

The evolution of jumping spiders (Araneae: Salticidae): the palaeontological evidence

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A recent review on the evolution of jumping spiders (Salticidae) by Hill and Richman (2009) proposed a Late Cretaceous origination, with speciation well underway by the Oligocene–Miocene. These conclusions were based on modern cladistic analyses, including both DNA and morphology, but only scant attention was paid to the existence (or not) of any supporting palaeontological evidence. Regardless of whether or not cladistic analyses provide sound reasoning to generate such hypotheses, any resulting ideas warrant corroboration through careful consideration of the fossil record. Fossil spiders are reasonably well studied, with more than 1,000 different species described. Palaeoarachnological data for all described fossil arachnids are readily available (*e.g.* Dunlop *et al.* 2010) on Platnick's (2010) World Spider Catalogue and have been now for several years. The aim of this comment is not to criticize the ideas generated via the cladistic methodologies, but merely to address the potential timelines for the origination of Salticidae, based on the available palaeontological evidence.

Hill and Richman (2009) rightly pointed out that Penney *et al.* (2003) assumed an early Cenozoic emergence of the family Salticidae. Despite considerable extensions in the known geological ranges for certain spider families in recent years, the evolutionary tree of spiders with regards to the origination of Salticidae and the other unresolved dionychan families remains unchanged (Selden & Penney 2010). The Burmese amber Thomisidae mentioned by Hill and Richman (2009), cited as recorded by Grimaldi *et al.* (2002) from Cretaceous Burmese amber from Myanmar, was based on a record cited by Rasnitsyn and Ross (2000). This juvenile specimen has not been described, so its identity as a thomisid has yet to be confirmed. Grimaldi *et al.* (2002) also mentioned a jumping spider (Salticidae) in the Cretaceous New Jersey amber collections of the American Museum of Natural History, a specimen was figured as Salticidae by Néraudeau *et al.* (2002) from Cretaceous amber of France, and a specimen was figured by Kaddumi (2005) as Salticidae in Cretaceous Jordanian amber. Although the aforementioned were misidentifications (Penney 2007), none were mentioned by Hill and Richman (2009), who concluded that at the present time, the spider fossil record is too fragmentary to draw any firm conclusions with respect to the origin of existing salticid groups. Whilst this may true to a large extent for subfamilial groups, the palaeontological evidence for an absence of the family Salticidae in the Cretaceous is rather compelling.

Extant salticids have a global distribution and are the most diverse spider family on the planet today, with 5,293 recognised species in 570 genera (Platnick 2010). They occur frequently as Tertiary fossils in amber (Figure 1) from the Baltic region (Wunderlich 2004) and the Dominican Republic (Penney 2008). As visual predators, they were presumably attracted to struggling insects trapped in sticky resin and eventually became entombed themselves, thus explaining the high frequency of occurrence of this family in Tertiary ambers. In a study of 701 Dominican amber spiders from 45 different families, Salticidae ranked second (after Theridiidae), with 107 specimens accounting for 15% of the total spider sample (Penney 2002). Given that different amber forming resins appear to have operated as an arthropod trap in the same way (Penney and Langan 2006), they should have been preserved in Cretaceous ambers if they were present at that time. Salticids are highly distinctive as a result of their large anterior median eyes, and can be easily identified from very tiny juvenile specimens, even in amber. Thus, they are unlikely to have been accidentally overlooked in Cretaceous amber spiders examined to date, which are not particularly scarce. Thus, the suggestion that the earliest salticids predated the Lower Cretaceous

breakup of Pangaea and that they would have been widely distributed on this landmass is unlikely to be true, especially as the distribution of major Salticoida clades is constrained by modern continental boundaries, established following the break up of Pangaea (Maddison and Hedin 2003), as noted by Hill and Richman (2009).

Figure 1. Mature male *Distanilinus nutus* Wunderlich 2004 in Eocene Baltic amber. Photo by D. I. Green (Manchester Museum).



Interestingly, the reasoning used by Hill and Richman (2009) to explain the divergence and rapid speciation of salticids serves to argue against a Cretaceous origin of this family. They suggested that tropical and subtropical climates (during the Tertiary) may have spurred on the diversification of the family. However, many of the Cretaceous amber forests grew under such climatic conditions (Penney 2010), yet salticids are absent in these faunas. Even more enigmatic is the absence of jumping spiders in Tertiary lowermost Eocene amber from Oise (France), which contains an otherwise diverse spider assemblage. Out of a total of 230+ spiders examined, not one was a salticid (Penney 2007). However, had they been widespread on Pangaea before its breakup in the Mesozoic, then they should be present in this deposit. It is also interesting to note that only one primitive salticid subfamily is known from Eocene Baltic amber, whereas four subfamilies occur in the geologically younger Miocene Dominican amber (Wunderlich, 2004), again suggesting diversification within the Cenozoic, rather than the Mesozoic.

Thus, at present, the fossil record points towards a Cenozoic origination for jumping spiders, although their presence in the Cretaceous cannot be ruled out entirely. Palaeoarachnologists researching Cretaceous (and older) spiders (both amber and non-amber fossils) are forever vigilant in the hope of discovering the first Mesozoic salticid. The search for a Mesozoic jumping spider has been, and will continue to be, one of the holy grails of palaeoarachnology.

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