

Taxonomy and systematics

Phylogenetic isolation of the jumping spider *Amilaps olivacea*, with notes on morphology and natural history (Salticidae: Spartaeinae: Lapsiini)

Aislamiento filogenético de la araña saltarina Amilaps olivacea, con notas sobre su morfología e historia natural (Salticidae: Spartaeinae: Lapsiini)

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Abstract

The rarely-seen jumping spider *Amilaps mayana* Maddison, 2019 has been enigmatic in its phylogenetic placement, having no synapomorphies known to unite it with any other subgroup of salticids. In recent field work in southern México, we found them to be common in limestone alcoves near the entrances of caves. Our phylogenomic analysis based on ultra-conserved elements (UCEs) shows *Amilaps* to be in the tribe Lapsiini, but phylogenetically isolated as the sister group to all other known genera of the tribe. A preliminary divergence dating analysis hints that it may be the single species most distant from others known within Salticidae. We describe the female for the first time, present photos of living specimens, and give details of its natural history. The discovery of the female reveals that *Amilaps mayana* is a junior synonym of *Sidusa olivacea* F.O. Pickard-Cambridge 1901, syn. nov., thus yielding the new combination *Amilaps olivacea* (F.O. Pickard-Cambridge, 1901), comb. nov.

Keywords: Grutas de Coconá; Karst topography; Phylogeny; Systematics; Taxonomy

Resumen

La araña raramente vista *Amilaps mayana* Maddison, 2019 ha sido uno de los salticidos filogenéticamente más enigmáticos, ya que no se conocen sinapomorfías que la relacionen con ningún otro clado de salticidos. En una recolecta reciente en el sur de México se encontraron ejemplares activos de esta especie sobre roca caliza, cerca de

la entrada de cuevas. Se llevó a cabo un análisis filogenómico basado en elementos ultraconservados (UCEs), cuyos resultados muestran que *Amilaps* pertenece a la tribu Lapsiini y dados los resultados de un análisis de divergencia preliminar, se puede suponer que es el grupo hermano de todos los demás lapsiinos conocidos. Lo cual sugiere que *Amilaps* es una de las especies de salticidos filogenéticamente más aisladas que se conocen. En esta contribución se describe la hembra, se presentan fotografías de ejemplares vivos y se aportan detalles de su historia natural, por primera vez. El descubrimiento de la hembra revela que *Amilaps mayana* es un sinónimo de *Sidusa olivacea* F.O. Pickard-Cambridge 1901, syn. nov., por lo que se propone la nueva combinación *Amilaps olivacea* (F.O. Pickard-Cambridge, 1901), comb. nov.

Palabras clave: Grutas de Coconá; Topografía kárstica; Filogenia; Sistemática; Taxonomía

Introduction

Few major phylogenetic mysteries remain among the jumping spiders. Almost all species that are known to any degree can be assigned easily to one of the 7 subfamilies, if not to tribe (Maddison, 2015). However, *Amilaps mayana* Maddison, 2019, of southern México and Guatemala, has remained enigmatic. Known from just 2 old male specimens, there has been no molecular phylogenetic data available for it. Its morphology excludes it from the 2 subfamilies containing all other salticids known from the North American continent, the enormous Salticinae and the smaller Lyssomaninae. Maddison (2019) placed it with hesitation in the Lapsiini, a small tribe of otherwise South American genera in the subfamily Spartaeinae. This placement was based primarily on *Amilaps* being in the Americas, like the lapsiines, but on little else. Their general morphological resemblance could very well be plesiomorphic to the family, and thus not an indication of relationship. The synapomorphy that unites all other lapsiines, a reduction to 2 retromarginal cheliceral teeth (Ruiz & Maddison, 2012), is absent in *Amilaps* (Maddison, 2019). No other synapomorphies are known to unite *Amilaps* with the remaining Lapsiini, with the Spartaeinae, or for that matter any other subgroup of Salticidae. Thus, with *Amilaps*'s generalized features, it could have been placed anywhere deep in the salticid tree, perhaps even as sister to the rest of the family. As such, it could play a major role in inferences of the evolution of salticids.

Using specimens obtained from recent field work at the type locality of *Amilaps mayana*, this paper gathers ultra-conserved element (UCE) data (Faircloth, 2017) to resolve the phylogenetic position of *Amilaps*. We give the first description of the female, characterize in general terms the natural history of the species, and present photographs and videos of living specimens. Finding the female led to the discovery of an older synonym, and thus the species will be hereafter referred to as *Amilaps olivacea* (F.O. Pickard-Cambridge, 1901), comb. nov.

Materials and methods

Specimens and morphology

Preserved specimens recently collected are deposited in the Colección Nacional de Arácnidos (CNAN), Instituto de Biología, Universidad Nacional Autónoma de México, and the Beaty Biodiversity Museum (BBM), University of British Columbia. The holotype female of *Sidusa olivacea* F. O. Pickard-Cambridge, 1901, is in the Natural History Museum, London (NHMUK).

The preserved specimens were examined under both dissecting microscopes and a compound microscope with reflected light. Drawings were made with a drawing tube on a Nikon ME600L compound microscope. Microscope photographs were made on the same microscope and focus-stacked using Helicon Focus v. 4.2.7.

Terminology is standard for Araneae. All measurements are given in mm. Descriptions of color pattern are based on the alcohol-preserved specimen. Carapace length was measured from the base of the anterior median eyes not including the lenses to the rear margin of the carapace medially; abdomen length to the end of the anal tubercle. Abbreviations used: ALE, anterior lateral eye; AME, anterior median eye; PLE, posterior lateral eye; PME, posterior median eye.

Phylogenomics

In order to place *Amilaps* phylogenetically, molecular data was newly gathered from 15 salticids (Table 1) by Ultraconserved Element (UCE) target enrichment sequencing methods (Faircloth 2017), using the RTA v3 probe set (Zhang et al., 2023), and with the assistance of Arbor Biosciences. These data were combined with previously-published data for 17 other salticids and 2 outgroups to assemble a UCE dataset of 34 species spanning all 7 subfamilies. All but 3 of the previously-published taxa are from Zhang et al. (2024); the 2 non-salticid taxa are from Zhang et al. (2023), and *Habronattus ophrys* Griswold, 1987 is from Maddison (2024a). The specimen information for previously-published data can

Table 1

Newly sequenced specimens. “j.” = Juvenile; SRA = accession number in Sequence Read Archive.

Species	Specimen	sex	SRA	Reads passed QC	Locality	Lat., long.
<i>Amilaps olivacea</i> (F.O. Pickard-Cambridge, 1901)	IDWM.24057	♀	SAMN53178949	3345230	México: Teapa	17.564, -92.928
<i>Ascylltus pterygodes</i> (L. Koch, 1865)	WL22.0288	j.	SAMN53178950	5745797	USA: Oahu	21.31, -157.79
<i>Asemonea sichuanensis</i> Song & Chai, 1992	MRB084	♂	SAMN53178951	5895745	China: Ningming Co.	21.83, 107.02
<i>Attulus fasciger</i> (Simon, 1880)	DDKM21.151	♀	SAMN53178952	2603659	Canada: Burlington	43.3507, -79.7593
<i>Bavia sexpunctata</i> (Doleschall, 1859)	AS19.2175	♂	SAMN53178953	2603659	Singapore	1.356, 103.774
<i>Breda apicalis</i> Simon, 1901	ECU10-2705	♂	SAMN53178954	2545037	Ecuador: Río Bigal	-0.5275, -77.4225
<i>Bristowia heterospinosa</i> Reimoser, 1934	IDWM.22045	♂	SAMN53178955	4292901	Singapore	1.38, 103.817
<i>Chinoscopus</i> sp.	DDKM23.006	j.	SAMN53178956	4296450	Panama: Gamboa	9.1584, -79.7425
<i>Cucudeta gahavisuka</i> Maddison, 2009	IDWM.22014	j.	SAMN53178957	4307698	Papua New Guinea	-6.0145, 145.4117
<i>Hispo sulcata</i> Wanless, 1981	IDWM.22011	♂	SAMN53178958	4256628	Madagascar	-21.2644, 47.4218
<i>Icius hamatus</i> (C. L. Koch, 1846)	d288	♂	SAMN53178959	5689752	Spain: Sitges	41.2383, 1.8244
<i>Idastrandia</i> sp. “WHSPS”	d517	♂	SAMN53178960	5709864	Malaysia: Mulu	4.049, 114.860
<i>Matinta</i> cf. <i>fonsecai</i> (Soares & Camargo, 1948)	IDWM.22018	♂	SAMN53178961	4191187	Ecuador: Jatun Sacha	-1.067, -77.617
<i>Portia</i> cf. <i>schultzi</i> Karsch, 1878	d131	♀	SAMN53178962	3299758	Madagascar	-22.592, 45.128
<i>Viciria pavesii</i> Thorell, 1877	IDWM.22044	♀	SAMN53178963	6469708	Singapore	1.44, 103.7

be found in those papers using the specimen ID code in Figure 26. Molecular protocols followed those of Marathe et al. (2024).

UCE loci were identified among the assembled contigs using the RTA probe set file and PHYLUCE 1.7.3 (Faircloth, 2016; Faircloth et al., 2012). After recovery, each locus was aligned with MAFFT v. 7.505 (Katoh & Standley, 2013) using the L-INS-i option. Poorly aligned areas were trimmed using PhyIN (Maddison, 2024b) as implemented in Mesquite v. 4.01 (Maddison & Maddison, 2025b), with parameters b = 10 d = 2 p = 0.5 e = true occ = 0.5. Loci were discarded if recovered in fewer than 50% of the taxa. The loci were concatenated and rogue subsequences trimmed using Spruceup v.2024.07.22 (Boroweic, 2019) as implemented in Mesquite, with parameters criterion:mean window_size:50 cutoffs:4.0 overlap:25 distance_method:uncorrected. The loci were

de-concatenated, after which sequences of less than 50 nucleotides were discarded. For each locus, a RAxML analysis (Stamatakis, 2014) was done to obtain a gene tree, and the locus was discarded if its gene tree had the ratio of the 2 longest branches greater than or equal to 5, a sign of possible paralogy (Maddison et al., 2020). Concatenations and de-concatenations of loci were done in Mesquite.

Maximum likelihood phylogenetic analyses on the concatenated alignment were performed with IQ-TREE version 3.0.1 (Wong et al., 2025) using the Zephyr 4.01 package (Maddison & Maddison, 2025a) in Mesquite 4.01 (Maddison & Maddison, 2025b). Analyses were run unpartitioned and used the TEST option (standard model selection followed by tree inference). A bootstrap analysis was done with 500 replicates.

A preliminary Bayesian estimate of relative divergence dates was made on the ML tree from the concatenated

alignment by MCMCtree in PAML (Yang, 2007) via special features in IQ-TREE 3.01 (Demotte et al. 2025) that communicate with MCMCtree via Hessians in order to implement the approximate likelihood method (Minh et al., 2025). We used a correlated rates clock model, unpartitioned, root age < 1.0, BDparas = 1,1,0.5. Because our goal is relative divergence dating rather than absolute, the root age specification is likely irrelevant, but dos Reis et al. (2017) suggest that specifying “root age <1.0” is a “safe constraint on root age, used if no fossil for root”. The analysis was run for 100 million MCMC generations (burn-in 10,000, sample every 1,000, number of samples 100,000), by which point the ESS of each node height was greater than 15,000.

Raw reads of new data are deposited in Sequence Read Archive (BioProject submission ID PRJNA1360076; see Table 1). Alignments and trees are deposited in FigShare (<https://doi.org/10.6084/m9.figshare.32680758>).

Results

Natural history

During field work 26 to 28 August 2024, 12 males, 21 females, and 2 juvenile *A. olivacea* were found at Grutas de Coconá, Teapa, Tabasco (17.564° N, 92.928° W [17°33'50" N, 92°55'40" W]), ca. 30 m elevation), at the base of a canyon in a small range of hills in tropical rainforest (Fig. 1).

The site is a small tourist park in karst topography, with entrances leading into caves. The steep-sided canyon walls have large patches of bare limestone, either vertical or in recessed alcoves where overhanging limestone shades and protects the surface from rain (Figs. 2-4). Some of the alcoves are shallow dimples (Fig. 3), while others continue inward into the cave system.

All individuals of *Amilaps* were found on this limestone in the liminal zone between cave and forest. The great majority were found in alcoves or under overhangs, on the outermost edge of the cave's limestone and in the shade, but within 1 or 2 metres from the forest's full light (Figs. 2-4). The surfaces on which they walked were typically dry, though some were found walking over wet patches. The spiders were not on webs or visibly associated with any web of their own or other spiders. None were found with prey. They were sometimes first seen walking, but most were seen motionless. The spiders moved primarily by walking, relatively slowly for a salticid. When disturbed they could run quickly, but were not seen to jump for escape. They have a distinctive gait like that seen in Spartaeini, Cocalodini, other Lapsiini, and some Hispaninae (Maddison, 2006, 2009, 2015), hesitant and yet fluid, waving first, second, and third pairs

of legs, seemingly randomly. Figures 5, 6, 17, and 18 show individuals waving 1 or both second legs. Photographs of living specimens are shown in Figures 5-25. A video is available at <https://youtu.be/heT9khLhRmE>, showing the habitat, locomotory behaviour, and the behaviour of a male interacting with a female.

Phylogenetic placement of *Amilaps*

Sequencing, cleaning, assembly, and UCE identification resulted in 3,680 RTAv3 UCE loci recovered among the taxa. Of these, 618 were discarded for being recovered in fewer than 50% of the taxa, 25 were discarded for having only sequences less than 50 nucleotides, and 10 were discarded because their gene trees failed the branch length ratio paralogy filter. The remaining 3,027 loci concatenated to an alignment of 1,117,290 sites.

Figure 26 shows the maximum likelihood tree from the concatenated alignment, placing *Amilaps olivacea* with strong support within the Lapsiini, as sister to the remaining lapsiines, all of which are South American. This is the placement suggested by Maddison (2019). The reduction to 2 retromarginal cheliceral teeth (Ruiz & Maddison, 2012) is therefore a synapomorphy of the South American lineage of lapsiines, but not of all lapsiines. There is still no known morphological synapomorphy for the tribe.

The relative dating analysis (Fig. 27) shows a deep divergence between *Amilaps* and the other lapsiines, older than the first divergence in the entire subfamily Salticinae.

Taxonomy

Amilaps olivacea (F. O. Pickard-Cambridge, 1901), comb. nov.

Figs. 5-25, 28-35

Sidusa olivacea F. O. Pickard-Cambridge, 1901. Holotype female in NHMUK, examined.

Amilaps mayana Maddison, 2019, syn. nov.

Description of female (measurements from specimen NA24.9873). Carapace length 1.8, width 1.3; abdomen length 2.4. Carapace (Figs. 28, 29): integument light to medium brown except for a central longitudinal band of pale honey, and black around the eyes. Band of pale scales extending posterior for side of AME breaks up into a few discrete spots on lower thoracic sides (Figs. 23, 29). Cream and orange-brown scales clothe the ocular quadrangle, pointing forward in the middle but to the side just anterior to the PLE. PMEs as far medial as the inner edge of the ALE. Fovea long, longer than diameter of PLE. Clypeus narrow, pale except for dark band extending laterally and downward from AME, thinly clothed with white hairs (Fig. 30). Chelicerae light brown proximally and distally, but dark brown centrally. Four small retromarginal and 3



Figures 1-4. Habitat of *Amilaps olivacea*. 1, Overview of the hills in which the Grutas de Coconá are embedded, just north of Teapa, Tabasco. In the lower center can be seen a limestone cliff. 2, 3, Examples of sites where *Amilaps* was found (blue arrows). Beating sheet is ~ 85 cm × 85 cm. 4, M. Menéndez searching for *Amilaps* on overhanging wall of boulder, on which several were found.

larger promarginal teeth. Palp with tarsal claw. Legs pale honey coloured, with darker annulae. First tibia with 3 pairs of ventral and 2 smaller anterior-lateral macrosetae; first metatarsus with 2 pairs of ventral macrosetae and 1 smaller anterior-lateral one. Leg formula 4132. Length of femur I 1.2, II 1.16, III 1.11, IV 1.49; patella + tibia I 1.51, II 1.4, III 1.3, IV 1.8; metatarsus + tarsus I 1.2, II 1.16, III 1.42, IV 1.9 Abdomen light to dark brown with paler cream-coloured medial markings forming a series of approximate triangles, the anteriormost the longest, the middle the widest, and the posteriormost the smallest. Epigyne (Figs. 31, 32) with a large pale posterior depression, framed at

the back by a lip along the epigastric furrow. At the front of the depression, openings lie beneath crescent shaped ridges. From the openings a heavily sclerotized twisted duct goes anteriorly, and a duct proceeds from the regions of the openings posteriorly to the spermathecae (Fig. 33). Whether the path to the posterior goes through the anterior twisted duct, or whether the duct forks into anterior and posterior branches, is not clear.

Material examined. México: Tabasco: Teapa, Grutas de Coconá, limestone walls and overhangs. 17.564, -92.928. 30 m elev. 26 to 28 August 2024. Maddison, Menéndez, Torres, González, Cuevas. WPM#24-047a



Figures 5-16. Living male *Amilaps olivacea*. 5, 8, 16, Male NA24.9670; 6, 12, male NA24.0078; 7, 10, 11, male NA24.9696; 9, 13-15, male NA24.9736. Figures 5, 6 show the spider waving the first and/or second pair of legs, as done by many non-salticid salticids. Scale bar 1.0 mm in 5; applies to all photos.



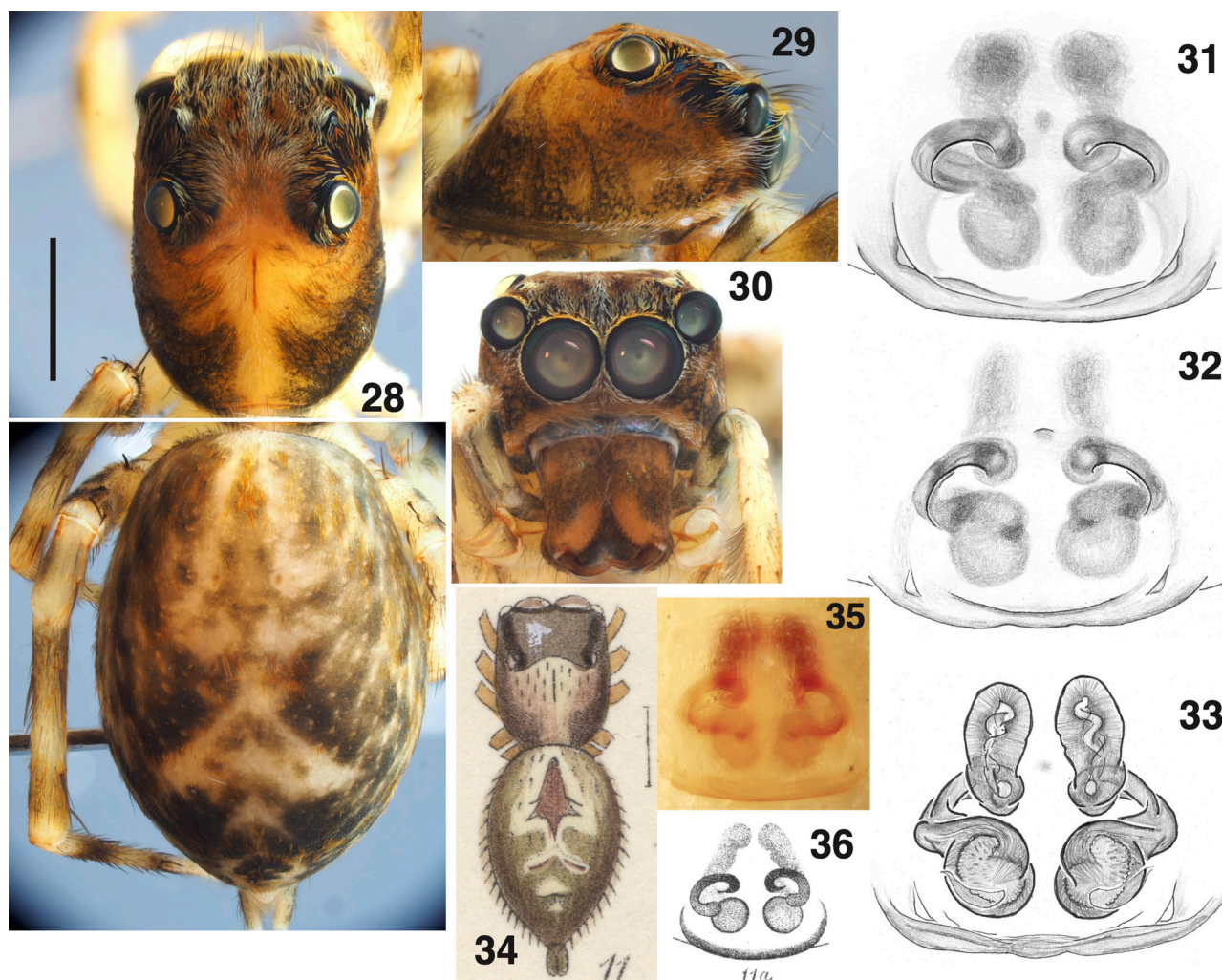
Figures 17-25. Living female *Amilaps olivacea*. 17, 18, 22, Female NA24.9789; 19, 23, female NA24.9777; 20, female NA24.9825; 21, 25, female NA24.9853; 24, female NA24.9806. Figures 17, 18 show the spider waving the first and/or second pair of legs, as done by many non-salticid salticids. Scale bar 1.0 mm in 25; applies to all photos.

(12 ♂, 21 ♀, 2 juv., CNAN-Ar017743). Chiapas: Mpo. Ocosingo, Area Natural Protegida Lacandonia, 16.7598, -91.0065. 159 m. elev. 31 May 2004, diurnal collecting (1 ♀ CNAN-Ar004581, CNAN).

Distribution. Southeastern Mexico and Guatemala. A male is known from Poptún, Guatemala (Maddison, 2019), and Pickard-Cambridge's (1901) female of *Sidusa olivacea*, collected by Sarg, is listed as from "Guatemala".

Remarks. The holotype female is now faded, but Pickard-Cambridge's (1901) Figure 11 (our Fig. 34) of it

shows markings matching those of *Amilaps mayana*. We include as well his illustration of the epigyne (his 11a, our Fig. 36) alongside its photograph (our Fig. 35) to show the accuracy of Pickard-Cambridge's drawings. Pickard-Cambridge's assigning this species to a euophryine genus, now placed in a different subfamily, may seem like a grave error, but not only has our understanding of phylogeny improved enormously, but also this species does have a superficial resemblance to some euophryines in the region, especially *Amphidraus* Simon, 1900 and *Chapoda*



Figures 28-36. Female *Amilaps olivacea*. 28-30, Female from Teapa; 28, dorsal; 29, carapace, lateral; 30 face; 31, female NA24.9964 from Grutas de Coconá, epigyne; 32, 33, female CNAN-Ar004581 from Ocosingo, epigyne and cleared vulva; 34, 36, holotype female *Sidusa olivacea* from Guatemala; 34, 36, illustrations by F. O. Pickard-Cambridge (1901). Scale bar for body photos 1.0 mm, for epigynes 0.1 mm.

Cocalodini (Maddison et al., 2016). It may be useful to establish a separate subtribe for *Amilaps*, but that would best wait for a comprehensive review of higher level salticid classification.

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