

Strike kinematics in the whip spider *Charon* sp. (Amblypygi: Charontidae)

Michael Seiter¹, Patrick Lemell¹, Rosa Gredler¹ and Jonas O. Wolff²: ¹Department of Integrative Zoology, University of Vienna, Faculty of Life Science, Althanstraße 14, 1090 Vienna, Austria. E-mail: michael.seiter@univie.ac.at;

²Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

Abstract. The speed, precision and impact of strikes often determines predatory success. Whip spiders (Arachnida: Amblypygi) are nocturnal ambushing predators that use massive raptorial pedipalps in rapid strikes. While prey capture behavior has been described for a number of amblypygids, the movements performed during the strike have never been resolved in detail, in spite of their strong relevance for the feeding ecology and evolutionary history of this group. Here we studied the attack behavior of *Charon* sp. on crickets and describe the kinematics of body and pedipalpal movements during the strike. We found that the total strike is performed within 30–180 milliseconds with the pedipalpal tip being accelerated up to 70 m/s² during closure. We found that *Charon* sp. is able to strike the prey at a lateral angle of up to 30°, which is achieved by non-parallel abduction of the laterigrade legs. These results contribute to our understanding of the evolution of high performance of predatory structures.

Keywords: Arachnida, prey capture, strike behavior, predator-prey interaction, high speed video.

The speed and impact of strikes can be important determinants of foraging success in predators (Dawkins & Krebs 1979). Therefore, strike performance has often evolved under high selective pressure, which repeatedly resulted in impressive performance (Abrams 2000). For instance, trap jaw ants and mantis shrimps perform a complete strike within milliseconds, which makes it nearly impossible for the prey to escape (Burrows 1969; Gronenberg et al. 1993). Such fast movements are achieved by the rapid release of stored elastic energy (Gronenberg 1996). In contrast, purely muscular driven movements are substantially slower. Their speed depends on muscle length and can be enhanced by leverage, such as in mantids (Ass 1973). In addition to fast movements, specialized appendages, such as clamps, pincers, hooks, fangs, or adhesive pads, play an important role for successful predatory strikes by enabling the seizing and subsequent securing of the prey (Betz & Kölsch 2004; Wolff & Gorb 2016; Wolff et al. 2016). Thus, clarification of the kinematics of strikes and the functional morphology of the body parts involved is crucial for our understanding of the adaptive mechanisms and ecological effects of predation.

Arachnids are among the most important and abundant invertebrate predators. An arachnid order that is known for its peculiar and large raptorial pedipalps are whip spiders (Amblypygi). These are nocturnal ambushing predators that occur in tropical and subtropical regions and can grow large (leg span up to 20 cm, excluding their elongated first legs). Whip spiders have a unique appearance: in general, they are cryptically colored, dorso-ventrally flattened with laterally tilted (laterigrade) legs, and have their first pair of legs modified into long and thin antenna-like sensory appendages (Weygoldt 2000). Prey is caught with two large and spinous appendages, the pedipalps. Since whip spiders do not possess venom glands, they need to dismember and eat the prey while it is alive and struggling using their two jack-knifed orthognath chelicerae. To prevent prey from escaping, the flexed pedipalps form a capture basket that holds the prey in place close to the chelicerae (Weygoldt 2000). Hence, a successful acquisition of prey depends on the accuracy and velocity of the predatory strike followed by a forceful flexion

of the pedipalps. Santer & Hebets (2009) were the first to study prey capture in these animals in detail by means of high-speed videography. They found that the attack is highly stereotypic and consists of an approach phase and the very rapid strike. Apart from these observations, the kinematics and functional morphology of the amblypygid pedipalps are unknown. Amblypygids show enormous inter- and intraspecific variation in pedipalp morphology from short and thick to very long and slender pedipalps, and it is conceivable that those differ in their strike kinematics and function. The species used by Santer & Hebets (2009) bears relatively short pedipalps. Here we studied strike kinematics in closer detail, in a species with comparably long pedipalps – *Charon* sp. (Charontidae). Thereby, we aimed to clarify the role of different pedipalpal segments, the chelicerae and the overall body movement in prey capture.

METHODS

We used captive bred juvenile individuals (four females and one male) of *Charon* sp., approx. 8 months old with a body size of 17.06 (\pm 1.38) mm (Amblypygi: Charontidae), which originated from Mindanao, Philippines. A charontid species was chosen because of its ability to securely walk on glass due to the presence of adhesive foot pads (arolia) (Wolff et al. 2015). This was important because we aimed to film prey capture behavior from below the walking substrate (i.e., the glass bottom of a terrarium) to observe the use of all pedipalpal segments and the chelicerae. Because the prey animals (crickets) cannot climb on steep smooth glass surfaces, it was necessary to place the arena horizontally and film from below. It should be noted, that *Charon* spp. usually hunt in a vertical position, e.g., on cave walls or tree stems. However, such positioning was no prerequisite to trigger prey capture behavior in our study animals.

The terminology of appendages follows Quintero (1981): the modified first pair of legs is called antenniform leg and the pedipalps are divided into coxa, trochanter, femur, tibia, basitarsus, distitarsus and claw.

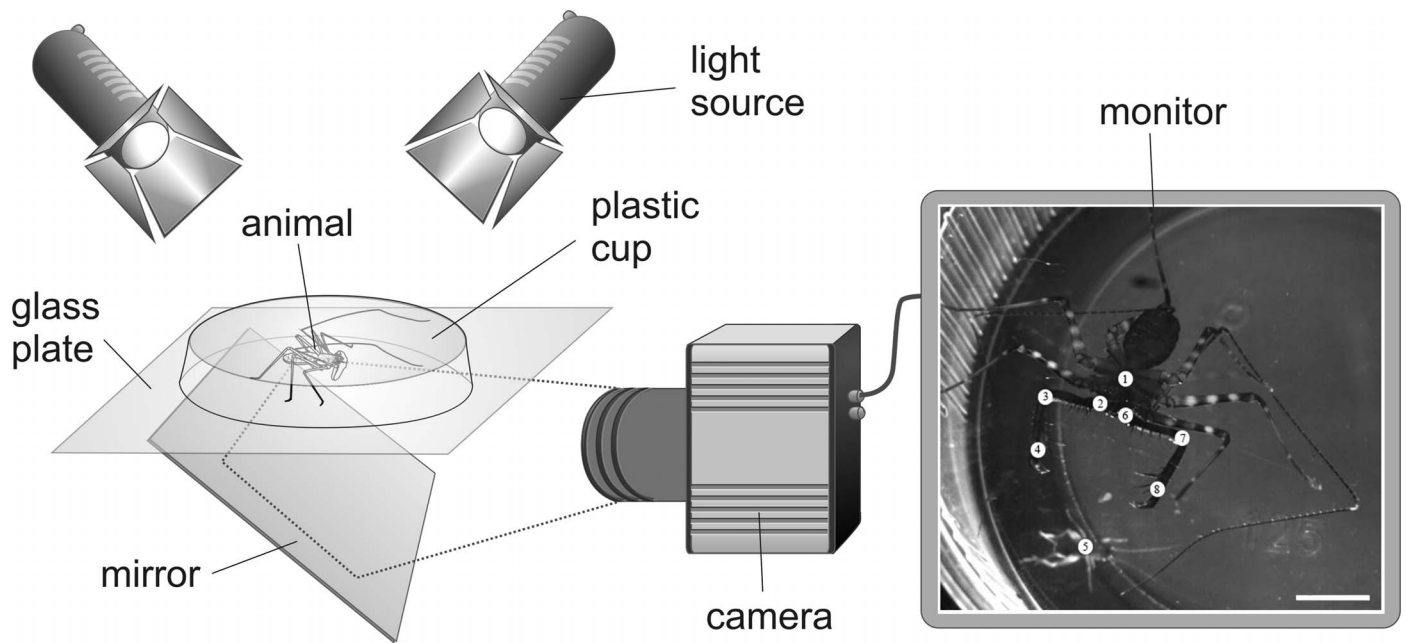


Figure 1.—Experimental set-up and anatomical landmarks (estimated centre). The experimental individuals (*Charon* sp.) were placed on a glass plate together with a single cricket (*Acheta domestica*). They were covered with a closed plastic box (1 cm high, 9 cm diameter). Light sources were mounted on the left and right sides, one meter above the arena. The high-speed camera was focused on a mirror which was beneath the glass plate at a 45° angle to the experimental individuals. Inset shows an example of a video frame with the tracked landmarks indicated. The landmarks comprised (1) the sternum, (2) the trochanter of the left pedipalp, (3) the femur-tibia joint of the left pedipalp, (4) the tibia-basitarsus joint of the left pedipalp, (5) the centre of the prey item, (6) the trochanter of the right pedipalp, (7) the femur-tibia joint of the right pedipalp, and (8) the tibia-basitarsus joint of the right pedipalp. Scale bar: 1 cm.

Video recordings were accomplished in a terrarium (50 × 30 × 30 cm) with a 45° mirror underneath to obtain a ventral view (Fig. 1). Animals were placed onto the glass bottom of the terrarium and covered by an upside-down plastic box (9 cm diameter, 1 cm height) to restrict their mobility, but providing enough space for free movement of prey and whip spiders within the camera's field of view. A few minutes later, a medium-sized cricket (approx. 8–9 mm body size), *Acheta domestica* (Linnaeus, 1758), was released into the box. Prey capture events were recorded with a high-speed camera (Photron FASTCAM, 1024PCI, San Diego, USA) and using control software (Photron FASTCAM Viewer, v3600_64bit, San Diego, USA) at 1000 frames per second (fps). For illumination, two light lamps with 250 W (Dedocool Coolh, Dedo Weigert Film GmbH; München, Germany) were placed laterally above the terrarium (Fig. 1).

A total of five complete strikes, each from a different individual, was used for the kinematic analysis. Supplementary file S1 (online at <http://dx.doi.org/10.1636/JoA-S-18-089.S1>) shows the attack motion of a *Charon* sp.

We submit that this limited number of replicates could not be increased despite repeated trials over a period of five months due to the elusive nature of amblypygid behavior.

The video sequences were analysed with a custom tracking program implemented in MATLAB (MathWorks, Inc., Natick, MA, USA) (Hedrick 2008). Further analyses and calculations were performed with custom-made scripts built in MATLAB R2015b. To convert distance measures from pixels into millimeters, a known distance in the image (a marking on the plastic box) was measured. The x-y-coordinates of eight

landmarks were tracked frame by frame. The landmarks comprised (1) the sternum, (2) the trochanter of the left pedipalp, (3) the femur-tibia joint of the left pedipalp, (4) the tibia-basitarsus joint of the left pedipalp, (5) the centre of the prey item, (6) the trochanter of the right pedipalp, (7) the femur-tibia joint of the right pedipalp, and (8) the tibia-basitarsus joint of the right pedipalp; all from ventral view (Fig. 1). Based on the landmark displacements, kinematic variables for the following motion components were determined (in the same order as in Table 1): (1) complete attack (attack motion): from start of forward movement to stop of backward movement; (2) entire strike: from start of forward movement to first contact with prey; (3) pedipalp opening and (4) pedipalp closing. For each of these components (except (1)), we calculated the following kinematic parameters: total duration (Δt), mean velocity (\bar{v}), and maximum velocity as the mean of five peak values ($V_{\max(5)}$). The maximal velocity was obtained by averaging five peak values since single values between two frames can be subject to tracking inaccuracies. Numbers for pedipalpal movements represent the mean of the movements of the left and the right pedipalp, because the movements were generally synchronous and differences between both pedipalps were minor. Pedipalp opening and closing velocities were described by the angular movement around the femur-tibia joint. Since calculation of acceleration frame by frame in a 1000 fps highspeed film is very noisy, the curve was smoothed with a Butterworth filter (order: 5; % of Nyquist-frequency: 20), and the maximum value of this smoothed curve was again rounded off. Raw data of

Table 1.—Summary of kinematic parameters of *Charon* sp. attack movements ($n = 5$). Δt – duration; \bar{v} – mean velocity; $V_{\max (5)}$ – maximum velocity (mean of 5 peak values); SD – standard deviation.

	Δt [s; mean \pm SD]	\bar{v} [cm/s; mean \pm SD]	$V_{\max (5)}$ [cm/s; mean \pm SD]
Complete attack	0.155 \pm 0.097		
Complete attack (forward motion)	0.082 \pm 0.063	25.14 \pm 12.75	63.62 \pm 15.13
Complete attack (backward motion)	0.073 \pm 0.062	24.17 \pm 7.79	48.26 \pm 18.58
Strike (until first prey contact)	0.074 \pm 0.065	25.04 \pm 14.34	60.01 \pm 15.37
Pedipalp opening	0.064 \pm 0.046	6.56 \pm 3.76	28.53 \pm 8.78
Pedipalp closing	0.050 \pm 0.017	22.79 \pm 9.32	72.31 \pm 16.77

kinematic measurements are presented in supplementary file S2 (online at <http://dx.doi.org/10.1636/JoA-S-18-089.S2>).

To provide a general description of the stereotypic strike movement, we aligned individual kinematic plots of landmark shifts from all trials. Either the starting position of the attack motion or the starting position of pedipalp closure served as a reference.

RESULTS

Attack behavior.—The terminology of the attack behavior follows the definitions by Santer & Hebets (2009). After these authors, the attack comprises four distinct behavioral phases: (1) detection and antenniform leg aiming; (2) body orientation and approach; (3) pre-strike; and (4) ultimate strike. It has to be noted that only the attack behavior of five complete strikes were used for the following description.

Detection and antenniform leg aiming: The first notable action by the whip spider occurred approximately 5 to 10 minutes after introducing the prey. The whip spider aimed one of its antenniform legs into the direction of the prey without any clear re-orientation of its body, while the prey was moving.

Body orientation and approach: Following the first phase, the whip spider re-orientated its body towards the prey. This was performed without any intermediate step of its six walking legs. One individual moved slightly forward towards the prey, but its leg IV remained in the same position, attached onto the ground with its arolia. Most of the time the body axis of the whip spider and the prey were aligned. During this phase the antenniform legs never touched the prey (in contrast to Santer & Hebets 2009) but the whip spiders already slowly unfolded its pedipalps.

Pre-strike: During this phase, the whip spider finally orientated its position into a suitable strike distance (2.35 cm \pm 0.85), partly stepping forward, or rotated its body, but always staying attached to the ground with at least one walking leg. At this time, the pedipalps were opened to their final pre-strike position (angle between femur and tibia up to 80°) (Figs. 2A, 3A–B) and the distance between the chelicera of the whip spider and the prey was reduced to 1–2 cm. Again, during this phase, the antenniform legs never touched the prey.

Ultimate strike: While the body of the whip spider rapidly rocked forward towards the prey by extending the hind legs, the pedipalps were rapidly opened further up to 105° (Fig. 2B), the chelicerae were extended and the antenniform legs swung back. During this rapid movement towards the prey, the whip spider could also rotate its body up to 30° by extension of the legs on one body side and the flexion of a front leg on the contralateral side. The first contact with the prey took place at a mean of 75° between pedipalp femur and tibia (Figs. 2C–F, 3A–B). In most cases, one pedipalp contacted the prey earlier than the other one (Figs. 2C–D). The pedipalps were immediately closed down to 35° strongly squeezing the prey, the legs relaxed again, and the body swung back into its original resting position (Fig. 4). In a single case, the eventual resting position was shifted forwards, because the hind legs

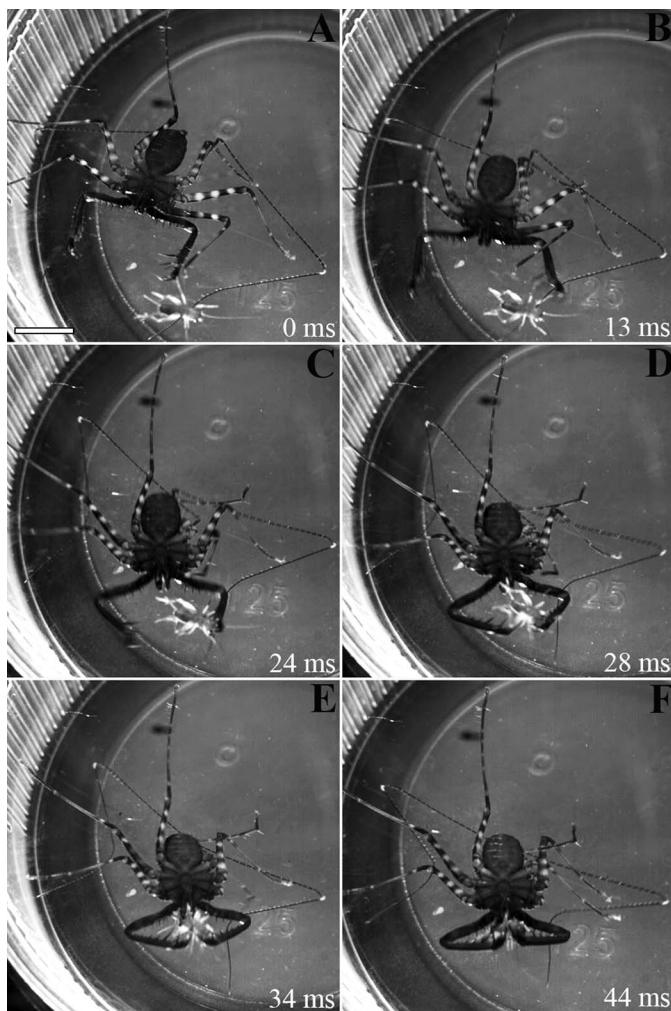


Figure 2.—Selected frame sequences of high speed-videos showing a typical prey capture event. (A) Start of the attack movement, (B) Highest angle between pedipalp femur and tibia, (C) First prey contact with the right pedipalp, (D) First prey contact with the left pedipalp, (E) First prey contact with the chelicera, (F) Closest position of the pedipalps with prey. Scale bar: 1 cm.

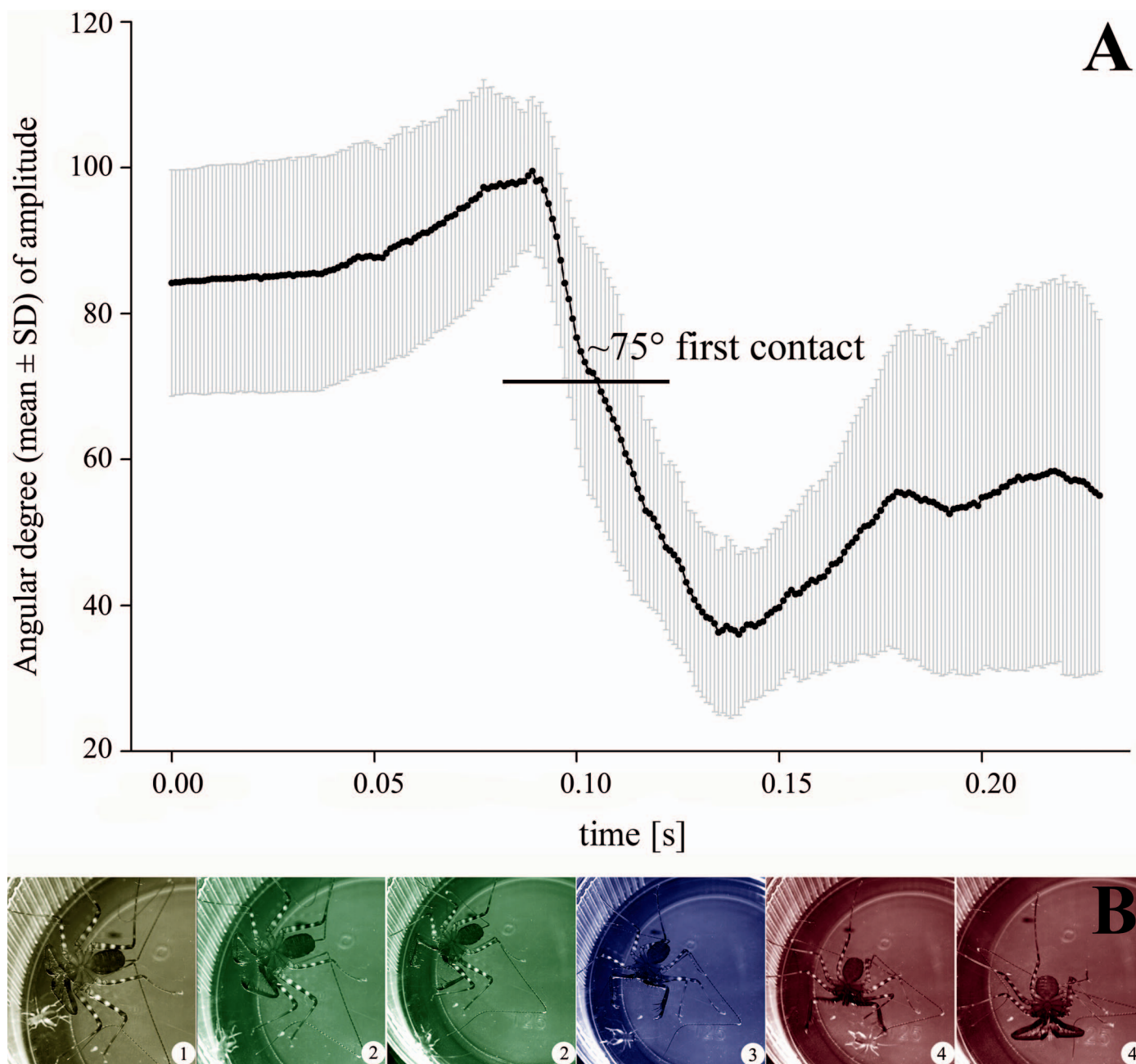


Figure 3.—Kinematics of the pedipalp during strike motion. (A) Angular movement of the pedipalp during strike (angular degree; mean \pm SD). The first contact with prey (indicated by horizontal line) took place at a pedipalpal opening angle of $\sim 75^\circ$. (B) Total cycle of opening, attacking and closing the pedipalps during strike motion. Usually, the pedipalps of whip spiders are completely folded (resting position with $\sim 10\text{--}20^\circ$). While preparing to strike, whip spiders slowly opened their pedipalps up to 80° , followed by a rapid opening up to 100° . After the fast strike the pedipalps were folded again. During consumption of the prey pedipalps were held with an angle of $\sim 20\text{--}35^\circ$. The colour- and number coding correspond with the distinct behavioral phases. Yellow (1) detection and antenniform leg aiming; Green (2) body orientation and approach; Blue (3) pre-strike; and Red (4) ultimate strike.

released the substrate and attached again during the forward strike. Moreover, we observed strikes not only at a linear axis, but also at an angle of $\pm 30^\circ$ by non-parallel leg abduction and adduction.

After the attack (Feeding): After the strike, the pedipalps were open at an angle of $\sim 50^\circ$ due to the prey filling the space in the capture basket. The prey was secured by the interlocking

of the pedipalpal spines with appendages of the prey and the jack-knife-like chelicerae began to cut into the prey's body. The prey was handled with both the pedipalps and the chelicerae during the feeding process.

Kinematics.—In total, we recorded five completed strikes with successful capture of prey. Kinematic parameters are summarized in Table 1. The full attack movement was

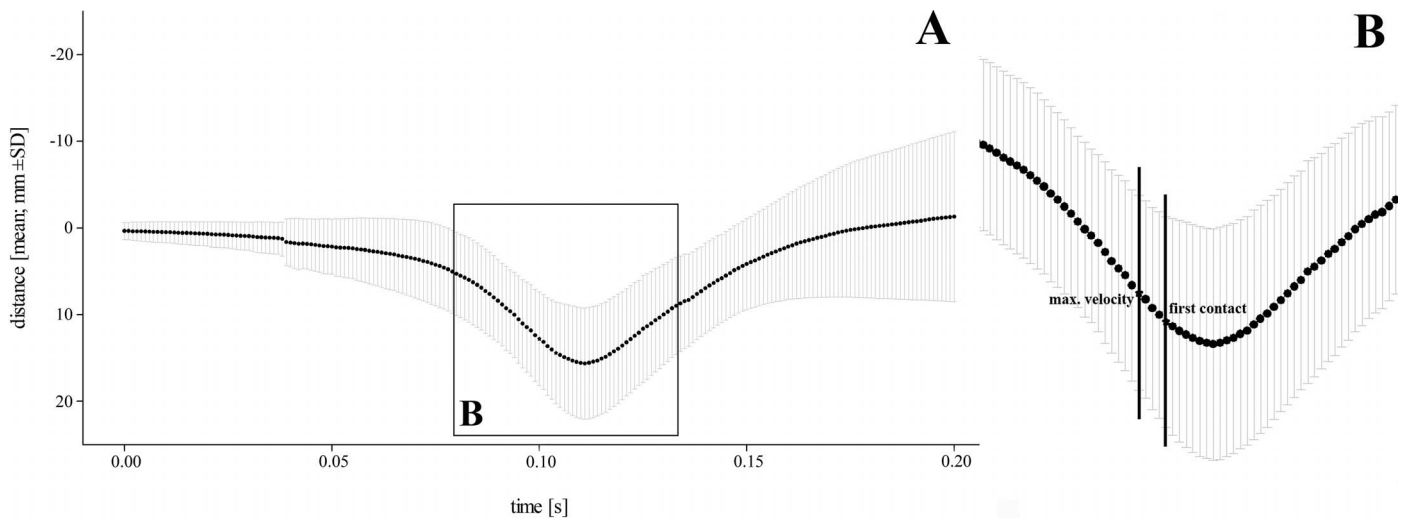


Figure 4.—Kinematic pattern of the body motion during the attack (Δd , the distance moved, in mm; mean \pm SD). (A) Complete forward and backward motion of the whip spider *Charon* sp. while striking. (B) Detail with marks at the points of peak velocity and the first contact of the whip spider with the prey.

performed in 0.07–0.27 s (mean of 0.16 s), with the actual strike being accomplished within 0.03–0.18 s (mean of 0.07 s). The maximum velocity was at 63.62 cm/s (\pm 15.13) with a mean acceleration of about 20 m/s². During the strike, pedipalps were opened with a mean speed of 1.27–10.42 cm/s (mean of 6.56 cm/s). Pedipalp closure was about three times that fast, reaching 10.31–39.74 cm/s (mean of 22.79 cm/s) with a mean maximal speed of 72.3 cm/s. During closure the pedipalp tip accelerated about 70 m/s² and reached its maximal velocity about 4 ms before the prey item was hit.

DISCUSSION

Whip spiders are nocturnal ambushing hunters that primarily prey on ground running insects, such as crickets and cockroaches (Weygoldt 2000; Chapin & Hebets 2016). Such insects may have a high burst speed and quick escape response. Whip spiders avoid an escape response by using careful, stealthy movements to get close enough to the prey to reach it with its pedipalps (Weygoldt 2000; Chapin & Hebets 2016). The eventual strike of the whip spider *Charon* sp. is highly stereotypic, precise and fast. This is in agreement with previous observations on *Phrynos marginemaculatus* (Santer & Hebets 2009). The mean strike speed of *Charon* sp. was about 0.25 m/s and thus higher than Santer & Hebets (2009) measured in *P. marginemaculatus* (0.17 m/s), whereas the acceleration of the pedipalpal tip was comparable (20 m/s² in *Charon* sp. and 8.74 m/s² in *P. marginemaculatus*). Santer & Hebets (2009) described that the strike of *P. marginemaculatus* consisted of a slow and a fast phase, however, we did not find this in *Charon* sp.

With 70–270 ms, the duration of the whip spider strike is within the range of hunting spiders (Eggs et al. 2015; Zeng & Crews 2018) and competes with the take-off speed of larger insects such as crickets and locusts (Brown 1967). Other arachnids can strike substantially faster, such as sabaconid harvestmen (few milliseconds, Wolff et al. 2016) and trap-jaw spiders (within a fraction of a millisecond, Wood et al. 2016),

but it should be noted that these are substantially smaller animals that prey on fast moving collembolans, and strike speed may be subject to allometric effects (Ilton et al. 2018). In whip spiders, the pedipalps not only function to immobilize the prey, but also to smash it. Accordingly, the pedipalps are quite massive in these arachnids, and larger masses take more time to accelerate. With a peak velocity of 0.7 m/s, the pedipalps close faster than many insects can move. However, some cockroaches can run two times faster (Full & Tu 1991), and hence the whip spider only attacks when the prey is resting or moving slowly. An interesting focus for future studies would be the measurement of the forces acting on the prey during the pedipalpal strike.

It remains unclear what drives the speed and impact of pedipalp closure, since information on pedipalp musculature and the morphology of the femur-tibial joint is lacking. It is conceivable that elastic elements in the joint are stressed during the forceful opening of the pedipalp, and rapidly release stored energy causing fast acceleration of the tibia and tarsus. Elastic elements have been shown to play an important role in opening and closure of arachnid joints (Sensenig & Shultz 2003; Wolff et al. 2016). A future morphological investigation of pedipalp musculature and joints may help to explain the underlying mechanism.

We also found that the chelicerae take part in grasping the prey, as previously noted by Weygoldt (2000). Chelicerae consist of a thick basal segment carrying sharp tooth-like protuberances, and the pointed terminal article (fang). This article may pierce the prey and be flexed against the sclerotized teeth of the basal segment to secure and dismember the prey.

Furthermore, we found that the whip spiders can perform the strikes not only at a linear axis, but also at an angle of $\pm 30^\circ$ by non-parallel leg abduction and adduction. While this range is far less than in some spiders that can fully turn around their body within milliseconds, whip spiders share the feature of laterigrade legs with those spiders, a character that was proposed to play an important role for rapid rotational movements (Zeng & Crews 2018).

Whip spiders are a fascinating example of arthropod predators showing a unique combination of adaptations such as laterigrade and antenniform legs and raptorial pedipalps. They perform a strike within a thirtieth to fifth of a second and are able to perform the attack non-linearly. Thereby the massive, spinated pedipalps have both the function to immobilize and to smash the prey and are assisted by the blade-like cheliceral fangs. This study is a starting point to comparatively study the kinematics and predatory efficiency of different pedipalpal shapes in whip spiders and also in their sister group the whip scorpions (Thelyphonida). This has a strong potential to understand evolutionary drivers of predatory structures and strike performance as well as balancing conflicting drivers from sexual selection as represented by pedipalp elongation in males of some whip spider species (McArthur et al. 2018).

ACKNOWLEDGMENTS

We are thankful to Christian Beisser (Department of Integrative Zoology, University of Vienna, Austria) for making his tracking and analysis software available for this study.

JOW was funded by a Macquarie University Research Fellowship by Macquarie University, Sydney.

LITERATURE CITED

- Abrams, P.A. 2000. The evolution of predator-prey interactions: theory and evidence. *Annual Review of Ecology and Systematics* 31:79–105.
- Ass, M. 1973. Die Fangbeine der Arthropoden, ihre Entstehung, Evolution und Funktion. *Deutsche Entomologische Zeitschrift* 20:127–152.
- Betz, O. & G. Kölsch. 2004. The role of adhesion in prey capture and predator defence in arthropods. *Arthropod Structure and Development* 33:3–30.
- Brown, R.H.J. 1967. Mechanism of locust jumping. *Nature* 214:939.
- Burrows, M. 1969. The mechanism and neural control of the prey capture strike in the mantid shrimps *Squilla* and *Hemisquilla*. *Zeitschrift für vergleichende Physiologie* 62:361–381.
- Chapin, K.J. & E.A. Hebets. 2016. The behavioural ecology of amblypygids. *Journal of Arachnology* 44:1–14.
- Dawkins, R. & J.R. Krebs. 1979. Arms races between and within species. *Proceedings of the Royal Society of London. Series B. Biological Sciences* 205:489–511.
- Eggs, B., J.O. Wolff, L. Kuhn-Nentwig, S.N. Gorb & W. Nentwig. 2015. Hunting without a web: how lycosoid spiders subdue their prey. *Ethology* 121:1166–1177.
- Full, R.J. & M.S. Tu. 1991. Mechanics of a rapid running insect: two-, four- and six-legged locomotion. *Journal of Experimental Biology* 156:215–231.
- Gronenberg, W. 1996. Fast actions in small animals: springs and click mechanisms. *Journal of Comparative Physiology* 178:727–734.
- Gronenberg, W., J. Tautz & B. Hölldobler. 1993. Fast trap jaws and giant neurons in the ant *Odontomachus*. *Science* 262:561–563.
- Hedrick, T.L. 2008. Software techniques for two- and three-dimensional kinematic measurements of biological and biomimetic systems. *Bioinspiration & Biomimetics* 3:034001, doi: 10.1088/1748-3182/3/3/034001
- Ilton, M., M.S. Bhamla, X. Ma, S.M. Cox, L.L. Fitchett, Y. Kim et al. 2018. The principles of cascading power limits in small, fast biological and engineered systems. *Science* 360: eaao1082.
- McArthur, I.W., G.S. Miranda, M. Seiter & K.J. Chapin. 2018. Global patterns of sexual dimorphism in Amblypygi. *Zoologischer Anzeiger* 273:56–64.
- Quintero, D.J. 1981. The amblypygid genus *Phrynus* in the Americas (Amblypygi, Phrynidae). *Journal of Arachnology* 9:117–166.
- Santer, R.D. & E.A. Hebets. 2009. Prey capture by the whip spider *Phrynus marginemaculatus* C.L. Koch. *Journal of Arachnology* 37:109–112.
- Sensenig, A.T. & J.W. Shultz. 2003. Mechanics of cuticular elastic energy storage in leg joints lacking extensor muscles in arachnids. *Journal of Experimental Biology* 206:771–784.
- Weygoldt, P. 2000. Whip Spiders. Their Biology, Morphology and Systematics. Apollo Books, Stenstrup.
- Wolff, J.O. & S.N. Gorb. 2016. Attachment structures and adhesive secretions in arachnids. *Biologically-inspired systems*, Vol. 7. Springer, Cham, Switzerland.
- Wolff, J.O., J. Martens, A.L. Schönhofer & S.N. Gorb. 2016. Evolution of hyperflexible joints in sticky prey capture appendages of harvestmen (Arachnida, Opiliones). *Organisms Diversity & Evolution* 16:549–557.
- Wolff, J.O., M. Seiter & S.N. Gorb. 2015. Functional anatomy of the pretarsus in whip spiders (Arachnida, Amblypygi). *Arthropod Structure and Development* 44:524–540.
- Wood, H.M., D.Y. Parkinson, C.E. Griswold, R.G. Gillespie & D.O. Elias. 2016. Repeated evolution of power-amplified predatory strikes in trap-jaw spiders. *Current Biology* 26:1057–1061.
- Zeng, Y. & S. Crews. 2018. Biomechanics of omnidirectional strikes in flat spiders. *Journal of Experimental Biology* 221:jeb166512.

Manuscript received 27 October 2018, accepted 18 March 2019.