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Repeated Evolution of Power-Amplified Predatory Strikes in Trap-Jaw Spiders

Highlights

- High-speed, power-amplified predatory strikes occur in the mecysmaucheniid spiders
- High-speed predatory strikes have evolved four times independently
- Novel morphologies are related to functional diversification

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In Brief

Using high-speed video, Wood et al. show that power-amplified predatory strikes have evolved independently four times within the mecysmaucheniid spider family. Several structural innovations may relate to the observed functional diversification.

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Repeated Evolution of Power-Amplified Predatory Strikes in Trap-Jaw Spiders

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SUMMARY

Small animals possess intriguing morphological and behavioral traits that allow them to capture prey, including innovative structural mechanisms that produce ballistic movements by amplifying power [1–6]. Power amplification occurs when an organism produces a relatively high power output by releasing slowly stored energy almost instantaneously, resulting in movements that surpass the maximal power output of muscles [7]. For example, trap-jaw, power-amplified mechanisms have been described for several ant genera [5, 8], which have evolved some of the fastest known movements in the animal kingdom [6]. However, power-amplified predatory strikes were not previously known in one of the largest animal classes, the arachnids. *Mecysmaucheniidae* spiders, which occur only in New Zealand and southern South America, are tiny, cryptic, ground-dwelling spiders that rely on hunting rather than web-building to capture prey [9]. Analysis of high-speed video revealed that power-amplified mechanisms occur in some *mecysmaucheniid* species, with the fastest species being two orders of magnitude faster than the slowest species. Molecular phylogenetic analysis revealed that power-amplified cheliceral strikes have evolved four times independently within the family. Furthermore, we identified morphological innovations that directly relate to cheliceral function: a highly modified carapace in which the cheliceral muscles are oriented horizontally; modification of a cheliceral sclerite to have muscle attachments; and, in the power-amplified species, a thicker clypeus and clypeal apodemes. These structural innovations may have set the stage for the parallel evolution of ballistic predatory strikes.

RESULTS AND DISCUSSION

Predatory Strike Kinematics

Mecysmaucheniid species are millimeter-sized (Figure 1), ranging in carapace length of 0.745–3.10 mm [9, 10] and in adult body

weight of 0.5–23.1 mg (N = 18, across 13 species). There are currently 25 described species in the family [11], but based on our work, there are at least 11 additional undescribed species (denoted here as “sp” followed by a number). The chelicerae are an average of 3.9% of the body weight (N = 24, across 14 species), but range from 1.3%–6.7% depending on the species. When in a resting position, the chelicerae are held close to the body (Figure 1A). However prior to a strike, the highly maneuverable chelicerae move upward and open and remain extended anterolaterally away from the body (Figures 2A, S1A, and S1B). This is in contrast to the typical left-right lateral movements of most spiders where the chelicerae remain close to the body (Figure 2B) [13]. A row of setae runs along the inner cheliceral margin and projects anteriorly when the chelicerae are opened (Figure 2A), similar to the trigger hairs seen in trap-jaw ants [5]. During high-speed recordings, contact with these setae preceded a strike. Immediately after a strike, the chelicerae project anterior-medially away from the body (Figure 2C). All observed species have the behavior of opening the chelicerae and holding them in position prior to a strike (Figures 2A, S1A, and S1B).

The chelicerae, which always moved synchronously in the high-speed recordings, were modeled as a thin rod of uniform density that rotates around a fixed point, with the point of rotation being the inter-cheliceral pivot (ICP) (Figures 2A, S1C, and S1D). High-speed videos of cheliceral closures from 14 different species revealed that there is a great range of cheliceral closing speeds, with the fastest species being more than two orders of magnitude faster than the slowest species (Table 1). Cheliceral closures in *Zearchaea* sp4 were the fastest among *mecysmaucheniid* species: all *Zearchaea*, which occur only in New Zealand, share similar carapace/chelicerae morphology, and most likely achieve similar speeds in their predatory strikes. Power output from four species (Table 1) exceeds the known power output of muscles [7], and these movements could not be directly powered by muscles given the short times and small distances covered during a strike. Structural mechanisms must be present in these species for storing energy to produce ballistic movements. However, these four species show a continuum of speeds, strike durations, and power outputs, showing that a variety of functional outcomes can be achieved.

Evolutionary History of Extreme Speeds

Phylogenetic analysis of molecular data from 26 *mecysmaucheniid* species, representing all seven genera, recovered a

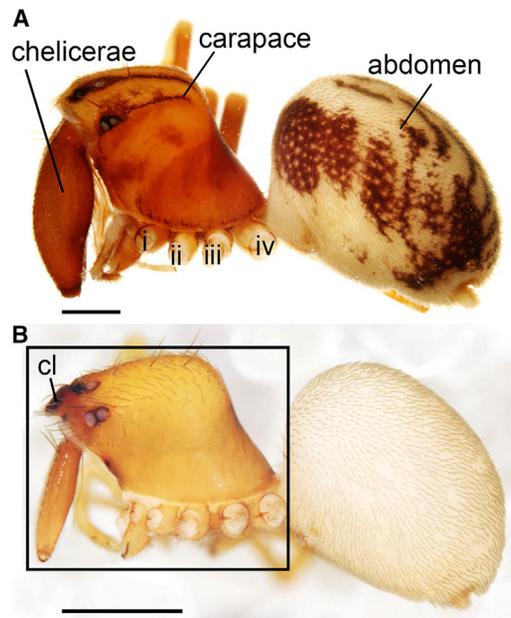


Figure 1. Mecysmaucheniid Spider

Specimens with left legs removed, lateral view. Scale bars, 0.5 mm. (A) Female *Aotearoa magna*. Leg attachment points are denoted i–iv. (B) Female *Zearchaea* sp3. “cl” indicates a thickened clypeus. The boxed section corresponds to the structure in Figure 2C.

phylogeny with well-supported branches (Figure S2). An ancestral character state reconstruction was performed on an ultrametric phylogeny with branches proportional to time (see the Supplemental Experimental Procedures) to examine evolution of power-amplification. Power amplification was treated as a discrete trait, scored as “present” if the output exceeded the limitation of muscles [7] (Table 1), and was mapped onto the phylogeny using likelihood methods. This revealed that ballistic movements have evolved at least four times independently within the mecysmaucheniid spiders (Figure 3). Independent evolution of the trap-jaw strike has occurred in the trap-jaw ants as well [14], with strike forces proportional to the size of the head [15].

Structural Innovations

In the typical spider body plan, the carapace is a convex plate that sits on top of the cephalothorax, and several sets of muscles that control the chelicerae run upward from the cheliceral bases and attach to the anterior portion of the carapace (Figure 2D) [12, 13]. Spiders typically have the greatest range of cheliceral movement in a transverse plane relative to the body’s anteroposterior axis [13] (Figure 2B). However, mecysmaucheniid spiders deviate greatly from this body plan, instead: (1) the carapace is highly modified, being greatly elevated, and with the carapace forming a circular opening around the cheliceral bases (Figures 1, 2C, and 2E); (2) the cheliceral muscles are oriented horizontally and not vertically (green and blue in Figures 2C and 2F); and (3) a small sclerite that sits between the inner margins of the cheliceral bases, which we term the “inter-cheliceral-pivot” (ICP) (Figures 2A, 2F, S1C, and S1D), has

muscle attachments (brown in Figures 2C, 2F, and S1C) to the carapace. This cheliceral sclerite exists in other spiders [13, 16], yet the presence of attached muscles has not been observed in other spiders [12, 13]. The modified carapace and muscular orientation in mecysmaucheniids allows for highly maneuverable chelicerae that can be projected anteriorly and perpendicularly away from the body, and that have a wide gape (Figures 2A, 2C, S1A, and S1B), important for launching a trap-jaw predatory strike.

3D visualizations and measurements of morphological structures revealed differences among the power-amplified species compared to the non-power-amplified species: apodemes (purple in Figures 2C and 2F) that run from the anterolateral basal edge of the chelicerae to the clypeus tend to be thicker (at least as thick as the cuticle), and the clypeus also tends to be thicker (at least 1.6 times thicker than the cuticle) in power-amplified species (Figures 1, 2E, 2G, and 2H; Table 1). These structures may be implicated in storing energy for ballistic movements. The chelicerae in preserved specimens of *Chilarchaea quellon* can be manually locked open through mechanical interactions of the ICP with protrusions on the cheliceral bases (Figure S1D).

Conclusions

The highly modified body plan and trap-jaw behaviors are in place in all mecysmaucheniid species regardless of the speed of the cheliceral strike, with only some lineages independently evolving power-amplified movements. The similarities shared between mecysmaucheniid spiders and trap-jaw ants, the amount of cheliceral functional variation among closely related species, and the independent origins of extremely rapid predatory strikes within the mecysmaucheniids, illustrate that universal evolutionary strategies are at play, where distantly related groups converge on the similar solution of power amplification to solve important biological tasks. In mecysmaucheniids, the modified carapace, the shifted cheliceral muscle orientation, and the ICP muscle attachments are likely innovative traits that have allowed for functional diversification to occur [17].

EXPERIMENTAL PROCEDURES

Molecular Phylogenetic Analysis

Molecular data were extracted, amplified, and sequenced using standard protocols [16]. A suite of primers was used to amplify a portion of the mitochondrial protein coding gene cytochrome c oxidase subunit 1 (CO1), the nuclear protein-coding gene histone 3 (H3), and the ribosomal nuclear genes 28S and 18S. Phylogenetic analyses were performed using Bayesian and parsimony methods (see the Supplemental Experimental Procedures).

High-Speed Video and Analysis

Using a Photron SA3 high-speed video camera, 98 recordings (1,000–40,000 frames per second) were made of cheliceral strikes from 14 species (Tables 1 and S2); the specimen was contained in a glass tube while an eyelash, affixed to an insect mounting pin, was used to stimulate the specimen. Calculations were based on the movement of one chelicera, so the starting angle and the chelicerae and muscle weights were halved. For kinematic, force, power, and energy calculations, the chelicera was treated as a thin rod of uniform density that rotates around a fixed point (see the Supplemental Experimental Procedures).

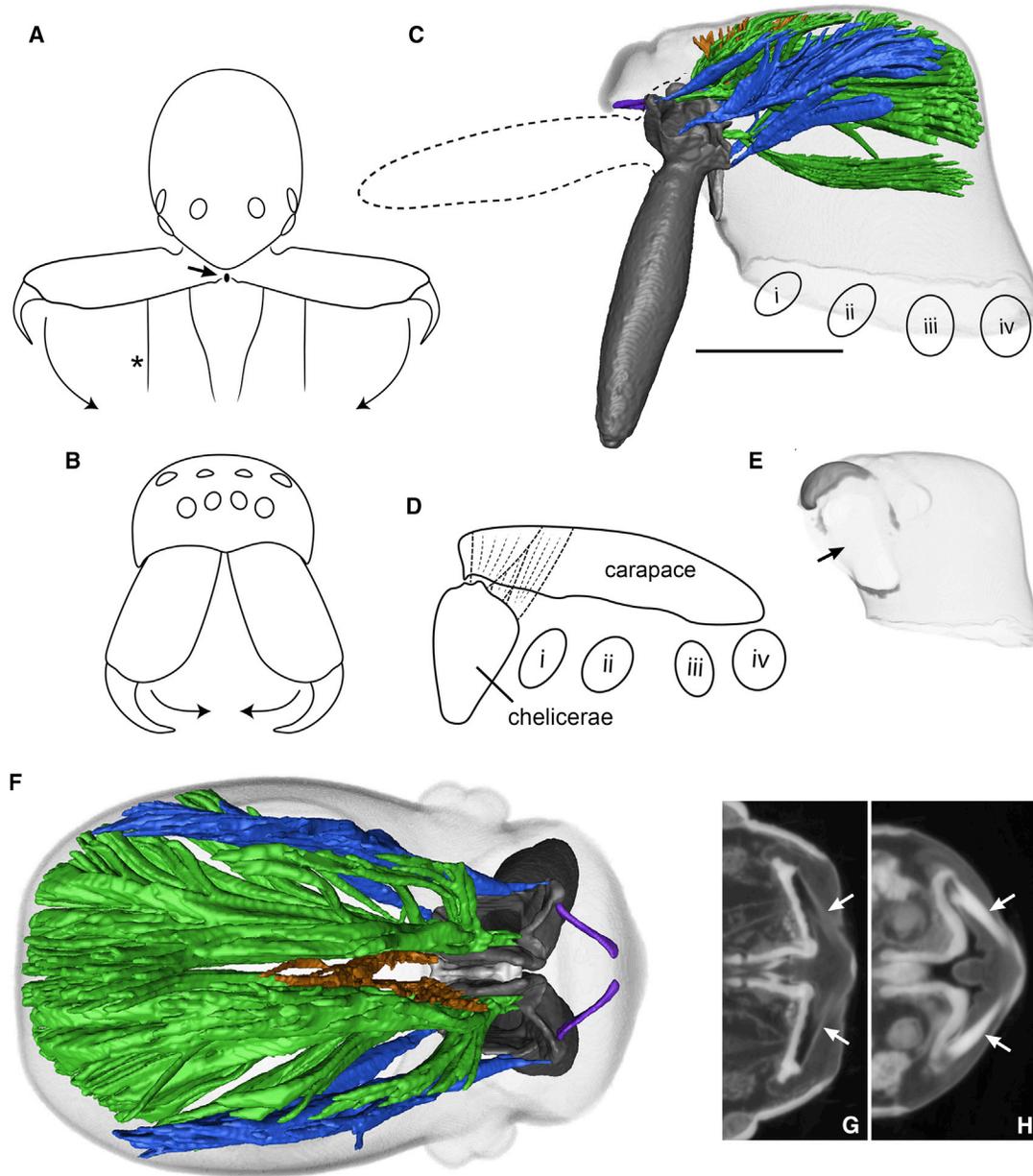


Figure 2. Carapace Modifications

(A) In mecysmauchenids, the cheliceral movements are best observed in the dorsal view, shown here (curved arrows). The straight arrow shows the ICP (point of rotation). Four setae project anteriorly from the chelicerae; one is denoted with an asterisk. The illustration is based on *Chilarchaea quellon*.

(B) In contrast, typical spider cheliceral movements (curved arrows) are best observed in the anterior view, shown here.

(C, E, and F) 3D surface mesh of segmented carapace/chelicerae in *Zearchaea* sp4, with the chelicerae in a relaxed position, showing the carapace (translucent), chelicerae (dark gray), ICP (light gray), cheliceral abductor muscles (blue), cheliceral adductor muscles (green), ICP muscles (brown), and cheliceral apodemes (purple). A lateral view is shown in (C). The dashed line shows chelicerae position immediately after a strike. Leg attachment points are denoted i–iv. Scale bar, 0.25 mm. An anterolateral view of the carapace is shown in (E). The color gradient shows the thickest parts. The arrow points to the circular opening that surrounds cheliceral bases. A dorsal view is shown in (F).

(D) Typical spider carapace, lateral view, with legs removed. Leg attachment points are denoted i–iv. Dashed lines show cheliceral muscle orientation. The illustration is based on *Araneus angulatus* from [12].

(G and H) Slice through a 3D reconstruction of the anterior portion of the carapace, dorsal view, showing the cheliceral apodemes (arrows). *Mecysmauchenius* sp1 (H), a species with a power-amplified strike, has thicker apodemes compared to *Mecysmauchenius* sp3 (G).

See also Figure S1.

Table 1. Summary of High-Speed Video Calculations and Clypeal Measurements

Species	n	i	Average Strike Duration (s)	Average Linear Speed (m/s)	Average Angular Speed (rad/s)	Average Power Output (W/kg)	Clypeus Thickness Ratio	Clypeal Tendons Ratio
<i>Zearchaea</i> sp4	3	2	0.00012	8.5	13,000	66,000	4.4	2.5
<i>Mecysmauchenius</i> sp1	10	1	0.00048	2.4	2,500	3,700	2.6	2.3
<i>Chilarchaea</i> quellon	2	2	0.00027	2.5	4,600	3,100	3.6	1.1
<i>Semysmauchenius</i> sp1	4	3	0.00056	1.3	1,700	1,300	1.6	1.1
<i>Mecysmauchenius osorno</i>	8	3	0.0094	0.13	100	0.78	0.98	0.60
<i>Mecysmauchenius chepu</i>	13	2	0.0077	0.20	140	1.1	0.98	–
<i>Mecysmauchenius victoria</i>	15	4	0.01	0.21	88	1.3	1.3	0.86
<i>Mecysmauchenius</i> sp4	2	2	0.012	0.035	51	0.048	1.2	0.74
<i>Mecysmauchenius</i> sp3	2	1	0.013	0.054	50	0.099	1.0	0.43
<i>Mecysmauchenius segmentatus</i>	13	6	0.017	0.074	52	0.12	1.0	0.79
<i>Mecysmauchenioides nordenskjoldi</i>	10	8	0.018	0.058	45	0.054	1.1	0.87
<i>Mecysmauchenioides quetrihue</i>	5	3	0.015	0.051	42	0.051	1.1	0.50
<i>Mecysmauchenius puyehue</i>	2	2	0.020	0.059	47	0.078	1.4	0.49
<i>Mecysmauchenius newtoni</i>	9	5	0.02	0.049	37	0.057	0.99	0.47

For each species, the calculations of one chelicera closing based on high-speed videos. n, number of recordings; i, number of individuals. Species in bold are scored as “present” for power amplification in the ancestral character state reconstruction. “Clypeus thickness ratio” indicates clypeus thickness/cuticle thickness; “clypeal tendons ratio” indicates clypeal tendons thickness/cuticle thickness (measurement unavailable for *M. chepu*). See also Table S2 for calculations of individual videos.

Morphological Visualization

All 26 species in the phylogeny were scanned by hard X-ray micro-tomography at the Lawrence Berkeley National Lab Advanced Light Source synchrotron. Prior to scanning, specimens were stained overnight in Lugol's solution, washed in water for 30 min, and then scanned in 70% ethanol. Some specimens were also scanned after critical point drying. Scans were performed at X-ray energies of 33.5 keV for the stained specimens, or between 20 and 25 keV. Most scans were performed using a 10× objective lens, yielding a reconstructed 3D voxel size of 0.65 × 0.65 × 0.65 μm. 3D reconstructions were created from these scans, and a number of structures were digitally labeled (“segmented”) by hand, and the boundaries of these labels were converted to a surface mesh to better visualize the data.

Character State Evolution

We reconstructed the ancestral character state of power amplification onto an ultrametric phylogeny (see the Supplemental Experimental Procedures) using likelihood methods in the program Mesquite [18]; power amplification was treated as a discrete trait and modeled using the Markov k-state 1 parameter model [19]. The four fastest species were scored as “present” and the remaining species as “absent” (Table 1). For species that were missing kinematic data, species that shared the same somatic morphology as a species that was scored were pruned, and morphologically unique species were retained and scored as “missing.”

ACCESSION NUMBERS

The accession numbers for the DNA sequences reported in this paper are GenBank: KP209033–KP209244 (Table S1).

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, two figures, two tables, and three movies and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2016.02.029>.

AUTHOR CONTRIBUTIONS

H.M.W. conceived the study, designed and performed experiments, analyzed the data, and wrote the manuscript. D.Y.P. supervised and contributed to the X-ray micro-tomography scanning and data processing. D.O.E. supervised and contributed to the high-speed video recording and video analysis. D.O.E., R.G.G. and C.E.G. supervised the entire project. All authors discussed the results and commented on the manuscript.

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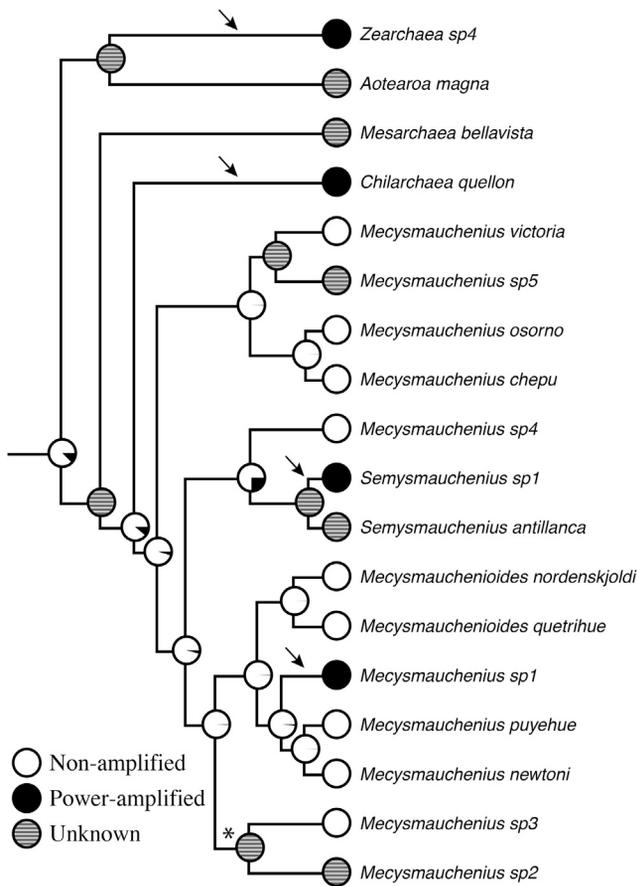


Figure 3. Maximum-Likelihood Ancestral Character State Reconstruction

Circles at terminals represent current species' states; pie graphs at nodes represent the most likely ancestral states, with black denoting power amplification. Duplicate taxa were pruned, and outgroup taxa are not shown. Arrows mark the four branches where a power-amplified predatory strike evolved. All branches have branch support values (posterior probabilities, pp) equal to or greater than 0.99 except where the asterisk signifies pp = 0.95. See also Figure S2 and Table S1.

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