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Extension of fangs during the predatory jumps of jumping spiders (Araneae: Salticidae)

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Abstract. Lateral extension of fangs during the predatory jump of salticid spiders, prior to contact with prey, is documented through use of a light beam trigger for still photographs, and slow motion (1920 fps) video. This movement, difficult to observe, demonstrates the role of fangs as primary weapons of attack by these spiders. Other important aspects of the functional design of these fangs, and their role in threat displays, are also discussed.

Key words. chelicera, *Colonus puerperus, Gorgonopsis,* microserration, *Paraphidippus aurantius,* paturon, *Phanias harfordi, Phidippus audax, Phidippus carolinensis, Phidippus mimicus, Psecas viridipurpureus,* serrated blade, therapod dinosaur, *Zygoballus sexpunctatus*

The predatory jumps of salticid spiders have been mentioned in many published accounts (e.g., Comstock & Gertsch 1965; Levi & Levi 1968; Bristowe 1971; Kaston 1978; Gertsch 1979; Preston-Mafham & Preston-Mafham 1984, 1996; Foelix 2011), as well as papers dealing with the mechanics of these jumps (e.g., Hill 2010, 2018b), but none of these have included a detailed description of the movement of chelicerae and fangs during these jumps. This is most certainly due to the fact that, although the resultant hold of prey with the chelicerae is evident (Figures 1-2), extension of the fangs is so rapid that it cannot be seen without special photographic techniques. Some published works even suggest that the chelicerae are not used until after the prey has been captured with the extended legs. Here (Figures 3-4) we document the extension of the fangs of salticids well in advance of their contact with intended prey. With reference to Figure 4, detailed photographs of an adult female *Psecas viridipurpureus* (Simon 1901) are also shown in Figure 5.

The chelicerae of spiders are sometimes described as *jaws*, but they are really not like our own mouthparts, but represent a pair of specialized appendages that begin their development just behind the mouth, from the segment just anterior to the segment bearing the pedipalps; during development they migrate to a more anterior position. The mouth itself lies behind the chelicerae in the fully-developed spider, and this has both an upper roof, the bottom of the labrum or rostrum, and a lower floor, the top of the labium. Thus the labrum and labium are more analogous to mammalian jaws (Hill 2011). The chelicerae, like the pedipalps, should be thought of as specialized appendages with no clear analog to be found in the mammals. Each chelicera is comprised of a basal segment, the *paturon*, equipped with a *fang* that, when not in use, is retracted into a distal sheath or *fang groove*, usually surrounded by a variable number of teeth on the anterior (pro) or posterior (retro) margins of that groove. Each venom gland in the prosoma discharges venom through a small pore near the tip of each fang (Figure 6).



Figure 1. Lateral view of sequence (positions 1-4; position 1 repeated in composite middle frame) showing the capture of a thomisid of the genus *Mecaphesa* by a penultimate male *Colonus puerperus* (Hentz 1846) from South Carolina (after Hill 2018a). Note the manner in which this *Colonus* held its prey, with fangs securely embedded in the rear of the prosoma.



Figure 2. Large grasshopper held safely and securely by the fangs of a *Phidippus carolinensis* Peckham & Peckham 1909, suspended on its dragline, and photographed at Ft. Sill, Oklahoma (1 JUL 2013). Photo credits: 1-3, © Victor W. Fazio III (iNaturalist), modified under a Creative Commons Attribution-Noncommercial International (<u>CC BY-NC 4.0</u>) license.



Figure 3. Photographs showing the lateral separation of chelicerae and extension of fangs by *Phanias harfordi* (Peckham & Peckham 1888) prior to contact with intended prey (*Drosophila*). In each case the camera shutter was triggered by interruption of a light beam (Appendix 1). Note the elevation of the pedipalps to enable attack with the chelicerae. **1**, Female, antero-lateral view. Only one of the chelicerae is visible in the perspective. Collected in Berkeley, California. **2**, Male, anterior view, showing both extended fangs in position to make a strike. Collected at Alpine Lake, Marin County, California.



Figure 4 (continued on next page). Selected frames from a 1920 fps video record of an adult female *Psecas viridipurpureus* leaping to capture a field cricket. The number of each frame is shown in brackets. **1,** The estimated scale and takeoff velocity (~120 cm/s) are based on Galiano's (1963) record of the size of a female *P. viridipurpureus* (~13 mm, prosoma length 4.8 mm, abdomen length 8.6 mm; see also Figure 5). Compared to earlier records (Hill 2018b), this represents a very high takeoff velocity for a salticid, comparable to that attained by *Colonus puerperus*. White arrows (1-4, 6) point to the extended fangs. In (6) both fangs are visible. Also note elevation of the pedipalps prior to contact with the prey. Locality: Rio Preto da Eva, Amazonas, 69117-000, Brasil (2.701472°S, 59.71042°W).



Figure 4 (continued from previous page). Selected frames from a 1920 fps video record of an adult female *Psecas viridipurpureus* leaping to capture an orthopteran. **7-18,** Contact with legs I and II preceded the bite of this spider with its chelicerae by several milliseconds, and simultaneous flexion of those legs appeared to contribute to the force of that bite. After legs IV were disengaged, legs I-III continued to hold the prey. If this prey were not held in place, recoil of the extended dragline may have pulled that prey free of its hold on a surface (Hill 2018a; see Figure 2).



Figure 5. Adult female *Psecas viridipurpureus* from French Guiana (4.0855°N, 52.6818°W, 12 MAR 2021). Photo credits: 1-2, © Sean McCann (iNaturalist), modified under a Creative Commons Attribution-Noncommercial International (<u>CC BY-NC 4.0</u>) license.



Figure 6. SEM images of the left chelicera of two *Phidippus audax* (Hentz 1845) from Iowa City, Iowa. **1**, Posterior-distal view, penultimate, adapted after Hill (1977). **2**, Posterior view, adult male. Note the presence of one large tooth on the posterior margin, and two successively smaller teeth on the anterior margin, of each fang groove. The opening of the venom duct is near the tip of each fang and, proximal to this duct, lies a sharp, microserrated interior edge.

Attack with the fangs has been described as follows (Hill 1977):

The two fangs of the jumping spider are versatile tools in the handling of prey. They are used in unison, like ice tongs, to seize the prey as it is jumped. The fangs extend as the chelicerae are moved laterally, and flex to impale the prey as the chelicerae are brought together, with a sudden force. Subsequently the fangs are employed in the injection of the venom, and the maceration (chewing) of the prey.

The spider fang has been compared to the tip of a syringe, with a sharp and strong, penetrating tip distal to the opening of the venom duct (Hill 1977; Foelix 2011, 2015; Politi et al. 2012, 2017; Bar-On et al. 2014). The presence of a sharp interior edge bearing microserrations (Figure 6) is also of particular interest. Similar serrations are found on the cutting edges of mosquito maxillae, as well as the cutting edges of the teeth of a number of vertebrates, to include therapod dinosaurs and varanid lizards, where this condition is termed *ziphodonty* (Figure 7; Brink et al. 2015; Giovanni et al. 2017).



Figure 7. Microanatomy of the teeth of the tyrannosaurid dinosaur *Gorgonopsis*. **1**, Drawing of the skull of *G. libratus* by Danielle Dufault. 2, Sagittal sections through the distal and mesial *carinae* (sharp edges) of a maxillary tooth (ROM 57981) of a cf. *Gogonopsis* sp. Abbreviations: **dej**, dentine-enamel junction; **e**, enamel; **if**, interdental fold; **is**, interdental sulcus; **pd**, primary dentine. Figure adapted from Brink et al. (2015), used under a Creative Commons Attribution 4.0 International (<u>CC BY</u> <u>4.0</u>) license.

Wheras therapod dinosaurs like *Gorgonopsis* (Figure 7) have teeth that cut to the front and rear, the salticid fang has a single sharp, serrated edge, on the interior or medial side of each fang. This corresponds to the medial movement of each fang during the bite of a salticid, where the two fangs work in opposition to securely hold the prey. Foelix & Erb (2011) suggested that the microserrations of the salticid fang reflected an adaptation for the cutting of silk lines, but this is clearly only one possible use. Those familiar with the use of serrated and straight-bladed knives understand that the former is more effectively used, like a saw blade, to grip and to cut through both hard and pliant surfaces, exemplified by baked bread with a hard exterior and a soft interior (Perry 2004; Crowley 2016). Recent studies have shown that microserrations reduce the force required to cut through mammalian skin layers by at least 20-30% (Giovanni & Ehmann 2016; Giovanni et al. 2017; Bollinger et. al 2020). Other recent studies have demonstrated the effectiveness of the design of spider fangs as weapons, to include the binding of metals like zinc to histidine residues in the cuticle to improve its hardness (Politi et al. 2012, 2017).

The notion that the salticid bite includes immediate injection of venom is supported by many observations of prey that are immobilized after a quick bite and release by a salticid. One of the authors (DEH) recently observed the attack of an adult female *Paraphidippus aurantius* (Lucas 1833) on an adult orchard spider, *Leucauge venusta* (Walckenaer 1849). After a fast bite, this *Paraphidippus* backed off by about 4 cm, apparently to avoid grappling with a dangerous spider, but waited only several seconds before advancing to feed on its now paralyzed prey. The same author (DEH) can also report the attack of an unprovoked adult female *Phidippus mimicus* Edwards 2004, jumping from a plant in the laboratory at a distance of ~10 cm to bite and then immediately release his hand (Figure 8). In this instance envenomation led to rapid inflammation in an area of ~1 cm in diameter, with intensive itching one week later, and subsequent healing within one month.



Figure 7. Adult female *Phidippus mimicus* from western Oaxaca. **1**, The dorsal color pattern of both males and females of this species may represent mimicry of mutillid wasps (Edwards 2004). **2**, Immediately after its bite this female continued to threaten one of the authors (DEH) with exposed chelicerae and venom dripping from the fangs. Between extended chelicerae the light-grey rostrum of this spider is visible (19 MAR 2019).

Beyond their role in attack and defense, chelicerae and fangs play an important role in the agonistic (ritual male:male combat) encounters of many salticid species (Figures 8-9).



Figure 8. Displays by adult male *Zygoballus sexpunctatus* (Hentz 1845), Greenville County, South Carolina. **1.** Frontal view of courtship display, as seen by the courted female. In this display the chelicerae are held close together, flanked by the vertically-oriented pedipalps. The bright, light-blue scales that cover the face and chelicerae are a major feature of this display, and the position of the chelicerae, with retracted fangs, is not threatening. **2.** Agonistic display while facing another male of similar size, engaged in the same kind of display. Here the large chelicerae and fangs are fully extended, supplemented by a large spine near the base of each chelicera that, like the anters of male deer, can play a role in a later, grappling stage of combat. Although this ritual display is formidible, this has not yet been observed to lead to damage to either combatant.



Figure 9. Sequential positions of two adult male *Paraphidippus aurantius* (Greenville County, South Carolina, 27 JUN 2021) during an agonistic encounter on a plant in the laboratory. Combat included alternating advance and retreat by each male (e.g., 3 steps forward followed by 2 steps to the rear, resulting in gradual advancement to direct contact). Like *Zygoballus* (Figure 7), these also have greatly enlarged chelicerae with large spines near the base that can play a role in later grappling stages of combat, if necessary. In this example, no harm was done as the spider on the left soon fled from the scene.

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Appendix 1. Use of a light beam to trigger a photograph of a jumping spider in motion

This technique was devised by one of the authors (DLG) to produce the photographs shown in Figure 3: The light source was a miniature halogen flashlight bulb collimated with a lens to a 1 cm diameter beam, and then focused on the sensor of a phototransistor. Interruption of the light beam by a moving spider altered the transistor signal to trigger a comparator, which in turn triggered an electronic leaf shutter placed in front of a 90 mm macro lens mounted to a DSLR. The flash exposure time was approximately 1/30,000 second. In order to stage the prey, a 0.5 x 0.5 cm piece of ripe fruit was placed on a similarly sized platform and wetted with two to three drops of cider vinegar. Approximately twenty Drosophila were released into the same room and, after a time, several found the fruit and alighted on it. At that point, one of the *Phanias harfordi*, which stalk stationary prey, was introduced onto a twig that was separated from the piece of fruit by 1 cm.