

The unknown *Enna* (Araneae: Trechaleidae), new species and first record of wrapped nuptial gifts in the genus

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Abstract. The spider family Trechaleidae includes 17 genera and 131 species distributed throughout the Neotropical region. Most of them are semiaquatic spiders living adjacent to streams and rivers. Very few species of the family have been studied for their natural history or behavior; however four genera (*Paratrechalea* Carico, 2005, *Trechalea* Thorell, 1869, *Paradosenus* F. O. Pickard-Cambridge, 1903 and *Trechaleoides* Carico, 2005) are already known to have males that offer wrapped nuptial gifts to females. Here we describe a new species from the genus *Enna* O. Pickard-Cambridge, 1897, namely *E. gloriae* sp. nov. from Quindío, Colombia. We additionally report the presence of males of this species offering nuptial gifts to females during courtship, being the first record of this sexual trait for the genus.

Keywords: Gift-giving, RTA clade, spider taxonomy, trechaleid

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The family Trechaleidae includes 17 genera and 131 described species distributed throughout the Neotropics from the southern USA to the south of Argentina, with a single species in Japan (World Spider Catalog 2020). Most of the species are semiaquatic, living in riparian habitats near rivers and streams. Individuals of this family are characterized by having legs with long and flexible tarsi, a character suggested to be an adaptation for walking along the water surface (Carico 1993, 2005; Silva et al. 2008). The diagnostic characters in males are the morphology of the median apophysis and the presence of a dorsal embolic groove and ‘guide’ on the pedipalps; while females typically present dark and sclerotized epigynes and carry the discoid egg sacs by their spinnerets (Carico 1993, 2005; Silva et al. 2008).

The trechaleid genus *Enna* O. Pickard-Cambridge, 1897 comprises 39 described species distributed from Central to South America (World Spider Catalog 2020). Species belonging to this genus present the anterior eye row straight to moderately recurved and the posterior row recurved. As in other trechaleids, the third pair of legs is smaller than the rest. The diagnostic generic characters are the female genitalia with globose spermathecae and a conspicuous middle field on the epigyne. In addition, the male pedipalps typically have a larger dorsal division of the median apophysis in relation to the ventral division, and the dorsal division is usually concave (Silva et al. 2008; Carico & Silva 2010). In general, the number of specimens from this genus that are available in collections is limited, and most species are only represented by one described sex (Silva & Lise 2011; Silva et al. 2012).

So far, biological characteristics of the genus *Enna* are largely unknown and unstudied (Silva et al. 2008). However, the biology of the family as a whole is of particular interest for evolutionary and behavioral studies, given that males of many species present wrapped nuptial gifts to females (Costa-Schmidt et al. 2008) – a behavior which has been suggested

to be an ancestral trait in the family (Albo et al. 2017). Several studies have described this gift-giving behavior, reporting it in eight species from four genera including *Paratrechalea* Carico, 2005 [*P. ornata* (Mello-Leitão, 1943), *P. azul* Carico, 2005, *P. galianoae* Carico, 2005], *Trechalea* Thorell, 1869 [*T. amazonica* F. O. Pickard-Cambridge, 1903, *T. tirimbina* Silva & Lapinski, 2012, *T. bucculenta* (Simon, 1898)], *Paradosenus* F. O. Pickard-Cambridge, 1903 [*P. longipes* (Taczanowski, 1874)] and *Trechaleoides* Carico, 2005 [*T. keyserlingi* (F. O. Pickard-Cambridge, 1903)] (Costa-Schmidt et al. 2008; Albo et al. 2009, Lapinski & Tschapka 2009; Silva & Lise 2009; Trillo & Albo 2019; Martínez-Villar et al. 2020). This sexual trait has also been described for some species of the family Pisauridae (Bristowe & Locket 1926; Itakura 1993, 1998; Bastos 2009; cf. Nitzsche 2011; Albo et al. 2014b), a family closely related to Trechaleidae (Albo et al. 2017). In all of the eight trechaleid species studied, nuptial gift production is similar and ritualized, and includes silk wrapping of the prey or inedible items and other associated sexual behaviors like hyperflexion (Lang 1996; Costa-Schmidt et al. 2008; Albo et al. 2009, 2011, 2014b; Brum et al. 2012).

Here, we studied a species of *Enna* from Colombia, where four described species of this genus occur: *E. caliensis* Silva, Lise & Carico, 2008, *E. caricoi* Silva & Lise, 2011, *E. jullieni* (Simon, 1898) and *E. minor* Petrunkevitch, 1925. We describe this species as new, and report the first known example of nuptial gift-giving behavior in the genus.

METHODS

Specimens.—For the species description, we collected 10 adult individuals (five females and five males) from Quindío, Colombia, during January 2018. The specimens are deposited in the Museo de Artrópodos de la Universidad Quindío (CIUQ; curator A.L. García-Hernández), Armenia, Colombia. For the behavioral studies, we performed field trips to the

same collecting locality during May 2018. We collected 20 individuals (10 males and 10 females) to study the species' sexual behavior under laboratory conditions (see details below).

Taxonomy.—We dissected male and female genitalia. Female genitalia were placed in a lactic acid solution for one hour and washed with distilled water. Measurements (in millimeters) and habitus photos were taken using a Carl Zeiss Stemi 2000c AxioCam ERc5s stereomicroscope, while the genitalia of both sexes were also imaged using a scanning electron microscope (FEI, model QUANTA 250). Image processing was performed using the software GIMP (The GIMP Development Team 2020).

We followed the same abbreviations used by Silva et al. (2008): *Eye diameters, inter-distances, and median ocular quadrangle*: ALE–AME, distance between anterior lateral eye and anterior median eye; ALE, diameter of anterior lateral eye; AME, anterior median eye; AME–AME, distances between anterior median eyes; OQA, width of ocular quadrangle anteriorly or width of anterior median eyes; OQH, height of ocular quadrangle or height of anterior median eye and posterior median eye; OQP, width of ocular quadrangle posteriorly or width of posterior median eyes; PLE, diameter of posterior lateral eye; PLE–PME, distance between posterior lateral eye and posterior median eye; PME, posterior median eye; PME–PME, distance between posterior median eyes. *Genitalia*: AF, internal field of the epigyne; AS, accessory spermathecae; DD, dorsal division of median apophysis; ECD, ectal division of retrolateral tibial apophysis (RTA); END, ental division of RTA; G, guide; HS, head of spermathecae; MF, middle field of epigyne; SC, scape; SS, stalk of spermathecae; ST, subtegulum; T, tegulum; VD, ventral division of median apophysis.

Behavior.—We studied the sexual behavior of spiders in the field, in particular by searching for males carrying nuptial gifts. Typically, individuals of this family are crepuscular or nocturnal (Jocqué & Dippenaar-Schoeman 2006). Thus, one of us (LR) carried out the observations during four hours at night, and additionally, performed behavioral assays under temperature-controlled conditions (17° C minimum and 25° C maximum). We transported spiders and placed them individually in plastic jars (of 11 cm diameter), each containing pebbles as substrate. We fed spiders twice a week with fruit flies (*Drosophila melanogaster*) and gave them water as required.

For the behavioral experiments, we placed each female ($n = 10$) into a cage (15 × 15 × 20 cm) containing pebbles and water, 24 hours before commencing observations (as it is known that the silk deposited by females is a relevant stimulus for male courtship and nuptial gift production; see Lang 1996; Albo et al. 2009). For each experiment, we placed the male in with the female and once he started to vibrate his forelegs and pedipalps (a typical courtship pattern) we placed a dead moth (family Geometridae) or a house fly (*Musca domestica*) on the substrate. We registered the following behavioral units: occurrence of nuptial gift production (silk wrapping of the prey), courtship and mating duration, and pedipalp insertions. We described nuptial gift construction using previously reported terminology (Costa-Schmidt et al. 2008; Albo et al. 2009). We measured the courtship duration from the time the

male contacted the female and initiated the first pedipalp insertion; and mating duration from the first to the last pedipalp insertion, calculating it as the sum of all insertions. We finished the experiments after 30 min of no contact between sexes, after an hour of male courtship and female rejection, or immediately after the end of the mating (Costa-Schmidt et al. 2008).

TAXONOMY

Family Trechaleidae Simon, 1890

Genus *Enna* O. Pickard-Cambridge, 1897

Enna glorieae sp. nov.

<http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:5F59BDD8-A193-4D58-92FB-BC73075CA158>
(Figs. 1–2)

Type material.—*Holotype male*. COLOMBIA: *Quindío*: Filandia, Quebrada Portachuelo, 4°40'48.7"N, 75°39'48.5"W, alt. 1870 m., 20 January 2018, L. Rengifo (CIUQ: 16203). *Paratypes*. COLOMBIA: *Quindío*: 5 ♀, 4 ♂, same data as holotype (CIUQ: 10252-55 and 16204-08).

Etymology.—This species is named in honor of the senior author's mother, Gloria A. Gutiérrez.

Diagnosis.—The male pedipalps of *Enna glorieae* sp. nov. resemble those of *E. caliensis* in the shape of the median apophysis (Silva et al. 2008), but can be distinguished by the long and acute guide (G) with a crest above it (Figs. 2A–E). This species can also be distinguished by the short, rounded tip of the ectal division (ECD) of the retrolateral tibial apophysis (Figs. 2A–E). The female epigyne is similar to *E. caliensis* in the general shape of the spermathecae and the presence of a pair of small accessory spermathecae (Silva et al. 2008), but can be distinguished by the globose and conspicuous head of each main spermatheca (Figs. 3A–D).

Description (male holotype).—Carapace brown, fovea with a dark mark, clypeus dark brown; chelicerae reddish-brown; labium dark brown; sternum light yellow scattered with dark brown; legs brown. Total length 7.70. Carapace 4.79 long, 4.22 wide. Clypeus 0.40 high. Eye diameters, inter-distances, and median ocular quadrangle: AME 0.26, ALE 0.22, PME 0.31, PLE 0.39; AME–AME 0.14, AME–ALE 0.11, PME–PME 0.45, PLE–PME 0.13, OQA 0.64, OQP 1.10, OQH 0.77 (Figs. 1C, D). Chelicerae light brown, without lateral carina, promargin with three teeth and retromargin with three teeth on fang furrow, equidistant and equal in size. Sternum 2.12 long, 2.28 wide. Labium 0.89 long, 0.69 wide. Leg measurements: relative length I, II, IV, III. Leg I femur 8.78, tibia-patella 11.73, metatarsus 9.92, tarsus 3.48, total 33.91; leg II 7.68, 10.25, 9.02, 3.12, 30.06; leg III 5.74, 6.94, 5.86, 2.03, 20.57; leg IV 7.35, 8.95, 9.58, 3.15, 29.02. Pedipalp with dorsal division of median apophysis concave; ventral division of median apophysis with prominent, acute projection. Retrolateral tibial apophysis short, with a rounded and subtriangular ectal division; ental division smaller than ectal division (Figs. 2A–E).

Description (female paratype CIUQ: 16206).—Coloration as in male. Total length 10.45. Carapace 4.63 long, 4.49 wide. Clypeus 0.42 high. Eye diameters, inter-distances, and median ocular quadrangle: AME 0.26, ALE 0.21, PME 0.32, PLE

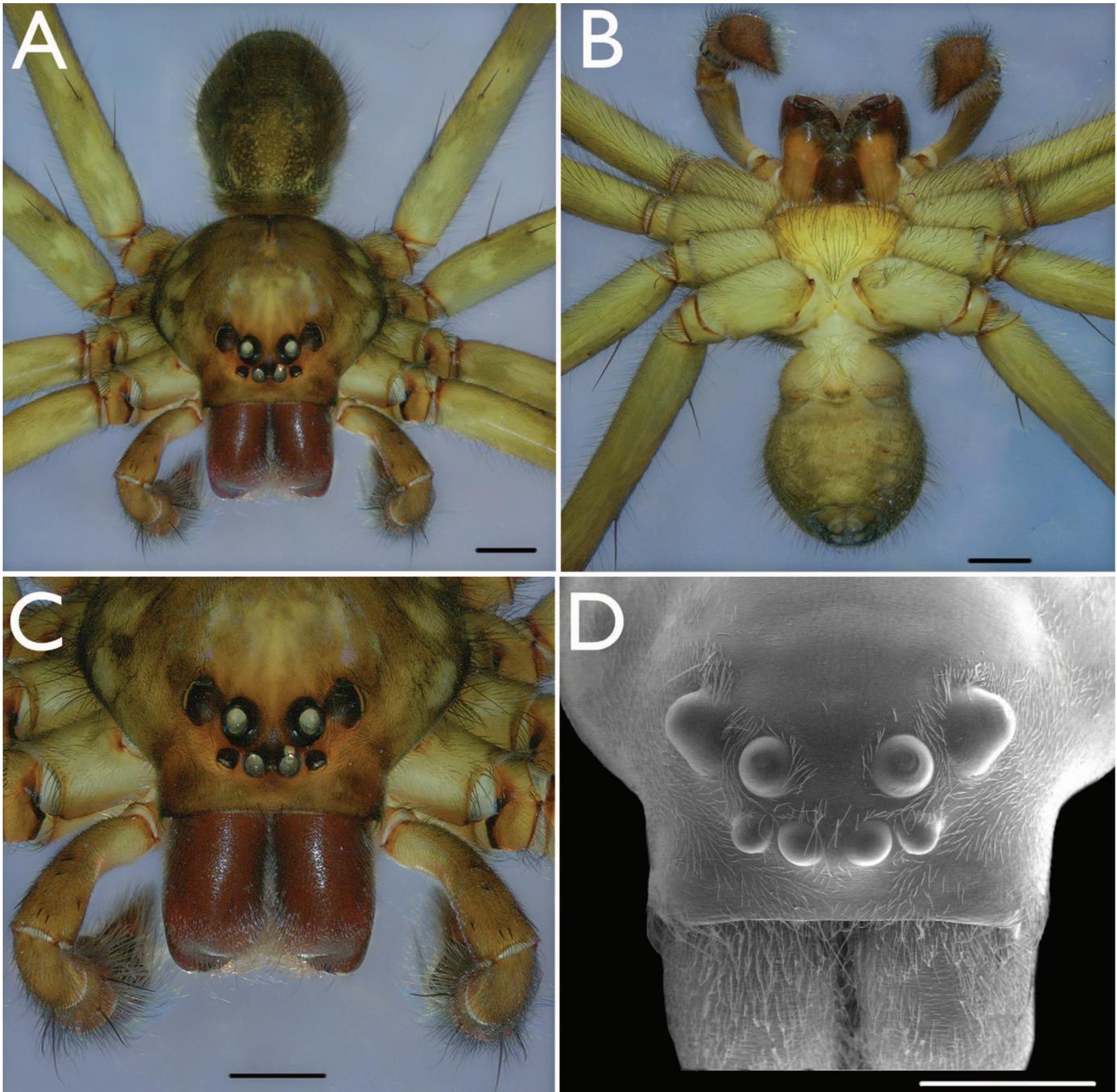


Figure 1.—*Enna gloriae* sp. nov., male holotype: A, cephalothorax and abdomen, antero-dorsal view; B, cephalothorax and abdomen, postero-ventral view; C, eyes, antero-dorsal view; D, scanning electron micrograph of eyes, antero-dorsal view. Scale bars = 1 mm.

0.39; AME–AME 0.20, AME–ALE 0.17, PME–PME 0.54, PLE–PME 0.22, OQA 0.66, OQP 1.15, OQH 0.59. Chelicerae with promargin and retromargin of fang furrow each with three teeth. Sternum 2.10 long, 2.41 wide. Labium 0.79 long, 0.66 wide. Leg measurements: relative length I, II, IV, III. Leg I femur 6.61, tibia–patella 9.11, metatarsus 7.09, tarsus 2.89, total 25.70; leg II 6.97, 8.73, 6.88, 2.76, 25.33; leg III 5.59, 6.59, 5.20, 2.01, 19.38; leg IV 6.60, 8.44, 5.20, 2.85, 23.08. Epigyne strongly sclerotized, with conspicuous globose, round sperma-

thecae including a pair of accessory spermathecae. Middle field of external epigyne hood-like (Figs. 3A–D)

Variation.—Males ($n = 4$): total length 8.79–11.21 (mean 10.1), carapace length 4.03–5.58 (4.81), carapace width 4.33–4.72 (4.53), femur 7.85–8.68 (8.26). Females ($n = 4$): total length 10.90–12.04 (11.47), carapace length 4.66–4.91 (4.79), carapace width 4.07–4.57 (4.32), femur 6.07–7.14 (6.61).

Distribution.—This species is known only from the type locality (Fig. 4).

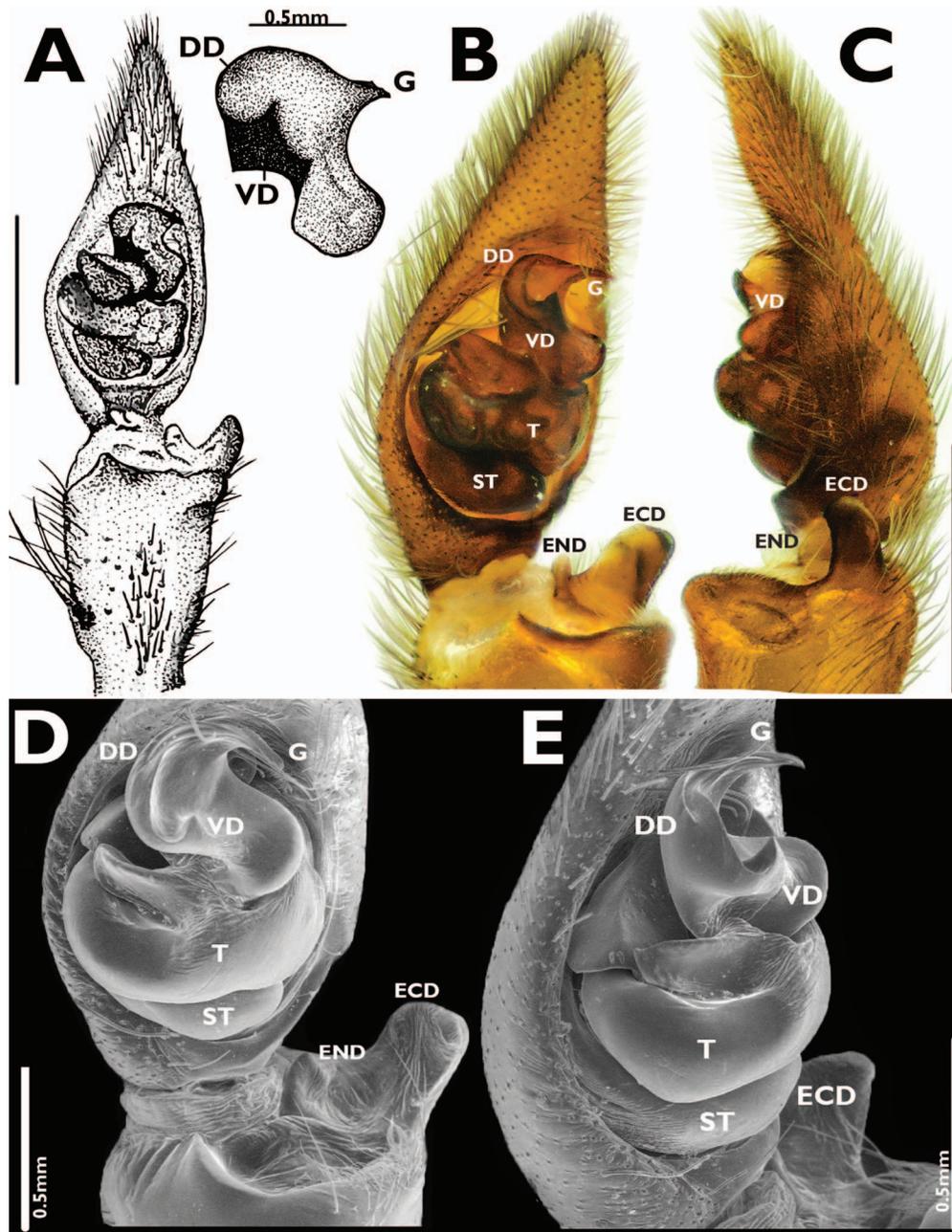


Figure 2.—*Enna glorioe* sp. nov., male holotype, pedipalp: A, illustration of tibia and cymbium in ventral view; B, C, cymbium and retrolateral tibial apophysis (RTA) in ventral (B) and retrolateral (C) views; D, E scanning electron micrographs of tegular sclerites and RTA in ventral (D) and prolateral (E) views. Abbreviations: DD, dorsal division of median apophysis; ECD, ectal division of retrolateral tibial apophysis; END, ental division of retrolateral tibial apophysis; ST, subtegulum; T, tegulum; VD, ventral division of median apophysis. Scale bars = 1 mm except where noted.

Natural history.—We found these spiders adjacent to streams and on the edge of riparian vegetation, which is characteristic of the family. Females and juveniles were mostly found on vegetation near streams or on the banks of streams, including females with egg sacs. Males were usually found perching on pebbles at the stream edge. Preliminary field studies at the same site showed that adult and juvenile individuals can be found throughout the year (Rengifo 2018).

RESULTS

Nuptial gifts in *Enna glorioe*.—In the field, we observed 15 males carrying wrapped nuptial gifts and courting females (Fig. 5). In the laboratory, all of the males courted females, although mating occurred in only four of 10 interactions. In three cases, a male offered a prey to the female (one wrapped in silk and two unwrapped); in the fourth case, the male courted and mated without a nuptial gift.

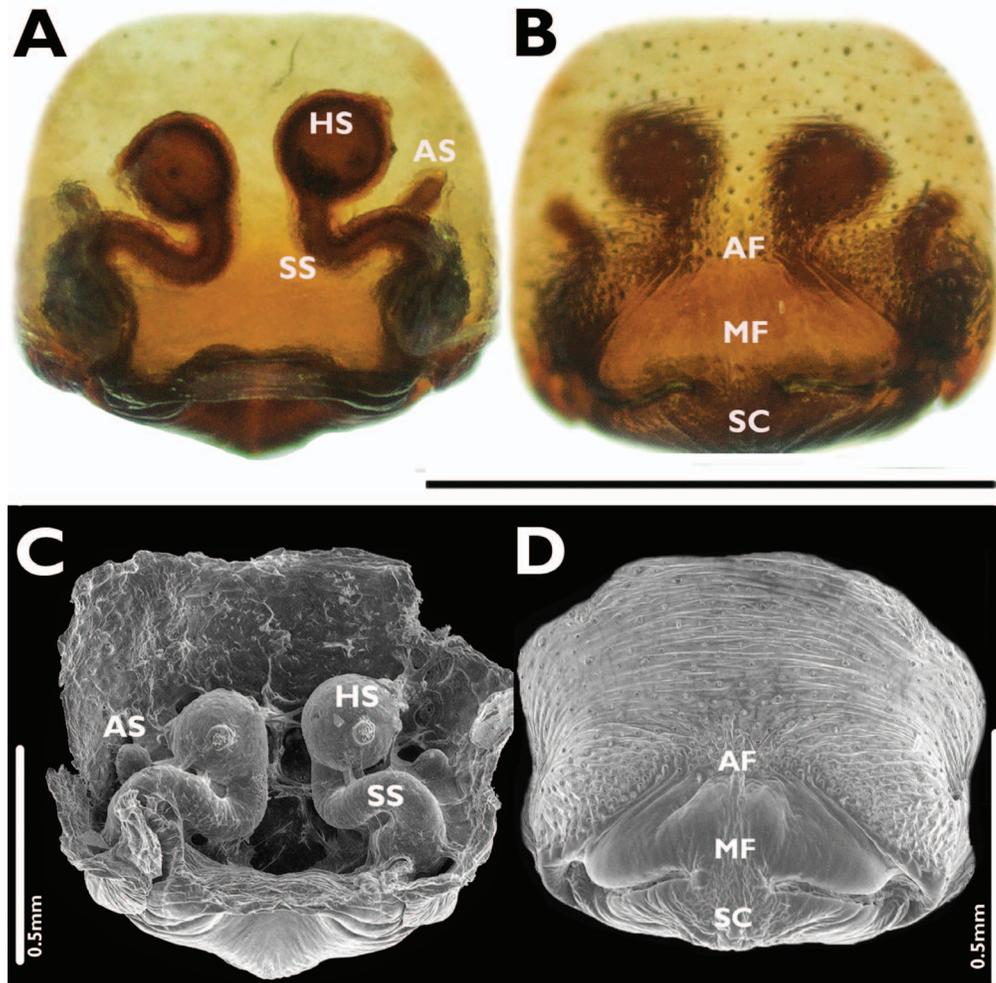


Figure 3.—*Enna glorioe* sp. nov., female paratype (CIUQ: 16206), epigyne: A, B, cleared genitalia in dorsal (A) and ventral (B) views; C, D, scanning electron micrograph of cleared genitalia in dorsal (C) and ventral (D) views. Abbreviations: AF, internal field of epigyne; AS, accessory spermathecae; HS, head of spermatheca; MF, middle field of epigyne; SC, scape; SS, stalk of spermatheca. Scale bars = 1 mm except where noted.

Nuptial gift production consisted of the following behavioral units: firstly, once a male held the prey in his chelicerae, he performed circular concentric movements by adhering silk threads to the substrate forming a sheet ('basal plate spinning'). Secondly, he placed the prey on the sheet and continued to cover it with silk ('item placement'). At the end, he held the prey with his chelicerae and with the help of his third pair of legs and pedipalps, removed the wrapped prey by lifting it from the substrate ('gift grabbing and wrapping'). The complete wrapping behavior of the nuptial gift included three repetitions of these three steps, after which the male courted and offered the nuptial gift to the female (see Supplementary Material, Video S1, online at <https://doi.org/10.1636/JoA-S-20-022.s1>).

The duration of pre-copulatory courtship was 0.73 ± 0.30 minutes (average \pm SD), during which the male started a fast and energetic tapping of the female's lateral abdomen using his first and second pairs of legs. When males offered the prey (wrapped or not) they performed this same behavior while also exposing the gift in front of the female ('hyperflexion posture'). Once the female grabbed the gift, the male began mating while also holding the gift with his third pair of legs. All males (even

the single male observed without a gift) adopted this last position with the third pair of legs next to the female's chelicerae. During mating, the male mounted the female in an opposite position to her, and commenced pedipalp insertion and sperm transfer. The average mating duration was 2.80 ± 1.41 minutes. Males performed alternate pedipalp insertions, which when males offered a gift lasted 0.53 ± 0.52 min, and lasted 0.69 ± 0.66 min when mating occurred without a gift. After each insertion, the male continued mounting by changing the side without return to the front position. During mating, the male courted by performing a series of rapid and short strokes with the first and second pairs of legs towards the lateral sides of the female's abdomen until she turned a little and facilitated pedipalp insertion. We also observed that males and females occasionally struggled over possession of the gift. Matings ended when males walked away and females remained with the gift.

DISCUSSION

Similar to other genera from the family Trechaleidae, males of *Enna glorioe* are capable of capturing and preparing prey for the purpose of presenting nuptial gifts to females during



Figure 4.—Map of northern South America, showing the collection locality of *Enna gloriae* sp. nov. in Colombia.

courtship (Costa-Schmidt et al. 2008; Albo et al. 2009; Lapinski & Tschapka 2009; Silva & Lise 2009; Trillo & Albo 2019; Martínez-Villar et al. 2020). Although relatively few nuptial gifts and matings were observed in the laboratory experiments, this was possibly because individuals were collected as adults from the field, and females may already have mated (Albo et al. 2014a). However, in the observed cases, males showed the same pattern of gift production and multiple similarities in the mating behavior relative to other gift-giving species of Trechaleidae (Costa-Schmidt et al. 2008; Albo et al. 2009), indicating these highly ritualized behaviors are shared by different genera (Costa-Schmidt et al. 2008; Albo et al. 2009; Lapinski & Tschapka 2009; Silva & Lise 2009; Trillo & Albo 2019; Martínez-Villar et al. 2020). For instance, males commonly use the third pair of legs to hold the gift during mating, a position retained even in the absence of a gift (Albo et al. 2014b). This may favor communication between the sexes during mating (Bilde et al. 2006), as well helping the male to grasp the gift while transferring sperm and therefore avoiding the female running away with it (Andersen et al. 2008). Another similarity is the struggle performed by males and females when they both grasp the gift in their chelicerae (Costa-Schmidt et al. 2008; Albo et al. 2009). Interestingly, two particular differences were observed when comparing the mating of *E. gloriae* with that observed in species of *Paratrechalea* (Costa-Schmidt et al. 2008; Albo et al. 2009). Firstly, the position of the male while offering the nuptial gift is less noticeable, and secondly, males do not return to grasp the gift between pedipalp insertions. Finally, while we never observed females attacking or cannibalizing males during encounters (with or without nuptial gifts), further research is needed to test whether the nuptial gift acts as a shield against sexual cannibalism (Toft & Albo 2015).



Figure 5.—*Enna gloriae* sp. nov., male with a wrapped nuptial gift in the field.

In conclusion, five out of 17 genera of Trechaleidae are now known to use wrapped nuptial gifts during courtship and mating. While this prevalence suggests that the trait may be symplesiomorphic for the family, new behavioral and phylogenetic studies including the remaining genera are necessary to further understand the evolution of this sexual trait in the family.

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SUPPLEMENTARY FILES

Video S1. Nuptial gift production in *Enna glorieae* sp. nov. The male wraps the prey in silk. Due to the dark coloration of the spiders, we placed a layer of white rocks in the terrariums to facilitate the contrast for the recording (Camera: Canon T5i). Online at <https://doi.org/10.1636/JoA-S-20-022.s1>

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