



The oldest fossils of the spider subfamily Modisiminae from the Americas: Description of a new species of the genus *Modisimus* Simon (Araneae: Pholcidae) from the amber of Mexico with a checklist of the extant Mexican species

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ABSTRACT

We present two new records and the description of a new fossil species of daddy long-legs spiders of the genus *Modisimus* Simon, 1893 from the Miocene Aquitanian amber in the state of Chiapas, Mexico. Of the two studied specimens, one of them is described based on adult male: *Modisimus chiapanecus* sp. nov. It is not possible to assign the second specimen as new species, because the epigynum it is not clearly visible, therefore we are presenting here the description of the female specimen only. *Modisimus chiapanecus* sp. nov. is the second fossil species of the family Pholcidae described from Mexico, and the 85th species described of the genus so far. The total number of species of *Modisimus* from Mexico increases to 20, including the new fossil species described herein. These species represent the oldest known fossils records of the subfamily Modisiminae from the Americas and of the genus so far (23 Mya). Additionally, an updated checklist of the extant Mexican species of the genus is provided.

1. Introduction

The spider family Pholcidae Koch, 1850 is the ninth largest family, with 1751 extant species including the new species described herein, classified in 94 genera (WSC, 2020). This family is subdivided into five subfamilies: Ninetinae Simon, 1890, Arteminae Simon, 1893, Modisiminae Simon, 1893, Smeringopinae Simon, 1893, and Pholcinae C.L. Koch, 1850 (Eberle et al., 2018). Until now, 15 fossil species of Pholcidae have been recorded worldwide, being the 24th spider family with the highest diversity in number of fossil known worldwide (Dunlop et al., 2019). Fossil specimens have been recorded from the French, Baltic and Chinese ambers (Wunderlich, 2004a; Penney, 2007), and the oldest fossil record of the family is from Le Quesnoy, Oise department, Paris Basin, France (53 Mya) (Penney, 2007). Most recent Pholcidae

fossil records come from the Bitterfeld (Middle Eocene-Upper Oligocene, 49-27 Mya; Ahrens et al., 2019) and the Dominican ambers (Middle Miocene, 20-15 Mya; Iturralde-Vincent and McPhee, 1996) (Wunderlich, 2004b). In the case of Dominican ambers, for the subfamily Modisiminae, six species of the genus *Modisimus* have been recorded: *M. calcar* Wunderlich (1988); *M. calcaroides* Wunderlich (1988); *M. crassifemoralis* Wunderlich (1988); *M. oculatus* Wunderlich (1988); *M. tuberosus* Wunderlich (1988); and *Modisimus* sp. in Wunderlich (1988). Recently, the family was recorded for the first time from the Mexican Chiapas amber (22.8 Mya), by García-Villafuerte (2019), with the description of *Metagonia esquincacanoi* García-Villafuerte (2019) based on one adult male.

The genus *Modisimus* Simon, 1893 is composed of 84 species worldwide, with 18 species recorded from Mexico, six of them from

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Chiapas (García-Villafuerte and Brescovit, 2019; WSC, 2020). The genus is distributed from southern North America south to Central America and the West Indies (Valdez-Mondragón and Francke, 2009). There are five species reported from South America: *M. culicinus* (Simon, 1893) (cosmopolitan), *M. globosus* Schmidt, 1956 from Colombia, *M. modicus* (Gertsch and Peck, 1992) from Galapagos Island, and *M. minima* (González-Sponga, 2009) and *M. simoni* Huber (1997) from Venezuela (Huber, 1997, 1998c; González-Sponga, 2009, 2010; Baert, 2013; Saaristo, 2010). However, these species must be included in a robust phylogenetic analysis to establish their taxonomic relations or probably a misplaced position into the genus.

Most species of the genus build dome-shaped webs in different habitats, mainly in humid places in tropical and subtropical forests, such as under tree trunks and rocks, in dark cavities on the floor, between the vegetation near the ground, and in cave entrances (Valdez-Mondragón and Francke, 2009; *per. obs.*). Adult specimens occur in any season, males and females are often found together on the same web, and the population density may fluctuate significantly depending on the season (Huber, 1998c; Valdez-Mondragón, *per. obs.*). *Modisimus* was originally established for a single species, *Modisimus glaucus* Simon (1893), from Hispaniola. Most subsequent species have been described by Gertsch (1941, 1971, 1973, 1977, 1992) and Huber (1997, 1998a, 1998b, 1998c). Morphologically, *Modisimus* is characterized by the presence of a long and prominent eye turret, a median elevation of the anterior part of the prosoma that carries the eyes (Simon, 1893; Gertsch, 1971; Brignoli, 1974; Huber, 1996, 1998c; 2000; Valdez-Mondragón and Francke, 2009). Another characteristic that unites most but not all *Modisimus* species is the high density of short vertical hairs on the male leg femora, but not on the tibiae (Huber et al., 2018). The spiders of this genus are small to medium sized (1.5–4 mm body length), usually with six eyes, rarely with punctiform anterior median eyes, and the male pedipalp femur with a pointed, upward projecting ventral apophysis (Huber, 1998c). In many species the elevation of the eye turret is quite distinct (Huber, 1998c: Figs. 164, 166, 183), but other species have elevations that are no higher than those of other New World genera (Huber, 1998c: Fig. 46).

Chiapas amber is the product of the polymerization of the resin produced by two species of the genus *Hymenaea* (Leguminosae), *H. mexicana* (Poinar and Brown, 2002) and *H. allendis* (Calvillo-Canadell et al., 2010). Concerning the Chiapas amber age, some authors have proposed it corresponds to the late Oligocene-Early Miocene (28 a 23 Mya) (Tomasini-Ortiz and Martínez-Hernández, 1984; Bousfield and Poinar, 1995). Other authors subsequently suggested that the stratigraphic units of Simojovel amber corresponded to the middle Miocene, and therefore correlating to the amber age of the Dominican Republic (20 Mya) (Meneses-Rocha, 2001). Recently, isotopic analyses using ⁸⁷Sr/⁸⁶Sr indicate that the age of amber-bearing sediments from Simojovel, Chiapas, corresponds to the Oligocene-Miocene boundary, with an age of 23–22.8 Mya (Vega et al., 2009; Serrano-Sánchez et al., 2015).

In this work, we contribute to the knowledge of the fossil spider fauna from Mexico, describing the first fossil species of the spider genus *Modisimus* from Chiapas amber and the record of one additional species, corresponding to the Miocene Aquitanian amber from Simojovel de Allende, Chiapas. Thus, the new fossil species, *Modisimus chiapanecus* sp. nov, and the undescribed fossil species based on one female, represent the oldest known fossils records of the genus and the subfamily Modisiminae so far. Additionally, an updated checklist of the extant Mexican species of *Modisimus* is provided.

2. Material and methods

2.1. Biological collections

The specimens are deposited in the Museum of Palaeontology “Eliseo Palacios Aguilera”, Dirección de Gestión, Investigación y Educación

Ambiental of the Secretaría de Medio Ambiente e Historia Natural (SEMAHN), Tuxtla Gutierrez, Chiapas, Mexico (Curator: Gerardo Fabio Carbot Chanona). The pieces of amber are from the “Los Cocos” mine, Simojovel de Allende (Fig. 1), acquired directly from a Simojovel craftsman. Abbreviations for institutions cited herein: AMNH, American Museum of Natural History, New York, U.S.A.; BMNH, British Museum of Natural History, London, United Kingdom; CARCIB, Colección Aracnológica del Centro de Investigaciones del Noroeste, Baja California Sur, Mexico; CNAN, Colección Nacional de Arácnidos, Institute of Biology, UNAM, Mexico City; MCZ, Museum of Comparative Zoology at Harvard, Massachusetts, U.S.A.

2.2. Geological setting

Three lithostratigraphic units interact in the Simojovel area: La Quinta Formation, Mazantic and Balumtum, where it is possible to find amber from the base to the top (Allison, 1967, Frost and Langenheim, 1974; Perrilliat et al., 2010; Solórzano-Kraemer, 2010; Serrano-Sánchez et al., 2015) (Fig. 2). These units are exposed in the Sierra Madre del Sur in Chiapas, from the northern end of the Central Depression to Palenque, near the coast of the Gulf of Mexico in the state of Tabasco (Solórzano-Kraemer, 2010). In the La Quinta Formation, the sandstone interspersed with the horizons of amber is fine to medium size, the grains of sand are subangular to semi-rounded in shape, with few well rounded clasts. It shows a low compaction, since the contacts between the grains are long or punctual with few concave/convex contacts. Sand grains are mostly monomineral, with quartz grains as the most abundant. It also contains abundant grains of feldspar, composed of pagoclase, pertite and orthoclase (Serrano-Sánchez et al., 2015). Detritic mica is very abundant and is mainly biotite with some muscovite and chlorite, which suggests a low influence of chemical weathering in the area of origin. The amber pieces of this unit have an irregular shape and vary in size, from less than 1 cm to 60 cm in length. Most of them have clear layers of various thicknesses, from one to 4 mm, which represent flows of individual resin separated by thin layers of sand (Serrano-Sánchez et al., 2015). The Mazantic Shale contains remains of plants, mollusks, small hepatids and pinnoterid crabs (Vega et al., 2009). The amber pieces from these sites are submerged in gray mud and generally have an ovoid shape, indicating relatively long distances of sand river transport (Serrano-Sánchez et al., 2015). Some of these pieces show oysters growing directly on the amber, indicating a final deposition in a marine environment or an estuarine environment, which was suggested by Frost and Langenheim (1974), Perrilliat et al. (2010) and Solórzano-Kraemer (2010). The Balumtum Sandstone is the superior unit where amber can occasionally be found and is distinguished by containing massive gray sandstone (Frost and Langenheim, 1974) (Fig. 2).

2.3. Specimens preparation

The amber pieces were cut and polished prior to being received by the authors. Subsequently, at the laboratory of the Museum of Paleontology “Eliseo Palacios Aguilera” the piece was cut with a hair hacksaw and polished using an abrasive of the Brasso® trademark, in order to reveal the morphological characters. The use of this material in amber has been shown to eliminate the scratches left by the finest sandpaper (García-Villafuerte, 2018). The specimen with catalog number IHNFG-5890 (male) is preserved in a cut piece of amber approximately 30 mm long, 19 mm wide and 4 mm thick. The specimen with catalog number IHNFG-5891 (female) is approximately 24 mm long, 11 mm wide and 5.5 mm thick. Anatomical data was gathered using a Zeiss Stemi 2000-C stereomicroscope. A Zeiss Axio Cam 506 color camera attached to a Zeiss Axio Zoom V16 stereomicroscope was used to photograph the different structures of the specimens. The digital photographs and map were edited using Adobe Photoshop version CS6. All measurements are in millimeters (mm).

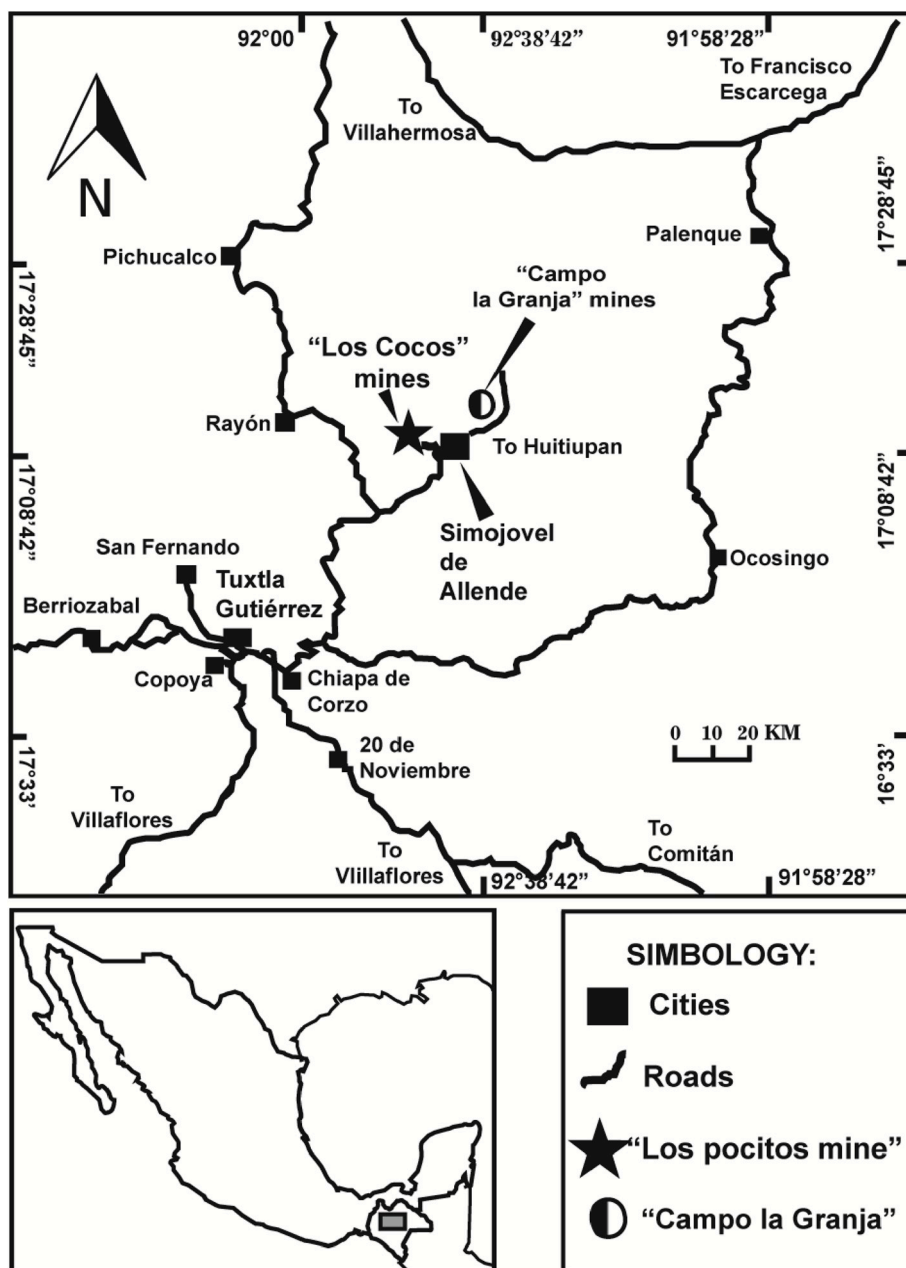


Fig. 1. Type Locality “Los Cocos” mine near Simojovel de Allende, Municipality of Simojovel, Chiapas, Mexico, where the specimens were obtained. Modified from García-Villafuerte (2019).

3. Results

3.1. Systematic paleontology

Family Pholcidae C. L. Koch, 1850.

Genus *Modisimus* Simon, 1893.

Type species: *Modisimus glaucus* Simon (1893).

***Modisimus chiapanecus* sp. nov.**

Figs. 3–17.

Type data.— MEXICO: *Chiapas*: Male holotype (IHNFG-5890) from the “Los Cocos” mine, Simojovel de Allende (Miocene Aquitanian amber), Municipality of Simojovel, located approximately 60 km North from Tuxtla Gutiérrez, in the north of Chiapas State (17°80'48"N, 92°42'30"W; 660 m) (Fig. 1).

Etymology.— The specific name is a noun in apposition and refers to the state where the type locality is found: Chiapas, Mexico.

Diagnosis.— *Modisimus chiapanecus* sp. nov. resembles *Modisimus deltoroi* Valdez-Mondragón and Francke (2009), from Comitán, Chiapas Mexico and *Modisimus propinquus* O. Pickard-Cambridge, 1896 from Teapa, Tabasco, Mexico, by the curved shape of the procurus, although in the new species the procurus is conical and less curved than the other two species, and bifurcated distally (Figs. 11 and 12). The embolus seems to be conical (Figs. 11 and 12), but is hard to observe complete in the specimen due to the position in the amber piece, and therefore it is impossible to compare it with the other two species.

Description: Male (Holotype).— *Measurements:* Total length 0.8 (approximately); prosoma length 0.5 mm, width ?; Leg formula: 1234 (tentatively). Leg lengths, I: total: ? (femur 4.95, patella 0.2, tibia-tarsus ?); II: 12.47 approximately (femur 4.08, patella 0.15, tibia 3.24, metatarsus 5?, tarsus ?); III: 10.82 (femur 3.06, patella 0.13, tibia 2.94, metatarsus 4.14, tarsus 0.55); IV: 10.37 (femur 3.0, patella 0.12, tibia 2.64, metatarsus 4.08, tarsus 0.53). Eyes diameter PME-PME ?, PME

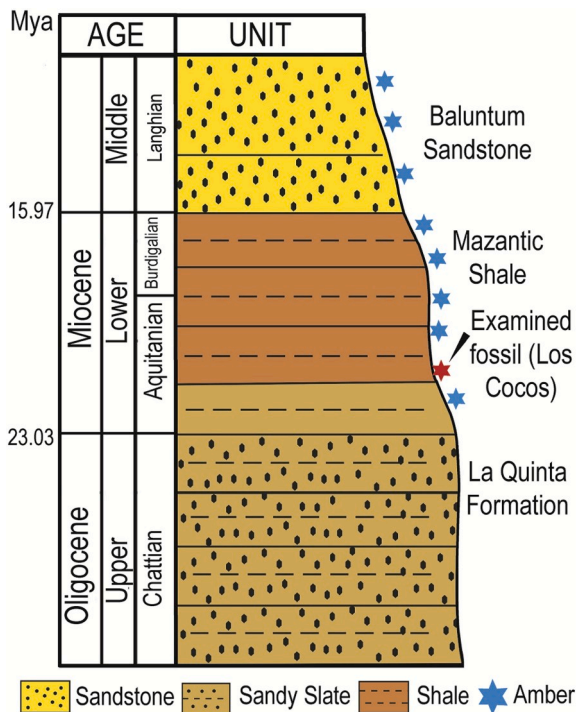


Fig. 2. Stratigraphy from the Simojovel de Allende area Chiapas, Mexico. Modified from Serrano-Sánchez et al. (2015).

0.06; PME-ALE 0.04; AME-AME 0.1 (approximately), AME 0.05, ALE 0.04. *Coloration in amber* (Figs. 3–8): Carapace pale brown, ocular area pale brown with a tiny dark line on the base, thoracic furrow medially dark; chelicerae apparently pale brown, sternum brown with white spots, endites not visible. Legs brown (Figs. 13–17). Abdomen dorsally light orange (Figs. 5 and 8), ventrally with a longitudinal brown region in the genital operculum (Fig. 5), lateroventrally pale yellow and with median brown longitudinal broadband. Ocular area strongly elevated (Figs. 5 and 8), with six eyes and several setae on top. Thoracic furrow distinct. Sternum wider than long, unmodified (Fig. 5). Chelicerae not visible. Opisthosoma long, longer than wide, covered dorsally and ventrally with long setae (Figs. 5 and 8). Legs with short spines dorsally and ventrally (Figs. 13–17); patella I and II with triangular ventral keel (Figs. 13 and 14). Dorso-basal trichobothria on metatarsus III. Tarsi pseudosegments (Fig. 17): I ?; II ?; III 13; IV 20. Tarsus III and IV both curved distally; probably also both tarsus I and II were curved distally. *Palp*: Femur conical, with pointed ventral apophyses (arrow, Figs. 11 and 12), directed towards the base of the procurus. Tibia with a long trichobothria dorsally (Figs. 9, 10 and 12). Procurus slightly curved, ending in sharpen tip (Fig. 12). Embolus parallel to procurus (Figs. 11 and 12).

Natural History.— In Miocene Aquitanian amber from Simojovel de Allende (23 Mya), Chiapas (Fig. 2); the estuarine environments (23 Mya) such as the vegetation type and habitat, are quite similar to current mangroves.

Distribution.— MEXICO: Chiapas (Fig. 1).

Modisimus sp.

Figs. 18–31.

Material data.— MEXICO: Chiapas: Male holotype from the “Los Cocos” mine, Simojovel de Allende (Miocene Aquitanian amber), Municipality of Simojovel, located approximately 60 km North from Tuxtla Gutiérrez, in the north of Chiapas State Date? (17°80'48"N, 92°42'30"W; 660 m) (Fig. 1).

Description: Female.— *Measurements*: Total length 1.65; prosoma length 0.65 mm, width ζ ? Leg formulae: 1,2,3,4. Leg 1: femur 3.52, patella 0.2, tibia 3.96, metatarsus 6, tarsus 0.34, total: 14.02; leg II: femur 2.25, patella 0.15, tibia 2.37, metatarsus 2.94, tarsus 0.58, total:

8.29; leg III femur 1.96, patella 0.17, tibia 1.47, metatarsus 2.46, tarsus 0.33, total 6.39; leg IV femur 1.77, patella 0.15, tibia 1.44, metatarsus 1.95, tarsus 0.43, total: 5.74. Eyes diameter and distances difficult to see, not measured. *Coloration in amber* (Figs. 18–23). Carapace pale ochre-white, with distinct thoracic furrow dark brown (Figs. 20 and 25). Ocular region brown, elevated (Figs. 23 and 24). Chelicerae light brown, endites and sternum brown (Fig. 24). Sternum wider than long, with long setae on posterior part (Figs. 23 and 24). Palps simple, unmodified, with paired long setae distally (Figs. 24 and 29). Legs femora medially olive green, tibia-metatarsus light brown to brown (Figs. 20 and 23). Patellae with long curved setae (Fig. 30). Legs with short spines in two dorsal rows on femora I, 39 (approximately) spines in each row and 33 spines in each row in femur II. Some spines on medially elevated bases; there are also spines in two ventral rows in both femora I and II from middle to the end (Fig. 23). Tibia-tarsi I-IV with very short spines in two dorsal and ventral rows (Fig. 31). Opisthosoma globose, higher than long, greenish gray, with some small brown spots (Figs. 18–23, 26, 27), except close to the pedicel, where a wide white region is present (Figs. 20 and 26). Epigynum brown, wider than long?, with long straight setae (Figs. 26–28). Pale yellow area in front of spinnerets (Fig. 23).

Remarks.— There are bubbles below the genital area (Figs. 23, 26–28) making it difficult to see the epigynum clearly, which is the reason why it is not possible to assign it as a new species or even co-specific with *M. chiapanecus* sp. nov. Also, the internal pore plates of the epigynum are impossible to observe, and it is not possible to see other features of the female such as the general coloration, color pattern on the carapace, opisthosoma or clypeus, and even the ventral pattern in the sternum; therefore we cannot conclude whether the specimen is a new different species or co-specific to *Modisimus chiapanecus* sp. nov.

Natural History.— In Miocene Aquitanian amber from Simojovel de Allende (23 Mya) (Fig. 2), Chiapas; the estuarine environments such as the vegetation type and habitat, are quite similar to current mangroves.

Distribution.— MEXICO: Chiapas (Fig. 1).

4. Checklist of the extant species of the genus *Modisimus* Simon, 1983 from Mexico

Modisimus beneficus Gertsch (1973).

M. beneficus Gertsch, 1973a: page 151, Fig. 18 (Description female).

Type locality. MEXICO: Veracruz: Female holotype and female paratype from Sótano de Botella Chica, 3 km NW Tequila, 5 August 1967 (J. Reddell, J. Fish Colls.).

Other records. None.

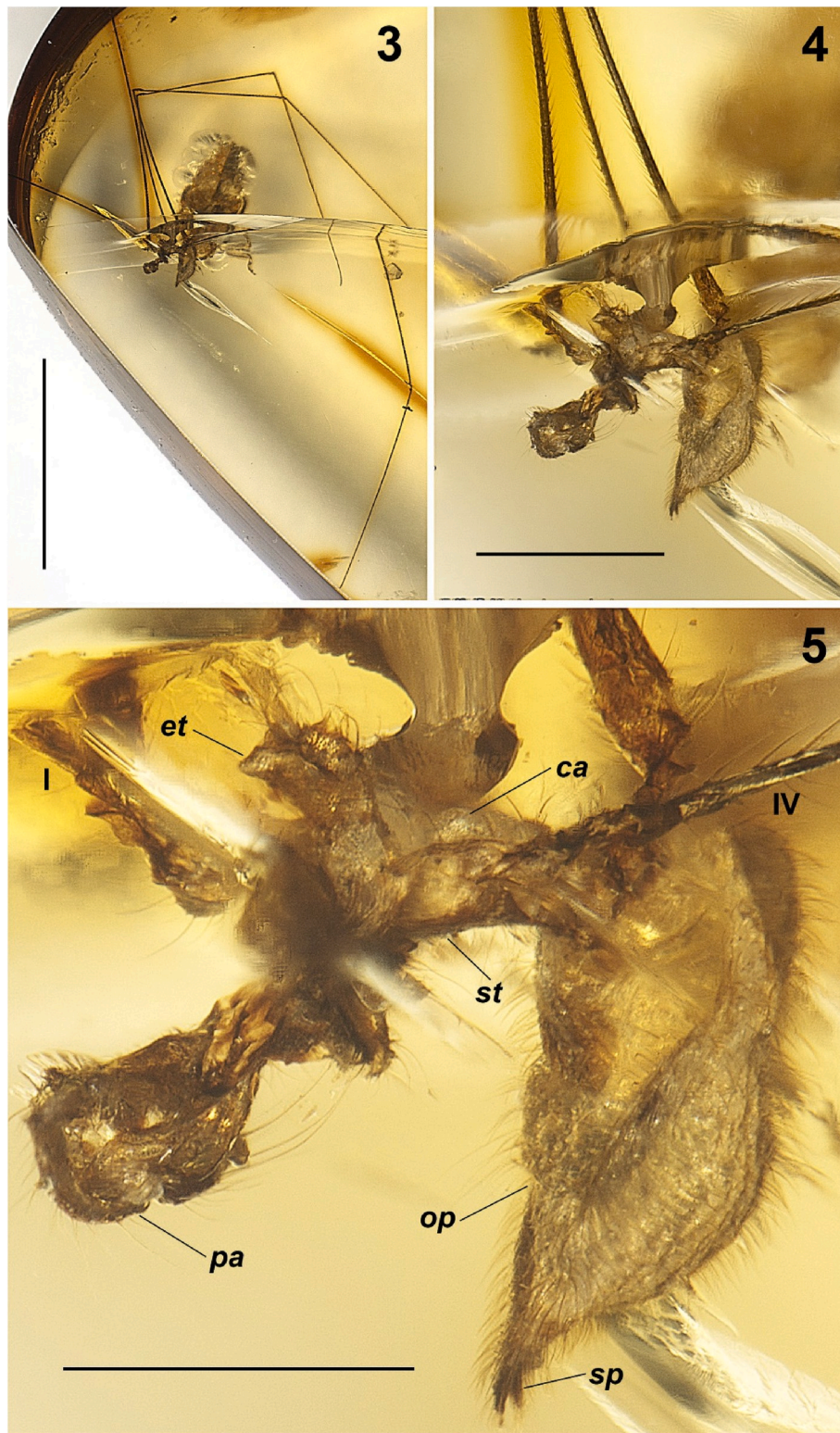
Distribution. Veracruz.

Modisimus boneti Gertsch (1971).

M. boneti Gertsch (1971): 66, Figs. 74–76 (Description male and female).

Type locality. MEXICO: San Luis Potosí: Male holotype from Cueva Chica, 2.5 km NE of El Pujal, 5 June 1967 (R. Mitchell Coll.).

Other records. MEXICO: San Luis Potosí: Next specimens belong to the same type locality: Males, females, juveniles, 4 April 1942, (C. Bolívar Coll.). Males, females, 12 March 1940 (W. Bridges Coll.). Female from deepest point in cave, 20 March 1940 (Bishop Coll.). Female, 26 March 1964 (T. Raines, D. McKenzie, B. Bell Colls.). Female, 23 May 1971 (W. Elliott Coll.). Male, four females, 5 June 1967 (R. Mitchell Coll.). Two males, one juvenile, 22 July 1969 (S. Peck, J. Peck Colls.). Female from Cueva (=Sótano) de los Monos, 15 km NE Valles, 30 December 1971 (D. Honea, R. Jameson Colls.) Female from Cueva de Taninul No. 1, 13 km SE Valles, 29 December 1970 (J. Hallan Coll.). immature female from Cueva de Puente de Dios, 22 km SSW Valles, 9 April 1968 (T. Raines Coll.). MEXICO: Tamaulipas: Male and female from main passage and bat dome from Cueva de la Florida, 7.5 km NE of Antiguo Morelos, 28 May 1968 (J. Reddell



Figs. 3–5. *Modisimus chiapanecus* sp. nov. Male holotype (IHNFG-5890). 3–4: Amber piece with specimen. 5, Detail of habitus, left view. Scale bars: 1 mm (Figs. 4 and 5), 5 mm (Fig. 3). Abbreviations: ca, carapace; et, eye turret; op, opisthosoma; pa, palp; sp, spinnerets; st, sternum.

Coll.). Juvenile from Cueva de la Florida, 7.5 km NE of Antiguo Morelos, 10 March 1969 (J. Reddell, S. Fowler, B. Cook Colls.).

Distribution. San Luis Potosí, Tamaulipas.

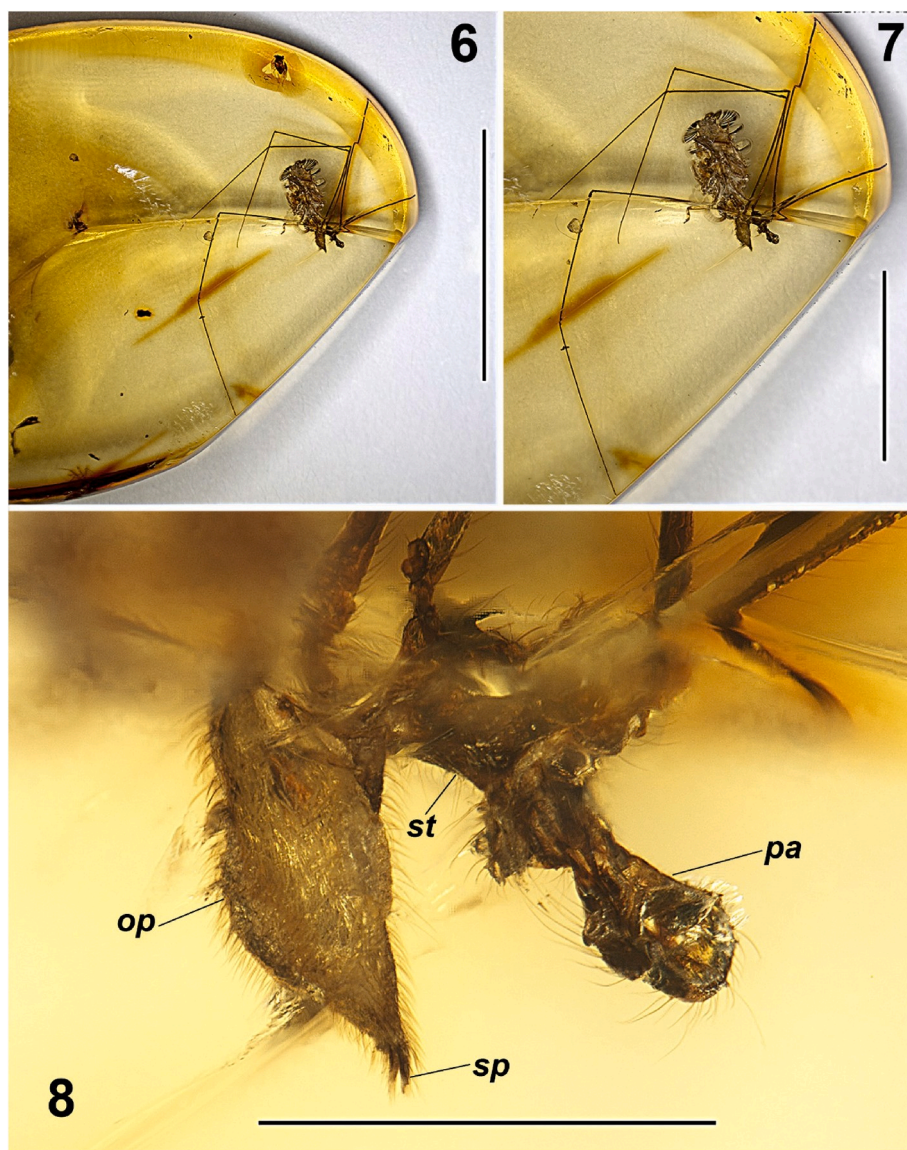
***Modisimus chiapa* Gertsch (1977).**

M. chiapa Gertsch (1977): 119, f. 60 (Description male, female unknown).

Hedysilus chiapa Gertsch and Peck (1992): 1191.

Type locality. MEXICO: Chiapas: Male holotype from hillside 8 km NE of Chiapa, 22 August 1966 (J. Ivie, W. Ivie Colls.).

Other records. None.



Figs. 6–8. *Modisimus chiapanecus* sp. nov. Male holotype (IHNFG-5890). 6–7: Amber piece with specimen. 8, Detail of habitus, right view. Scale bars: 1 mm (Fig. 8), 5 mm (Figs. 7), 10 mm (Fig. 6). Abbreviations: *op*, opisthosoma; *pa*, palp; *sp*, spinnerets; *st*, sternum.

Distribution. Chiapas.

***Modisimus deltoroi* Valdez-Mondragón and Francke (2009).**

M. deltoroi Valdez-Mondragón and Francke (2009): 58, Figs. 1–9 (Description male and female).

Type locality. MEXICO: *Chiapas*: Male holotype (CNAN-T0283) from Cueva Ch'en-bajlám "Cueva del Tigre" (N 16° 41' 12", W 90° 49' 30"), 200 m, Reserva Ecológica Chan-Kin, Municipio de Ocosingo, 7 November 2006 (A. Valdez, H. Montaña, R. Paredes, G. Montiel, F. Bertoni Colls.). Female paratype (CNAN-T0284), same locality, 19 October 2006 (A. Valdez, O. Francke, H. Montaña, A. Ballesteros Colls.). Male paratype (CNAN T-0285) same locality, 10 August 2006 (A. Valdez, H. Montaña, I. Mondragón, S. Rubio, N. Perez Colls.). Male paratype (CNAN T-0286) from Cueva Kolem-Ch'en "Cueva Grande" (N 16° 41' 28", W 90° 49' 26"), 189 m, Reserva Ecológica Chan-Kin, 10 August 2005 (A. Valdez, J. Castelo, E. Cabrera, R. Paredes, G. Montiel Colls.). Female paratype (CNAN-T0287) from "Cueva del Tigre", 19 October 2006 (A. Valdez, O. Francke, H. Montaña, A. Ballesteros Colls.). Female paratype (CNAN

T-0288), same locality, 10 August 2006 (A. Valdez, H. Montaña, I. Mondragón, S. Rubio, N. Pérez). Male and female paratypes (AMNH), same locality, 7 November 2006 (A. Valdez, H. Montaña, R. Paredes, G. Montiel, F. Bertoni Colls.).

Other material. None.

Distribution. Chiapas.

***Modisimus guerrerensis* Gertsch and Davis (1937).**

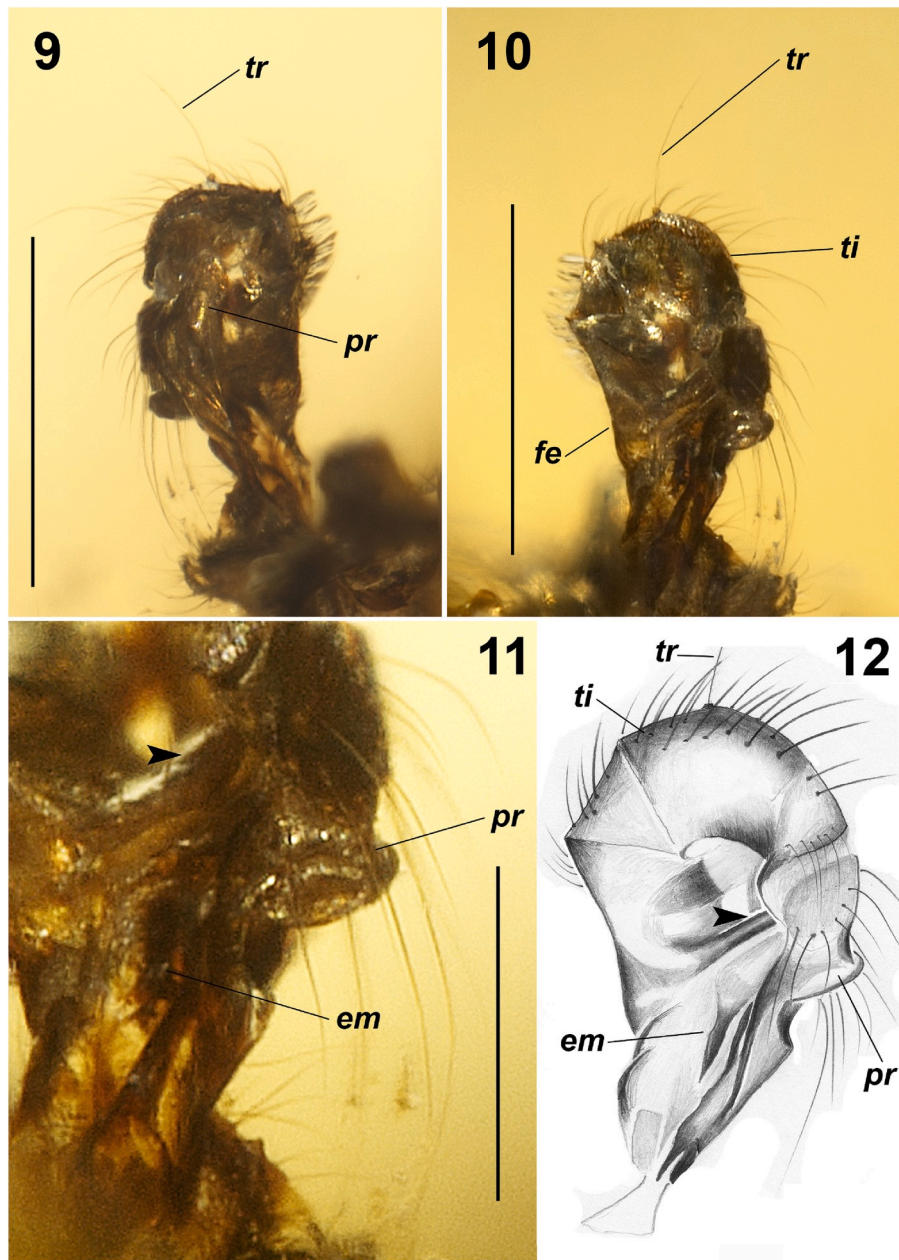
M. guerrerensis Gertsch and Davis (1937): 5, f. 3–5 (Description male and female).

Type locality. MEXICO: *Guerrero*: Male holotype and female paratype from 99 km N of Acapulco, 18 July 1936 (A. M. Davis, L. I. Davis Colls.).

Other material. MEXICO: *Guerrero*: female, same data as type locality. *Hidalgo*: Immature male and female paratype from Jacala, 13 June 1936 (Davis Coll.).

Distribution. Guerrero, Hidalgo.

***Modisimus inornatus* O. Pickard-Cambridge, 1895**



Figs. 9–12. *Modisimus chiapanecus* sp. nov. Male holotype (IHNFG-5890). 9, Right palp, prolateral view; 10, right palp, retrolateral view; 11, Detail of the procurus, retrolateral view. 12, Palp showing the details of the procurus and embolus. Arrows indicate the embolus. Scale bars: 0.25 mm (Figs. 11 and 12), 0.5 mm (Figs. 9 and 10). Abbreviations: *em*, embolus; *fe*, femur; *pr*, procurus; *ti*, tibia; *tr*, trichobothria.

M. inornatus O. Pickard-Cambridge, 1895a: 149, plate 20, Fig. 7 (Description female).

M. propinquus O. Pickard-Cambridge, 1896a: 223, plate 27, Fig. 8F (female).

M. inornatus O. Pickard-Cambridge, 1899a: 303, plate 32, Fig. 4 (Description male).

M. inornatus F. O. Pickard-Cambridge, 1902a: 367, Figs. 17–19 (male and female).

M. inornatus Huber, 1998e: 54, Figs. 158–163 (male and female).

Type locality. MEXICO: *Tabasco*: Female holotype (BMNH) from Teapa, Date? (H. H. Smith).

Other material. MEXICO: *Tabasco*: Female from Teapa, Date? (H. H. Smith). Male from Teapa, Date?, (H. H. Smith).

Distribution. *Tabasco*.

***Modisimus iviei* Gertsch (1973).**

M. iviei Gertsch, 1973a: 149, f. 12–14 (Description male and female).

Type locality. MEXICO: *Yucatán*: Female holotype from Xmahit Cave, Tekax, 31 July 1936 (A. S. Pearse Coll.), from 6 m deep in cave.

Other material. One damage male, same data as holotype.

Distribution. *Yucatán*.

***Modisimus maculatipes* O. Pickard-Cambridge, 1895**

M. maculatipes O. Pickard-Cambridge, 1895a: 148, plate 20, Fig. 5 (Description female, male unknown).

M. putus O. Pickard-Cambridge, 1895a: 148, plate 20, Fig. 6 (Description female).

M. maculatipes F. O. Pickard-Cambridge, 1902a: 367, plate 34, Fig. 20 (female).

M. putus F. O. Pickard-Cambridge, 1902a: 368, plate 34, Fig. 21 (female).

M. maculatipes Huber, 1998e: 55, Figs. 164–167 (female).

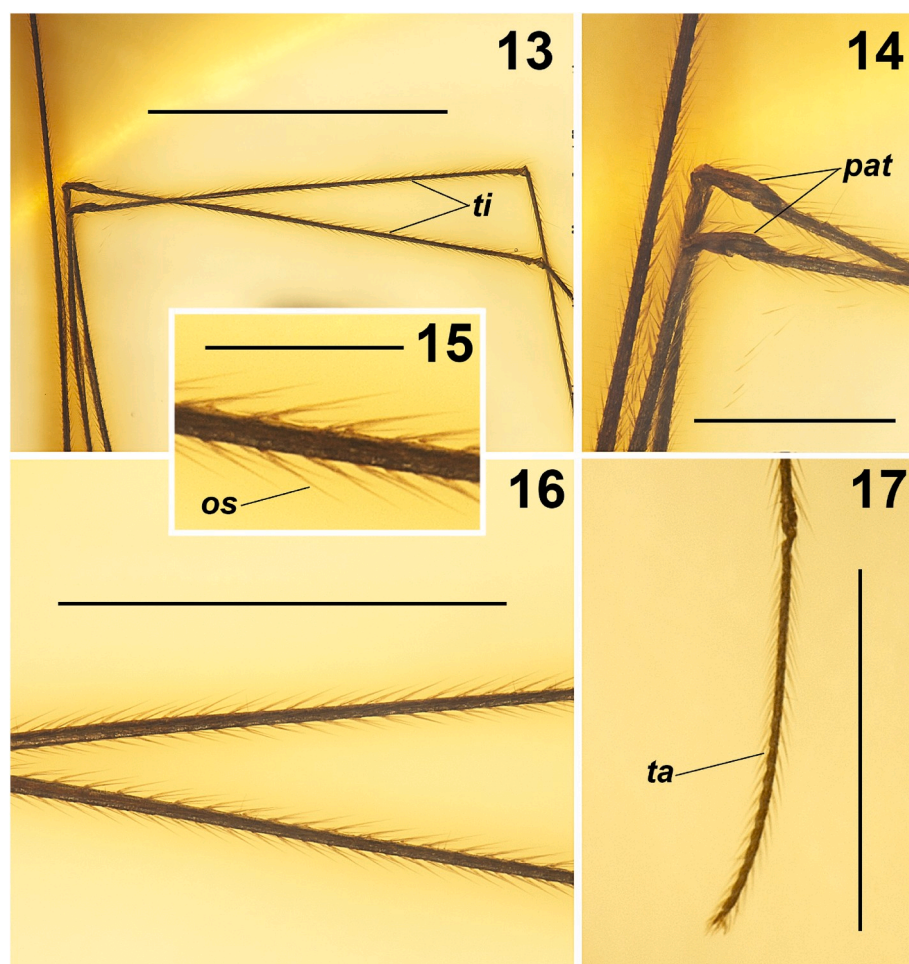


Fig. 13–17. *Modisimus chiapanecus* sp. nov. Male holotype (IHNFG-5890). Legs. 13, Patellae and tibiae of legs IV. 14, Detail of patellae. 15, Detail of oblique setae on tibiae. 16, Detail of tibiae IV. 17, Tarsi of right leg IV, retrolateral view. Scale bars: 0.2 mm (Figs. 15), 0.5 mm (Figs. 14 and 17), 1 mm (Fig. 16), 2 mm (Fig. 13). Abbreviations: os, oblique setae; pat, patella; ta, tarsus; ti, tibia.

Type locality. MEXICO: *Tabasco*: Female paratype (BMNH) from Teapa, Date? (H. H. Smith).

Other material. None.

Distribution. Tabasco.

***Modisimus mckenziei* Gertsch (1971).**

M. mckenziei Gertsch (1971): 71, Figs. 62–63 (Description male and female).

Type locality. MEXICO: *Tamaulipas*: Male holotype and female paratype from Sótano del León, Gómez Farías, 20 May 1971 (W. Elliot Coll.).

Other material. MEXICO: *Tamaulipas*: Female from Bee Cave, 17 km NE Ocampo, 10 April 1966 (J. Fisher, E. Alexander, D. McKenzie, R. Felton Colls.). Immature female from Cueva de la Paloma, 1 km NE Gómez Farías, 18 May 1971 (W. Russell Coll.).

Distribution. Tamaulipas.

***Modisimus mitchelli* Gertsch (1971).**

M. mitchelli Gertsch (1971): 70, Figs. 57–60 (Description male and female).

Type locality. MEXICO: *Tamaulipas*: Male holotype from Cueva de la Capilla, 13.5 km NW of Gómez Farías, El Porvenir, 13 January 1971 (J. Reddell, R. Mitchell and group Colls.).

Other material. MEXICO: *Tamaulipas*: Three males, four females, juvenile from same data as type locality. Male, two females from type

locality, 28 January 1968 (J. Reddell, R. Mitchell, F. Rose, J. Geroge Colls.). Female from Cueva de la Mina (CM), 7 km NW of Gómez Farías, 3 June 1967 (R. Mitchell Coll.). two males from CM, 24 March 1967 (R. Mitchell Coll.). Male and two females from CM, 3 June 1967 ((R. Mitchell Coll.). Female and juvenile from CM, 1 July 1969 (S. Peck, R. Norton Colls.). Female from CM, 9 March 1968 (J. Reddell Coll.). Female and juvenile from CM, 27 January 1968 (J. Reddell, R. Mitchell, F. Rose, J. George Colls.). Male, female and juvenile from Harrison Sinkhole, Rancho del Cielo, 25 March 1967 (R. Mitchell Coll.). Male, three females and juvenile from Rancho del Cielo, 12 January 1971 (J. Cooke, M. Brownfield, W. Elliott Colls.). Female and juvenile from Crystal Cave, Rancho del Cielo, 10 January 1971 (J. Reddell, J. Cooke, S. Wylie, V. Tipton Colls.). Three females and juvenile from Cueva del Infiernillo, San José, 4 June 1967 (R. Mitchell Coll.). Immature male from Cueva Chica de la Perra, 13.5 km NW of Gómez Farías, 2 July 1969 (S. Peck, R. Norton Colls.). Four males and female from Sótano de la Joya de Salas (SJS), 21 km NW of Gómez Farías, 23 January 1965 (D. McKenzie Coll.). Two males and two females from SJS, 25 November 1966 (O. Knox, E. Alexander Colls.). male and juvenile from Cueva de Rancho del Cielo #3, Rancho del Cielo, 4 July 1967 (S. Peck, J. Peck Colls.). Two males and two females from Sótano de El Porvenir, El Porvenir, 13 January 1971 (W. Elliott, J. Cooke Colls.). Male, two females and juvenile from Sótano de El Refugio, 20 km SW of Gómez Farías, 14 July 1967 (J. Fish Coll.).

Distribution. Tamaulipas.

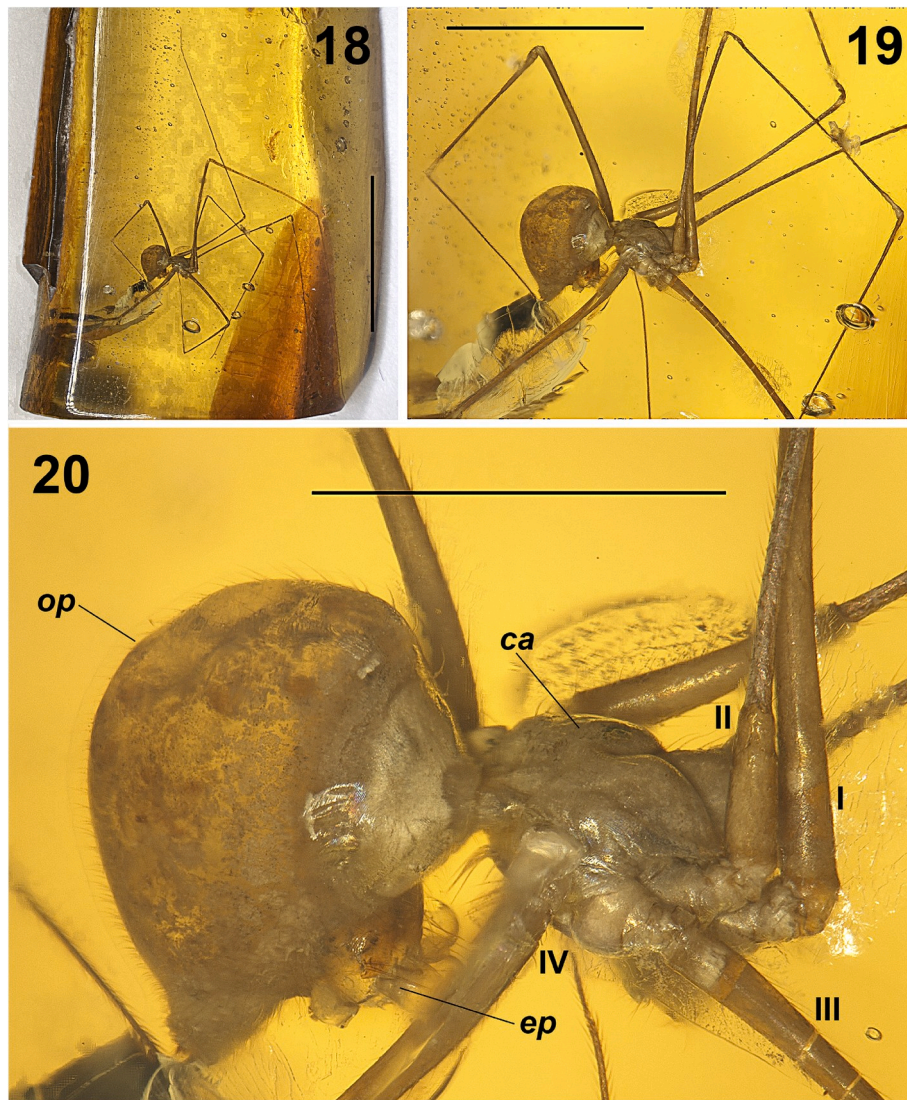


Fig. 18–20. *Modisimus* sp. Female. Amber piece with specimen IHNFG-5891. 18–19, habitus, right view. 20, Detail of habitus, right view. Scale bars: 1 mm (Fig. 20), 2 mm (Fig. 19), 5 mm (Fig. 18). Abbreviations: *ca*, carapace; *ep*, epigynum; *op*, opisthosoma.

***Modisimus palenque* Gertsch (1977).**

M. palenque Gertsch (1977): 117, Figs. 61–63 (Description male and female).

Type locality. MEXICO: *Chiapas*: Male holotype from 1 km N Palenque, 25 July 1973 (J. Reddell, R. Mitchell and group Colls.).

Other material. MEXICO: *Chiapas*: Female from Ruinas de Palenque, 25 July 1973 (J. Reddell, J. M. Rowland Colls.).

Distribution. Chiapas.

***Modisimus propinquus* O. Pickard-Cambridge, 1896**

M. propinquus O. Pickard-Cambridge, 1896a: 223, plate 27, Fig. 8 (Description male, female unknown).

M. propinquus Huber, 1998e: 57, Figs. 168–174 (male).

Type locality. MEXICO: *Tabasco*: One male, one female from, Teapa, Data? (H. H. Smith Coll.).

Other material. None.

Distribution. Tabasco.

***Modisimus pusillus* Gertsch (1971)**

M. pusillus Gertsch (1971): 72, Figs. 56, 73 (Description female, male unknown).

Type locality. MEXICO: *Nuevo León*: Female holotype from Grutas de García, 14 June 1942 (F. Bonet, B. Osorio, D. Peláez Colls.).

Other material. None.

Distribution. Nuevo León.

***Modisimus rainesi* Gertsch (1971).**

M. rainesi Gertsch (1971): 68, Figs. 70–72 (Description male and female).

Type locality. MEXICO: *Nuevo León*: Male holotype from Cueva de la Boca, 5 km NE of Santiago, 27 January 1967 (T. Raines Coll.).

Other material. MEXICO: *Nuevo León*: Five males, female from type locality, 13 July 1942 (C. Bolívar, Maldonado, B. Osorio, D. Peláez Colls.). Male, two females, juvenile from type locality, 1 May 1966 (J. Fish, E. Alexander Colls.). Tw males, two females from type locality, 4 December 1969 (T. Raines Coll.). Three females from type locality, 17 June 1944, (F. Bonet Coll.). Male and female from type locality, 20 June 1969 (S. Peck, J. Peck Colls.).

Distribution. Nuevo León.

***Modisimus reddelli* Gertsch (1971).**

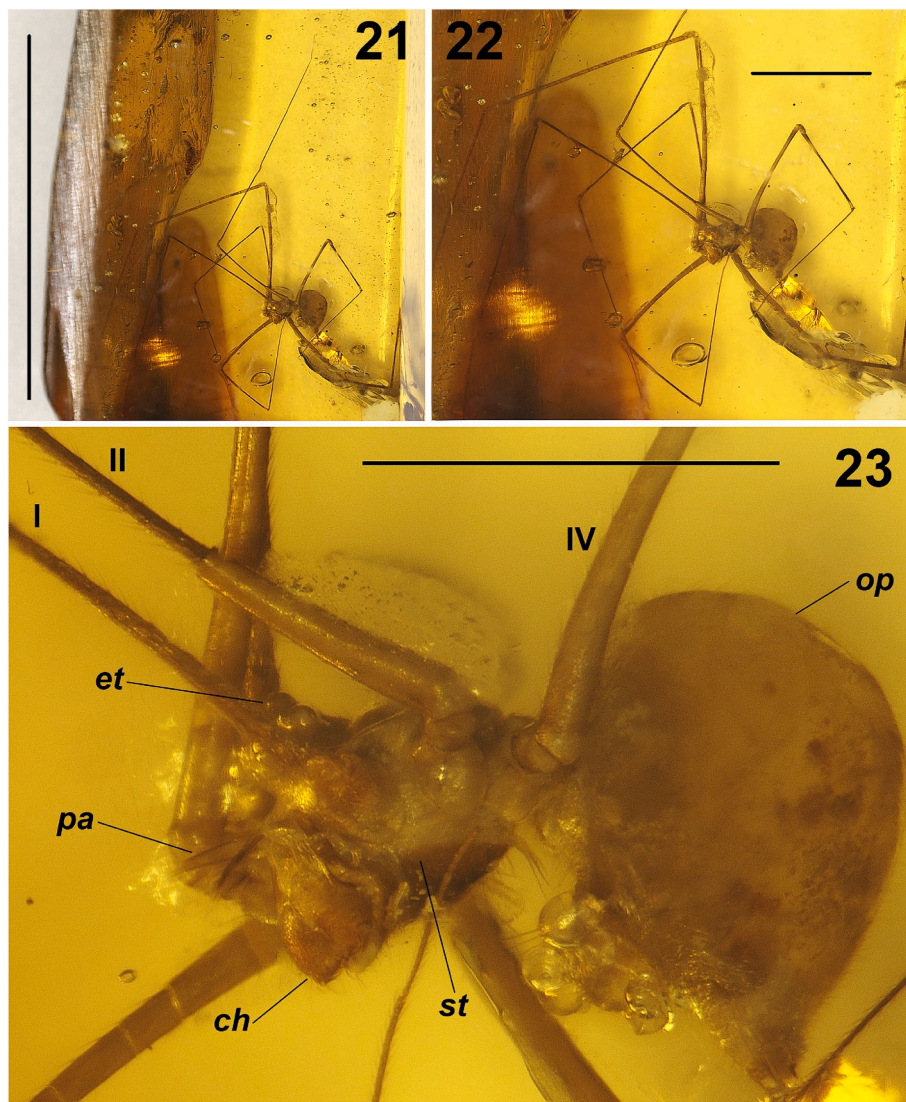


Fig. 21–23. *Modisimus* sp. Female. 21–22, habitus, left view. 23, Detail of habitus, left view. Scale bars: 1 mm (Fig. 23), 2 mm (Figs. 21 and 22). Abbreviations: *ch*, chelicerae; *et*, eye turret; *op*, opisthosoma; *pa*, palp; *st*, sternum.

M. reddelli Gertsch (1971): 70, Figs. 53–55 (Description male and female).

Type locality. MEXICO: *Tamaulipas*: Male holotype and female paratype from Cueva Bonita, 30 km SW of Victoria, 19 June 1967 (J. Fish Coll.).

Other material. None.

Distribution. Tamaulipas.

Modisimus sanpedro Jiménez & Palacios-Cardiel, 2015

M. sanpedro Jiménez & Palacios-Cardiel, 2015: 595, Figs. 1–13 (Description male and female).

Type locality. MEXICO: *Baja California Sur*: Male holotype (CARCIB 0014), Paratypes: 4 males (CARCIB 0087–0090), 10 females (CARCIB 0091–100) from San Pedro Oasis, Municipality La Paz (23°23′22.4″N, 110°12′30.2″W, 6 m.a.s.l.), 4 March 2013 (C. Palacios, M. L. Jiménez Colls.).

Other material. None.

Distribution. Baja California Sur.

Modisimus texanus Banks, 1906

Modisimus texanus Banks, 1906b: 94 (Description female).

Modisimus texanus Huber, 1998e: 58, Figs. 182–191 (female, Description male).

Type locality. UNITED STATES: *Texas*: Female holotype (MCZ) from Austin, March (no year) (J. H. Comstock).

Other material. MEXICO: *Nuevo León*: Male and female from 45 km N of Monterrey, 7 July 1936 (L. I. Davis).

Distribution in Mexico. Nuevo León.

Modisimus tzotzile Brignoli (1974).

M. tzotzile Brignoli (1974), figure: 218, Fig. 7E (Description female, male unknown).

Type locality. MEXICO: *Chiapas*: Female holotype from Ocozocoautla, Col. Galeana, Sima del Ojito, 950 m, 21 March 1971 (V. Sbordoni Coll.).

Other material. None.

Distribution. Chiapas.

5. Discussion

This is the first time that a new species of *Modisimus* is described from

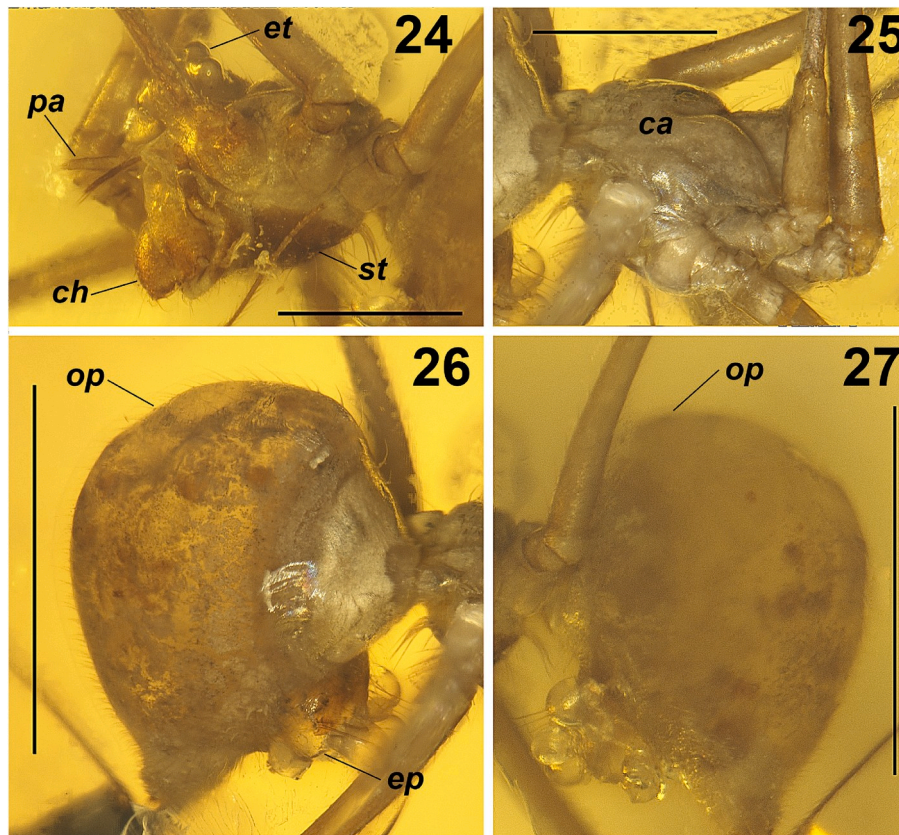


Fig. 24–27. *Modisimus* sp. Female. 24, Prosoma, left-frontal view. 25, Carapace, dorso-lateral right view. 26–27, Opisthosoma, right and left views respectively. Scale bars: 0.5 mm (Figs. 24 and 25), 1 mm (Figs. 26 and 27). Abbreviations: ca, carapace; ch, chelicerae; ep, epigynum; et, eye turret; op, opisthosoma; pa, palp; st, sternum.

the Miocene Aquitanian amber from Simojovel de Allende, Chiapas. With this contribution, the geological age for the subfamily and the genus is extended by approximately 3 Mya so far, considering the Dominican fossil record of *Modisimus calcaroides* Wunderlich (1988). The other fossil *Modisimus* species (*Modisimus calcar* Wunderlich, 1988; *Modisimus crassifemoralis* Wunderlich, 1988; *Modisimus oculatus* Wunderlich, 1988; and *Modisimus tuberosus* Wunderlich, 1988) are considered younger (Huber et al., 2010), since ether tests and the fact that the resins smear when ground suggest that all fossil *Modisimus* species from the Dominican amber, except for *M. calcaroides*, might be preserved in copal rather than amber.

According to and within the framework of modern taxonomy (Simon, 1893; Gertsch, 1971; Brignoli, 1974; Huber, 1996, 1998c, 2000; Valdez-Mondragón and Francke, 2009; Huber et al., 2018), we are pointing out the putative synapomorphies with the extant genus *Modisimus*, as it is suggested by others authors (Harms and Dunlop, 2009; Penney et al. 2012; García-Villafuerte, 2018, 2020). Harms and Dunlop (2009) mentioned that there has been a tendency to assign new species of fossils spiders rather liberally, often using characteristics which are either unstable within and between taxa, or otherwise phylogenetically uninformative. Even at genus level, some morphological characters are not completely informative, such as the putative synapomorphies that support the genus *Modisimus*. Based on molecular evidence, Eberle et al. (2018) demonstrated that *Modisimus* is not a monophyletic group clustered with the genera *Anopsicus* Chamberlin & Ivie, 1938 and *Platnickia* Jocqué, 1991. Besides, Magalhães et al. (2020) carried out a deep bibliographical analysis in relation to the fossil record of spiders from the Mesozoic, and after a careful review of the fossil descriptions, they found that in many cases the fossil spiders lack putative synapomorphies with extant clades.

It is not possible to make a deep dating phylogenetic analysis on the fossil record from Mexican Chiapas amber or those from the Dominican

amber, because the deposits are too young compared to those of the Mesozoic (Magalhães et al., 2020), but even so, they are closely allied to extant forms. However, when making a correct taxonomic interpretation, it is possible to provide data useful for calibration points for the extant families, subfamilies and genera. With this idea in mind, we decided to describe only the male fossil *Modisimus* as a new fossil species. The female is probably not co-specific with the male fossil *Modisimus chiapanecus* sp. nov.

On the other hand, prior to the work of Huber et al. (2010), eight extant *Modisimus* species had been recorded for the West Indies, seven specifically from Cuba and three more from the Hispaniola, and among them *M. glaucus*, the type species of the genus (World Spider Catalog, 2020). With the 22 extant species of *Modisimus*, Hispaniola harbors the highest number of species, also with a high endemism level (Huber et al., 2010). Likewise, Mexico ranks second with 18 described extant species (see updated list in this work). However, it is very likely that the species richness of *Modisimus* in Mexico, which is 26 times the size of the Hispaniola (Huber et al., 2010), will increase considerably, as there are many areas in the country where methodical sampling has not been carried out. In the case of Chiapas, serious and methodical sampling work has not been carried out with the family Pholcidae. To date, there are 24 valid records of spider species, distributed in six genera (García-Villafuerte and Brescovit, 2019), of which six species belong to *Modisimus* (Brignoli, 1974; Gertsch, 1977; Valdez-Mondragón and Francke, 2009). Regarding the fossil record, five species of Pholcidae have been recorded from the Dominican amber (Wunderlich, 1988; Dunlop et al., 2019), and those recorded from Mexican Chiapas amber herein.

Tectonic and sedimentary evolution of Central America, including Mexico and the Antilles, affected and modified not only the environment, but also the climate in those areas (James, 2007). The geological evolution of Chiapas, since Oligocene to Pliocene, is also linked to the

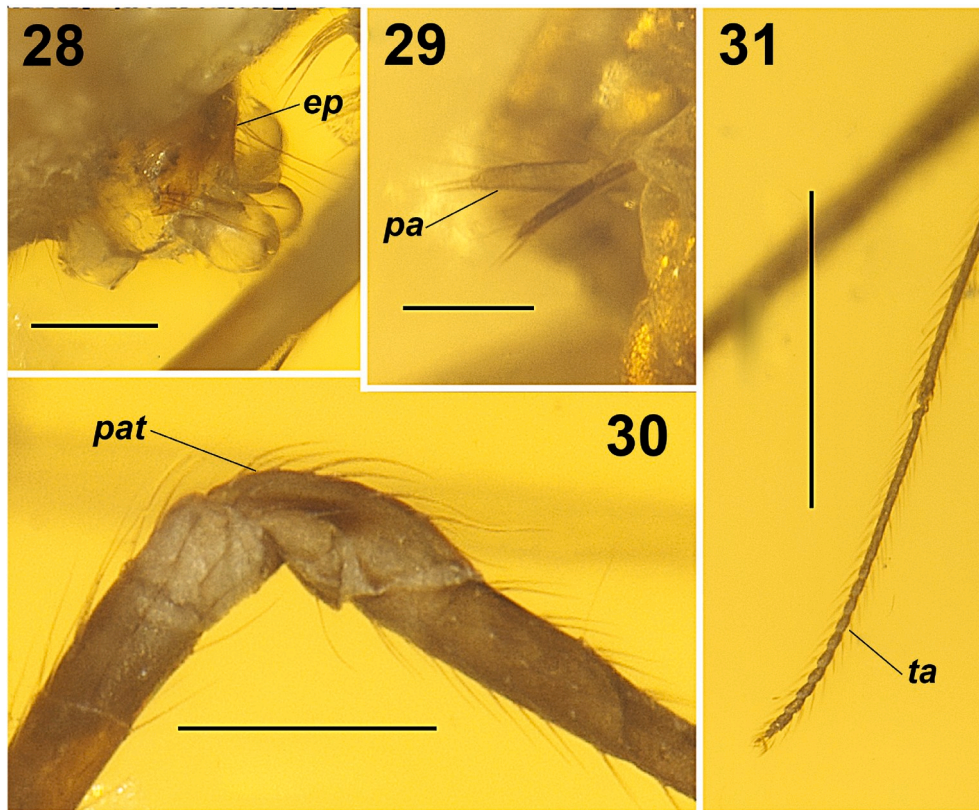


Fig. 28–31. *Modisimus* sp. Female. 28, Epigynum, right view. 29, Palps, left view. 30, Leg II, detail of right patella, retrolateral view. 31, Leg II, right tarsus, retrolateral view. Scale bars: 0.2 mm (Figs. 28–30), 0.5 mm (Fig. 31). Abbreviations: *ep*, epigynum; *pa*, palp; *pat*, patella; *ta*, tarsus.

formation of Central America (Meneses-Rocha, 2001; Mandujano-Velázquez and Keppie, 2009). Thus, the tectonic phenomena and sedimentary materials that formed the current mountains in Chiapas during the Oligocene-Miocene altered the distribution of the basins and modified dispersal barriers for many species. At present, the area of Simojovel de Allende is characterized by a warm subhumid climate, with rains in the summer and tropical rainforest vegetation (Inafed, 2017). However, 23 Mya prior, based on paleontological evidence, *Hymenea* communities probably developed near the ancient coast in estuarine environments very similar to modern mangroves (e. g., Langenheim et al., 1967; Cobben, 1971; Frost and Langenheim, 1974; Poinar, 1992; Langenheim, 1995; Graham, 1993; Poinar and Brown, 2002; García-Villafuerte, 2008; Calvillo-Canadell et al., 2010; Solórzano-Kraemer, 2010; Serrano-Sánchez et al., 2015), and the genus *Modisimus* was part of the spider fauna back then. Evidently, the geological evolution of Central America did not affect its existence in Chiapas. In fact, the genus has been documented from the modern mangrove in Chiapas (Santos-González, 2005), from a rainforest at 200 m (Valdez-Mondragón and Francke, 2009), from the modern area of Simojovel de Allende at 660 m (García-Villafuerte, pers. obs.), and even from the cloud montane forest at 2000m (Ibarra-Niñez et al., 2011).

Nevertheless, an analysis of the genus in each of these modern ecosystems from Chiapas has not been presently carried out as it has been done in other areas, for example, Costa Rica and the Hispaniola (Huber, 1998b; Huber et al., 2010). Huber (1998b) mentioned that representatives of *Modisimus* from Costa Rica might be found in all of these environments; most are found in shady and humid places near the ground; other are found under leaves or webs built higher in the vegetation; and most have been found in the rain forest. We consider that it is very important to carry out a similar work in the modern Chiapas ecosystems. Although Chiapas ranks first in terms of spider species richness nationwide due to the sampling bias (García-Villafuerte and Brescovit, 2019), specific and systematized sampling of the genus *Modisimus*, and of the

family Pholcidae in general, is necessary to have a better knowledge of the pholcid fauna from Chiapas.

Author statement

Alejandro Valdez-Mondragón: Original draft preparation, writing, rewriting, editing, photographs and plates, discussion. **Miguel Ángel García-Villafuerte:** Writing, reviewing, obtaining the material, measure of the specimens, discussion.

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Declaration of competing interest

None.

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