (ed) *Klassen und Ordnungen des Tierreichs*. Akademische Verlagsgesellschaft Geest & Portig, Leipzig, pp 850–970
- Brannoch SK, Wieland F, Rivera J, Klass K-D, Béthoux O, Svenson GJ (2017) Manual of praying mantis morphology, nomenclature, and practices (Insecta, Mantodea). *Zookeys* 696:1–100
- Corrette BJ (1990) Prey capture in the praying mantis *Tenodera aridifolia sinensis*: coordination of the capture sequence and strike movements. *J Exp Biol* 148:147–180
- Ehrmann R (2002) *Gottesanbeterinnen der Welt*. Natur und Tier Verlag, Münster, p 519
- Friedrich F, Matsumura Y, Pohl H, Bai M, Hörnschemeyer T, Beutel RG (2014) Insect morphology in the age of phylogenomics: innovative techniques and its future role in systematics. *Entomol Sci* 17:1–24
- Gerson U (1982) Bryophytes and invertebrates. In: Smith AJE (ed) *Bryophyte ecology*. Chapman & Hall, London, pp 291–332
- Godfray H CJ (2007) Linnaeus in the information age. *Nature* 446:259–260
- Kelly BE, Bhattacharya I, Heidari H, Shusteff M, Spadaccini CM, Taylor HK (2019) Volumetric additive manufacturing via tomographic reconstruction. *Science*. <https://doi.org/10.1126/science.aau7114>
- Li D, Zhang K, Zhu P, Wu Z, Zhou H (2011) 3D configuration of mandibles and controlling muscles in rove beetles based on micro-CT technique. *Anal Bioanal Chem* 40:817–825
- Maldaner C, Agudelo AA, Rafael JA (2015) Rediscovery of *Mantellias pubicornis* Westwood, 1889, a rare praying mantis from the Amazon (Mantodea, Thespidae, Oligonictinae). *Zootaxa* 3973:195–199
- Maldonado H, Levin L, Pita JB (1967) Hit distance and the predatory strike of the praying mantis. *Z Vgl Physiol* 56:237–257
- McKinney ML, McNamara KJ (2013) *Heterochrony: the evolution of ontogeny*. Springer Science & Business Media, p 437
- McNamara KJ (2012) Heterochrony: the evolution of development. *Evolution: Educ Outreach* 5(2):203–218
- McNamara KJ, McKinney ML (2005) Heterochrony, disparity, and macroevolution. *Paleobiology* 31(S2):17–26
- Murphy EAK, Patek SN (2012) Strike mechanics of an ambush predator: the spearing mantis shrimp. *J Exp Biol* 215:4374–4384
- Nguyen CV, Lovell DR, Adcock M, La Salle J (2014) Capturing natural-colour 3D models of insects for species discovery and diagnostics. *PLoS One* 9:1–11
- Nyffeler M, Maxwell MR, Remsen JV Jr (2017) Bird predation by praying mantises: a global perspective. *Wilson J Ornithol* 129:331–344
- Oufiero CE, Nguyen T, Sragner A, Ellis A (2016) Patterns of variation in feeding strike kinematics of juvenile ghost praying mantis (*Phyllocrania paradoxa*): are components of the strike stereotypic? *J Exp Biol*:jeb-139675
- Pye GH (1984) Optimal foraging theory: a critical review. *Annu Rev Ecol Evol Syst* 15:523–575
- Qing X, Bert W (2018) 3D printing in zoological systematics: integrative taxonomy of *Labrys chinensis* gen. nov., sp. nov. (Nematoda: Tylenchomorpha). *J Zool Syst Evol Res*, 56: 35–47
- Rehn JA (1935) The Orthoptera of Costa Rica, part I: Mantidae. *Proc Acad Nat Sci Philadelphia* 87:167–272
- Rivera J (2010) A historical review of praying mantid taxonomy and systematics in the Neotropical region: state of knowledge and recent advances (Insecta: Mantodea). *Zootaxa* 2638:44–64
- Rivera J, Svenson GJ (eds) (2014) A revived focus on the praying mantises (Insecta: Mantodea). *Zootaxa* 3797:1–273
- Rivera J, Svenson GJ (2016) The Neotropical ‘polymorphic earless praying mantises’— part I: molecular phylogeny and revised higher-level systematics (Insecta: Mantodea, Acanthopoidea). *Syst Entomol* 41(3): 607–649
- 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* 4337:361–389

- Rivera J, Yagui H, Ehrmann R (2011) Mantids in the mist – taxonomy of the Andean genus *Pseudopogonogaster* Beier, 1942, a cloud forest specialist, with notes on its biogeography and ecology (Mantodea: Thespidae: Mioteryginae). *Insect Syst Evol* 42:313–335
- Rodrigues HR, Rivera J, Reid N, Svenson GJ (2017) An elusive Neotropical giant, *Hondurantemna chespiritoi* gen. n. & sp. n. (Antemniinae, Mantidae): a new lineage of mantises exhibiting an ontogenetic change in cryptic strategy. *ZooKeys* 680:73–104
- Roy R (2014) A historical review of nomenclature and high-level classification of praying mantises (Mantodea), including a provisional checklist of the names associated to suprageneric ranks. *Zootaxa* 3797(1):9–28
- Salazar-E JA, Gomes-Dias L (2018) Descripción de una nueva especie de mantis-lichen para Colombia: *Carrikerella amazonica* n. sp. (Mantodea: Thespidae, Oligonychinae). *Bol Cient Mus His Nat* 22:106–118
- Santos BF, Scherrer MV, Loss AC (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*:1–9
- Saussure H, Zehntner L (1894) Familia Mantidae. *Biol Cent-Amer* 1:123–197
- Scharf FS, Juanes F, Rountree RA (2000) Predator size-prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Mar Ecol Prog Ser* 208:229–248
- Scherrer M (2014) A revision of *Miobantia* Giglio-Tos, 1917 (Mantodea: Thespidae, Miobantiinae), with molecular association of dimorphic sexes and immature stages. *Zootaxa* 3797:207–268
- Schwarz CJ, Roy R (2019) The systematics of Mantodea revisited: an updated classification incorporating multiple data sources (Insecta: Dictyoptera). *Ann Soc Entomol France (NS)* 55(2):101–196
- Ströbe B, Schmelzle S, Blüthgen N, Heethoff M (2018) An automated device for the digitization and 3D modelling of insects, combining extended-depth-of-field and all-side multi-view imaging. *ZooKeys* 759:1–27
- Svenson GJ, Whiting MF (2009) Reconstructing the origins of praying mantises (Dictyoptera, Mantodea): the roles of Gondwanan vicariance and morphological convergence. *Cladistics* 25:468–514
- Terra PS (1980) Ontogênese da perna raptoria em “louva-a-deus” (Mantodea): um estudo comparativo de alometria. *Rev Bras entomol* 24:117–122
- Travassos Filho LP, Urban H (1954) Sobre a criação de pequenos Mantodea com insetos da ordem collembola. *Rev Bras entomol* 1:159–161
- Van Der Wal C, Ah Yong ST, Ho SY, Lo N (2017) The evolutionary history of Stomatopoda (Crustacea: Malacostraca) inferred from molecular data. *PeerJ* 5:e3844
- Wieland F (2013) The phylogenetic system of Mantodea (Insecta: Dictyoptera). *Species, Phylogeny Evol* 3:3–222
- Wieland F, Svenson GJ (2018) Biodiversity of Mantodea. In: Foottit RG, Adler PH (eds) *Insect biodiversity: science and society*, vol 2. Wiley-Blackwell, New Jersey, pp 389–416
- Wobber V, Wrangham R, Hare B (2010) Application of the heterochrony framework to the study of behavior and cognition. *Commun Integr Biol* 3:337–339
- Wulff NC, Lehmann AW, Hipsley CA, Lehmann GUC (2015) Copulatory courtship by bushcricket genital titillators revealed by functional morphology, μ CT scanning for 3D reconstruction and female sense structures. *Arthropod Struct Dev* 44:388–397
- Yanoviak SP, Nadkarni NM, Gering JC (2003) Arthropods in epiphytes: a diversity component that is not effectively sampled by canopy fogging. *Biodivers Conserv* 12:731–741
- Yanoviak SP, Walker H, Nadkarni NM (2004) Arthropod assemblages in vegetative vs. humic portions of epiphyte mats in a neotropical cloud forest. *Pedobiologia* 48:51–58
- Yanoviak SP, Nadkarni NM, Solano JR (2007) Arthropod assemblages in epiphyte mats of costa rican cloud forests. *Biotropica* 39:202–210
- Zimmermann D, Randolph S, Metscher BD, Aspöck U (2011) The function and phylogenetic implications of the tentorium in adult Neuroptera (Insecta). *Arthropod Struct Dev* 40:571–582

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