

Insights into amber salticids from the Neogene of Middle America, with the first report of Marpissinae (Araneae: Salticidae) from the Chiapas amber

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Abstract. The genera and species of fossil salticids from the European Baltic amber (Paleogene) are more diverse than salticids from the geologically younger Neogene deposits of Dominican and Chiapas amber. However, the latter are more diverse than Baltic amber at the subfamily level and also include close relatives of modern species. This diversity may reflect the presence of ancestor taxa for extant North American groups. The relatively modern forms of the Neogene suggest a broader divergence since the Miocene within the tropics. Here we add the discovery of a fossil salticid that appears to be a marpissine (cf. *Maevia* C. L. Koch, 1846) from the Miocene Chiapas amber (southern México). The tectonic and sedimentary evolution of South México, Central America and the Antilles from the Paleogene to Neogene that caused short-term cyclical changes in climate may have also driven the early dispersal and introduction of marpissines from Middle America into southern North America.

Key words: Chiapas amber, Miocene, Middle America, Salticidae, Marpissinae

Resumen. Los géneros y las especies de salticidos fósiles del ámbar Báltico en Europa (Paleógeno) son más diversos que los salticidos de los más recientes depósitos de ámbar del Neógeno de República Dominicana y Chiapas. Sin embargo, estos últimos son más diversos que los del ámbar del Báltico a nivel de subfamilias y también muestran parentescos cercanos con especies modernas. Las formas relativamente modernas del Neógeno sugieren una más amplia divergencia desde el Mioceno en los trópicos. Se incluye aquí el descubrimiento de un salticido fósil, según parece marpissino (cf. *Maevia* C. L. Koch, 1846), en el ámbar de Chiapas (Mioceno) al sur de México. La evolución tectónica y sedimentaria del Sur de México, Central América y las Antillas durante el Paleógeno al Neógeno que causó cambios cíclicos de periodos cortos en el clima también puede haber conducido a una temprana dispersión e introducción de marpissinos desde la América Media hacia el sur de Norte América.

Palabras clave: Ámbar de Chiapas, Mioceno, América Media, Salticidae, Marpissinae

Introduction

Fossil spiders, including amber salticids, have been fully cataloged based on criteria used for living spiders (Dunlop, Penney and Jekel, 2013). Several monographs of amber and copal spiders from the Cretaceous to Tertiary of Europe, Africa, Asia and America have also been published separately by Wunderlich (2004a, 2008, 2011, and 2012), reflecting his use of different criteria. Fossil representatives of the Salticidae occur in the amber deposits of the Paleogene and Neogene of Europe and the Americas (Wunderlich, 2004a; Penney and Selden, 2011; Dunlop, Penney and Jekel, 2013). This includes the Paleogene amber deposits from Bitterfeld, Baltic, Rovno and younger (Neogene) strata from the Dominican Republic. These recent reviews do not include the salticid records from the Neogene Chiapas amber (Southern México) that were previously published by Petrunkevitch (1971) and García-Villafuerte and Penney (2003). Both reports of Chiapas salticids were associated with the Simojovel quarries that belong to the Lower Miocene Balumtum and Mazantic Shale strata. Petrunkevitch (1971) described a representative of Salticidae *incertae sedis* since this specimen was too poorly preserved to identify further, while García-Villafuerte and Penney (2003) described a representative of the genus *Lyssomanes*. Additionally, a putative new member of the subfamily Marpissinae (Araneae: Salticidae) from the Chiapas amber is reported here for the first time. Although limited, this fossil record increases our knowledge of

the amber salticids from the Neogene of Middle America, complementing previously published fossil records from Dominican amber.

Material and Methods

The piece of amber containing the salticid shown here was collected in the Rio Salado locality near the town of Totolapa, 66 km south of Simojovel, State of Chiapas, southern México. A first stratigraphy report of the Totolapa amber outcrops can be found in Duran-Ruiz *et al.* (2013: Fig. 1-2). Totolapa amber is currently thought to be Lower Miocene in age. The single specimen IGM6264 is housed at the Colección Nacional de Paleontología belonging to the Instituto de Geología, UNAM, México.

Results and Discussion

This putative member of the subfamily Marpissinae (Araneae: Salticidae) is tentatively placed in the genus *Maevia* C. L. Koch, 1846 (Figure 1).

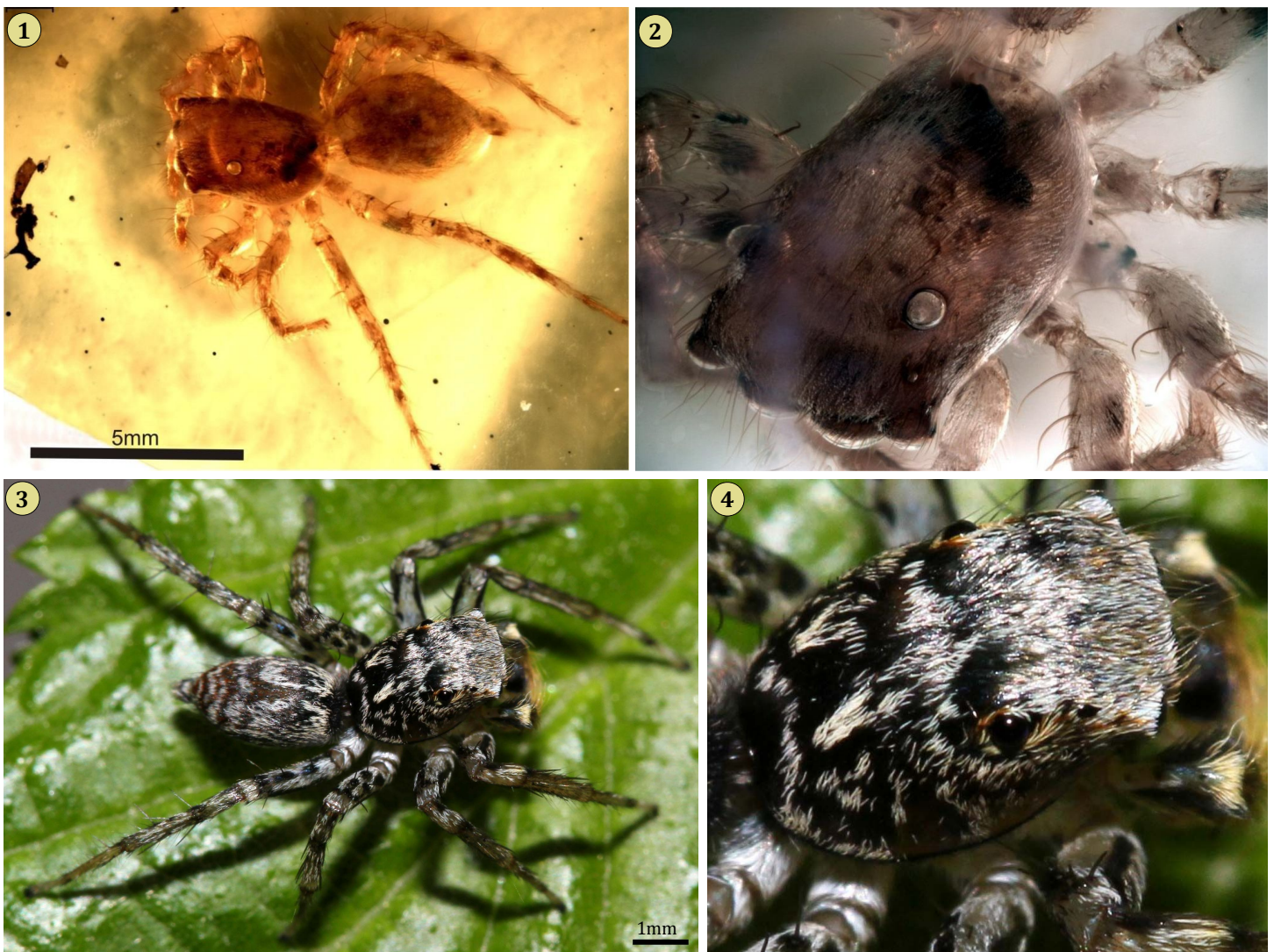


Figure 1. 1, A single specimen preliminarily identified as new member of the Marpissinae from the Miocene Totolapa amber, Chiapas, México. 2, Closer view of the of prosoma from (1). 3, ♂ *Maevia inclemens* (Walckenaer 1837), 'light form' from the forest understory of southern Greenville County, South Carolina, USA (12 MAY 2012). 4, Detail of prosoma from (3). In many details including size, carapace shape, placement of eyes, relative leg lengths, and setation, the amber specimen resembles this living *Maevia*.

This specimen is presently being studied and a formal description at the species level will be published when this has been completed. The fossil record of salticids from North America is unknown to date, so the discovery of this fossil marpissine in the Miocene Chiapas amber at the physiographic boundaries between southern North America and Central America can have a major impact on our hypotheses regarding the minimum age of the origin and divergence of related taxa.

The Chiapas amber is associated with a resin-producing tree of the genus *Hymenaea* that formed a dominant plant cover in temperate, subtropical and tropical areas from the Miocene until recently (Langenheim, 2003). The paleobiological affinities of the Neotropical Chiapas amber that are shared with Dominican amber, including the *Hymenaea* forest, mangrove-like environments, and their coeval faunas, are suggested elsewhere (Poinar, 1992; Langenheim, 2003; Solórzano-Kraemer, 2010; Penney, 2008; others). In this context, according to Wunderlich (2004b) the fossil record of salticids in Dominican amber is most abundant at the subfamily level reflecting a higher diversity than the Baltic amber. Penney (2008) reported that the family Salticidae has the second most abundant fossil spider record in Dominican amber, after Theridiidae. The amber salticids of Chiapas mentioned above expand the known subfamily diversity of Neotropical America during the Tertiary. Accordingly, the diversity of these Miocene salticids may reflect the presence of ancestor taxa for the recent North American groups.

The hypothesis of salticid origin during the Upper Cretaceous on the basis of the molecular phylogenetics and available biogeography literature has been reviewed elsewhere (Hill and Richman, 2009). Penney (2010) saw a need to integrate the fossil record into this kind of analysis. In this sense, the huge gap in the Mesozoic fossil record of salticids including the Cretaceous fossiliferous amber and the absence of relative modern forms in the Eocene Baltic amber (Wunderlich, 2004b) have suggested that the divergence of salticid groups occurred during the Cenozoic instead of the Mesozoic (Wunderlich, 2004b; Penney, 2010; Penney and Selden, 2011). Some of the most 'primitive' or basal salticids representing few subfamilies are known from the Eocene Baltic amber, suggesting a poor diversification of modern groups during the lower part of the Cenozoic (Wunderlich, 2004b). According to Wunderlich, a significant divergence may have started after the Eocene Baltic amber extinction during the Oligocene (when we have a fossil record gap), persisting into the Miocene. Hill and Richman (2009) also suggested that the divergence and rapid speciation of the salticids probably took off in the Paleocene-Miocene. The subfamily diversity and the presence of relatively modern forms of salticids from the Middle American amber indicate a broader divergence of salticids since the Miocene within the tropics.

Geological notes on the Miocene Chiapas amber with implications for salticid dispersal

Central America lies at the western end of the Caribbean plate (James, 2007; Bundschuh and Alvarado, 2007). Its geological history is clearly important to biodispersal between North and South America. Central America is part of a complex of fragmented continental, oceanic and volcanic arc crust between the larger continental masses of North and South America. This includes pre-Mesozoic blocks, Mesozoic and Cenozoic units (James, 2007; Bundschuh and Alvarado, 2007). The Caribbean plate is thought to have a Pacific origin, moving from north to south (Bundschuh and Alvarado, 2007; others). Readers are urged to consult the abundant available literature for a more detailed discussion, which is only briefly mentioned here. The tectonic and sedimentary evolution of so-called Middle America includes southern México, Central America and the Antilles (James, 2007; Bundschuh and Alvarado, 2007). This evolution drastically modified paleobasins in this area and also affected climate change in a manner that is consistent with the early introduction of marpissines from Neogene ancestors in Middle America to southern North America.

It is important to note that the Neogene Dominican and Chiapas amber strata, as part of the geological history of the Middle America, shared the same time scale and orogeny at convergent boundaries during

the geological evolution of southern México and Central America (James, 2007). This and their similar nearshore depositional regimes spanning the Lower to Middle Miocene eventually favored similar patterns of biodispersal in the two areas.

Wunderlich (2004a), Penney (2008), and Penney and Selden (2011) suggested that nearly all families and genera of fossil spiders from Dominican amber are still extant in the same geographical area. The accuracy of this statement can be a subject of debate, but this diversity may also reflect a center of origin for several groups. Poinar (1992) and Nudds and Selden (2008) compared the Dominican fossil assemblages with the similar, living tropical biota. They suggested that paleobiota trapped in Dominican amber was forced to disperse and became extinct due to climatic fluctuations during the ice ages (Neogene to Pleistocene), which altered the poles and also affected the tropics. According to this hypothesis, plant and animal groups could retreat back to Central and South America, and elsewhere to Australasia. Because this approach is based on a general climate inference (glaciation cycles), it remains to be demonstrated in accordance with the geological history of the Dominican Republic region as part of the Central America orogenies.

On the other hand, the Chiapas amber deposits of southern México are part of the Mazantic Shale and Balumtum Sandstone strata ranging from Lower to Middle Miocene (ca. 23-13 Ma). These are associated with nearshore and lowland continental settings (Perrilliat *et al.*, 2010). The geological evolution of Chiapas from the Oligocene to Pliocene is also linked to the formation of Central America (Meneses-Rocha, 2001; Bundschuh and Alvarado, 2007; Mandujano-Velázquez and Keppie, 2009; others). The tectonic phenomena and sedimentary input that formed the Mountains of Chiapas (where the Chiapas amber is now collected) during the Oligocene-Miocene altered the distribution of basins and generated and modified barriers to dispersal (Meneses-Rocha, 2001). This caused changes in local ecosystems and represents a potential driver of diversification, forcing the dispersal of Chiapas amber paleobiota.

Accordingly, the intense tectonic activity by a general uplift that thrust and folded the basal rocky units during the Oligocene-Miocene of Chiapas (ca. 28-13 Ma) and a subsidence post-orogenic phase ending at the Lower Pliocene (ca. 5 Ma) significantly altered the paleogeography of the region (Riquelme *et al.*, 2013: Fig. 2). The rising blocks triggered by tectonics produced mountain ranges, marine sea level fluctuations, and also affected climatic processes progressively. Thus, the shoreline was forced to recede toward the north and cyclic alternation of depositional environments occurred, alternating from lacustrine to alluvial and stream-flood systems that reflect episodic, severe climate changes (Meneses-Rocha, 2001). This is consistent with the Oligocene to Miocene depositional record in the Chiapas amber area. The rocks exposed here show alternate, compositional changes in carbonate, siliciclastic and organic-rich carbonaceous beds that suggest a system eventually controlled by short-term cyclical changes in climate (Riquelme *et al.*, 2013). It seems that the dispersal and extinction of Chiapas amber paleobiota took place in allopatry by land changes. This was followed by a forced dispersion to new areas over long periods of time spanning the Miocene to Pliocene.

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